EVOLUTION OF THE SIDE-NECKED TURTLES: THE FAMILIES BOTHREMYDIDAE, EUREXEMYDIDAE, AND ARARIPEMYDIDAE

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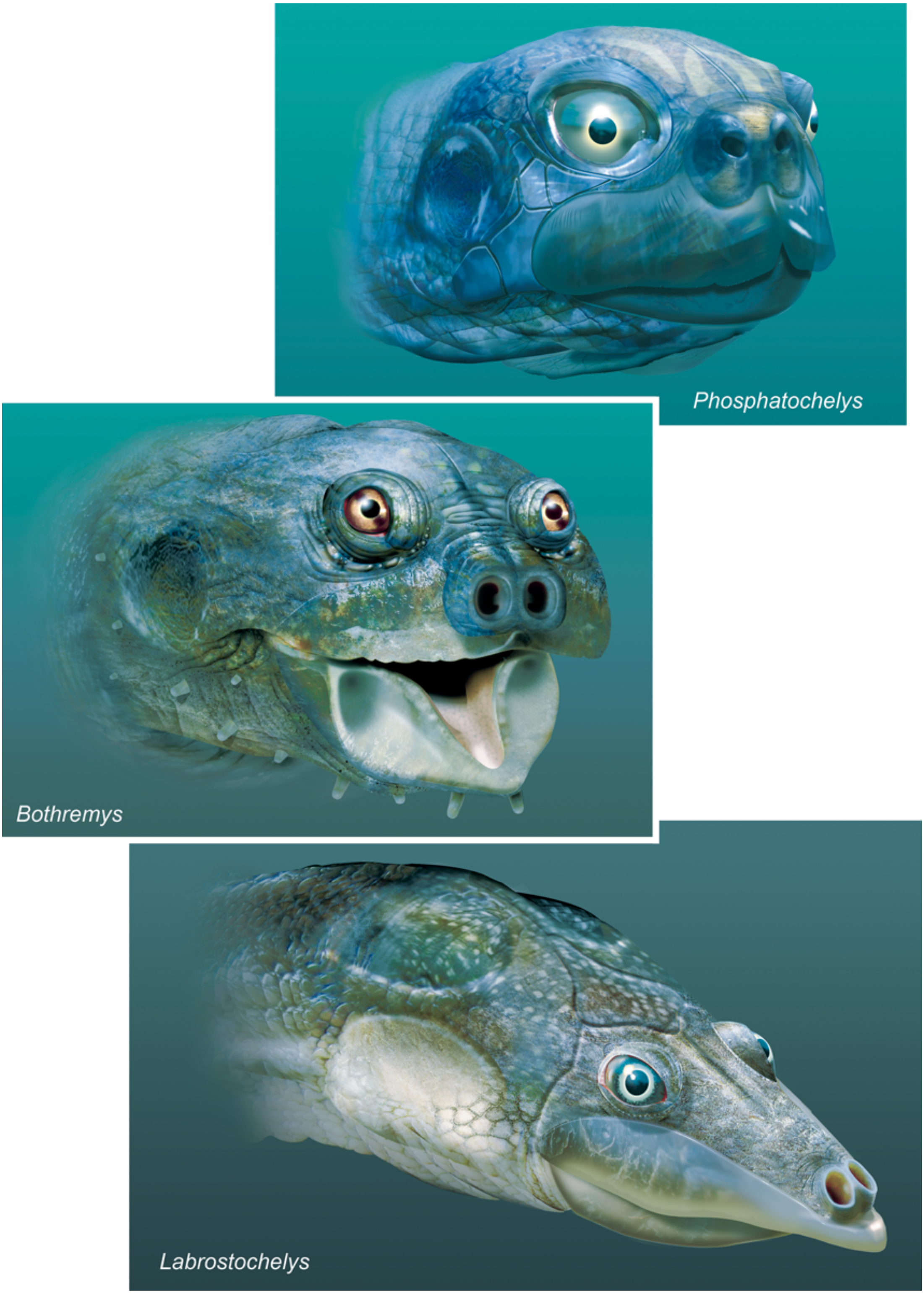

Frontispiece. Speculative reconstructions of the heads of extinct bothremydid pleurodires from the early Tertiary of Morocco. Upper, *Phosphatochelys tedfordi* (tribe Taphrosphyini), Eocene; middle, *Bothremys maghrebiana* (tribe Bothremydini), Paleocene; lower, *Labrostochelys galkini* (tribe Taphrosphyini), Paleocene. See figure 318 (p. 697) for the views of the skulls that are the basis for these reconstructions. [F. Ippolito, del.]

CONTENTS

ABSTRACT

Although pleurodires have been considered significantly less diverse than their sister group, the cryptodires, current discoveries show that pleurodires had a more complex and extensive evolutionary history than had been realized. Previously unknown radiations, particularly in the near-shore marine realm, are revealed by taxa with diverse cranial morphology, indicating many different feeding and sensory strategies. The pleurodire group that is changed the most by the new discoveries is its largest group, the hyperfamily Pelomedusoides. The hyperfamily Pelomedusoides now consists of the families Pelomedusidae, Podocnemididae, Bothremydidae, Araripemydidae, and Euraxemydidae, new family. The families Bothremydidae, Araripemydidae, and Euraxemydidae, new family, are documented with descriptions of skulls, lower jaws, and shells. The relationships of the family Podocnemididae to its sister taxa *Hamadachelys* and *Brasilemys* are recognized by placing them in the epifamily Podocnemidinura. The epifamily Podocnemidinura is the sister group to the family Bothremydidae, and together they form the superfamily Podocnemidoidea.

The family Araripemydidae consists of one taxon, *Araripemys barretoi*, from the Aptian-Albian of Brazil. Description of new cranial material suggests that it is the sister group to all other Pelomedusoides or the sister group to the Pelomedusidae, but these relationships are only weakly supported. There is strong support for a multichotomy of *Araripemys*, Pelomedusidae, and remaining Pelomedusoides. *Araripemys* is characterized by very thin triturating surfaces and by a shell that lacks mesoplastra and has the first costals reaching the shell margin.

The new family Euraxemydidae consists of two new genera: *Euraxemys essweini*, n. gen. et sp., from the Albian Santana Formation of Brazil, and *Dirqadim schaefferi*, n. gen. et sp., from the Cenomanian Kem Kem beds of Morocco. Members of the Euraxemydidae are united by the unique possession of a medial process of the quadrate partially covering the prootic and narrowly contacting a ventral process of the exoccipital, in contrast to all other pleurodires, which have either complete exposure or complete covering of the prootic ventrally. Furthermore, members have a ventral process of the exoccipital that is exposed at the lateral margin of the basioccipital in an elongate foot. The Euraxemydidae is hypothesized as the sister group to the superfamily Podocnemidoidea.

The family Bothremydidae and the epifamily Podocnemidinura (consisting of the family Podocnemididae, *Hamadachelys*, and *Brasilemys*) are united as the superfamily Podocnemidoidea based on the possession of a quadrate-basioccipital contact, the complete or nearly complete ventral covering of the prootic, and the extension of the pectoral scales onto the entoplastron.

The family Bothremydidae is a large and diverse group extending from the Albian to the Eocene in North and South America, Europe, Africa, and India. Its monophyly is supported by the presence of a wide exoccipital-quadrate contact, a eustachian tube separated from the incisura columellae auris usually by bone to form a bony canal for the stapes, absence of a fossa precolumellaris, a supraoccipital-quadrate contact (except in the tribe Taphrosphyini), and a posterior enlargement of the fossa orbitalis. Although there is a diversity of triturating surfaces within the family, primitively bothremydids have a posteriorly wide triturating surface with a significant palatine contribution in the upper jaw.

The family Bothremydidae consists of four newly recognized, monophyletic groups: the tribes Kurmademydini, Cearachelyini, Bothremydini, and Taphrosphyini. The tribe Kurmademydini consists of two taxa: *Kurmademys kallamedensis*, from the Maastrichtian Kallamedu Formation of India, and *Sankuchemys sethnai*, from the Maastrichtian Intertrappean beds of India. The tribe Kurmademydini is characterized by extensive temporal and cheek emargination, a large fossa precolumellaris, and a small, anterior exposure of the prootic on the ventral surface. The tribe Kurmademydini is the sister group to the subfamily Bothremydinae (consisting of the tribes Cearachelyini, Bothremydini, and Taphrosphyini). Members of the subfamily Bothremydinae all possess a foramen stapedio-temporale that faces anteriorly.

The tribe Cearachelyini consists of *Cearachelys placidoi*, from the Albian Santana Formation of Brazil, and *Galianemys emringeri* and *Galianemys whitei*, both from the Cenomanian Kem Kem beds of Morocco. The tribe Cearachelyini is characterized by a jugal retracted from the orbital margin and a fenestra postotica formed into a short slit. The tribe Cearachelyini is the sister group to the infrafamily Bothremydodda (consisting of the tribes

Bothremydini and Taphrosphyini). The infrafamily Bothremydodda is characterized by a quadrate shelf formed below the cavum tympani, a foramen stapedio-temporale and foramen nervi trigemini that are very close together on the anterior face of the otic chamber, and a condylus occipitalis and occipital neck that are formed only by the exoccipitals.

The tribe Bothremydini consists of *Foxemys mechinorum*, from the Campanian-Maastrichtian of France; *Polysternon provinciale*, from the Campanian of Europe; *Zolhafah bella*, from the Maastrichtian Dakla Formation of Egypt; *Rosasia soutoi*, from the Campanian-Maastrichtian of Portugal; *Araiochelys hirayamai*, n. gen. et sp., from the Danian phosphates of Ouled Abdoun Basin, Morocco; *Bothremys cooki*, from the Maastrichtian Navesink Formation of New Jersey; *Bothremys maghrebiana*, n. sp., from the Danian phosphates of Ouled Abdoun Basin, Morocco; *Bothremys kellyi*, n. sp., from the Ypresian phosphates of Ouled Abdoun Basin, Morocco; *Bothremys arabicus*, from the Santonian of Jordan; *Chedighaii hutchisoni*, n. gen. et sp., from the Campanian Kirtland Formation of New Mexico; and *Chedighaii barberi*, n. gen., from the Campanian of Arkansas, Alabama, Kansas, and New Jersey. The tribe Bothremydini is the sister group to the tribe Taphrosphyini.

The tribe Taphrosphyini is characterized by the presence of a jugal-quadrate contact, the absence of a maxilla-quadratojugal contact, and the absence of a supraoccipital-quadrate contact. Members of the tribe Taphrosphyini have a considerable variety of triturating surfaces but they lack the wide, triangular surfaces typical of the other bothremydids. The tribe Taphrosphyini consists of *Taphrosphys sulcatus*, from the Danian Hornerstown Formation of New Jersey; *Taphrosphys congolensis*, from the Paleocene of Cabinda, west Africa; *Taphrosphys ippolitoi*, n. sp., from the Danian phosphates of the Ouled Abdoun Basin, Morocco; *Labrostochelys galkini*, n. gen. et sp., from the Danian phosphates of the Ouled Abdoun Basin, Morocco; *Phosphatochelys tedfordi*, from the Ypresian phosphates of the Ouled Abdoun Basin Morocco; *Ummulisani rutgersensis*, n. gen. et sp., from the Ypresian phosphates of the Ouled Abdoun Basin, Morocco; *Rhothonemys brinkmani*, n. gen. et sp., from the Paleogene phosphates of the Ouled Abdoun Basin, Morocco; *Azabbaremys moragjonesi*, from the Paleocene Teberemt Formation of Mali; *Nigeremys gigantea*, from the Maastrichtian of Niger; and *Arenila krebsi*, from the Maastrichtian Dakla Formation of Egypt.

Among the Bothremydidae, the Taphrosphyini is the most diverse morphologically. The triturating surfaces show a wide range of variation. The long, narrow skull of *Labrostochelys* differs significantly from the very short skull of *Phosphatochelys*. Other genera, such as *Azabbaremys* and *Arenila*, have large and massive skulls, but without broadly expanded triturating surfaces, while *Ummulisani* has very narrow and deep labial ridges. The nasal regions of Taphrosphyini also show wide diversity. *Rhothonemys* has nasal openings and cavities more than twice the size of the orbits, but the nasal openings in *Labrostochelys* are smaller than the relatively small orbits. This diversity of Taphrosphyini skull morphology is mostly evident in the Paleogene of North Africa.

A phylogenetic analysis of the core dataset of 41 taxa, 122 cranial characters, and 52 postcranial characters relies on comparative descriptions of these taxa. The analysis using PAUP results in one most parsimonious cladogram of 382 steps with a consistency index of 0.6. A Bremer decay analysis shows that the family Bothremydidae is strongly supported at five steps: the tribes Kurmademydini and Cearachelyini have an index of 2, and the tribe Taphrosphyini has an index of 3. The tribe Bothremydini becomes unresolved at one step and is the most weakly supported of these groups. The addition of selected shell-only taxa with low missing data values to the core dataset results in one equally parsimonious cladogram that is resolved as: (*Proterochersis* (Platychelyidae (*Dortoka* (Chelidae (Pelomedusidae + *Araripemys*) (Euraxemydidae (*Teneremys* (Podocnemididae + *Hamadachelys* + *Brasilemys* (Bothremydidae)))))))). A partitioned dataset consisting only of cranial characters (excluding all shell-only taxa) results in one equally parsimonious cladogram identical to the most parsimonious cladogram resulting from the whole dataset; however, a partitioned dataset consisting only of postcranial characters (excluding all skull-only taxa) resulted in 2704 trees, the consensus of which lacks resolution for nearly all Pelomedusoides, but which does resolve more basal pleurodires.

When the skull morphology of the Bothremydidae is placed in the context of all other turtles, it becomes apparent that this family has the greatest range of skull forms of any turtle family yet known. In fact, the skull morphologies of many turtle families seem remarkably uniform in

comparison (e.g., Testudinidae, Kinosternidae, Pelomedusidae, Trionychidae, Carettochelyidae). There are other turtle families with bizarre skull morphologies (e.g., Nanhsiungchelyidae; Meiolaniidae) but these are not taxonomically diverse, at least as they are now known. In no other family do we see the extremes exemplified by the skulls of forms like *Cearachelys*, *Bothremys*, *Labrostochelys*, *Azzabaremys*, *Rhothonemys*, and *Phosphatochelys*. It is this remarkable variation in skull morphology that has allowed us to formulate a strong hypothesis of bothremydid relationships in spite of the presence in Pelomedusoides of remarkably uniform shells.

INTRODUCTION

Early in their history, before the Late Triassic, turtles split into two main groups, the cryptodires and the pleurodires. Although initially neither group had neck retraction mechanisms, later members evolved different mechanisms that persisted to become major characteristics for each group. Recent cryptodires ("hidden neck") withdraw the head by bending the neck in a vertical plane, while pleurodires ("side neck") bend the neck in a horizontal plane. Many species of both groups survive to the present, but the pleurodires are less diverse than the cryptodires and are more restricted geographically, living at present only in the southern hemisphere. Living pleurodires are restricted to freshwater environments and they do not live in the open marine and arid habitats to which some cryptodires have adapted. However, the fossil record of pleurodires illustrates a different story that tells of great diversification. During the Cretaceous and Paleogene, pleurodires were geographically widespread, reaching all land masses except central Asia and Antarctica, and occupying at least the littoral marine realm, as well as diverse freshwater environments. The recently discovered morphologic diversity of pleurodire skulls described here demonstrates a level of ecological diversity previously unknown (figs. 1, 2).

Systematic study of both fossil and recent pleurodires has lagged behind study of their more diverse and more accessible (to northern hemisphere workers) sister taxon, the cryptodires. Some studies of fossil forms are available (see below), but much of the known diversity of the group has not been documented by descriptions and has not been analyzed using explicit character distributions. Most named taxa (see list in Pritchard and Trebbau, 1984) are so poorly known as to be barely diagnosable, let alone sufficiently described to be included in explicit character analyses. Some taxa (e.g., "*Carteremys*" and "*Sokotochelys*") are even without specimens (see Dubious Taxa below). In recent years, however, fossil pleurodires have been getting more attention (e.g., Fuente and Fernandez, 1989; Fernandez and Fuente, 1994; Meylan, 1996; Gaffney et al., 1998; Tong et al., 1998; Lapparent de Broin and Werner, 1998; Lapparent de Broin and Murelaga, 1999; Lapparent de Broin, 2000a; Gaffney, Campos, and Hirayama, 2001; Gaffney, Chatterjee, and Rudra, 2001; Gaffney, Moody, and Walker, 2001; Lapparent de Broin and Fuente, 2001; Gaffney, Tong, and Meylan, 2002; Fuente, 2003; Gaffney, DeBlieux, Simons, Sánchez-Villagra, and Meylan, 2003; Gaffney and Forster, 2003; Gaffney and Tong, 2003; Rueda and Gaffney, 2005), but a large amount of fossil and recent material remains undocumented and unanalyzed. This study attempts to correct this situation by documenting much of the previously unknown diversity of the extinct Pleurodira and analyzing the morphology phylogenetically. The results of the present work, which emphasize bothremydids but include all pleurodires except podocnemidids and chelids, are summarized in figures 1 and 2. The most parsimonious cladogram (referred to as MPC, which is cladogram 1; cladogram 2, is the same dataset but analyzed with a series of shell-only taxa added; see Phylogenetic Analysis for discussion) for Pelomedusoides is shown in figure 288.

The pleurodire literature has been dominated by systematic work based on shell morphology and by the announcement of new taxa. The usefulness of shell-only taxa in phylogenetic analysis is limited by the comparatively simpler morphology of shells compared with skulls, but also by the relatively conservative shell morphology, particularly in the Pelomedusoides. Although there have been 150 years of descriptions of pleurodire shells, the range of diversity now seen in skulls (figs. 3–11) is not even suggested in the shell-dominated pleurodire literature.

Although pleurodires have not received the attention given to other turtle or most reptile groups, this relative paucity of previous scholarly work belies their evolutionary significance. The oldest pleurodire, *Proterochersis*, is probably the oldest turtle, with specimens apparently occurring stratigraphically below *Proganochelys* in the Late Triassic of Germany (specimens in Staatliches Museum für Naturkunde, Stuttgart, Ger-

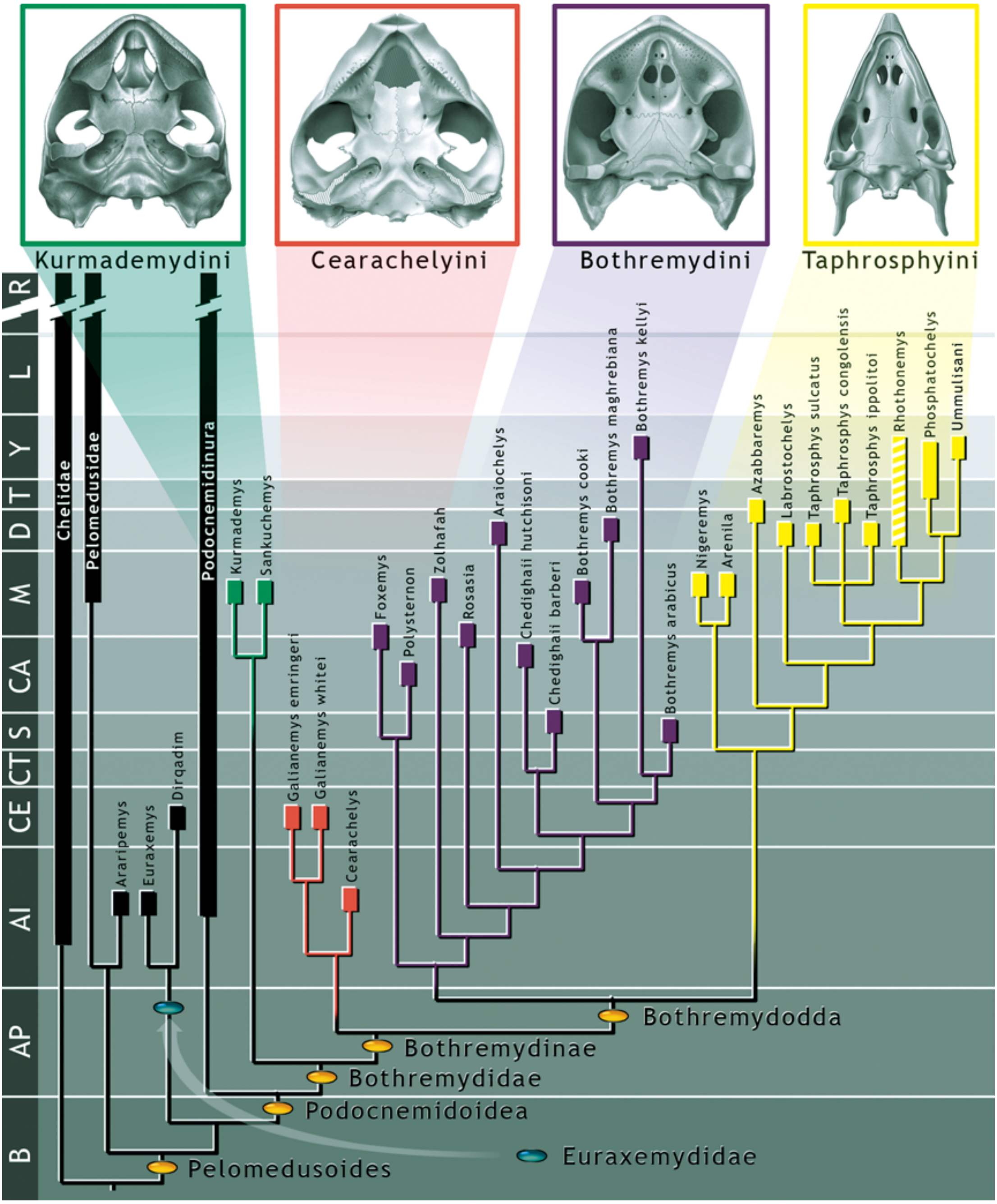

Fig. 1. Cladogram of the families Bothremydidae, Euraxemydidae, Araripemydidae, and other pleurodire groups superimposed on a geologic timescale (based on Harland et al., 1990). Palatal views of representatives of the four tribes of the Bothremydidae are shown above the chart. Only records that can be adequately diagnosed and identified to species are indicated. Colors identifying the tribes also refer to map in figure 2. See figure 288 for complete cladogram. Abbreviations: AL, Albian; AP, Aptian; B, Barremian; CA, Campanian; CE, Cenomanian; CT, Coniacian and Turonian; D, Danian; L, Lutetian; M, Maastrichtian; R, Recent; S, Santonian; T, Thanetian; Y, Ypresian. [F. Ippolito, del.]

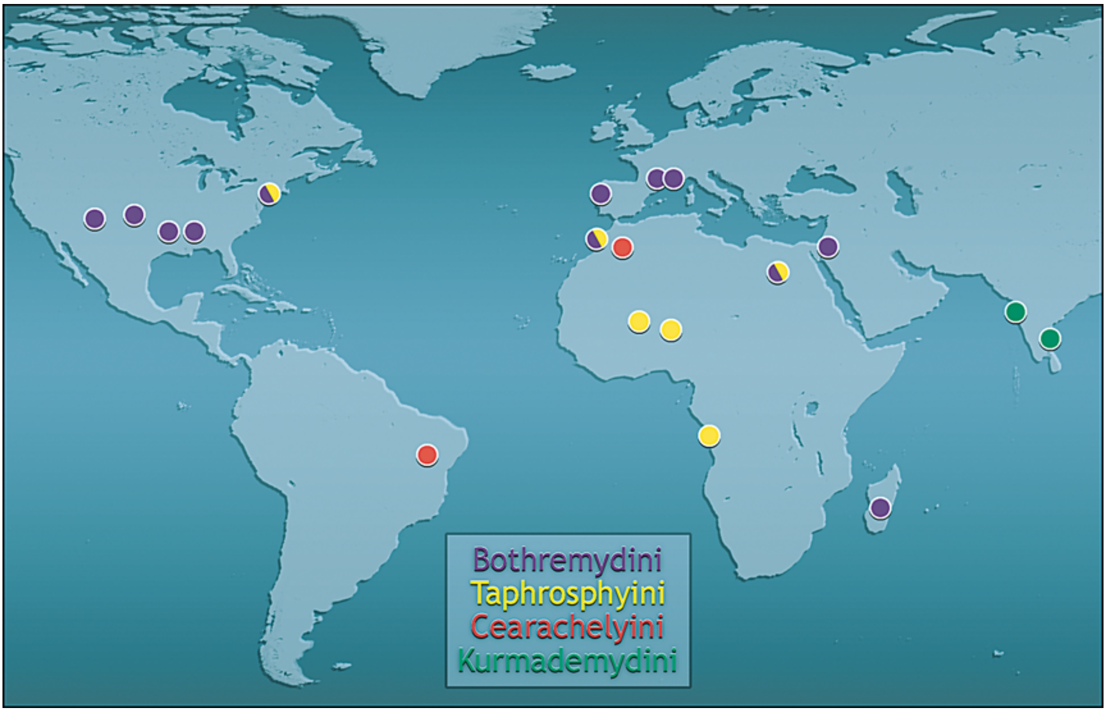

Fig. 2. World map showing distribution of the family Bothremydidae. Tribes identified by colors from figure 1. Only records that can be identified to tribe are indicated; Bothremydidae incertae sedis are not indicated. [F. Ippolito, del.]

many). Pleurodires are usually considered to have had a relatively conservative evolutionary history compared to cryptodires, but this is a misconception based on a spotty fossil record and a comparatively low recent diversity, especially as reflected in the recognition of family-level taxa (until recently, 2 families of pleurodires and 12–13 of cryptodires in the Recent fauna). Pleurodires certainly do not seem to have ever been as speciose as cryptodires, and they do not seem to have radiated into the pelagic realm, but it is now apparent from their fossil record that they have had a long and complex history that includes several previously unrecognized radiations. The extremely diverse feeding mechanisms seen in extinct pleurodires, from extensive secondary palates to deep labial ridges and projections, suggest a wide range of feeding strategies. Habitats varying from near-shore marine to freshwater and terrestrial were occupied by extinct pleurodires. Although the available record is still relatively sparse, there are now enough specimens to show that pleurodires had a much richer and more diverse history than had been thought.

Previous Work

Gaffney (1984) provided an historical overview of theories of chelonian relationships from the Linnaean concept of a single genus for all turtles through the advent of cladistics, as well as tracing the recognition of pleurodires as a natural group. In one of the earliest classifications of turtles, Dumeril (1806) recognized pleurodires (Gaffney, 1984), but Gray (1831) was the first to definitely unite the then known pleurodires as a group, Chelydae. Dumeril and Bibron (1835) coined the terms “cryptodérés” and “pleurodérés”. Among the more influential classifications of pleurodires are those of Cope (1871), Boulenger (1889), Lydekker (1889), and Hay (1908). More recently, Gaffney (1972a, 1975b) used the phylogenetic systematics of Willi Hennig to develop synapomorphies for cryptodires and pleurodires, with Pelomedusoides (= Pelomedusi-

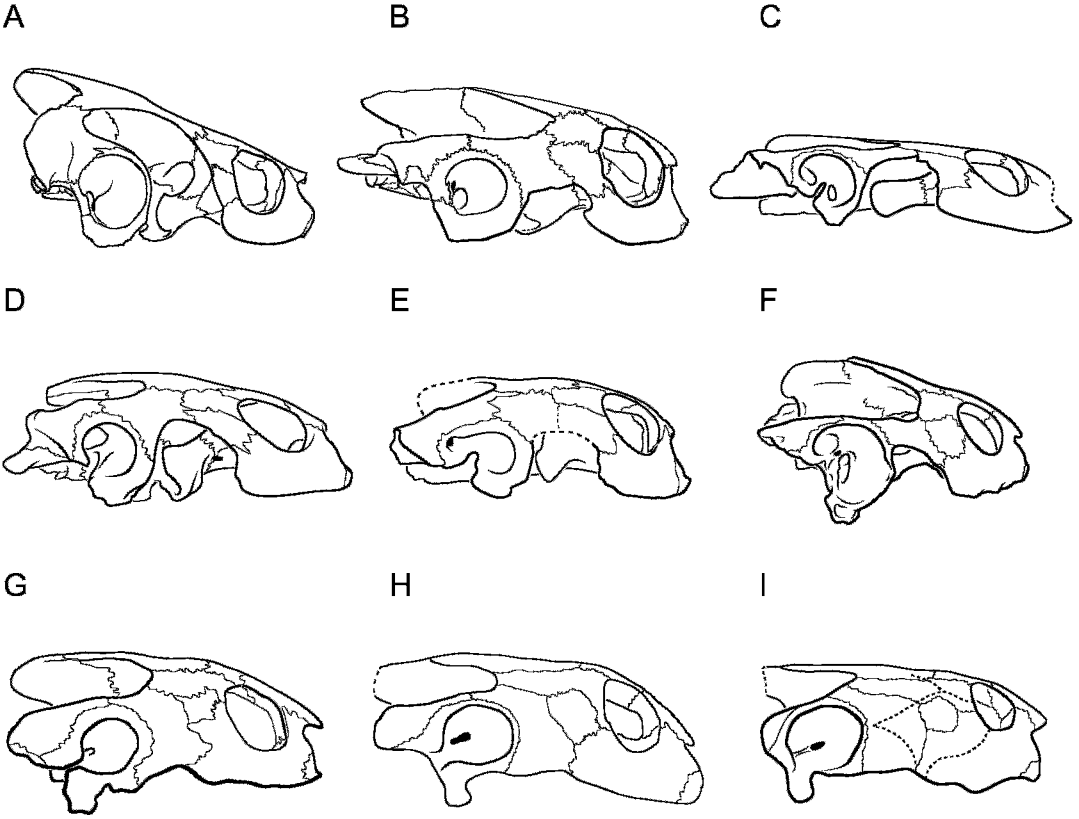

Fig. 3. Comparisons of lateral views of skulls of families Chelidae, Pelomedusidae, Araripemydidae, Euraxemydidae, and the Bothremydidae tribes Kurmademydini and Cearachelyini. **A**, *Emydura macquarrii* (Chelidae); **B**, *Pelomedusa subrufa* (Pelomedusidae); **C**, *Araripemys barretoi* (Araripemydidae); **D**, *Euraxemys essweini* (Euraxemydidae); **E**, *Dirqadim schaefferi* (Euraxemydidae); **F**, *Kurmademys kallamedensis* (Bothremydidae, tribe Kurmademydini); **G**, *Cearachelys placidoi* (Bothremydidae, tribe Cearachelyini); **H**, *Galianemys whitei* (Bothremydidae, tribe Cearachelyini); **I**, *Galianemys emringeri* (Bothremydidae, tribe Cearachelyini). [A. Venjara and various artists, del.]

dae sensu lato) and Chelidae having been diagnosed with synapomorphies in Gaffney (1977b). Gaffney (1988) and Gaffney and Meylan (1988) published a cladogram of Pelomedusoides (= Pelomedusidae sensu lato), but it consisted of relatively few taxa (e.g., the only ones diagnosable by skull characters at that time).

Antunes and Broin (1988) published a phylogeny of the Bothremydidae that was presented within the context of recognizing three family-level taxa (Pelomedusidae Cope, 1868, Podocnemididae Cope, 1868, Bothremydidae Baur, 1891) equivalent to the former family Pelomedusidae, which was raised to the hyperfamily Pelomedusoides. Baur (1888) had already suggested the higher category Pelomedusoidea, which included essentially the same taxa, so the idea of multiple familial categories to recognize diversity within this group is not new. Although Antunes and Broin (1988) used cranial characters to diagnose some of the groups within their Pelomedusoides, many of the terminal taxa in their phylogeny were not known from skulls. Broin (1988) presented a more general branching diagram of the group but without characters. Meylan (1996) provided the first computer-assisted parsimony analysis of Pelomedusoides known at that time. More recent computer-assisted analyses (discussed below) are Tong

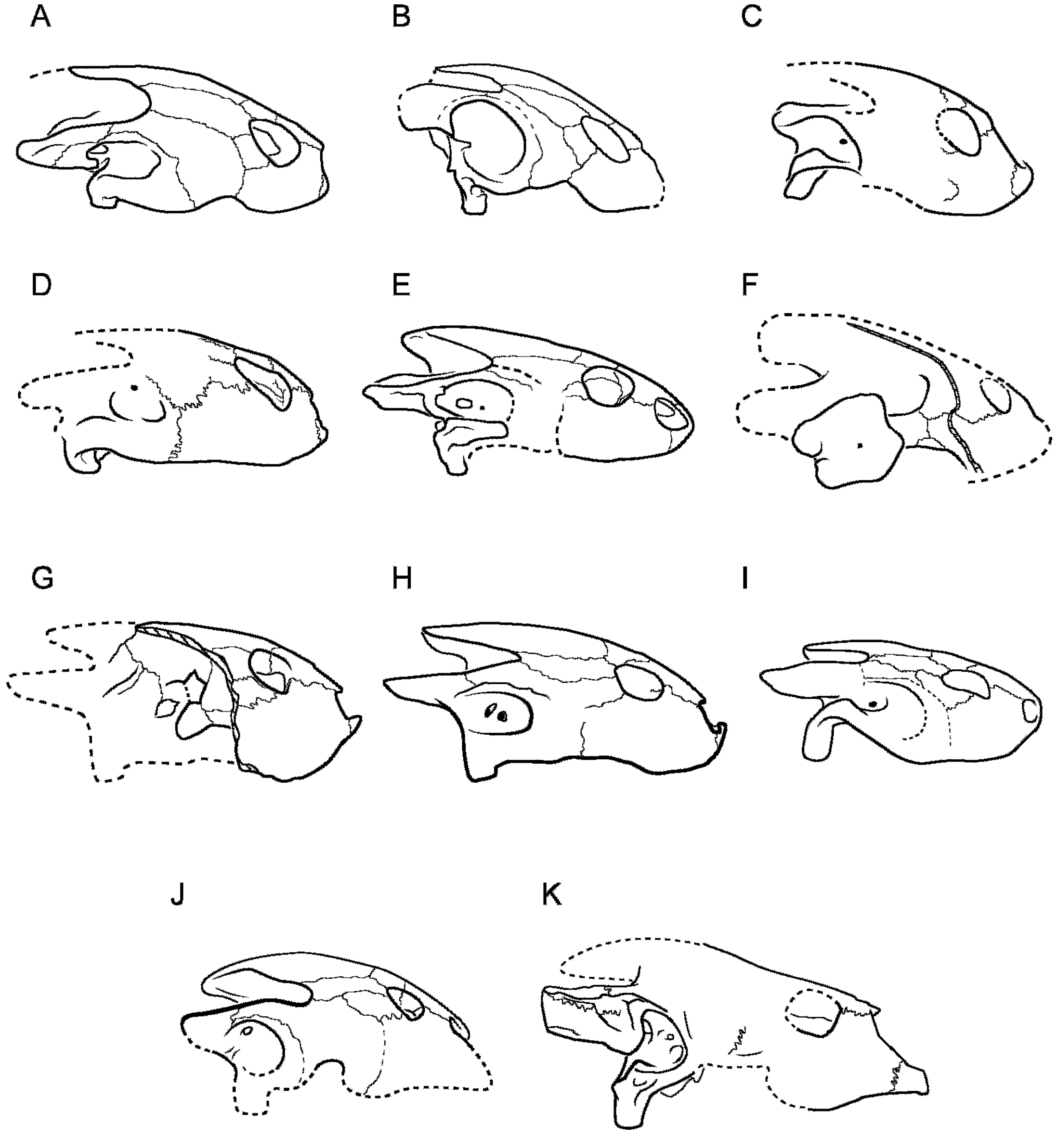

Fig. 4. Comparisons of lateral views of skulls of the family Bothremydidae, tribe Bothremydini. **A**, *Foxemys mechinorum*; **B**, *Polysternon provinciale*; **C**, *Zolhafah bella*; **D**, *Rosasia soutoi*; **E**, *Araiochelys hirayamai*, n. gen. et sp.; **F**, *Bothremys arabicus*; **G**, *Bothremys cooki*; **H**, *Bothremys maghrebiana*, n. sp.; **I**, *Bothremys kellyi*, n. sp.; **J**, *Chedighaii hutchisoni*, n. gen. et sp.; **K**, *Chedighaii barberi*, n. gen. [A. Venjara and various artists, del.]

et al. (1998), Lapparent de Broin and Murelaga (1999), and Fuente and Iturralde-Vinent (2001).

Although many fossil species of Pelomedusoides have been described, mostly on the basis of partial or complete shells, most are incertae sedis within Pelomedusoides or higher. For example, more than 60% of the Pelomedusidae (sensu lato, = Pelomedusoides) listed in Pritchard and Trebbau

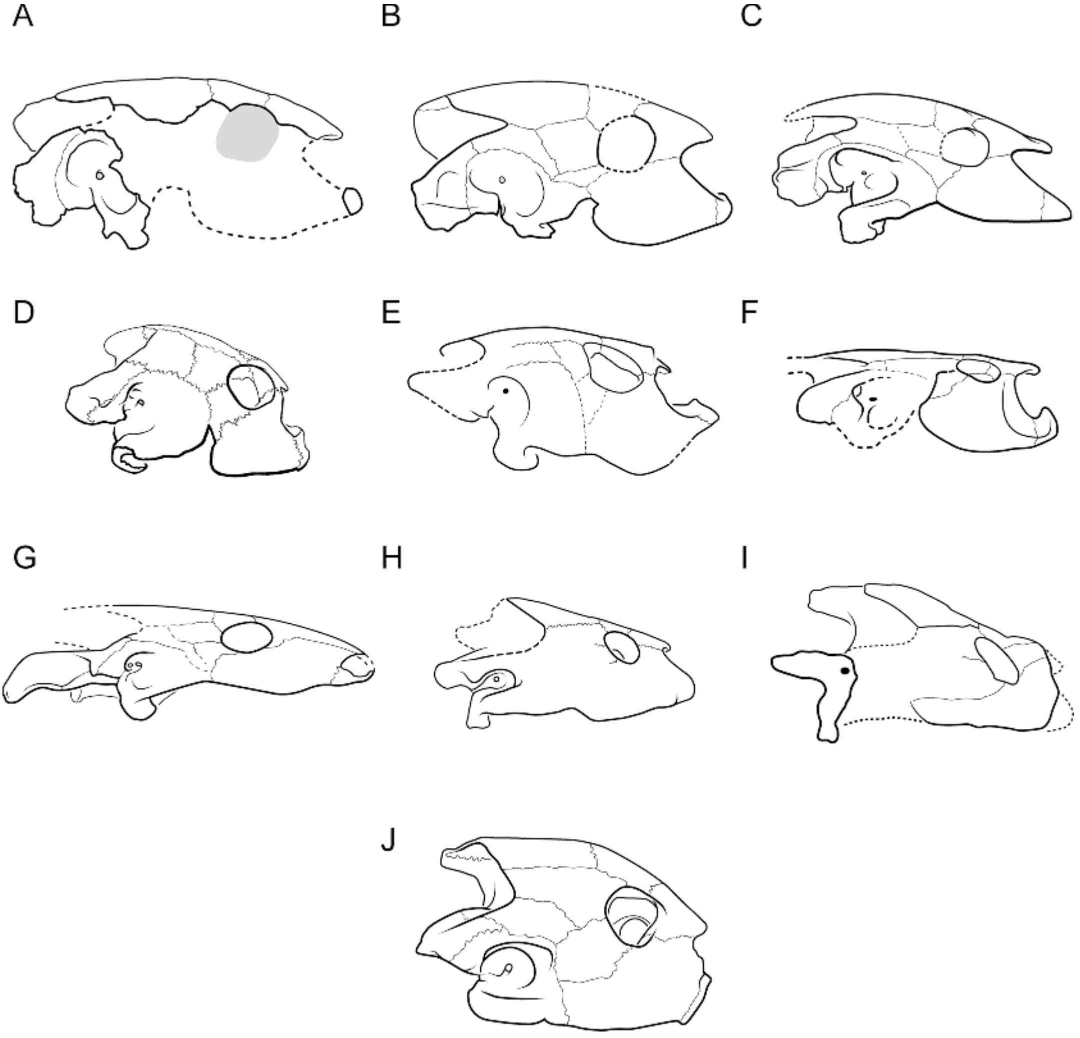

Fig. 5. Comparisons of lateral views of skulls of the family Bothremydidae, tribe Taphrosphyini. **A**, *Taphrosphys sulcatus*; **B**, *Taphrosphys congolensis*; **C**, *Taphrosphys ippolitoi*, n. sp.; **D**, *Phosphatochelys tedfordi*; **E**, *Ummulisani rutgersensis*, n. gen. et sp.; **F**, *Rhothonemys brinkmani*, n. gen. et sp.; **G**, *Labrostochelys galkini*, n. gen. et sp.; **H**, *Nigeremys gigantea*; **I**, *Arenila krebsi*; **J**, *Azabbaremys moragjonesi.* [A. Venjara and various artists, del.]

(1984: 34) are nomina dubia that are of little use in a character-based phylogenetic analysis. Most are differentiated on geographic or stratigraphic grounds, with the conservative shells providing few diagnostic characters.

Specific literature on Pelomedusoides is discussed below, but there are more general references. Named fossil taxa are listed in Kuhn (1964), Mlynarski (1976), Pritchard and Trebbau (1984), Broin (1988), Lapparent de Broin (2000a), and Fuente (2003). King and Burke (1989) and Iverson (1992) listed recent Pelomedusoides species.

The only comprehensive compilation of cranial morphology of fossil and recent Pelomedusoides is Gaffney (1979a), but individual genera are variably described in Merwe (1940, *Pelomedusa*), Gaffney and Zangerl (1968, *Bothremys*), Tronc and Vuillemin (1974, *Erymnochelys*), Antunes and Broin (1977, *Neochelys*), Broin (1988, *Rosasia*), Meylan (1996, *Araripemys*), Tong and Buffetaut (1996, *Hamadachelys*),

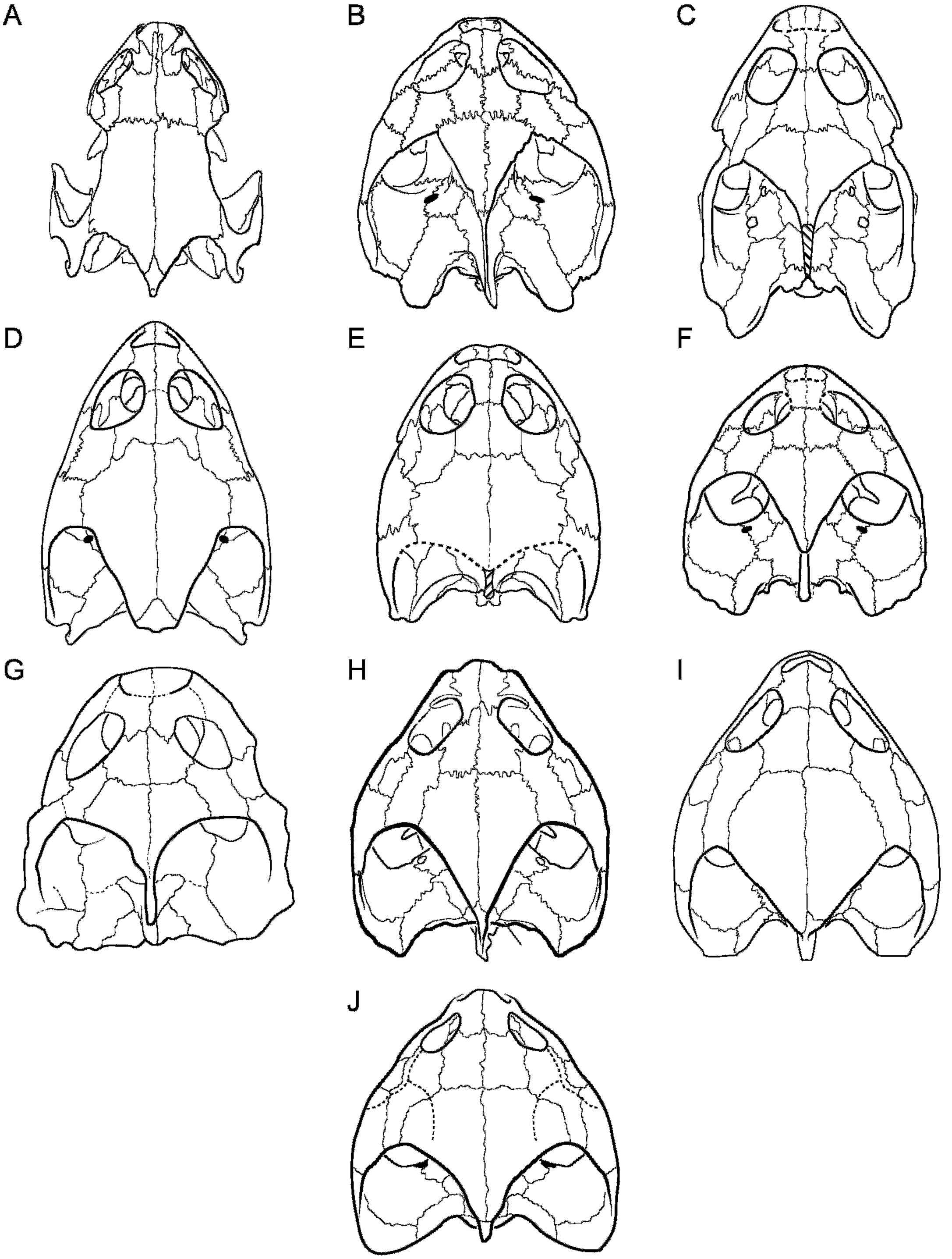

Fig. 6. Comparisons of dorsal views of skulls of families Chelidae, Pelomedusidae, Araripemydidae, Euraxemydidae, and the Bothremydidae tribes Kurmademydini and Cearachelyini. **A**, *Emydura macquarrii* (Chelidae); **B**, *Pelomedusa subrufa* (Pelomedusidae); **C**, *Araripemys barretoi* (Araripemydidae); **D**, *Euraxemys essweini* (Euraxemydidae); **E**, *Dirqadim schaefferi* (Euraxemydidae); **F**, *Kurmademys kallamedensis* (Bothremydidae, tribe Kurmademydini); **G**, *Sankuchemys sethnai* (Bothremydidae, tribe Kurmademydini); **H**, *Cearachelys placidoi* (Bothremydidae, tribe Cearachelyini); **I**, *Galianemys whitei* (Bothremydidae, tribe Cearachelyini); **J**, *Galianemys emringeri* (Bothremydidae, tribe Cearachelyini). [A. Venjara and various artists, del.]

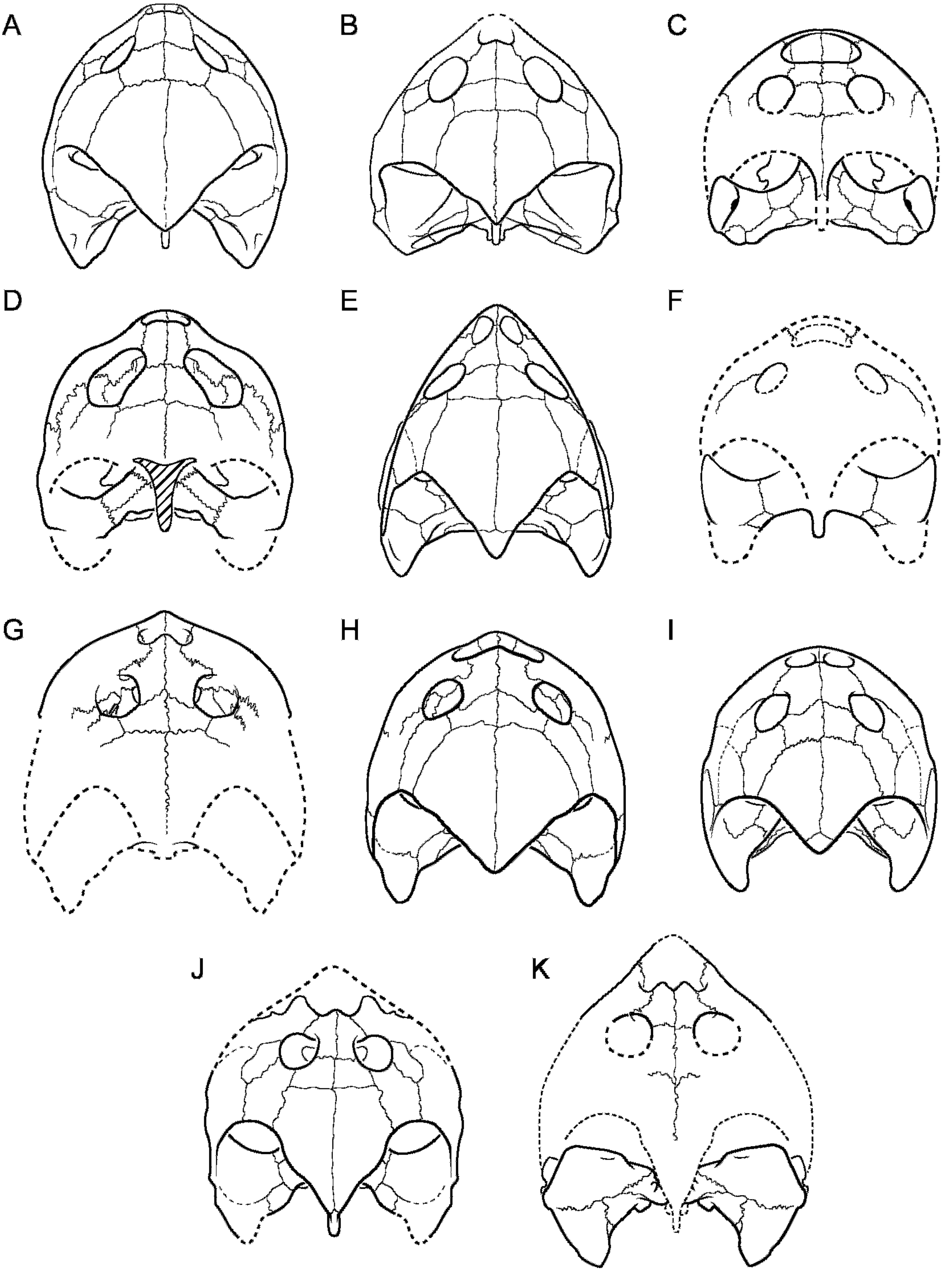

Fig. 7. Comparisons of dorsal views of skulls of the family Bothremydidae, tribe Bothremydini. **A**, *Foxemys mechinorum*; **B**, *Polysternon provinciale*; **C**, *Zolhafah bella*; **D**, *Rosasia soutoi*; **E**, *Araiochelys hirayamai*, n. gen. et sp.; **F**, *Bothremys arabicus*; **G**, *Bothremys cooki*; **H**, *Bothremys maghrebiana*, n. sp.; **I**, *Bothremys kellyi*, n. sp.; **J**, *Chedighaii hutchisoni*, n. gen. et sp.; **K**, *Chedighaii barberi*, n. gen. [A. Venjara and various artists, del.]

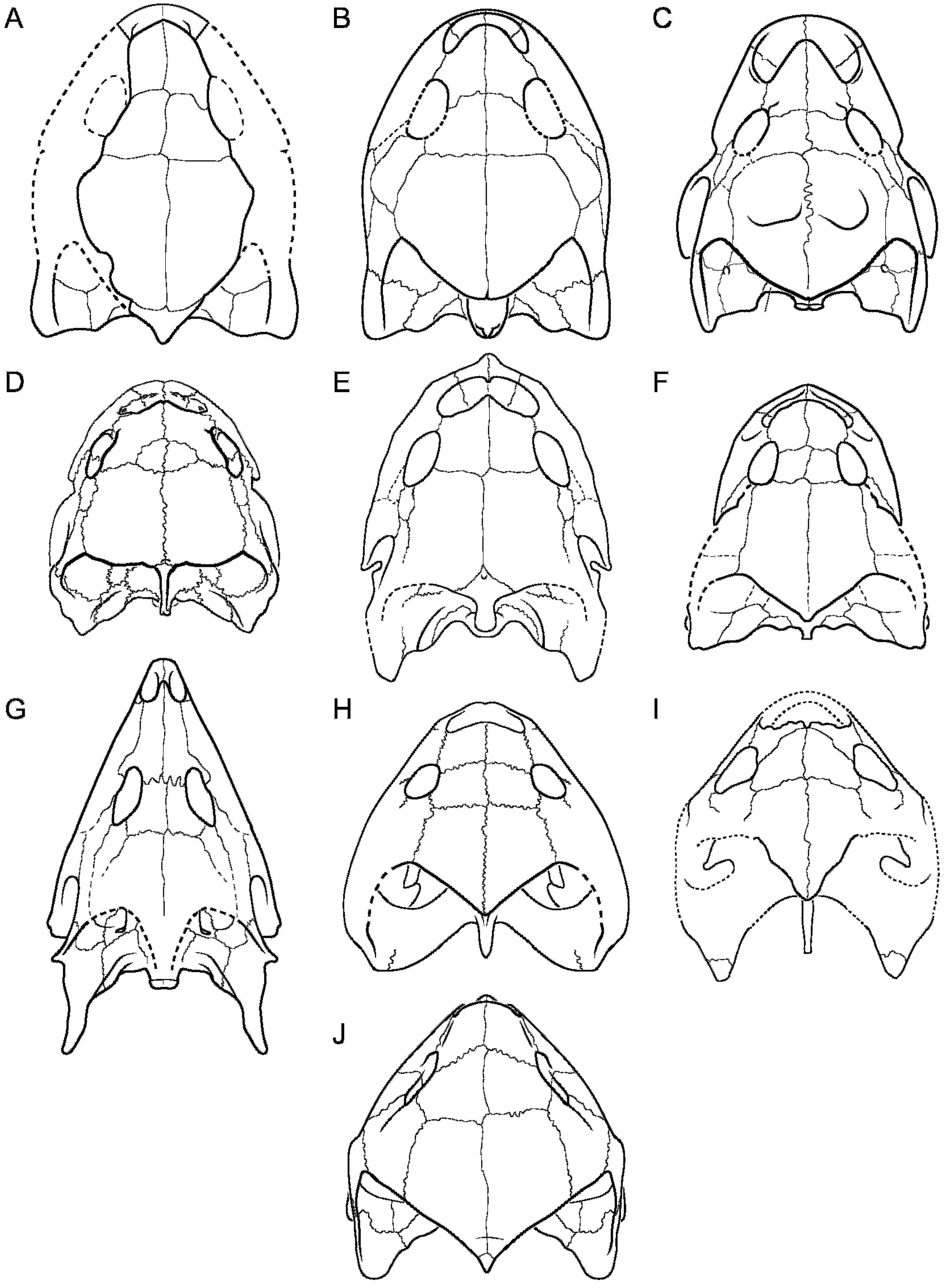

Fig. 8. Comparisons of dorsal views of skulls of the family Bothremydidae, tribe Taphrosphyini. **A**, *Taphrosphys sulcatus*; **B**, *Taphrosphys congolensis*; **C**, *Taphrosphys ippolitoi*, n. sp.; **D**, *Phosphatochelys tedfordi*; **E**, *Ummulisani schaefferi*, n. gen. et sp.; **F**, *Rhothonemys brinkmani*, n. gen. et sp.; **G**, *Labrostochelys galkini*, n. gen. et sp.; **H**, *Nigeremys gigantea*; **I**, *Arenila krebsi*; **J**, *Azabbaremys moragjonesi.* [A. Venjara and various artists, del.]

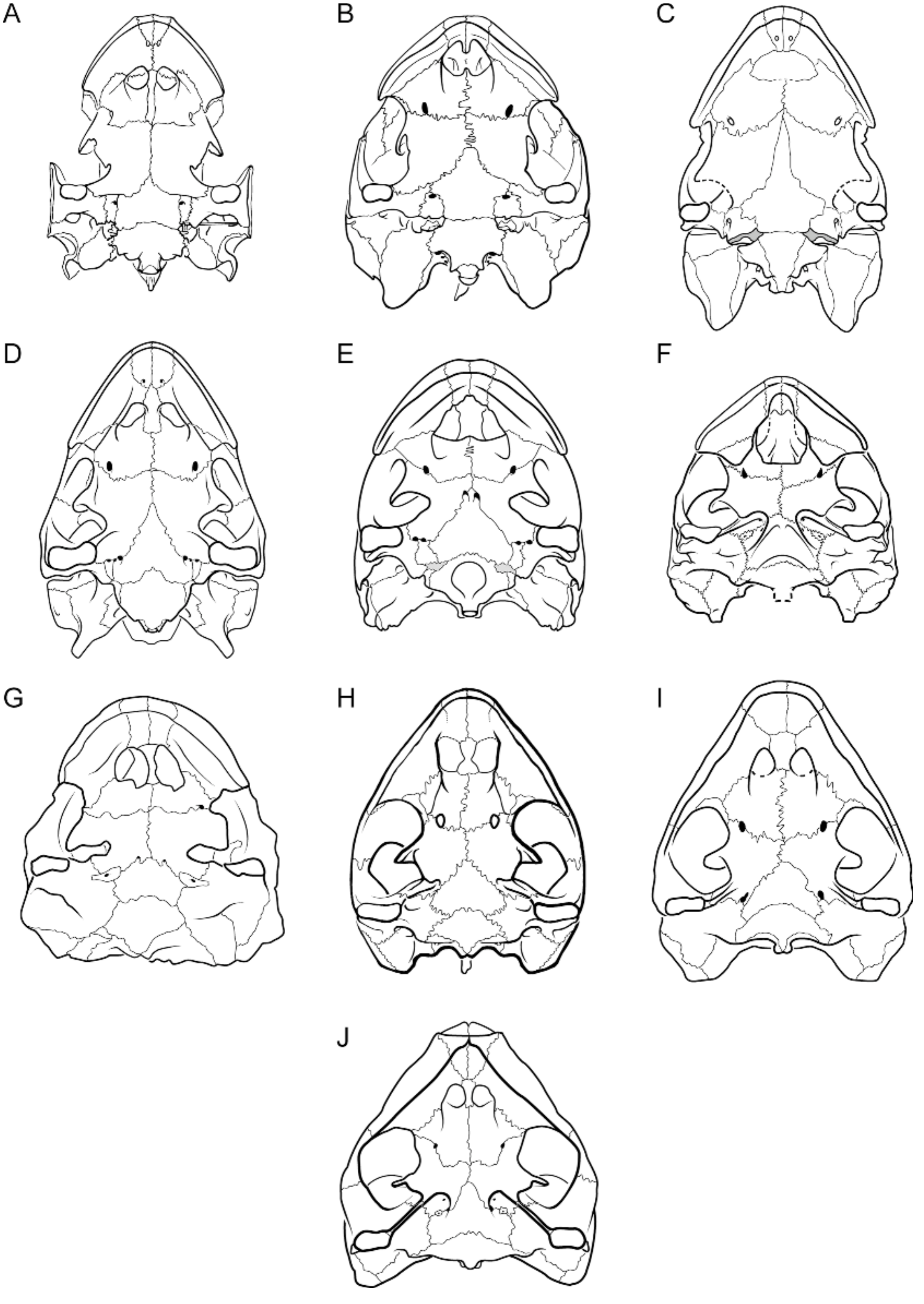

Fig. 9. Comparisons of ventral views of skulls of the families Chelidae, Pelomedusidae, Araripemydidae, Euraxemydidae, and the Bothremydidae tribes Kurmademydini and Cearachelyini. **A**, *Emydura macquarrii* (Chelidae); **B**, *Pelomedusa subrufa* (Pelomedusidae); **C**, *Araripemys barretoi* (Araripemydidae); **D**, *Euraxemys essweini* (Euraxemydidae); **E**, *Dirqadim schaefferi* (Euraxemydidae); **F**, *Kurmademys kallamedensis* (Bothremydidae, tribe Kurmademydini); **G**, *Sankuchemys sethnai* (Bothremydidae, tribe Kurmademydini); **H**, *Cearachelys placidoi* (Bothremydidae, tribe Cearachelyini); **I**, *Galianemys whitei* (Bothremydidae, tribe Cearachelyini); **J**, *Galianemys emringeri* (Bothremydidae, tribe Cearachelyini). [A. Venjara and various artists, del.]

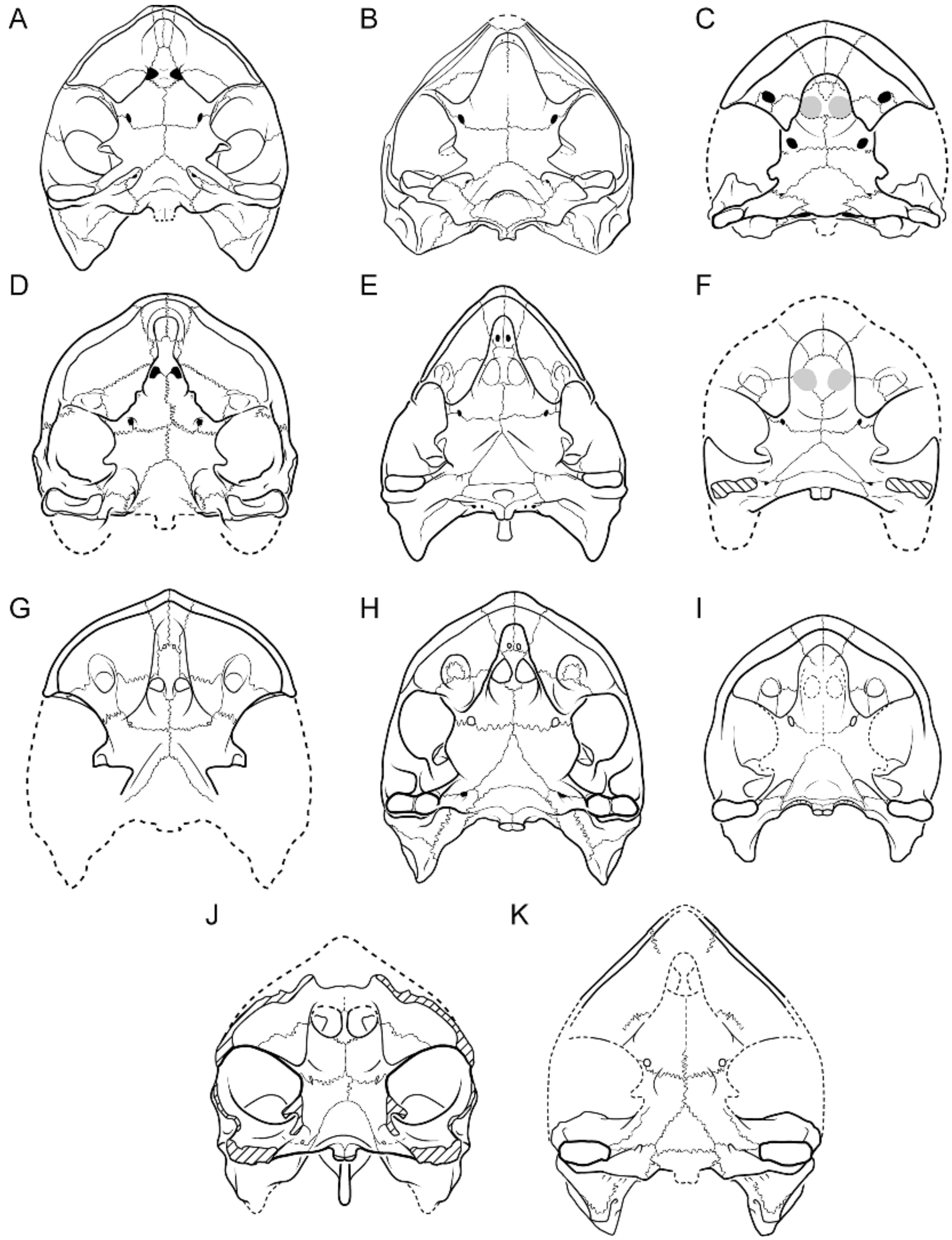

Fig. 10. Comparisons of ventral views of skulls of the family Bothremydidae, tribe Bothremydini. **A**, *Foxemys mechinorum*; **B**, *Polysternon provinciale*; **C**, *Zolhafah bella*; **D**, *Rosasia soutoi*; **E**, *Araiochelys hirayamai*, n. gen. et sp.; **F**, *Bothremys arabicus*; **G**, *Bothremys cooki*; **H**, *Bothremys maghrebiana*, n. sp.; **I**, *Bothremys kellyi*, n. sp.; **J**, *Chedighaii hutchisoni*, n. gen. et sp.; **K**, *Chedighaii barberi*, n. gen. [A. Venjara and various artists, del.]

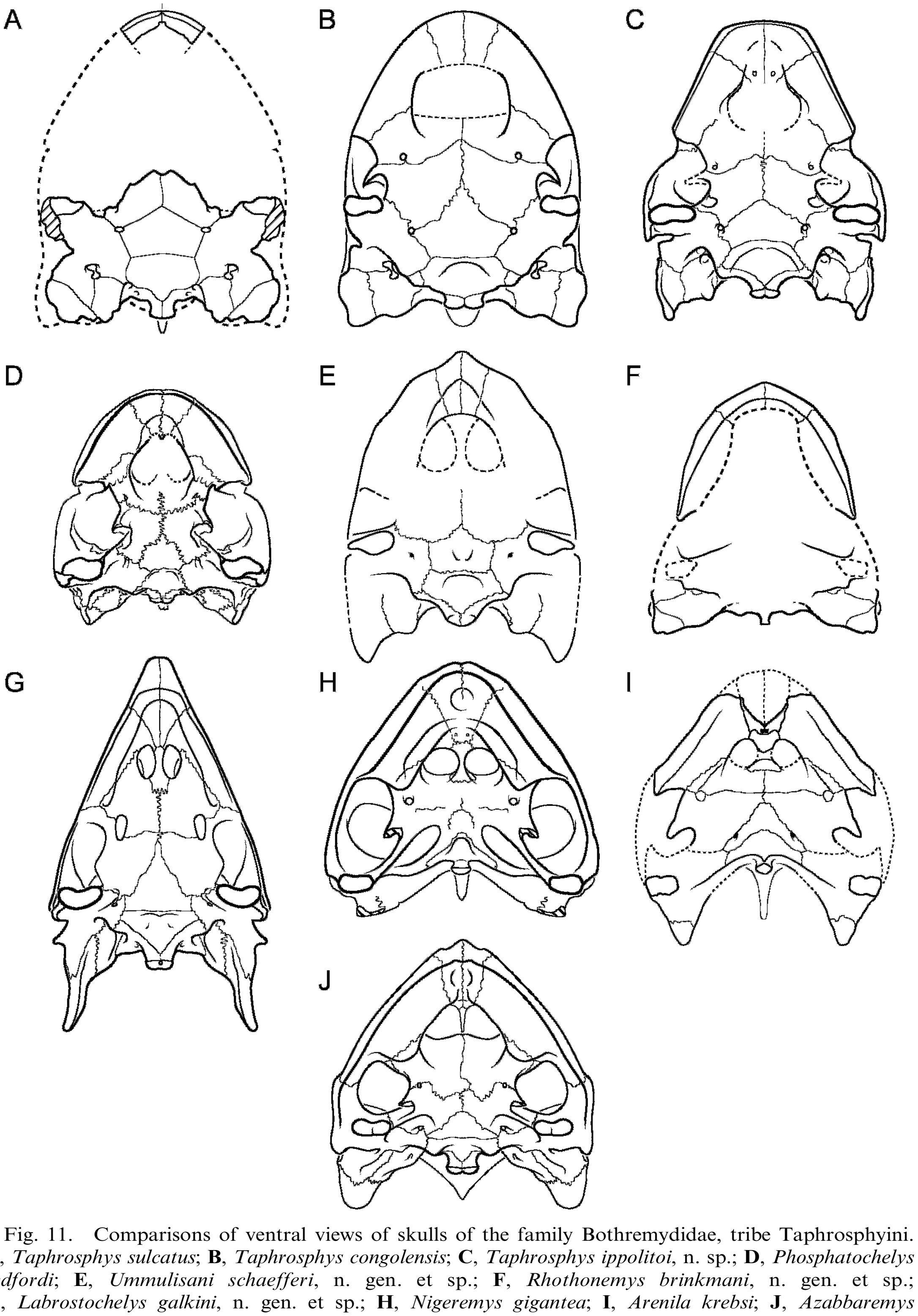

Fig. 11. Comparisons of ventral views of skulls of the family Bothremydidae, tribe Taphrosphyini. **A**, *Taphrosphys sulcatus*; **B**, *Taphrosphys congolensis*; **C**, *Taphrosphys ippolitoi*, n. sp.; **D**, *Phosphatochelys tedfordi*; **E**, *Ummulisani schaefferi*, n. gen. et sp.; **F**, *Rhothonemys brinkmani*, n. gen. et sp.; **G**, *Labrostochelys galkini*, n. gen. et sp.; **H**, *Nigeremys gigantea*; **I**, *Arenila krebsi*; **J**, *Azabbaremys moragjonesi*. [A. Venjara and various artists, del.]

Tong et al. (1998, *Foxemys*), Tong and Gaffney (2000, *Polysternon*), Gaffney, Campos, and Hirayama (2001, *Cearachelys*), Gaffney, Moody, and Walker (2001, *Azabbaremys*), Gaffney, Chatterjee, and Rudra (2001, *Kurmademys*), Gaffney, Tong, and Meylan (2002, *Galianemys*), Gaffney, DeBlieux, Simons, Sánchez-Villagra, and Meylan (2003, *Dacquemys*), and Gaffney and Tong (2003, *Phosphatochelys*).

The only developmental study of Pelomedusoides is Fuchs (1931), a study of the lower jaw in *Podocnemis*. Schumacher (1973, a summary but see earlier papers listed) and Albrecht (1976) described jaw muscles and arteries, respectively, in turtles and included some Pelomedusoides. Nonetheless, the anatomical literature on Pelomedusoides, living and fossil, is very thin, a situation we hope to correct to some extent.

More specific previous work is dealt with within the systematics sections for the groups concerned under the Previous Work subsections (see especially the extensive review of previous work in the review of Bothremydidae).

ORGANIZATION

The text is organized with the systematics section first, then the descriptive section, followed by the phylogenetic analysis and character descriptions. An introduction to pleurodire skull morphology precedes the longer cranial morphology description section. The systematics and descriptive arrangement is based on a classification derived from the MPC (cladogram 1, fig. 288 with skull-only taxa, and cladogram 2, fig. 292 with some shell-only taxa added; both use the same dataset, appendix 3) and are presented on a stratigraphic chart as figure 1. Reference to figure 1 and to the summary classification below will help orient the reader. The cranial morphology section describes 29 taxa that have well-preserved skulls. A comparison of Pelomedusoides skulls in three views is given in figures 3–11. To give the reader at least a chance to wade through this oh-so-interesting mass, it is organized using a common outline, with the bones in a consistent, repeating order, with the same subheadings describing the same topics in the same bone under the same heading for each genus or species. For example, this outline allows the reader to find the description of the foramen posterius canalis carotici under "Pterygoid,-Structures on ventral surface" in the same relative position in the text for *Galianemys* and *Arenila*, as well as any of the other 27 described taxa. The outline listing the bones and topics is summarized as appendix 1. In general, topics begin with the state of preservation of the bone, followed by its contacts, and then its structures. Although an effort has been made to adhere to this outline, there are places where circumstances made modifications more useful. The lower jaws are also included in this outline, although they are treated in a separate section.

Shell material is described following the skull, particularly shells that are known to be associated with skulls. Only a few unassociated shells provide enough characters to be included in our character analysis.

The taxa described in the Cranial Morphology section are in the same order as in the Systematics section. The bones are arranged in the same order and with the same subheadings as in appendix 1. The bone abbreviations in the list of abbreviations are the same ones used by the senior author in previous works. The figure references are to the best figure that shows the bone or feature, not to all figures showing that bone or feature. Most figures have a photograph associated with a labeled line drawing. The figure references in the text are to the labeled line drawing, rather than to both the line drawing and the photograph. The skull figures are usually ordered as follows: three views of the restored skull; shaded palatal drawing, photographs in six views with associated labeled line drawings; and oblique photograph and labeled line drawing. The oblique views are in the same orientation as the oblique ear views in Gaffney (1979a: figs. 85–102). Supplemental figures are usually placed between the six-view figures and the oblique views. Not all taxa lend themselves to this pattern, and there are some exceptions. The reader should be aware that the Character Description sections have comparative figures of the basicranium and the quadrate for many taxa. The restored views were determined by rotating structures from right to left, or by adding structures from other specimens where stated. There are no hypothetical additions or additions from other taxa unless stated. A number of taxa described here have been scanned with computed tomography by Tim Rowe and colleagues at the University of Texas (see http://www.digimorph.org).

Much of the work on this project by the senior author is in a series of notebooks in the AMNH Department of Paleontology archives, including preliminary drawings of all figures, photographs of nearly all specimens (many in stereo), and material not directly figured here.

ABBREVIATIONS

Institutional

AE	Costa Collection, Montpellier, France
ALAB	Alabama Museum of Natural History, Tuscaloosa, Alabama, USA
AMNH	American Museum of Natural History, New York, USA
ANSP	Academy of Natural Sciences of Philadelphia, Pennsylvania, USA
BMNH	Natural History Museum, London, Great Britain
BSP	Bayerische Staatssammlung für Paläeontologie und Historische-Geologie, Munich, Germany
ChM	Charleston Museum, Charleston, South Carolina, USA
CNRST SUNY	Centre National de la Recherche Scienctifique et Technologique, Bamako, Mali—Stony Brook University, New York
CSU, CC	Columbus State University, Columbus, Georgia, USA
DGM-DNPM	Divisao de Geologia e Mineralogia, Departmento Nacional de Produçao Mineral, Rio de Janeiro, Brazil
FMNH	Field Museum (formerly Field Museum of Natural History), Chicago, Illinois, USA
FR	Forschungsinstitut Senckenburg, Frankfurt, Germany
ISI, ISIR	Indian Statistical Institute, Calcutta, India
KUVP	University of Kansas, Lawrence, Kansas, USA
MC	Musée de Cruzy, Cruzy, France
MCNA	Museo de Ciencias Naturales de Alava, Vitoria-Gasteiz, Spain
MDEt	Musée des Dinosaures, Espéraza, France
MHNL	Muséum dHistoire Naturelle de Lyon, Lyon, France
MHNM	Muséum d'Histoire Naturelle de Marseille, Marseille, France
MNHN	Muséum National d'Histoire Naturelle, Paris, France
MPSC	Museu Paleontologico de Santana do Cariri, Ceará State, Brazil (types may be stored at DNPM)
MRAC	Musée Royal de l'Afrique Centrale, Tervuren, Belgium
NCSM	North Carolina Museum of Natural Sciences, Raleigh, North Carolina, USA
NJSM	New Jersey State Museum, Trenton, New Jersey, USA
PAM	Patrick and Annie Méchin, Vitrolles, France
SCSM	South Carolina State Museum, Columbia, South Carolina, USA
SDS/VPL	Vertebrate Paleontology Laboratory, Panjab University, Chandigarh, India
SMNS	Staatliches Museum für Naturkunde, Stuttgart, Germany
THUg	Teikyo Heisei University, Chiba, Japan
TUB	Technische Universität Berlin, Berlin, Germany
UA	Université d'Antananarivo, Madagascar
UCMP	University of California, Museum of Paleontology, Berkeley, USA
UNL	Universidad Nova de Lisboa, Lisbon, Portugal
USNM	United States National Museum, Washington, DC, USA
YPM	Yale Peabody Museum, New Haven, Connecticut, USA
YPM PU	Yale Peabody Museum (formerly Princeton University collection), New Haven, Connecticut, USA
YUP-HUS	Yarmouk University, Paleontological Collection of Huseinia, Irbid, Jordan

Anatomical

A	unnamed foramen in floor of canalis nervi vidiani of *Araripemys*
ab	abdominal scale
am	area articularis mandibularis
ana	anal scale
ax	axillary buttress

ane	apertura narium externa
ang	angular
ani	apertura narium interna
ap	antrum postoticum
art	articular
ast	aditus canalis stapedio-temporalis
bc	basis columellae
bo	basioccipital
bs	basisphenoid
ca	columella auris
cai	canalis alveolaris inferior
caj	cavum acustico jugulare
car	carapace
cas	canalis alveolaris superior
cc	canalis cavernosus
cci	canalis caroticus internus
ccl	canalis caroticus lateralis
ccm	canalis cartilaginis meckelii
ccr	cavum cranii
cf	"chelid" foramen
cio	canalis infraorbitalis
cip	canalis intrapalatinus
cl	cavum labyrinthicum
cm	condylus mandibularis
cna	canalis nervi abducentis
cnf	canalis nervi facialis
cnv	canalis nervi vidiani
co	condylus occipitalis
cor	coronoid
cos	costal bone
cp	crista pterygoidea
cs	crista supraoccipitalis
csa	canalis semicircularis anterior
csh	canalis semicircularis horizontalis
csp	canalis semicircularis posterior
cst	canalis stapedio-temporalis
ct	cavum tympani
ctm	canalis chorda tympani mandibularis
ctq	canalis chorda tympani quadrati
den	dentary
ds	dorsum sellae
ent	entoplastron
eof	exoccipital-opisthotic foramen
epi	epiplastron
ex	exoccipital
facci	foramen anterius canalis carotici interni
fact	foramen anterius chorda tympani
fae	foramen arteriaevidianae
faf	fossa acustico-facialis
fai	foramen alveolare inferius
fas	foramen alveolare superius
fav	foramen aquaducti vestibuli
fc	foramen cavernosum
fcl	foramen caroticum laterale
fcti	foramen chorda tympani inferius
fcts	foramen chorda tympani superius
fd	foramen dentofaciale majus
fe	fissura ethmoidalis
fem	femoral scale
fib	foramen intermandibularis oralis
fic	foramen intermandibularis caudalis
fim	foramen intermandibularis medius
fio	foramen interorbitale
fja	foramen jugulare anterius
fjp	foramen jugulare posterius
fm	foramen magnum
fmk	fossa meckelii
fn	fossa nasalis
fna	foramen nervi auriculotemporalis
fnf	foramen nervi facialis
fnt	foramen nervi trigemini
fnv	foramen nervi vidiani
fo	fenestra ovalis
fon	foramen orbito-nasale
for	fossa orbitalis
fp	foramen praepalatinum
fpa	foramen palatinum accessorium
fpc	fossa precolumellaris
fpcci	foramen posterius canalis carotici interni
fpct	foramen posterius chorda tympani
fpe	fenestra perilymphatica
fpo	fenestra postotica
fpp	foramen palatinum posterius
fpt	fossa pterygoidea
fr	frontal
fs	fenestra subtemporalis
fsm	foramen supramaxillare
fso	foramen supraorbitale
fst	foramen stapedio-temporale
fti	fossa temporalis inferior
fts	fossa temporalis superior
gu	gular scale
ha	hiatus acusticus
hu	humeral scale
hum	humerus
hyo	hyoplastron
hypo	hypoplastron
ib	inguinal buttress
ica	incisura columellae auris
ils	iliac scar
in	intergular scale
isc	ischiac scar
IXe	foramen externum nervi glossopharyngei
IXi	foramen internum nervi glossopharyngei
IXm	foramen medialis nervi glossopharyngei
ju	jugal
la	lacrimal
lar	labial ridge
lhv	lateral head vein
lir	lingual ridge
ma	marginal scale

me	mesoplastron
mx	maxilla
ne	neural bone
nu	nuchal bone
op	opisthotic
pa	parietal
pal	palatine
pas	processus articularis
pc	processus coronoideus
pec	pectoral scale
pel	pelvis
per	peripheral bone
pf	prefrontal
pg	pygal bone
pi	processus interfenestralis
pip	processus inferior parietalis
pl	processus clinoideus
pla	plastron
plu	pleural scale
pm	premaxilla
po	postorbital
pp	processus paroccipitalis
pr	prootic
pra	prearticular
prt	processus retroarticularis
ps	pubis scar
pt	pterygoid
ptf	pterygoid flange
ptp	processus trochlearis pterygoidei
qj	quadratojugal
qp	quadrate pocket
qs	quadrate shelf
qu	quadrate
rb	rostrum basisphenoidale
rlo	recessus labyrinthicus opisthoticus
rlp	recessus labyrinthicus prooticus
rls	recessus labyrinthicus supraoccipitalis
rst	recessus scalae tympani
sa	stapedial artery
sc	sulcus cavernosus
scm	sulcus cartilaginis meckelii
se	sulcus eustachii
sep	sulcus eustachii ventral process
sf	sulcus olfactorius
sh	shell
sl	sella turcica
so	supraoccipital
sot	septum orbitotemporale
sp	splenial
spg	suprapygal
spt	sulcus palatinopterygoideus
sq	squamosal
sqf	squamosal flange
st	sella turcica
sur	surangular
sv	sulcus vomeri
tb	tuberculum basioccipitale
tr	trigeminal ridge
ve	vertebral scale
VI	foramen nervi abducentis
VII	foramen nervi facialis
VIII	foramen nervi acustici
vo	vomer
vt	vertebrae
XII	foramen nervi hypoglossi
xip	xiphiplastron

Other

del.	"delineator", to identify the artist of the figure indicated
MFL	Main Fossil Layer of Hornerstown Formation, New Jersey
MPC	Most Parsimonious Cladogram (see Phylogenetic Analysis)

SYSTEMATICS

The translation of a cladogram into a text-only arrangement of names in the form of a classification is, unfortunately, not a hypothesis subject to test by observation; instead, it is a social process governed (if at all) by consensus and agreement, usually assisted by appeal to a set of agreed-upon rules. During the development of phylogenetic systematics, most classifications attempted to be an ordered set of hierarchical names of monophyletic taxa, determined by an associated cladogram and governed, to the extent possible, by Linnaean precedent. Although cladistic analysis has been the norm for phylogenetic work (at least in morphology) for decades, recently some have argued that there are limitations in the Linnaean classification system that require its complete abandonment in favor of an alternative, the PhyloCode, incorrectly called by some, "Phylogenetic Taxonomy" (De Queiroz and Gauthier, 1992). Although we do see some problems with the Linnaean system as a mirror image of a cladogram, with taxon names that can change in content with every addition or subtraction of a basic taxon or character, we do not think creation of a new system is the answer. We take a more traditional view, similar to that expressed by Nixon and Carpenter (2000; see also Carpenter, 2003; Janovec et al., 2003; Keller et al., 2003; Kojima, 2003; Moore, 2003; Nixon et al., 2003; and Schuh, 2003), that it is better to modify the Linnaean system where convenient, rather than set up a new one, particularly a rankless one.

An extreme example of the abandonment of the more traditional system of turtle classification is the Joyce et al. (2004) version of the PhyloCode in which most of the previously named higher taxa of turtles have been replaced or redefined with new content. Although this exercise claimed to improve stability in turtle nomenclature, it is obvious to the senior author that the opposite is the case. In fact, the proponents of new higher category definitions and names for turtles (Lee, 1995; Joyce et al., 2004) do not themselves agree on the taxon names or definitions. However, while the ongoing controversy over essentialism in nomenclature, the definition of definition, and the existence of individuals versus classes all may provide interesting activity for those that have the time to contemplate them, many practicing systematists seem to continue with a pluralistic methodology in translating cladograms into classifications (e.g., Wyss and Meng, 1996; Simmons and Geisler, 1998; Sereno, 2005). There has always been a struggle of content versus character ("node" versus "stem", for some authors) in the recognition of higher categories, even when the taxa are agreed upon (e.g., Simpson, 1945; McKenna and Bell, 1997). Most systematists change their own diagnoses of higher taxa, maintaining concepts using a mix of characters and content, as new species and new characters become available. Sereno (2005) pointed out that the senior author consistently maintained the same usage for higher categories in turtles when new taxa were discovered, altering some diagnoses to maintain Pleurodira, Cryptodira, and Casichelydia, for example, showing that he "never rigidly linked apomorphies with taxa" (Sereno, 2005: 614). The persistence of ill-defined taxa is of course poor science. However, so long as the basis of a taxon is clearly stated, it can be used or abused by other workers, without strict compliance to a complex set of rules like the PhyloCode (that do not seem to be agreed upon by their advocates in any case). So the "Panpleurodira" and "Pleurodiromorpha" are out there for those who prefer strict content-based definitions, while the senior author continues to alter Pleurodira with content considerations but based on a diagnosis consisting of characters. Therefore, all of the following higher taxa are primarily character-based but with consideration of historical content.

Another troublesome aspect of some recent classifications is the use of geological range in naming groups, the "stem" and "crown" nomenclature, referring to whether taxa include living species. Since extinction is not an element of the cladogram, it should not be an element of the classification, which is cumbersome enough without the added burden of geological range. The new classi-

CLASSIFICATION OF PLEURODIRES

Order Testudines Linnaeus, 1758 or Batsch, 1788

SUBORDER PROGANOCHELYDIA ROMER, 1966

SUBORDER CASICHELYDIA GAFFNEY, 1975b

INFRAORDER CRYPTODIRA COPE, 1868

INFRAORDER PLEURODIRA COPE, 1864

Parvorder Minipleurodira, new
    Family Proterochersidae Nopcsa, 1928
        Proterochersis robusta Fraas, 1913

Parvorder Megapleurodira, new
    Family Dortokidae Lapparent de Broin and Murelaga, 1996, Megapleurodira incertae sedis
        Dortoka vasconica Lapparent de Broin and Murelaga, 1996
        Ronella botanica Gheerbrant, Codrea, Hosu, Sen, Guernet, Lapparent de Broin, and Riverline, 1999

Nanorder Platychelira, new
    Family Platychelyidae Bräm, 1965
        Platychelys oberndorferi Wagner, 1853
        Notoemys zapatocaensis Rueda and Gaffney, 2005
        Notoemys oxfordiensis (Fuente and Iturralde-Vinent, 2001)
        Notoemys laticentralis Cattoi and Freiburg, 1961

Nanorder Eupleurodira Gaffney and Meylan, 1988, new rank
 Hyperfamily Cheloides Gray, 1825
    Family Chelidae Gray, 1825
 Hyperfamily Pelomedusoides Cope, 1868
  Magnafamily Pelomedusera Cope, 1868
    Family Pelomedusidae Cope, 1868
        Pelusios Wagler, 1830
        Pelomedusa Wagler, 1830
    Family Araripemydidae Price, 1973
        Araripemys barretoi Price, 1973
  Magnafamily Podocnemidera Cope, 1868
        Teneremys lapparenti Broin, 1980, Podocnemidera incertae sedis
   Superfamily Euraxemydoidea, new
    Family Euraxemydidae, new
        Euraxemys essweini, n. gen. et sp.
        Dirqadim schaefferi, n. gen. et sp.
   Superfamily Podocnemidoidea Cope, 1868
    Epifamily Podocnemidinura Cope, 1868
        Brasilemys josai Lapparent de Broin, 2000a
        Hamadachelys escuilliei Tong and Buffetaut, 1996
    Family Podocnemididae Cope, 1868

- Nanorder Eupleurodira (*continued*)
  - Epifamily Bothremydinura Baur, 1891
    - Family Bothremydidae Baur, 1891
      - Subfamily Kurmademydinae, new
        - Tribe Kurmademydini, new
          - *Kurmademys kallamedensis* Gaffney, Chatterjee, and Rudra, 2001
          - *Sankuchemys sethnai* Gaffney, Sahni, Schleich, Singh, and Srivastava, 2003
      - Subfamily Bothremydinae Baur, 1891
        - Infrafamily Cearachelyodda, new
          - Tribe Cearachelyini, new
            - *Cearachelys placidoi* Gaffney, Campos, and Hirayama, 2001
            - *Galianemys emringeri* Gaffney, Tong, and Meylan, 2002
            - *Galianemys whitei* Gaffney, Tong, and Meylan, 2002
        - Infrafamily Bothremydodda Baur, 1891
          - Tribe Bothremydini, new
            - Subtribe Foxemydina, new
              - *Foxemys mechinorum* Tong, Gaffney, and Buffetaut, 1998
              - *Polysternon provinciale* (Matheron, 1869)
              - *Polysternon atlanticum* Lapparent de Broin and Murelaga, 1996
              - *Elochelys perfecta* Nopcsa, 1931
              - *Elochelys convenarum* Laurent, Tong, and Claude, 2002
            - Subtribe Bothremydina, new
              - *Zolhafah bella* Lapparent de Broin and Werner, 1998
              - *Rosasia soutoi* Carrington da Costa, 1940
              - *Araiochelys hirayamai,* n. gen. et sp.
              - *Bothremys cooki* Leidy, 1865
              - *Bothremys maghrebiana,* n. sp.
              - *Bothremys kellyi,* n. sp.
              - *Bothremys arabicus* (Zalmout, Moustafa, and Wilson, 2005)
              - *Chedighaii hutchisoni,* n. gen. et sp.
              - *Chedighaii barberi* (Schmidt, 1940)
          - Tribe Taphrosphyini, new
            - Subtribe Taphrosphyina, new
              - *Taphrosphys sulcatus* (Leidy, 1856)
              - *Taphrosphys ippolitoi,* n. sp.
              - *Taphrosphys congolensis* (Dollo, 1913)
              - *Labrostochelys galkini,* n. gen. et sp.
              - *Phosphatochelys tedfordi* Gaffney and Tong, 2003
              - *Ummulisani rutgersensis,* n. gen. et sp.
              - *Rhothonemys brinkmani,* n. gen. et sp.
              - *Azabbaremys moragjonesi* Gaffney, Moody, and Walker, 2001
            - Subtribe Nigeremydina, new
              - *Nigeremys gigantea* (Bergounioux and Crouzel, 1968)
              - *Arenila krebsi* Lapparent de Broin and Werner, 1998

fications of Lee (1995) and Joyce et al. (2004) produce confusion for no advantage.

Therefore, the classification below is a ranked and named reflection of cladogram 2, shown in figure 292, without modifications based on extinction or strict definitions based on content. The taxa are named on the basis of monophyly; monophyletic groups are ranked on the basis of the cladogram in figure 292. Cladogram 2 differs from cladogram 1 (fig. 288) in the addition of some shell-only taxa, some of which are incertae sedis in the classification although they are fully resolved in cladogram 2. Some of the incertae sedis taxa are listed at their level of uncertainty. The traditional Linnaean higher categories are used to make it easier to find groups and to keep track of position within the cladogram. All possible monophyletic groups are not named, but there are some "empty" higher taxa, named so that there are matching levels of categories for ease in navigating the classification. The diagnoses of higher categories are primarily based on the apomorphy list (ACCTRAN optimization) produced for cladogram 2, with some distinguishing characters added when considered helpful. The species diagnoses consist of autapomorphies not in the dataset, as well as other distinguishing features. The classification of pleurodires developed in this paper is summarized on pages 26–27 and expanded in the Systematics section below.

ORDER TESTUDINES
INFRAORDER PLEURODIRA COPE, 1864

DIAGNOSIS: Casichelydian turtles with the following cranial characters: processus trochlearis pterygoidei, a lateral process of the pterygoid covered with infolded oral mucosa articulating with a cartilaginous nodule within the main adductor tendon present; sulcus palatinopterygoideus and associated septum orbitotemporale present; quadrate with ventral process extending medially to braincase below cranioquadrate space; hyomandibular branch of facial nerve (VII) usually subdivided within canalis cavernosus in its own canal; epipterygoid absent; foramen palatinum posterius lies behind orbit, usually posterior to fossa orbitalis; fossa precolumellaris deep and well defined primitively; condylus mandibularis anterior to basioccipital-basisphenoid suture primitively; foramen posterius canalis carotici interni completely enclosed by prootic primitively; cheek emargination present primitively.

Postcranial characters are: cervical ribs absent, cervical and caudal centra formed; sutural articulation of ilium with costal bones and pubis and ischium with xiphiplastron; tenth thoracic centrum incorporated into sacrum; dorsal part of ilium expanded; ilia close to midline; shoulder on lateral side of humeral head; anal notch present.

DISCUSSION: The cranial characters are as indicated by the ACCTRAN optimization in PAUP* (version 4.0b10, Swofford, 2002) for "cladogram 2 (fig. 292). However, with skulls absent in the four basal taxa, the distribution for some or all of these characters could be in any of these taxa up to the Eupleurodira. In the absence of shell-only taxa, cladogram 1 (fig. 288), all these characters are at Pleurodira with no ambiguity. See also table 1.

PARVORDER **MINIPLEURODIRA**, NEW

TYPE GENUS: *Proterochersis* Fraas, 1913.

INCLUDED TAXA: Family Proterochersidae Nopcsa, 1928.

DIAGNOSIS: Same as for family.

FAMILY PROTEROCHERSIDAE NOPCSA, 1928

TYPE AND ONLY INCLUDED GENUS: Proterochersis Fraas, 1913.

DISTRIBUTION: Late Triassic, Germany.

REVISED DIAGNOSIS: Pleurodire with these unique characters: two pairs of mesoplastra meeting in midline; nine pairs of plastral scales plus one on midline on xiphiplastra; 14 marginal scales, in contrast to 16 or more in *Proganochelys* and 12 or fewer in other turtles; other characters unique among pleurodires are: thyroid fenestra small; pygal notch present, narrow and spherical; three supramarginal scales (also in *Platychelys*); dorsal process of epiplastron very large; gular scales forming large projections.

PREVIOUS WORK: See Fraas (1913) for original description and Gaffney (1990) for a current reconstruction of the shell.

DISCUSSION: Known from nearly two dozen shells from the Late Triassic of

TABLE 1
Comparison of Early Pleurodires

	Proganochelys	*Proterochersis*	Platychelyidae	*Dortoka*	Eupleurodira
Pelvis sutured to shell	no	yes	yes	yes	yes
Mesoplastra	1 pair	2 pairs	1 pair	absent	1 pair, absent
Plastral scales	7 pair	9 pair	6 pair	6 pair	6 pair
Marginal scales	16–17	14	12	12	12
Vertebral scales	4	5	5	5	5
Supramarginal scales	12	3	0, 3	0	0
Caudal centra	platycoelous	?	variable?	variable	procoelous
Thyroid fenestra	small	small	large	large	large
Nuchal bone width 2× wider than length	yes	?	yes	no	usually no
Pygal notch present	yes	yes	no	no	no
Position of 4-sided neural	?	?	2nd	1st	1st, 2nd, 3rd
Neural series "regular" (see text)	?	?	no	no	yes
Axillary process reaches peripheral 3	no	no	no	yes	yes
Vertebral scales ≥ pleural scales	yes	yes	yes	no	no
1st thoracic rib small, close to 2^{nd}	no	no	no	yes	yes
Costovertebral tunnel large entire length	no	no	yes	no	no
Thoracic rib 1 with anterior facet	no	no	yes	no	no
Mesoplastra meet on midline	yes	yes	no	no	no[a]
Epiplastra meet on midline	no	no	yes	yes	yes
Large dorsal epiplastral process	yes	yes	no	no	no
Intergular scales	2	2	1	1	1
Gular projections	yes	yes	no	no	no
Posterior plastral lobe wider than pelvis	no	yes	yes	yes	yes
Anal notch present	no	yes	yes	yes	yes

[a] Except for *Pelusios*.

Germany, *Proterochersis* is a pleurodire on the basis of its sutured pelvis and shell and its xiphiplastral notch (see table 1). Although the two pairs of mesoplastra may be expected to be primitive for turtles, *Proganochelys* and other turtles with mesoplastra have only one pair, so two pairs is unique to *Proterochersis*.

Karl and Tichy (2000) have named a new taxon, "*Murrhardtia staeschei*", from the Late Triassic of Germany. This taxon is a junior synonym of *Proterochersis robusta* Fraas, 1913. Karl and Tichy mistakenly used Fraas' reconstruction of the type, SMNS 12777 (Fraas, 1913: figs. 1, 2), as a figure of the actual type specimen for comparison, and they named a more complete specimen of *Proterochersis robusta* (unnumbered shell in the Carl Schweizer Museum, Murhardt, Germany) as a new taxon. SMNS 12777 has only the internal mold of the carapace, plus a partial plastron, while the Karl and Tichy shell is nearly complete. However, two of us (E.S.G., P.A.M.) have studied these specimens, as well as nearly two dozen other *Proterochersis* shells, and have concluded that they all belong to a single species. In the areas that overlap in the type specimen of *Proterochersis robusta* and the type specimen of "*Murrhardtia staeschei*", they are nearly identical.

PARVORDER **MEGAPLEURODIRA**, NEW

TYPE GENUS: *Pelomedusa* Wagler, 1830.

INCLUDED TAXA: Families Dortokidae, Platychelyidae, Chelidae, Araripemydidae, Pelomedusidae, Euraxemydidae, Podocnemididae, Bothremydidae.

DIAGNOSIS: Pleurodires with fewer than two pairs of mesoplastra, in contrast to

Proterochersis, epiplastra meet in midline; single intergular scale rather than a pair as in *Proterochersis*; mesoplastra not meeting in midline (except in *Pelusios*); axillary and inguinal scales absent; axillary process contacts costal one.

DISCUSSION: This taxon is created for all pleurodires above *Proterochersis* in cladogram 2 (fig. 292, also table 1). The family Dortokidae is placed here incertae sedis even though in cladogram 2 it is resolved as the sister taxon to the nanorder Eupleurodira. The few characters allowing this resolution are poorly known.

MEGAPLEURODIRA INCERTAE SEDIS FAMILY DORTOKIDAE LAPPARENT DE BROIN AND MURELAGA, 1996

TYPE GENUS: *Dortoka* Lapparent de Broin and Murelaga, 1996.

INCLUDED GENERA: *Dortoka* Lapparent de Broin and Murelaga, 1996; *Ronella* Gheerbrant et al., 1999.

DISTRIBUTION: Late Cretaceous, Spain; Paleocene, Romania. Other possible localities based on fragmentary material from the Barremian of Spain and the Late Cretaceous of France reported in Lapparent de Broin et al. (2004).

DIAGNOSIS: Lapparent de Broin et al. (2004).

PREVIOUS WORK: Lapparent de Broin and Murelaga (1996, 1999), Gheerbrant et al. (1999), Lapparent de Broin et al. (2004).

DISCUSSION: See below.

Dortoka Lapparent de Broin and Murelaga, 1996

TYPE AND ONLY INCLUDED SPECIES: *Dortoka vasconica* Lapparent de Broin and Murelaga, 1996.

DISTRIBUTION: Late Cretaceous of Spain and possibly of France; Paleocene of Romania (Lapparent de Broin et al., 2004).

ETYMOLOGY: "Turtle" in Basque.

DIAGNOSIS: See Lapparent de Broin and Murelaga (1999).

Dortoka vasconica Lapparent de Broin and Murelaga, 1996

TYPE SPECIMEN: MCNA 6313, a partial shell (Lapparent de Broin and Murelaga, 1996: fig. 1a, b; 1999: pl. 3, fig. 1a, b).

TYPE LOCALITY: Laño, Condado de Treviño, Spain (Lapparent de Broin and Murelaga, 1996, 1999).

HORIZON: Upper Campanian (Lapparent de Broin and Murelaga, 1996).

DIAGNOSIS: See Lapparent de Broin et al. (2004).

ETYMOLOGY: In reference to Pais Vasconica, the Basque country (Lapparent de Broin and Murelaga, 1996).

REFERRED MATERIAL: "more than 461 numerated specimens" (Lapparent de Broin and Murelaga, 1999: 136). Although there are a few partial shells, most consist of disarticulated single bones. More complete shells are described in Lapparent de Broin et al. (2004).

PREVIOUS WORK: Lapparent de Broin and Murelaga (1996, 1999).

DISCUSSION: *Dortoka* consists only of partial shells and many isolated shell and other postcranial elements. If the claimed associations (Lapparent de Broin and Murelaga, 1996, 1999; Lapparent de Broin et al., 2004) are correct, then nearly all of the shell characters in the dataset are determinable (see also table 1). Consequently, this taxon can be resolved as the sister group to the Eupleurodira (i.e., Chelidae + Pelomedusoides), despite the large amount of missing data. In Lapparent de Broin and Murelaga (1999), their preferred cladogram showed *Dortoka* as sister group to Pelomedusoides and within Eupleurodira. In view of the limited data available, both cladograms must be considered strong possibilities until skull material provides more phylogenetic information.

Considering the ambiguous nature of the phylogenetic results, we are loath to diagnose a new higher category on the group *Dortoka* (or Dortokidae) + Eupleurodira, and simply list *Dortoka* along with its presumed relative, *Ronella*, as Megapleurodira incertae sedis.

Ronella Gheerbrant, Codrea, Hosu, Sen, Guernet, Lapparent de Broin, and Riveline, 1999

TYPE AND ONLY INCLUDED SPECIES: *Ronella botanica* Gheerbrant, Codrea, Hosu, Sen, Guernet, Lapparent de Broin, and Riveline (1999).

Considered by Lapparent de Broin et al. (2004: 207) as "*Ronella botanica* Lapparent de Broin, 2000, in Gheerbrant et al. 1999, type species of the genus." However, according to normal bibliographic pratice, the author attribution should be based on the authors listed on the title page. The reason for the difference in date is not known.

DISTRIBUTION: Paleogene of Romania.

ETYMOLOGY: In reference to the type horizon, the "calcaires de Rona" (Gheerbrant et al., 1999: 523).

DIAGNOSIS: See Lapparent de Broin et al. (2004).

Ronella botanica Gheerbrant, Codrea, Hosu, Sen, Guernet, Lapparent de Broin, and Riveline, 1999

TYPE SPECIMEN: A partial plastron, JBB-21, University Babes-Bolyai, Cluj, Romania.

TYPE LOCALITY: JBB-21 of Gheerbrant et al. (1999: 519), botanical garden of Jibou, Romania.

HORIZON: Calcaires de Rona, Sparnacian/Thanetian (Gheerbrant et al., 1999); Late Paleocene, Late Thanetian, Rona Limestone (Lapparent de Broin et al., 2004).

DIAGNOSIS: See Lapparent de Broin et al. (2004).

ETYMOLOGY: For the botanical garden type locality (Gheerbrant et al., 1999: 519).

REFERRED MATERIAL: 117 fragments belonging to at least six individuals (Gheerbrant et al., 1999). More complete shells are described in Lapparent de Broin et al. (2004).

PREVIOUS WORK: Gheerbrant et al. (1999), Lapparent de Broin et al. (2004).

DISCUSSION: This series of partial shells and shell elements are pleurodiran, as shown by the pelvic scars on the plastron. A recent description of new material (Lapparent de Broin et al., 2004) provided a nearly complete shell for this species, which substantiated it as a close relative of *Dortoka*.

NANORDER **PLATYCHELIRA**, NEW

TYPE GENUS: *Platychelys* Wagner, 1853.

INCLUDED TAXA: Family Platychelyidae.

DIAGNOSIS: Same as family Platychelyidae.

FAMILY PLATYCHELYIDAE BRÄM, 1965

TYPE GENUS: *Platychelys* Wagner, 1853.

INCLUDED GENERA: *Platychelys* Wagner, 1853; *Notoemys* Cattoi and Freiburg, 1961 (= *Caribemys* Fuente and Itturalde-Vinent, 2001).

DIAGNOSIS: Pleurodires differing from all other pleurodires (except *Chelus*) in having very wide costovertebral tunnel, differing from all other pleurodires in having an articulation tubercle on anterior edge of first thoracic rib, and carapace shape with anterior edge wide and straight, posterior sides tapering; other distinguishing characters: neurals alternating in size, as in *Dortoka*; first thoracic rib nearly as large as second thoracic rib; thoracic vertebral centra flat ventrally, thoracic ribs flat and broad without ventral keel; first thoracic central articulation concave, wider than high; thoracic ribs 9, 10, and 11 forming sacrum and attaching to ilium; iliac scar on costals 7 and 8 and suprapygal.

DISCUSSION: *Notoemys* and *Platychelys* are united by Rueda and Gaffney (2005) to form the Platychelyidae. *Platychelys oberndorferi* has been described by Lang and Rütimeyer (1866), Rütimeyer (1873), Zittel (1877), Bräm (1965), and Lapparent de Broin (2001). *Notoemys laticentralis* has been described by Cattoi and Freiburg (1961), Fuente and Fernandez (1989), and Fernandez and Fuente (1994). Rueda and Gaffney (2005) have described another species, *N. zapatocaensis*, and have argued that "*Caribemys*" *oxfordiensis* belongs in *Notoemys*, a conclusion we accept. *Notoemys laticentralis* is known from the shell, some vertebrae, some appendicular elements, and a partial skull. Although we have been unable to examine the partial skull, we suspect that the bone anterolateral to the basisphenoid in Fernandez and Fuente (1994: fig. 2B) is the pterygoid rather than the quadrate, as in chelids and pelomedusids. Because this partial skull of *Notoemys* is incomplete, we have been able to code only a few characters for it, and, at least for the present, we consider *Notoemys* as another shell-only taxon.

NANORDER EUPLEURODIRA GAFFNEY AND MEYLAN, 1988

DIAGNOSIS: Only procoelous caudal articulations; neural bones from number 2 posterior are hexagonal in shape, with ante-

TABLE 2
Major Groups of Pleurodira

	Chelidae	Pelomedusidae	Araripemydidae	Euraxemydidae	Bothremydidae	Podocnemididae
Nasals	present	absent	absent	absent	absent	absent
Prefrontals meet on midline	no	yes	yes	yes	yes	yes
Prefrontal	narrow	narrow	narrow	narrow	wide & narrow	wide & narrow
Quadratojugal-parietal contact	absent	absent	absent	present	present & absent	present
Squamosal-parietal contact	present	absent	absent	present & absent	absent	absent
Temporal emargination	slight	extreme	extreme	slight to moderate	extreme to slight	slight
Quadratojugal	absent	present	present	present	present	present
Wide triturating surfaces	yes and no	no	no	no	yes & no	yes & no
Accessory triturating ridge	no	yes & no	no	yes	yes & no	yes & no
Maxilla-quadratojugal contact	absent	absent	absent	absent	present primitively	absent
Maxilla-vomer contact	present	absent	?	present	present & absent	absent
Vomer	present	absent	?	present	present	present
Incisura columellae auris closed or a narrow fissure	no	no	no	no	yes	no
Fossa precolumellaris	deep	deep	deep	shallow	usually absent	usually deep
Quadrate-basioccipital contact	absent	absent	absent	absent	present	present
Pterygoid enters foramen posterius canalis carotici interni	no	no	no	yes	yes	yes
Supraoccipital-quadrate contact	absent	absent	absent	absent	present[a]	absent
Foramen jugulare posterius	closed	closed	variable	open	open & closed	closed
Exoccipital-quadrate contact	absent	absent	absent	present, narrow	present, extensive	absent
Exoccipital ventral process	usually absent	absent	—[b]	present	absent	absent
Basioccipital	long	long	long	long	short	short
Foramen stapedio-temporale visible dorsally	yes	yes	yes	yes	no[c]	yes
Foramen stapedio-temporale and foramen nervi trigemini close together	no	no	no	no	—[d]	no
Prootic covered ventrally	no	no	no	partly	yes	yes
Wedge-shaped prootic	no	yes	yes	no	no	no
Processus interfenestralis opisthotic covered ventrally	no	no	no	yes	yes	yes
Processus paroccipitalis of opisthtoic projects posteriorly beyond squamosal	no	yes	yes	yes	no	yes
Basisphenoid-quadrate contact	absent	narrow to absent	absent	absent	wide & narrow	wide
Prootic-quadrate contact	present	present	present	present	absent	absent
Exoccipital-basisphenoid contact	absent	absent	absent	present & absent	absent	absent
Condylus occipitalis	EX + BO	EX	EX + BO	EX + BO	EX, EX + BO	EX + BO

rolateral contacts shorter than posterolateral contacts; mesoplastra equidimensional and not meeting in midline except in *Pelusios* (mesoplastra absent in most but not all Chelidae); axillary process of hyoplastron reaches third peripheral (also in *Dortoka*); cervical postzygapophyses elevated on neural spine.

Discussion: The Eupleurodira was named by Gaffney and Meylan (1988) for the living pleurodires, consisting of the family Chelidae and the (then) family Pelomedusidae. These authors used the absence of medially meeting mesoplastra and supramarginal scales as the diagnosis. In cladogram 2, the mesoplastron character is still diagnostic for Eupleurodira, but the absence of supramarginals is more ambiguous due to their presence in the Platychelyidae, which requires either a reversal in *Platychelys* or independent loss in *Notoemys*. Other postcranial characters are also useful to diagnose this group. The main ambiguity is *Dortoka*, a shell-only genus that falls outside the Eupleurodira in cladogram 2, but this placement requires a few reversals (see also table 1).

In cladogram 1, with deletion of the shell-only taxa, Eupleurodira is the same as Pleurodira and has 41 synapomorphies diagnosing it.

TABLE 2
Continued

	Chelidae	Pelomedusidae	Araripemydidae	Euraxemydidae	Bothremydidae	Podocnemididae
Basioccipital-opisthotic contact	present	present	absent	absent	absent	present
Anteroventral part of exoccipital large	no	no	yes	no	no	no
Foramen posterius canalis carotici interni formed by prootic	yes	yes	yes	no	no	no
Degree of enclosure of cavum acustico-jugulare	less	less	less	more	more	more
Splenial	present	absent	absent	absent	absent	absent
Processus retroarticularis	short	short	short	short	long	long
Biconvex cervical	5th	2nd	2nd	2nd	?	2nd
Cervical scale	present	absent	absent	absent	absent	absent
Complete neural series reaching suprapygal	yes	no	yes	yes	yes & no	no

[a] Except Taphrosphyini and *Zolhafah*.
[b] Extensive ventral exposure.
[c] Except *Kurmademy*.
[d] Only in Taphrosphyini and Bothremydini.

HYPERFAMILY CHELOIDES GRAY, 1825

Type Genus: *Chelus* Duméril, 1806.

Included Taxa: Family Chelidae.

Diagnosis: Same as family Chelidae.

FAMILY CHELIDAE GRAY, 1825

Type Genus: *Chelus* Duméril, 1806.

Included Genera: *Chelus* Duméril, 1806; *Acanthochelys* Gray, 1873; *Chelodina* Fitzinger, 1826; *Elseya* Gray, 1867; *Emydura* Bonaparte, 1836; *Hydromedusa* Wagler, 1830; *Phrynops* Wagler, 1830; *Platemys* Wagler, 1830; *Pseudemydura* Siebenrock, 1901; *Rheodytes* Legler and Cann, 1980; *Elusor* Cann and Legler, 1994; *Bonapartemys* Broin and Fuente, 2001; *Lomalatachelys* Broin and Fuente, 2001; *Prochelidella* Broin and Fuente, 2001; *Palaeophrynops* Broin and Fuente, 2001; *Yaminuechelys* Fuente, Lapparent de Broin, and Manera de Bianco, 2001.

DISTRIBUTION: Early Cretaceous to Recent, South America and Australia (see King and Burke, 1989; Iverson, 1992; Broin and Fuente, 2001; Fuente et al., 2001).

DIAGNOSIS: Eupleurodires with the following unique characters: cheek emargination uniquely extensive, reaching parietal and usually squamosal; quadratojugal absent; cervical formula (2((3((4((5))6))7((8).

DISCUSSION: Monophyly of the Chelidae is well corroborated. Within-group relationships based on morphology (Gaffney, 1977b; Gaffney and Meylan, 1988; Bona and Fuente, 2005) and molecules (Seddon et al., 1997; Shaffer et al., 1997; Georges et al. 1998; Krenz et al., 2005) differ significantly, and the molecular phylogenies seem to be well supported. Nonetheless, we have not adopted a within-group cladogram and have therefore coded some characters as variable. Note that recent discoveries of Cretaceous chelids (Fuente et al., 2001; Lapparent de Broin and Fuente, 2001; Fuente, 2003; Bona and Fuente, 2005) support the morphology-based analyses. See King and Burke (1989), Iverson (1992), and Cann (1998) for literature on the living species. See also table 2 for characters of the Chelidae.

The chelid cervical formula of (2((3((4((5))6))7((8) has been suggested for the Platychelyidae and possibly *Dortoka* by Lapparent de Broin and Murelaga (1999), in which case this would become a synapomorphy at the level of Pleurodira or Megapleurodira. However, this is based on only a few cervicals, and our own examination of these taxa makes this generalization questionable.

HYPERFAMILY PELOMEDUSOIDES COPE, 1868, NEW RANK

TYPE GENUS: *Pelomedusa* Wagler, 1830.

INCLUDED TAXA: Families Pelomedusidae, Araripemydidae, Euraxemydidae, Podocnemididae, Bothremydidae.

DIAGNOSIS: Pleurodires with the unique possession of prefrontals meeting on the midline and nasals absent; parietal-squamosal contact absent; splenial absent; cervical scale absent; cervical vertebrae procoelous with biconvex second vertebra; primitively, processus paroccipitalis of opisthotic projects posteriorly beyond squamosal, and prearticular-angular contact present; anterior plastral lobe usually reaches anterior carapace margin.

MAGNAFAMILY PELOMEDUSERA COPE, 1868

TYPE GENUS: *Pelomedusa* Wagler, 1830.

INCLUDED GENERA: *Pelomedusa* Wagler, 1830; *Pelusios* Wagler, 1830; *Araripemys* Price, 1973.

DIAGNOSIS: Pelomedusoides with extensive temporal and cheek emargination (also in Kurmademydini and *Teneremys*); axillary process not reaching costal one (not in *Pelomedusa*).

DISCUSSION: This taxon is based on cladogram 2 (fig. 292), which shows the Pelomedusidae and *Araripemys* as sister taxa. However, if the high-missing-value shell-only taxa are deleted (cladogram 1, fig. 288), then *Araripemys* is outside the Pelomedusidae and there is no Pelomedusera. Even when the shell-only taxa are included, the few shared characters do not strongly support this group. However, the clade does exist in this analysis and is worth recognizing in regard to relationships of the Pelomedusidae (sensu stricto). This clade is also proposed by Kischlat (1996b). Another way to reflect this relationship would be to put *Araripemys* into the family Pelomedusidae.

The axillary process reaches the first costal in *Pelomedusa*, the preseumed primitive condition for the Pelomedusidae, because the process reduction in *Pelusios* seems to be related to the hinge mechanism unique to that genus.

FAMILY PELOMEDUSIDAE COPE, 1868a

TYPE GENUS: *Pelomedusa* Wagler, 1830.

INCLUDED GENERA: *Pelomedusa* Wagler, 1830; *Pelusios* Wagler, 1830.

DIAGNOSIS: Pelomedusoides with condylus occipitalis formed only by exoccipitals; foramen caroticum laterale absent; neural series not complete to suprapygal; vomer absent; basioccipital-opisthotic contact present (also in Podocnemididae); incisura columellae enclosing eustachian tube and stapes (also in Podocnemididae).

DISCUSSION: Although the published fossil record for this family is very poor, Lapparent de Broin (2000a) listed a number of new records extending back to the Paleocene. Unfortunately, the basis for these new identifications is not known. See King and Burke (1989) and Iverson (1992) for literature on the living species of *Pelusios* and *Pelomedusa*. See table 2 for a comparison of the Pelomedusidae to other families of Eupleurodira.

FAMILY ARARIPEMYDIDAE PRICE, 1973

Type Genus: *Araripemys* Price, 1973.

Included Genus: *Araripemys* Price, 1973 (see below for *Taquetochelys* Broin, 1980, discussion).

Diagnosis: As for genus.

Discussion: *Taquetochelys decorata* Broin, 1980 was described from the Aptian of Gadoufaoua, Niger, on the basis of a series of shell fragments (Broin, 1980: pl. 2, figs. 1a, 1b, pl. 3, figs. 2–11). The fragments have a characteristic surface texture, similar to that of *Araripemys*. Broin (1980) placed the genus in the Araripemydidae on the basis of the texture. It has small, lateral mesoplastra, absent in *Araripemys*. At present, the material is inadequate to establish a proper diagnosis and is considered Pelomedusoides incertae sedis (see Dubious Taxa below); however, it is possible that better specimens from the type locality could make the taxon diagnosable.

Fuente and Lapparent de Broin (1997) described a partial carapace as being a new but unnamed taxon of Pelomedusoides too incomplete to place in a family, but similar in some characters to *Araripemys*. They discussed the inadequate nature of *Taquetochelys* and listed presumed occurrences of *Araripemys*.

See also table 2 for comparisons among families of Pelomedusoides.

Araripemys Price, 1973

Type and Only Included Species: *Araripemys barretoi* Price, 1973.

Distribution: Albian Late Aptian (Early Cretaceous), Ceará, Brazil.

Etymology: For the Araripe Chapada, the region where the type was found (Price, 1973).

Revised Diagnosis: A member of the Pelomedusoides with extensive temporal and cheek emargination as in Pelomedusidae, but in contrast to the roofed condition of Podocnemididae, Bothremydidae, and Euraxemydidae, and to the extreme cheek emargination of Chelidae; basisphenoid very long, nearly reaching palatines, with posterior expansion resulting in a shape unique among Pelomedusoides; narrow triturating surface without accessory ridges and with thin labial ridge, in contrast to Bothremydidae and Podocnemididae; incisura columellae auris not enclosed by bone; fossa precolumellaris deep, as in Chelidae and Pelomedusidae; quadrate-basioccipital contact absent, as in Chelidae and Pelomedusidae; ventral exposure of exoccipital extensive, in contrast to all other Pelomedusoides; prootic widely exposed ventrally and forming foramen posterius canalis carotici interni, in contrast to Euraxemydidae, Bothremydidae, and Podocnemididae; processus interfenestralis of opisthotic widely exposed ventrally, in contrast to Euraxemydidae, Bothremydidae, and Podocnemididae.

Very flat, sculptured carapace in which first costals reach shell margin between nuchal and first peripherals, very long neck, reduced plastron lacking mesoplastra and gular scutes, inverted V-shaped entoplastron, J-shaped epiplastra forming a sharp point anteriorly, three midplastral fontanelles, postzygapophyses joined forming a single articular surface in cervical vertebrae 2–8, first thoracic strongly sutured to nuchal, and medial and lateral centralia absent (Meylan, 1996).

Discussion: The cranial part of the diagnosis has been revised on the basis of the new skull material and reexamination of previous material. The postcranial part of the diagnosis is essentially from Meylan (1996).

Araripemys barretoi Price, 1973

Araripemys arturi Fielding, Martill, and Naish, 2005.

Type Specimen: Divisao de Geologia e Mineralogia, Departamento Nacional de Produçao Mineral, Rio de Janeiro, DGM-DNPM 756-R; shell lacking anterior margin, part and counterpart (Price, 1973: figs. 1–5).

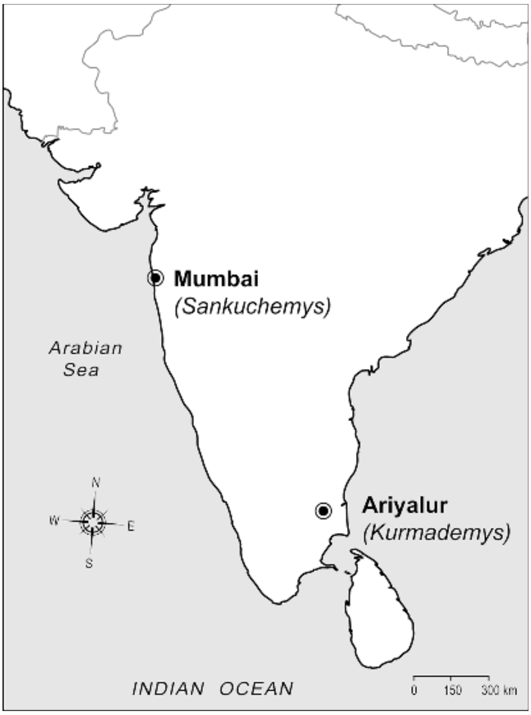

Fig. 12. Map showing localities of the family Bothremydidae, tribe Kurmademydini, in India. Only generically identifiable specimens are indicated. [A. Venjara, del.]

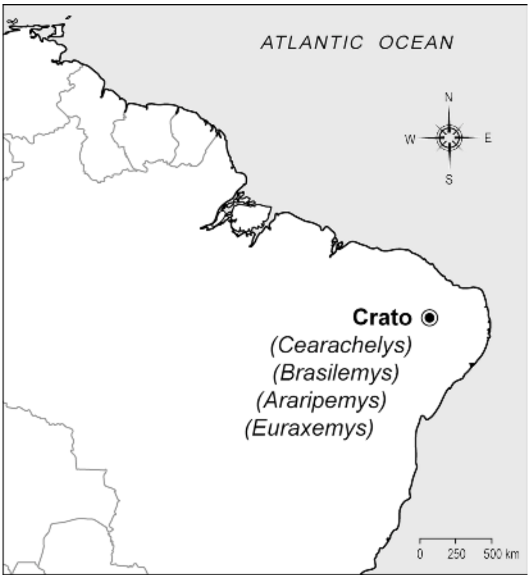

Fig. 13. Map showing locality of the family Bothremydidae, tribe Cearachelyini (*Cearachelys*); family Euraxemydidae (*Euraxemys*); family Araripemydidae (*Araripemys*); and family Brasilemydidae (*Brasilemys*) in Brazil. Only generically identifiable specimens are indicated. [A. Venjara, del.]

TYPE LOCALITY: Gypsum mine, ca. 2 km NE Santana do Cariri, Ceara, Brazil (Price, 1973) (fig. 13).

HORIZON: The Romualdo Member of the Santana Formation lies between the Crato Member of the Santana Formation (below) and the Exu Formation, which overlies the Santana Formation. Both of the latter horizons are most likely Albian in age. This suggests an Albian age (Early Cretaceous ±110 mya) for the Romualdo Member of the Santana Formation and for nearly all specimens of *Araripemys* (Maisey, 1990, 1991). Fielding et al. (2005) described an *Araripemys* from the Crato Formation that probably extends the taxon back to the Late Aptian.

DEPOSITIONAL ENVIRONMENT: Near-shore marine (Maisey, 1990) with probable freshwater episodes (Maisey, 2000). Also occurs with the chelonioid *Santanachelys* (Hirayama, 1998), the bothremydid *Cearachelys*, and the euraxemydid *Euraxemys*. Maisey (2000) made the argument that the Crato has significant freshwater deposits with saline influxes. *Araripemys* is rare in the Crato and its relation to freshwater/saline deposits is ambiguous. Maisey (2000) also showed that the Santana Formation proper also has freshwater episodes. Considering that *Araripemys* is much more common in this unit, it may also be fresh water in habit. The life environment of the Santana turtles is still unclear.

DIAGNOSIS: As for genus.

ETYMOLOGY: In recognition of Abel Barreto, the discoverer of the type (Price, 1973).

REFERRED MATERIAL: THUg 1357, skull (figs. 28, 29), shell, cervicals, some limb elements; near Crato (or Jardim?), Ceara, Brazil (label), purchased from "J. Karl 9/11/1990 (Rhg 9)", Romualdo Member, Santana Formation; THUg 1907, skull (figs. 32, 33) with articulated cervicals, associated shell fragments; Santana do Cariri?, Ceara, Brazil, Romualdo Member, Santana Formation, purchased from "Schwickert (Kranz)", Germany, 6/6/1994; AMNH 22550, fully prepared carapace and plastron; carapace complete, plastron complete anteriorly but lacking both xiphiplastra; both scapulae and coracoids, proximal left and complete right humeri, both femora, left tibia and fibula, right pubis, ischium and ilium, left ilium, left astragalus, eighth cervical and numerous caudal vertebrae; AMNH 22556, fully prepared, partial shell with most proximal parts of postcranial skeleton, plastron complete except for lateral parts of bridge, central part of the carapace, thoracics, proximal caudals, and last two cervical (seven and eight) vertebrae, pectoral girdles and humeri, and pelvis with both femora; AMNH 24452, partially prepared, small, badly fractured shell, left otic region of skull preserved in epoxy adjacent to shell, right coracoid, both femora, posterior caudals, cervicals seven and eight, and left humerus; AMNH 24453, large shell with plastron and carapace complete, complete cervical series folded over carapace; partial skull, including right half of basicranium, right otic region, parts of both maxillae and dentaries; both scapulae, humeri, femora, pelvis, articulated right carpus (fixed to carapace), and disarticulated elements from both feet; AMNH 24454, anterior quarter of shell with complete cervical series, complete right front limb, skull (figs. 30, 31, 282), lower jaws, hyoid, posterior parts of shell preserved but unprepared; AMNH 22551, unprepared shell with cervical vertebrae exposed; AMNH 24455, partially prepared shell with both hands and feet in articulation; AMNH 24456, unprepared shell and partial skull; AMNH 24457–24461, five unprepared shells; Staatliches Museum für Naturkunde, Karlsruhe, PAL 3979, lateral edge of shell exposed ventrally.

PREVIOUS WORK: Price (1973) described *Araripemys barretoi* on the basis of a partial shell (Price, 1973: figs. 1–5; Meylan and Gaffney, 1991: photo on p. 329). Price erected the family Araripemydidae for *Araripemys* and placed it in the superfamily Pleurosternoidea in the suborder Amphichelydia. Gaffney (1972a, 1975b) argued that the Amphichelydia was a paraphyletic "wastebasket" taxon, largely consisting of cryptodires and pleurodires lacking more derived features. All authors subsequent to Price (1973) have placed *Araripemys* in the Pleurodira (Broin, 1980, 1988; Schleich, 1990; Kischlat and Campos, 1990; Hirayama, 1991; Meylan and Gaffney, 1991; Kischlat, 1996a, 1996b; Meylan, 1996).

Broin (1980) was the first to refer *Araripemys* to the Pleurodira. Along with a new genus, *Tacquetochelys*, based on shell fragments, she suggested the family had affinities to chelids. In 1988, Broin moved the Araripemydidae to the Pelomedusoides. Schleich (1990) described the first new shell material of *Araripemys* since Price (1973) and followed Broin's identification of it as a pleurodire. Kischlat and Campos (1990) described the first vertebral and limb material of *Araripemys*, and concluded that it was "nearer to the chelids ancestors than to pelomedusids (sensu latissimo) ancestors [sic]" (Kischlat and Campos, 1990: 387). In an abstract, Kischlat (1996a: 45A) mentioned *Araripemys* as having "uncertain affinities", but in another abstract (1996b) he said it "is a sister-group of *Pelomedusa* + *Pelusios*", a conclusion in agreement with our analysis that would support the magnafamily Pelomedusera clade.

Kischlat and Campos (1990) figured a number of limb and vertebral elements, as well as a plastron. Schleich (1990) figured shell material. Meylan and Gaffney (1991) have a limited description and photographs. The most extensive description of *Araripemys* to date is Meylan (1996). This described and figured nearly the complete osteology: shell, limbs, and vertebrae. The skull restoration (Meylan, 1996: fig. 4) is modified here by the discovery of new material, but the detailed stereophotographs of a partial skull, AMNH 24453, are still important.

Meylan and Gaffney (1991) presented a list of characters and figures of the first skull known of *Araripemys* (a restoration altered by new material described here). They concluded that *Araripemys* is not a chelid but a "pelomedusid" (= Pelomedusoides) based on cervical and cranial characters. The only detailed phylogenetic analysis of *Araripemys* published to date is Meylan (1996), who presented a character analysis and dataset. He concluded that *Araripemys* and *Euraxemys* (at that time, "FR 4922") were sister taxa and the sister group to all other Pelomedusoides, a conclusion that we now dispute.

Fielding et al. (2005) named a new species, *A.* "*arturi*", considered here a synonym of *A. barretoi*, discussed below.

DISCUSSION: Two new specimens, THUg 1357 and THUg 1907, and further preparation of the two skulls available to Meylan (1996) allow a reinterpretation of the skull morphology of *Araripemys* and a reassessment of its relationships. The interpretation of *Araripemys* as the sister group of the Pelomedusoides or the alternative of *Araripemys* as the sister group to the Pelomedusidae, does not rest on a large number of characters (see discussion above). A multichotomy with Pelomedusidae and all other Pelomedusoides, however, is well supported.

Broin (1980) identified "?*Araripemys* sp." from the Aptian of Gadoufaoua, Niger, on the basis of a group of shell fragments, one of which is figured (Broin, 1980: pl. 3, fig. 1). The surface texture is similar to *Araripemys*, and there is an eighth costal showing the iliac suture, so it is a pleurodire. However, the shell texture is not unique to *Araripemys*, and it alone is insufficient to extend the range of *Araripemys* to Africa. This specimen must be considered Pleurodira incertae sedis.

Fielding et al. (2005) described a new species of *Araripemys* from the Upper Aptian/Lower Albian Crato Formation south of Nova Olinda in the Araripe Basin, northeast Brazil (using Maisey, 1991, terminology; Fielding et al. [2005] used Crato and Santana as distinct formations). They used a slightly different peripheral shape, shell outline (Fielding et al., 2005: fig. 7), and difference in the shape of the terminal phalanges to differentiate their new species, *A.* "*arturi*", from *A. barretoi*. These characters are insufficient to diagnose a new species. The type of *A.* "*arturi*" is a small individual, about 180 mm carapace length, and these supposed differences could be a result of minor ontogenetic variation, sexual dimorphism, or individual variation. The shell shape of *A.* "*arturii*" was determined (Fielding et al., 2005) by extrapolation of a portion of one side lacking the midline, and the restoration could easily be flawed due to slight preservational bias. The preservation of the type appears to be inadequate to be certain of the shape of the terminal phalanges. The type is in a block that has been split, and it appears that there has been some loss of bone from the area of the specimen from which the terminal phalanges are known. Notched or "arrow-shaped" unguals are related to claw development, which is variable within recent turtle species. Examination of *Araripemys barretoi* specimens (AMNH 24453–24455) also shows that all unguals are not arrow-shaped. Given the weakness of these diagnostic characters, we place *A.* "*arturi*" in the synonymy of *A. barretoi* until a stronger argument can be made for its recognition as a separate species. Nonetheless, the specimen does belong to *Araripemys* and its discovery in the Crato Formation makes it the oldest described *Araripemys*. Although the age of the unit has some ambiguity (see also Berthou, 1994; Maisey, 2000), at least some of the Crato seems to be Aptian. The type horizon of *Araripemys barretoi* is the Albian Romualdo Member of the Santana Formation.

MAGNAFAMILY PODOCNEMIDERA COPE, 1868

TYPE GENUS: *Podocnemis* Wagler, 1830.

INCLUDED TAXA: Families Euraxemydidae, Podocnemididae, Bothremydidae; *Teneremys lapparenti* Broin, 1980.

DIAGNOSIS: Pelomedusoides with these unique characters: at least half of prootic covered ventrally by quadrate and basisphenoid; processus interfenestralis of opisthotic covered ventrally; foramen posterius canalis carotici interni formed at least in part by pterygoid (formed by pterygoid and basisphenoid primitively); inguinal buttress extends to center of fifth costal (not known for Euraxemydidae).

DISCUSSION: The monophyly of the magnafamily Podocnemidera, consisting of the Euraxemydidae plus the epifamily Podocnemidinura (Podocnemididae and near relatives) plus the Bothremydidae, seems relatively robust using the above basicranial characters. The poorly known *Teneremys lapparenti* de Broin, 1980 might be better resolved when skull material is described.

MAGNAFAMILY PODOCNEMIDERA, INCERTAE SEDIS

Teneremys de Broin, 1980

TYPE AND ONLY INCLUDED SPECIES: *Teneremys lapparenti* de Broin, 1980.

DISTRIBUTION: Aptian, Niger (Broin, 1980).

ETYMOLOGY: From Ténéré Desert, Niger, type locality.

DIAGNOSIS: Same as species.

Teneremys lapparenti Broin, 1980

TYPE SPECIMEN: MNHN GDF 820, a partial carapace and skull.

TYPE LOCALITY: Gadoufaoua, Niger (Broin, 1980).

HORIZON: "GAD 5" Aptian (Broin, 1980).

DIAGNOSIS: Podocnemidera with these distinguishing characters: extensive temporal emargination; basisphenoid very elongate, in contrast to all other Pelomedusoides (except *Araripemys*); foramen posterius canalis carotici interni formed in anterior part of basisphenoid-pterygoid suture, in contrast to all other Pelomedusoides; nuchal embayment present (also in some Bothremydidae). See Broin (1980) for the original diagnosis.

ETYMOLOGY: For Albert de Lapparent, uncle of F. Lapparent de Broin.

REFERRED MATERIAL: MNHN GDF 819, 821–829.

PREVIOUS WORK: Only the type description (Broin, 1980).

DISCUSSION: *Teneremys* is represented by a series of skulls and associated shells and skeletons from the Aptian of Niger, not well prepared, partially described by Broin (1980). Although key areas of the quadrate and basicranium are undescribed, enough skull characters are visible to place *Teneremys* in the magnafamily Podocnemidera, the group formed by Euraxemydidae + epifamily Podocnemidinura (Podocnemididae + close relatives) + Bothremydidae. Because the material is still not well known, it seems best to place *Teneremys* as incertae sedis within this group. The analysis presented here is in contrast to Lapparent de Broin's assertion (2000a: 67) that *Teneremys* is a close relative of the Pelomedusidae.

The shell material of *Teneremys* shows a carapace that seems to lack the cervical scale, and a neural series that may or may not reach the suprapygal and allow medial contact of costals 7 and 8. The plastron has the intergular scale completely separating the gulars and extending onto the entoplastron. The pectoral scale extends onto the mesoplastron.

The skull material of *Teneremys* is very limited at present. Although at least three entire skulls are available, poor preservation and preparation leave many characters undeterminable. The skull roof is clearly emarginate, to the extent seen in Pelomedusidae and *Araripemys*. The ventral view is obscured by the lower jaws, incomplete preparation, and poor preservation. The processus trochlearis pterygoidei is present and similar to that in Pelomedusidae. The basisphenoid is very elongate, almost completely separating the pterygoids, as in *Araripemys*. There are what appear to be two small foramina at the anterior end of the basisphenoid-pterygoid suture. It is possible that these are for the carotids, but if so, they are in a unique position for pleurodires. Unfortunately, the key area of the prootic and medial process of the quadrate is badly damaged and lacking preserved bone.

Teneremys has 56% missing data and resolves as the sister taxon to "*Platycheloides*" cf. *nyasae*, GDF 801 (below). Because *Teneremys* is represented by a number of skulls and skeletons, after further preparation, hopefully it will become a significant taxon in future character analyses.

"*Platycheloides*" cf. *nyasae* Haughton, 1928

SPECIMEN: MNHN GDF 801, shell, figured and described in Broin (1980); GDF 800, carapace; a third uncataloged carapace (Broin, 1980).

LOCALITY: Gadoufaoua, Niger (Broin, 1980).

HORIZON: "GAD 5" Aptian (Broin, 1980).

DISCUSSION: A nearly complete shell of a small pleurodire was figured and described by Broin (1980: pl. 1). The type and only specimen of "*Platycheloides*" *nyasae* Haughton, 1928 is too poorly preserved to usefully diagnose, and, as suggested by Broin (1980), MNHN GDF 800 is probably a different taxon anyway. It is listed in Lapparent de Broin (2000a) as "Pelomedusidae Cope 1868, Plesions to still extant genera of Pelomedusidae" (Lapparent de Broin, 2000a: 67). The type of "*Platycheloides*" *nyasae* is too incomplete to be resolved in the dataset (and is considered here a nomen dubium), but MNHN GDF 800 is a nearly complete shell that resolves as the sister taxon to *Teneremys*. These two taxa together are the sister group to the superfamily Podocnemidoidea, but they are placed as incertae sedis within the magnafamily Podocnemidera due to extensive missing data and the ease with which they move around the cladogram with a few changes to the character and taxon list.

SUPERFAMILY **EURAXEMYDOIDEA**, NEW

TYPE GENUS: *Euraxemys*, n. gen.

INCLUDED GENERA: *Euraxemys*, n. gen.; *Dirqadim*, n. gen.

DIAGNOSIS: Same as family Euraxemydidae.

FAMILY **EURAXEMYDIDAE**, NEW

TYPE GENUS: *Euraxemys*, n. gen.

INCLUDED GENERA: *Euraxemys*, n. gen.; *Dirqadim*, n. gen.

DISTRIBUTION: Albian of Brazil, Cenomanian of Morocco.

DIAGNOSIS: A member of the hyperfamily Pelomedusoides characterized by the unique possession of a medial process of the quadrate partially covering the prootic and narrowly contacting a ventral process of the exoccipital, in contrast to other pleurodires, which have either complete exposure or complete covering of the prootic ventrally; ventral process of exoccipital, which is exposed at lateral margin of basioccipital in an elongate foot (fig. 44), in contrast to nearly all pleurodires, which lack a ventral process or which have broad exoccipital exposure (*Araripemys*); other characters include an accessory ridge on mandibular triturating surface; fossa precolumellaris present but shallow, in contrast to absent (bothremydids) or deep (all other pleurodires except some Podocnemididae); foramen posterius canalis carotici interni formed by basisphenoid and pterygoid (also prootic in *Dirqadim*); quadratojugal-parietal contact present, quadratojugal large; foramen jugulare posterius partially closed (also in some Bothremydidae and in *Brasilemys*); sutured dentary symphysis (not known for *Dirqadim*); cervical articulations procoelous with biconvex second (not known for *Dirqadim*); complete neural series reaching suprapygal (not known for *Dirqadim*); abdominal scale midline length less than anal scale length (not known for *Dirqadim*).

DISCUSSION: This group of two taxa is strongly corroborated. The present analysis argues that it is the sister group to the superfamily Podocnemidoidea (Bothremydidae + Podocnemididae). See also tables 2 and 3.

Euraxemys, new genus

"FR 4922" Gaffney and Meylan, 1991; Meylan, 1996.

TYPE AND ONLY INCLUDED SPECIES: *Euraxemys essweini*, n. gen. et sp.

DISTRIBUTION: Early Cretaceous of Brazil.

ETYMOLOGY: *Eurax*, Greek for sideways; *emys*, Greek for turtle, in allusion to its pleurodiran nature.

DIAGNOSIS: A member of the family Euraxemydidae differentiated from *Dirqadim* by parietal-squamosal contact absent; temporal emargination more extensive; quadratojugal exposed in temporal emargination; skull longer and narrower; labial ridge thinner and straight in lateral view; accessory ridge on premaxilla absent; median concavity on premaxilla absent; triturating surface more expanded anteriorly; accessory ridge on maxilla weakly developed; antrum postoticum larger; prootic-opisthotic contact much shorter; median pterygoid contact longer; no ventral opening into canalis cavernosus; foramen posterius canalis carotici interni formed by pterygoid and basisphenoid without prootic contribution; foramen nervi vidiani exposed lateral to foramen posterius canalis carotici interni.

DISCUSSION: See table 3 for generic comparison.

Euraxemys essweini, new species

TYPE SPECIMEN: FR 4922, a nearly complete skeleton (figs. 39–46, 231, 232, 252–254, 281), also figured in Gaffney and Meylan (1991). A cast of the carapace made before embedding in plastic is AMNH 30568.

TYPE LOCALITY: Araripe Basin, Brazil (fig. 13).

HORIZON: Santana Formation, Albian, Early Cretaceous (Maisey, 1990, 1991).

TABLE 3
Genera of Euraxemydidae

	Euraxemys	*Dirqadim*
Parietal-squamosal contact	no	yes
Temporal emargination	more extensive	less extensive
Quadratojugal exposed on temporal margin	yes	no
Width/length ratio	0.78	0.92
Skull shape	longer, narrower	shorter, wider
Apertura narium externa	narrower	wider
Labial ridge	thinner	broader
Accessory ridge on premaxilla	no	yes
Median concavity on premaxilla	no	yes
Labial ridge in lateral view	straight	curved
Accessory ridge on maxilla	weakly developed	strongly developed
Triturating surface expanded anteriorly	yes	no
Antrum postoticum	larger	smaller
Prootic-opisthotic contact	narrow or absent	broad
Median pterygoid contact	longer	shorter
Opening into canalis cavernosus lateral to foramen posterius canalis carotici interni	absent	present
Foramen posterius canalis carotici interni	PT + BS	PT + BS + PR
Foramen nervi vidiani exposed lateral to foramen posterius canalis carotici interni	yes	no

DEPOSITIONAL ENVIRONMENT: Near-shore marine (Maisey, 1990) with freshwater episodes (Maisey, 2000). See *Araripemys* for more discussion.

DIAGNOSIS: Same as genus.

ETYMOLOGY: In honor of Stephan Esswein, a student of pleurodire development at Tübingen University, who passed away prematurely in 1993.

REFERRED MATERIAL: None.

PREVIOUS WORK: *Euraxemys* has appeared in print as "primitive pelomedusid turtle" in Gaffney and Meylan (1991) and as "FR 4922" in Meylan (1996). The shell as illustrated (Gaffney and Meylan, 1991: 326) has errors that are corrected in the figure presented here (fig. 254). Meylan (1996) had FR 4922 in his pleurodire dataset and concluded that it was the sister group to *Araripemys*, together making up the Araripemydidae.

DISCUSSION: The present analysis argues that *Euraxemys* and its sister taxon, *Dirqadim*, are related to the superfamily Podocnemidoidea, not to *Araripemys*, as proposed by Meylan (1996).

Dirqadim, new genus

TYPE AND ONLY INCLUDED SPECIES: *Dirqadim schaefferi*, n. sp.

DISTRIBUTION: Cenomanian, Late Cretaceous of Morocco.

ETYMOLOGY: *Dir*, Arabic for armor; *qadim*, Arabic for ancient. We are very grateful to the help of Mark Caponigro for this etymology.

DIAGNOSIS: Euraxemydid Pelomedusoides differentiated from *Euraxemys* by parietal-squamosal contact present; temporal emargination less extensive; quadratojugal not exposed on temporal margin; skull shorter and wider; labial ridge broader; accessory ridge on premaxilla present; median concavity on premaxilla present; labial ridge curved, convex ventrally in lateral view; triturating surface parallel sided; accessory ridge on maxilla strongly developed; antrum postoticum smaller; prootic-opisthotic contact broader; median pterygoid contact shorter; ventral opening into canalis cavernosus just lateral to foramen posterius canalis carotici interni present; foramen posterius canalis carotici interni with prootic in margin as well as pterygoid and basisphenoid; foramen nervi vidiani not exposed in ventral view.

DISCUSSION: See table 3 for generic comparison.

Dirqadim schaefferi, new species

TYPE SPECIMEN: MDEt 41, a nearly complete skull (figs. 44–53).

TYPE LOCALITY: Eastern Morocco, Kem Kem region (figs. 14, 15). The fossil turtles (*Hamadachelys*, *Galianemys*, and *Dirqadim*) were collected by the local people and obtained from private collectors and dealers; their exact geological origin is therefore uncertain. However, all specimens clearly come from the Cretaceous red beds in the region called Hamada du Guir, or Kem Kem, in the southeast part of Morocco. The area is also called the Tafilalt by the local people. These terms are sometimes confusing. In fact, according to Lavocat (1954), the Hamada du Guir is a vast desert plateau east of the town of Taouz, extending from north to south, and the Kem Kem is southwest of Taouz, which is quite different from the Hamada in its structure and physiognomy (Lavocat, 1954). The vertebrate-bearing red beds, termed as "Kem Kem beds" by Sereno et al. (1996), outcrop along the border of the Hamada du Guir to the Kem Kem, from north of the town of Erfoud to the south for some 250 km. Along this distance, local people dig underground galleries to find vertebrate fossils, for the local and international fossil market.

The most important work on the geology of this region was made by Lavocat in the late 1940s and early 1950s (Lavocat, 1954). The continental red beds from which the vertebrate remains are derived are represented by a formation of ca. 200-m maximum thickness. They include two units: the lower unit is composed of red detritic cross-stratified sandstones, of channel-fill deposits, and the upper unit is composed of red to tan sandstones intercalated with mudstones, indicating a change in sedimentation rates. Both units contain vertebrate remains. These red beds lie unconformably on the Paleozoic basement and are covered by a limestone platform formed by the Cenomanian–Turonian transgression. The vertebrate-bearing beds have therefore been termed "Infra-Cenomanian" by Lavocat (1954) and were long considered as Albian in age (Forey and Grande, 1998; Taquet, 1976). The base of the overlying Cenomanian–Turonian limestones in the area of Erfoud Errachidia and the Taouz region is dated by the occurrence of the ammonite *Neolobites vibrayeanus* (Basse and Choubert, 1959; Ferrandini et al., 1985). The *vibrayeanus* Zone, which is known in many parts of the Tethyan regions, corresponds to the base of the late Cenomanian (Courville et al., 1991). The age of the vertebrate-bearing red beds is therefore older than late Cenomanian, but their oldest age is not well constrained stratigraphically.

Comparisons have been made between the vertebrate assemblage of Kem Kem beds and those from nonmarine deposits of other parts of Sahara and surrounding areas. As recognized by Lavocat (1954), the Kem Kem vertebrate fauna closely resembles that of Baharia, discovered by Stromer (1936) in Egypt. Several theropod dinosaurs, *Spinosaurus* and *Carcharodontosaurus*, and crocodilian *Libycosuchus* occur in both localities (Buffetaut, 1989a, 1989b, 1989c; Sereno et al., 1996; Tong and Buffetaut, 1996; Wellnhofer and Buffetaut, 1999). The Baharia assemblage was considered as Cenomanian in age by Stromer (1936). More recent works on fossil fishes from Baharia confirm Stromer's opinion (Slaughter and Thurmond, 1974; Schaal, 1984). According to Dominik (1985), the main vertebrate-bearing bed of the Baharia Formation includes marine intercalations, and the occurrence of the ammonite *Neolobites* indicates a late Cenomanian age for the Baharia deposits.

According to Sereno et al. (1996), nine elasmobranch species from the Kem Kem beds support a Cenomanian age for the deposits; seven of them occur also in the Cenomanian Baharia Formation, including four species limited to these formations (*Distobatus nutiae*, "*Lissodus*" *bartheli*, *Markgrafia libyca*, and *Peyeria libyca*), and one species (*Serratolamna amonensis*) occurs with a broad distribution and is restricted to the Cenomanian. The later species "*Serratolamna*" *amonensis*, probably called *Carcharias amonensis*, is indeed restricted to the Cenomanian according to Cappetta and Case

(1999). Thus, even though the shark and ammonite evidence does not precisely agree, the Cenomanian age for the Kem Kem beds is now widely accepted.

The Cenomanian Kem Kem beds have yielded abundant and very diverse vertebrate assemblages, which consist mostly of nonmarine species: fishes (Wenz, 1981; Martin 1984a, 1984b; Tong and Buffetaut, 1996; Forey, 1997; Forey and Grande, 1998; Dutheil, 1999a, 1999b; Taverne and Maisey, 1999; Cavin and Brito, 2001; Cavin et al., 2001), lizards, crocodiles (Buffetaut, 1994; Larsson and Sidor, 1999), turtles (Tong and Buffetaut, 1996; Gaffney, Tong, and Meylan, 2002), pterosaurs (Mader and Kellner, 1999; Wellnhofer and Buffetaut, 1999), and dinosaurs (Lavocat, 1951; Buffetaut, 1989a, 1989b; Russell, 1996; Sereno et al., 1996). The depositional environment is supposed to be deltaic or fluvial (Sereno et al., 1996; Cavin et al., 2001), and some fossil fishes found in one limited site indicate a still-water environment, like a lake or pool (Dutheil, 1999a).

HORIZON: Cenomanian Kem Kem beds.

DEPOSITIONAL ENVIRONMENT: Deltaic or fluvial (Sereno et al., 1996; Cavin et al., 2001), found with dinosaurs and other freshwater/terrestrial fauna.

DIAGNOSIS: Same as genus.

ETYMOLOGY: In honor of Dr. Bobb Schaeffer (1913–2004), former Curator of Fossil Fishes at the Department of Vertebrate Paleontology, American Museum of Natural History, and close friend and mentor of the senior author.

REFERRED MATERIAL: AMNH 30038, skull lacking anterior half, Kem Kem, Morocco.

PREVIOUS WORK: None.

SUPERFAMILY PODOCNEMIDOIDEA COPE, 1868

TYPE GENUS: *Podocnemis* Wagler, 1830.

INCLUDED TAXA: Family Bothremydidae and epifamily Podocnemidinura (consisting of the family Podocnemididae, genera *Hamadachelys* Tong and Buffetaut, 1996; *Brasilemys* Lapparent de Broin, 2000b; and *Portezueloemys* Fuente, 2003).

DIAGNOSIS: Magnafamily Podocnemidera uniquely in possession of a quadrate-basioccipital contact; prootic completely or almost completely covered ventrally by quadrate, basisphenoid, and pterygoid; dentary symphysis fused, not sutured, as in Euraxemydidae, *Teneremys*, and *Araripemys*; pectoral scales on entoplastron (except in a few Bothremydidae).

DISCUSSION: This taxon consists of the epifamily Podocnemidinura (the Podocnemididae plus its near relatives, *Hamadachelys*, *Brasilemys*, and, presumably, *Portezueloemys*) and the Bothremydidae. This superfamily name is in the sense of its original author, Broin (1988), and later, Lapparent de Broin (2000b, 2001). Meylan (1996) used "Podocnemoidae" for this group, which we have avoided.

EPIFAMILY PODOCNEMIDINURA COPE, 1868

TYPE GENUS: *Podocnemis* Wagler, 1830.

INCLUDED TAXA: Family Podocnemididae, genera *Hamadachelys* Tong and Buffetaut, 1996; *Brasilemys* Lapparent de Broin, 2000b; and *Portezueloemys* Fuente, 2003.

DIAGNOSIS: A member of the superfamily Podocnemidoidea uniquely possessing a cavum pterygoidei formed by basisphenoid, pterygoid, prootic, and quadrate, underlain by pterygoid and basisphenoid (in contrast to fossa pterygoidea of some Bothremydidae); processus retroarticularis of articular oriented posteroventrally; basioccipital-opisthotic contact present (also in Pelomedusidae and some Chelidae, not known in *Brasilemys*).

DISCUSSION: Our analysis agrees with Lapparent de Broin (2000b) and Fuente (2003) in that the close relatives of the Podocnemididae have this relationship: (*Brasilemys* (*Hamadachelys* (Podocnemididae))). We also follow their restricted use of the family Podocnemididae and do not place *Brasilemys* or *Hamadachelys* (or *Portezueloemys*) within it. Table 4 compares the skull in the three groups; the shell is not yet known for *Hamadachelys*.

We do not use the Lapparent de Broin (2000b) name "Podocnemidoidae." Instead, we create a new name, the epifamily Podocnemidinura, for the identical content and concept, even though the Lapparent de Broin name is older. The "Podocnemidoidae" is so close in spelling to Podocnemidoidea, which

TABLE 4
Comparison of Podocnemidinura

	Brasilemys	*Hamadachelys*	Podocnemididae
Cavum pterygoidei size	partial	partial	complete
Quadratojugal-parietal contact	absent	present	present
Basioccipital-opisthotic contact	indet	present	present
Processus retroarticularis long and posteroventral	yes	yes	yes
Incisura columellae auris enclosing stapes and eustachian tube in bone	no	yes	yes
Dentary widely exposed on lateral surface	yes	yes	no
Fossa precolumellaris	shallow	deep	usually deep
Foramen jugulare posterius	partly closed	closed	closed
Exoccipital-quadrate contact	present	absent	absent

has a different content, that we think its continued use too confusing. This is permissible under the current rules for higher categories.

Although we agree with Fuente (2003) that *Portezueloemys* is a closer relative of the Podocnemididae than either *Brasilemys* or *Hamadachelys*, we have not included it in our analysis due to the high missing values in the skull characters and because we have been unable to examine the specimen.

Brasilemys Lapparent de Broin, 2000b

TYPE AND ONLY INCLUDED SPECIES: *Brasilemys josai* Lapparent de Broin, 2000b.

DISTRIBUTION: Albian, Brazil.

ETYMOLOGY: For Brazil, country of origin (Lapparent de Broin, 2000b).

REVISED DIAGNOSIS: Member of the epifamily Podocnemidinura with the cavum pterygoidei partially developed, as in *Hamadachelys*, but in contrast to complete as in Podocnemididae; quadratojugal-parietal contact absent, in contrast to *Hamadachelys* and Podocnemididae; incisura columellae auris not enclosing stapes and eustachian tube with bone, in contrast to *Hamadachelys* and Podocnemididae; dentary widely exposed on lateral surface of lower jaw, as in *Hamadachelys*, but in contrast to Podocnemididae; fossa precolumellaris shallow, in contrast to *Hamadachelys* and Podocnemididae; foramen jugulare posterius partially closed, in contrast to open, as in *Hamadachelys* and Podocnemididae; exoccipital-quadrate contact present, in contrast to *Hamadachelys* and Podocnemididae. See also Lapparent de Broin, 2000b.

Brasilemys josai Lapparent de Broin, 2000b

TYPE SPECIMEN: Museu de Geologia de Barcelona, Catalunya, Spain, MGB 37911, partial skull and partial carapace (Lapparent de Broin, 2000b).

TYPE LOCALITY: Chapada do Araripe, Ceará State, Brazil (Lapparent de Broin, 2000b) (fig. 13).

HORIZON: Romualdo Member, Santana Formation, Albian (Lapparent de Broin, 2000b).

DIAGNOSIS: As for genus; see also Lapparent de Broin (2000b).

ETYMOLOGY: For Joan Josa (Lapparent de Broin, 2000b).

REFERRED MATERIAL: None.

PREVIOUS WORK: Only the type description (Lapparent de Broin, 2000b).

DISCUSSION: This partial skull and partial carapace provide enough characters for a resolution showing it as the sister taxon to *Hamadachelys* + Podocnemididae, a result that agrees with the branching diagram (no character matrix is presented) in Lapparent de Broin (2000b) and the computer-assisted cladogram of Fuente (2003).

Hamadachelys Tong and Buffetaut, 1996

TYPE AND ONLY INCLUDED SPECIES: *Hamadachelys escuilliei* Tong and Buffetaut, 1996.

DISTRIBUTION: Cenomanian of Morocco.

ETYMOLOGY: From Hamada du Guir (Tong and Buffetaut, 1996).

REVISED DIAGNOSIS: Podocnemidinura with a partially developed cavum pterygoidei, as in *Brasilemys*, but in contrast to Podocnemididae; quadratojugal-parietal contact present, as in Podocnemididae, but in contrast to *Brasilemys*; incisura columellae auris fully enclosing stapes and eustachian tube, as in Podocnemididae, but in contrast to *Brasilemys*; dentary widely exposed laterally, as in *Brasilemys*, but in contrast to Podocnemididae; fossa precolumellaris deep, as in most Podocnemididae, but in contrast to *Brasilemys*; foramen jugulare posterius completely enclosed, as in Podocnemididae, but in contrast to *Brasilemys*; exoccipital-quadrate contact absent, as in Podocnemididae, but in contrast to *Brasilemys*.

Hamadachelys escuilliei Tong and Buffetaut, 1996

TYPE SPECIMEN: MDEt-T-03, a nearly complete skull and jaws.

TYPE LOCALITY: Hamada du Guir, near Taouz, Morocco (Tong and Buffetaut, 1996).

HORIZON: Kem Kem red beds, Cenomanian (Sereno et al., 1996; Tong and Buffetaut, 1996).

DIAGNOSIS: As for genus; see also Tong and Buffetaut, 1996.

ETYMOLOGY: For F. Escuillié (Tong and Buffetaut, 1996).

PREVIOUS WORK: Tong and Buffetaut (1996).

DISCUSSION: This taxon is represented by skull material but no shells. A significant number of characters (but not all) can be coded. The resolution in the MPC shows *Hamadachelys* as the sister taxon to the Podocnemididae, in agreement with Fuente (2003). *Hamadachelys*, as well as *Brasilemys*, could be included in the Podocnemididae. We exclude both from an expanded Podocnemididae to reflect current usage (e.g., Tong and Buffetaut, 1996; Lapparent de Broin, 2000b; Fuente, 2003), which is more restricted (see table 4).

FAMILY PODOCNEMIDIDAE COPE, 1868

TYPE GENUS: *Podocnemis* Wagler, 1830.

INCLUDED GENERA: *Podocnemis* Wagler, 1830; *Peltocephalus* Duméril and Bibron, 1835; *Erymnochelys* Baur, 1888; *Bairdemys* Gaffney and Wood, 2002; *Dacquemys* Williams, 1954c; *Neochelys* Bergounioux, 1954; *Shweboemys* Swinton, 1939; *Bauruemys* Kischlat, 1994; *Stupendemys* Wood, 1976; *Stereogenys* Andrews, 1901.

DIAGNOSIS: Member of the epifamily Podocnemidinura uniquely possessing a fully developed, medially extensive cavum pterygoidei and a dentary covered laterally by the surangular, in contrast to *Brasilemys* and *Hamadachelys*; agreeing with *Hamadachelys* in basioccipital-opisthotic contact (not known in *Brasilemys*, may be at Podocnemidinura level), incisura columellae auris enclosing stapes and eustachian tube, usually deep fossa precolumellaris, completely closed foramen jugulare posterius, and exoccipital-quadrate contact absent, all in contrast to *Brasilemys*.

DISCUSSION: The formation of the family name has varied between "Podocnemididae" (Broin, 1977, 1988; Lapparent de Broin, 2000a, 2000b, 2001, and many earlier papers; Fuente, 2003) and "Podocnemidae" (Meylan, 1996). We choose to use "Podocnemididae", mostly because it is the name most frequently used and has the longest usage. It has been the experience of the senior author that classical authorities have different opinions on the correct root for "-nemis" or "-emis", which is usually (but not always) considered comparable to "-emys" (as in Emydidae). Yes, it's true. I don't give a rat's ass which is used.

EPIFAMILY BOTHREMYDINURA BAUR, 1891

TYPE GENUS: *Bothremys* Leidy, 1865.

INCLUDED TAXA: Family Bothremydidae.

DIAGNOSIS: Same as family Bothremydidae.

FAMILY BOTHREMYDIDAE BAUR, 1891

TYPE GENUS: *Bothremys* Leidy, 1865.

INCLUDED GENERA: *Kurmademys* Gaffney, Chatterjee, and Rudra, 2001; *Sankuchemys* Gaffney, Sahni, Schleich, Singh, and Srivastava, 2003; *Cearachelys* Gaffney, Campos, and Hirayama, 2001; *Galianemys* Gaffney, Tong, and Meylan, 2002; *Foxemys* Tong, Gaffney, and Buffetaut, 1998; *Polysternon* Portis, 1882; *Elochelys* Nopcsa, 1931; *Zolhafah* Lapparent de Broin and Werner, 1998; *Rosasia* Carrington da Costa, 1940; *Araiochelys*, n. gen.; *Bothremys* Leidy, 1865;

Chedighaii, n. gen.; *Taphrosphys* Cope, 1869a; *Labrostochelys*, n. gen.; *Phosphatochelys* Gaffney and Tong, 2003; *Ummulisani*, n. gen.; *Rhothonemys*, n. gen.; *Azabbaremys* Gaffney, Moody, and Walker, 2001; *Nigeremys* Broin, 1977; *Arenila* Lapparent de Broin and Werner, 1998.

DISTRIBUTION: Late Cretaceous of India, Late Cretaceous and Paleocene of Europe, Late Cretaceous and Paleogene of North and Central Africa (including Middle East), Late Cretaceous of Madagascar, Late Cretaceous and Paleocene (if *Taphrosphys* from New Jersey is Paleocene) of North America, Early Cretaceous of South America.

REVISED DIAGNOSIS: Member of the superfamily Podocnemidoidea with wide prefrontals, in contrast to Pelomedusidae and Euraxemydidae, wide premaxillary depression (narrow in some Bothremydini and some Taphrosphyini); triturating surfaces highly diverse but primitively moderately wide; moderate to large palatine contribution to triturating surface (except in Taphrosphyini), in contrast to all other pleurodires except *Araripemys*; maxilla-quadratojugal contact present (except in Taphrosphyini); wide exoccipital-quadrate contact present, in contrast to all other pleurodires, which have narrow or no contact; processus paroccipitalis does not project posterior to squamosal, in contrast to all other Pelomedusoides; eustachian tube separated from stapes by bone, in contrast to all other pleurodires; incisura columellae auris closed and stapes contained in bony canal (except *Cearachelys*, *Foxemys*, *Polysternon*), in contrast to all other pleurodires; fossa precolumellaris absent (except in *Kurmademys*), in contrast to all other pleurodires; cavum pterygoidei as seen in Podocnemididae absent; fossa orbitalis posterior enlargement present (except in *Cearachelys*), in contrast to all other pleurodires; supraoccipital-quadrate contact present (except in Taphrosphyini and *Zolhafah*); prootic partially or completely covered in ventral view; foramen posterius canalis carotici interni not in prootic, in contrast to Araripemydidae, Chelidae, and Pelomedusidae; basisphenoid-quadrate contact present, as in Podocnemididae, but in contrast to all other pleurodires; high lingual ridge on lower jaw.

PREVIOUS WORK: In 1891, George Baur recognized three living families of pleurodires, the Sternothaeridae (the Pelomedusidae of former usage), the Podocnemididae, and the Chelyiidae (Chelidae of current usage) (Baur, 1891: 420). Based on the presence of deep pits in the jaws, which he thought might be alveoli for large tusks, he thought that *Bothremys* Leidy should be placed in a family of its own, and he coined the term Bothremydidae (Baur, 1891: 424). Thus, Baur's (1891) Pleurodira consisted of four families rather than the two that have been recognized for much of the last century.

Baur (1893) reiterated the uniqueness of the Bothremydidae and used the superfamily name Pelomedusoidea for a group of three of his four pleurodire families: the Pelomedusidae, which he restricted to two genera, *Pelomedusa* and *Sternothaerus* (= *Pelusios*); the Podocnemididae, in which he placed *Podocnemis*, *Peltocephalus* and *Erymnochelys*; and "the intermediate extinct family Bothremydidae". This is very close to the current usage developed for "Pelomedusoides".

Baur's Bothremydidae was adopted by Hay (1908) in his classic monograph on North American fossil turtles. It was also used by Nopcsa (1923) and Dollo (1924) but then nearly disappeared from use for about 65 years. In his treatment of North American bothremydids, Hay (1908) included *Bothremys* Leidy, *Taphrosphys* Cope, and two new genera, *Amblypeza* and *Naiadochelys* (both considered invalid here). Schmidt (1940), in his description of *Podocnemis barberi* (now *Chedighaii barberi*), assigned his new taxon to a Pelomedusidae, which he acknowledged was used in an inclusive sense. He specifically mentioned the Bothremydidae, stating that *Taphrosphys*, which was placed in the Bothremydidae by Hay (1908), may be allied to *Podocnemis*, but he left the issue of revision of the Pleurodira for future workers.

Carrington da Costa (1940) tentatively referred his new genus *Rosasia* to the family Pelomedusidae and the "subfamily" Bothremydidae. He was explicit in his conclusion (apparently in consultation with F.-M. Bergounioux) that the Bothremydidae should be treated as a subfamily. He contemplated referring *Rosasia* to the Bothremydidae again in 1958 (Carrington da Costa, 1958), but instead referred it to the Pelomedusinae. Williams (1950) used Bothremydinae as a subfamily of the Pelomedusidae, along with the Pelomedusinae. However, in the turtle classification of Romer (1956), which was significantly influenced by Williams, the Bothremydinae is gone; only the Pelomedusidae and Chelyidae make up the Pleurodira.

Baur's Bothremydidae appeared next in a review of the genus *Bothremys* (Gaffney and Zangerl, 1968), which was prompted by the discovery of the first skull–shell association of a bothremydid, a specimen of *Bothremys* (now *Chedighaii*) *barberi* from the Selma Formation of Alabama. In this paper several shell taxa previously assigned to *Podocnemis* were referred to *Bothremys*. Although formal recognition of the family Bothremydidae was deferred, the uniqueness of the *Bothremys* lineage was noted. Gaffney (1975b) gave the group formal recognition as a subfamily of the Pelomedusidae. The subfamily was formally resurrected for the genera *Taphrosphys* and *Bothremys* in this paper, which gave a detailed description of the shell of *Taphrosphys* from the Late Cretaceous (now considered Paleocene) of New Jersey.

This family group name was also briefly considered by Broin (1977) in her treatise on French fossil turtles. In that work she reviewed the higher categories of pleurodires and considered the taxonomy of Baur (1888, 1891) to be the most satisfactory. She suggested that reuniting the genera *Bothremys*, *Nigeremys*, and *Taphrosphys* in the Bothremydidae would be desirable, but she did not follow the lead of Gaffney (1975b) until she published a further review of fossil pleurodires (Broin, 1988). In this stratigraphic treatment of geographic dispersion of pleurodires, she referred a series of genera to the family Bothremydidae, which she included in the hyperfamily Pelomedusoides along with the Podocnemididae. The genera referred to the Bothremydidae included *Taphrosphys*, *Bothremys*, *Nigeremys*, *Rosasia*, *Apertotemporalis*, *Apodichelys*, and *Sokotochelys* (Broin, 1988). We consider the last three to be invalid or incertae sedis.

The redescription of the bothremydid *Rosasia* by Antunes and Broin (1988) provided the first review of the family Bothremydidae. It included a tentative phylogeny and a detailed description of the skull of *Rosasia*, a taxon that was previously known only from shell material. The cladogram showed that the Bothremydidae is the sister group of the Podocnemididae. Furthermore, within the Bothremydidae, *Bothremys*, *Nigeremys*, and *Taphrosphys* informal groups were recognized. However, the phylogenetic position of many named taxa, especially those known only from shells, remained unresolved. The genera treated as members of the Bothremydidae in Antunes and Broin (1988) included *Apodichelys*, *Apertotemporalis*, *Bothremys*, *Elochelys*, *Nigeremys*, *Rosasia*, and *Taphrosphys*.

In Antunes and Broin (1988), the Bothremydidae was characterized by five skull, seven shell, and one vertebral character. Skull characters included (Broin's character numbers) (C_1) eustachian tube excluded from stapedial canal by quadrate, (C_2) strong development of the jaws and vomer, and secondary closure of temporal and cheek emargination, (C_3) low wide external narial openings, (C_4) ventral coverage of the prootic by the pterygoid, and (C_5) flattening of the anterior part of the muzzle. Shell features characteristic for the family included (C_6) large and depressed form of the subquadrangular carapace, with a smooth semicircular arc without inflations or keels and a trapezoidal ventral profile, (C_7) anterior plastral lobe particularly short and wide at its base, trapezoidal or subtrapezoidal, (C_8) vascular sculpture of the carapace consisting of dichotomous (branching) grooves well developed, and more so in the marine *Taphrosphys* group, (C_9) frequent suturing of the ilium to the suprapygal (this was considered to be a reversal to the primitive condition), (C_{10}) reduction in the number of neurals to seven or fewer, which is acknowledged to occur several times in pleurodires, (C_{11}) reduction of the width of vertebral 1, which does not cover all of the nuchal bone, and with the following vertebrals having an anterior width less than or equal to their median length (parallelism in this character was acknowledged), and (C_{12}) pectoral–abdominal sulcus crossing the anterior part of the mesoplastra (parallelism in this character was acknowledged). A single character of the vertebrae (C_{13}) was acknowledged to be variable in the three taxa for which cervical vertebrae were known.

In the same paper, the *Bothremys* group of the Bothremydidae was characterized by three skull and two shell characters: (D_1) maximum enlargement of the triturating surfaces with a deep fossa present in the palatine and jugal and in the dentary, (D_2) secondary covering of the cheek emargination by posterior extension of the maxilla, ventral enlargement of the quadratojugal, and anterior expansion of the quadrate, (D_3) foreshortening of the bones at the back of the skull, particularly the supraoccipital, the basisphenoid, and the basioccipital, such that the occipital condyle is in line with the articular facets of the quadrate, (D_4) tendency for elongation of the bridge, and (D_5) formation of a more-or-less strongly developed nuchal embayment that affects the nuchal scute.

The *Nigeremys* group was characterized by four characters: (F_1) deep ventral premaxillary pit but without formation of a recurved beak, (F_2) deep carotid fossa in the area of the quadrate–basisphenoid suture, (F_3) flattening and anterior enlargement of the snout with pronounced posterior elevation of the skull roof with a tectiform or subtectiform profile, and (F_4) marked increase in size.

Nearly all of these characters from Antunes and Broin (1988), or modifications of them, have been used in the dataset presented here (appendices 2 and 3). This work provided the basis for future analyses of the Bothremydidae.

A byproduct of Meylan's (1996) phylogenetic analysis of *Araripemys* was the first computer-assisted cladistic analysis of the Bothremydidae. Three bothremydids with available skull information were included in that analysis: *Bothremys*, *Rosasia*, and *Taphrosphys*. The Bothremydidae was monophyletic in this analysis and was the sister group of the Podocnemididae, as suggested by Antunes and Broin (1988) and Broin (1988). Beginning with this work, paleontologists have generally followed the taxonomy of Baur (1891) as suggested by Broin (1988) in recognizing more family-level taxa in the pleurodires. Neontologists have generally followed this development by splitting the living Pelomedusidae (sensu lato) into a more restricted Pelomedusidae and recognizing the family Podocnemididae (Pough et al., 1998, 2001; Zug et al., 2001).

In her description of *Brasilemys*, Lapparent de Broin (2000b) provided an explicit hypothesis for the phylogenetic position of the Bothremydidae. This family, including an undescribed form from Erfoud, Hamada de Guir, Morocco (now known as *Galianemys* Gaffney, Tong, and Meylan, 2002), was argued to be the sister group of the Podocnemididae plus the genera *Hamadachelys* and *Brasilemys*, a group that she termed the Podocnemidoidae (here renamed the Podocnemidinura).

A diverse fauna of bothremydid turtles was described by Lapparent de Broin and Werner (1998) from the Maastrichtian of Egypt. They described what they thought to be five taxa representing three separate lineages of bothremydid turtles. Two were described from skulls and three from shell fragments. Their new genus *Zolhafah* was based on a single skull and allied with members of the "*Bothremys* group", *Bothremys* and *Rosasia*. A second new genus, *Arenila*, was based on a poorly preserved skull and allied with *Nigeremys* in the "*Nigeremys* group". A carapacial disc was also provisionally referred to this new taxon. Two other poorly known genera, *Sokotochelys* and *Apertotemporalis* (here considered nomina nuda), were referred to this group. The "*Taphrosphys* group" was represented by two carapace fragments.

Lapparent de Broin and Werner (1998) characterized the skull of members of the *Bothremys* group as having pits in the triturating surface and as having a tendency to a flat posterior palatal surface with reduction of the "podocnemidoid fossa". Lapparent de Broin and Werner (1998) characterized the shell of this group as "a rather wide rectangular-rounded shell with a notched nuchal, an anterior trapezoid-rounded [plastral] lobe, short and posteriorly wide, a posterior [plastral] lobe narrower at its base than the anterior lobe and with straight posteriorly converging borders."

They characterized the skull of members of the *Nigeremys* group as having: (1) a much enlarged depression in the area of the pterygoid-basisphenoid and pterygoid-quadrate suture (this depression, the fossa pterygoidea, was considered by them to be homologous to the "podocnemidoid fossa" or cavum pterygoidei, a conclusion we dispute), (2) an enlarged snout, (3) basioccipital participating in occipital condyle, and (4) an enlarged and posteromedially projecting trochlear process (here interpreted as an artifact of preservation in *Arenila*). The shell of members of the *Nigeremys* group differed from other podocnemidoids in having the axillary buttress cross the second rather than the third peripheral to reach the first costal bone.

Lapparent de Broin and Werner (1998) relied entirely on shell characters to distinguish the *Taphrosphys* group for which they said skulls were too poorly known. Referral of new fossil shell material appeared to be based largely on the "typical very marked decoration of small prominent polygons and granulation and rounded crests." *Elochelys* and *Taphrosphys* were reported to share a shell that is "elongated rounded ovoid anteromedial shell, intergular separating the gulars and meeting the pectorals, rounded posterior lobe in most *Taphrosphys* specimens and in *Elochelys*, well trapezoid anterior lobe." They considered *Gafsachelys* Bergounioux, 1956 to be a member of this group on the basis of shell decoration.

These authors suggested that the shell shapes common to the *Taphrosphys* and *Bothremys* groups indicated that they formed a monophyletic sister group to the *Nigeremys* group (Lapparent de Broin and Werner, 1998: 164). This was a refinement of the trichotomy indicated for these groups in Antunes and Broin (1988).

Since 1998, the number of genera referred to the Bothremydidae has more than doubled. In addition to *Zolhafah* and *Arenila* discussed above (Lapparent de Broin and Werner, 1998), Tong et al. (1998) described the French bothremydid *Foxemys* and presented a cladogram with a resolution of (*Foxemys* (*Taphrosphys* (*Bothremys, Rosasia*))), a result (provided by the senior author) that is inconsistent with our current results, due to the smaller data set. More recently, Gaffney and colleagues have described six additional genera. *Phosphatochelys* (Gaffney and Tong, 2003) was described on the basis of a single skull of a short-faced member of the *Nigeremys* group. Another new member of the *Nigeremys* group is the remarkable skull taxon *Azabbaremys* from the Paleocene of Mali (Gaffney, Moody, and Walker, 2001). The large and strongly roofed skull of the type is quite similar in many respects to *Nigeremys* itself. The oldest bothremydid described to date is the Albian genus *Cearachelys* (Gaffney, Campos, and Hirayama, 2001), which was described from two nearly complete skeletons from the Chapada do Araripe in Ceara, Brazil. The three well-preserved skulls and shells of this taxon provide excellent evidence for the primitive skeletal morphology of the family. This taxon was referred by its describers to the *Bothremys* group of Lapparent de Broin and Werner (1998). A morphologically similar and apparently related genus, *Galianemys* (Gaffney, Tong, and Meylan, 2002), has been described from the Cenomanian Kem Kem Redbeds of Morocco. The two Indian bothremydids *Sankuchemys* (Gaffney et al., 2003) and *Kurmademys* (Gaffney, Chatterjee, and Rudra, 2001) considerably extend the geographic range of the Bothremydidae.

DISCUSSION: As a result of the discovery of many new bothremydid skulls that are used as the basis for a phylogenetic analysis of the Bothremydidae presented here, four monophyletic groups are recognized as tribes within the Bothremydidae (figs. 1, 2; table 5). The idea of the "*Bothremys* group" has been documented and confirmed in this analysis, but the "*Nigeremys* group" and "*Taphrosphys* group" of Lapparent de Broin and Werner (1998) are combined in the tribe Taphrosphyini.

The possible extension of the Bothremydidae into the Miocene is based on a single questionable record. Roger et al. (1994) reported on a damaged braincase from Miocene rocks from Oman in the Arabian Peninsula. The braincase, an uncataloged specimen with no institutional collection indicated, was not described in detail and was figured only in ventral view, but it was reported to have a "fosses ptérygoido-carotidiennes obliques" (Roger et al., 1994: 11) and an incisura columellae auris separated

TABLE 5
Tribes of Bothremydidae

	Kurmademydini	Cearachelyini	Bothremydini	Taphrosphyini
Preorbital skull broad	no	no	yes[a]	no
Fenestra interorbitale	high	high	low	high
Temporal emargination	extreme	intermediate	slight to absent	slight to absent
Jugal-quadrate contact	absent	absent	absent	present
Fossa precolumellaris	present	absent	absent	absent
Shelf below cavum tympani	absent	absent	present	present
Supraoccipital-quadrate contact	present	present	present[b]	absent
Foramen jugulare posterius	closed	open	closed[c]	closed
Exoccipitals completely form neck and condylus occipitalis	no	no	yes	yes
Foramen stapedio-temporale visible dorsally	yes & no	no	no	no
Foramen stapedio-temporale and foramen nervi trigemini very close	no	no	yes	yes
Small part of prootic exposed ventrally	yes	yes & no	no	no
Fenestra postotica	closed	open	closed	closed
Fenestra postotica a short slit	no	yes	no	no
Dorsal ridge on opisthotic	no	no	yes	no
Basisphenoid pentagonal	yes	no	yes & no	yes & no
Jugal nearly or completely retracted from orbit	no	yes	no	no
Condylus mandibularis anterior to main body of basisphenoid	yes	no	no[d]	yes & no
Pectoral scales on entoplastron	indet	no	yes	yes
Neurals to suprapygal	indet	yes	no	no
Maxilla-quadratojugal contact	present	present	present	absent
Dorsally arched palate	no	no	no	yes[e]
Palatine extent in triturating surface	greater	greater	greater	lesser
Triturating surfaces very wide	no	no	yes[f]	no

[a] Except *Araiochelys.*
[b] Except *Zolhafah.*
[c] Except Foxemydina.
[d] Except *Polysternon.*
[e] Except *Labrostochelys.*
[f] Except in a few species.

from the eustachian tube. Unfortunately, we have been unable to see this specimen and cannot confirm these characters. The photograph (Roger et al., 1994: pl. 1, fig. 1) shows a worn braincase in ventral view that certainly has large depressions in the position of what we would call the fossa pterygoidea. This is a character found in only a few bothremydids as a deep fossa, namely *Foxemys*, *Polysternon*, *Nigeremys*, and *Arenila*. However, the specimen is clearly eroded on its surface and it is possible that the fossae are actually cavum pterygoidei, with the ventral covering eroded away along the anterior and medial edges, making this a podocnemidid and not a bothremydid character. There is some evidence for this conclusion in the photograph, which shows the two depressions with different shapes, requiring at least some erosion on the right fossa. The second character, the closed incisura columellae auris, is restricted only to bothremydids and does not occur outside the group. However, this character is not visible in ventral view. Furthermore, the specimen is eroded extensively on both sides and is missing most if not all of each cavum tympani, so this character may not be determinable at all in this specimen. It is unfortunate that this specimen is not available for further study, as it represents the best possibility for bothremydids extending past the Eocene. As it stands, however, the published claim, while certainly possible, is inadequate for a range extension past the Eocene into the Miocene.

Extension of the range of bothremydids into the Late Cretaceous of Madagascar is based on the report of Gaffney and Forster (2003). This consists of a partial lower jaw (fig. 247) that has the symphyseal edge and lateral pits typical of the tribe Bothremydini.

A short, wide anterior lobe of the plastron has been used as a diagnostic character for the Bothremydidae (Broin, 1977, 1988; Lapparent de Broin, 2000a, 2001). However, *Bairdemys venezuelensis* has a short, wide anterior plastral lobe and a plastral morphology (fig. 275) that is very similar to that in such bothremydids as *Chedighaii* (fig. 264). However, *Bairdemys* is clearly a podocnemidid based on the skull morphology (Gaffney and Wood, 2002). Therefore, this character is not diagnostic for the family Bothremydidae and the records based on this feature are in doubt.

SUBFAMILY **KURMADEMYDINAE**, NEW

TYPE GENUS: *Kurmademys* Gaffney, Chatterjee, and Rudra, 2001.

INCLUDED GENERA: *Kurmademys* Gaffney, Chatterjee, and Rudra, 2001; *Sankuchemys* Gaffney, Sahni, Schleich, Singh, and Srivastava, 2003.

DIAGNOSIS: As for tribe Kurmademydini.

TRIBE **KURMADEMYDINI**, NEW

TYPE GENUS: *Kurmademys* Gaffney, Chatterjee, and Rudra, 2001.

INCLUDED GENERA: *Kurmademys* Gaffney, Chatterjee, and Rudra, 2001; *Sankuchemys* Gaffney, Sahni, Schleich, Singh, and Srivastava, 2003.

DISTRIBUTION: Late Cretaceous Maastrichtian of Peninsular India.

DIAGNOSIS: Bothremydid pleurodires with the following unique characters: extreme degree of posterior temporal emargination characterized by a short postorbital and no parietal-quadratojugal contact; large fossa precolumellaris (unknown for *Sankuchemys*); condylus mandibularis well anterior to main body of basioccipital; small part of prootic exposed on ventral surface at junction of basisphenoid, pterygoid, and quadrate, containing foramen nervi facialis; other differentiating characters are: preorbital part of skull narrow, in contrast to Bothremydini; jugal-quadrate contact absent and supraoccipital-quadrate contact (unknown for *Sankuchemys*) present, in contrast to Taphrosphyini; foramen stapedio-temporale not very close to foramen nervi trigemini, in contrast to Bothremydini and Taphrosphyini; fenestra postotica closed, in contrast to Cearachelyini; basisphenoid pentagonal, in contrast to Cearachelyini; jugal not retracted from orbit, in contrast to Cearachelyini; triturating surfaces narrower than in Bothremydini; parietal contacts pterygoid (unknown for *Sankuchemys*, also occurs in some Bothremydini and Taphrosphyini).

TABLE 6
Genera of Kurmademydini

	Kurmademys	*Sankuchemys*
Posterior temporal emargination	extensive	extensive
Triturating surface	wide	narrow
Accessory ridge on triturating surface	absent	present
Site of foramen posterius canalis carotici interni	BS	PT & BS
Foramen stapedio-temporale visible in dorsal view	yes	no

DISCUSSION: The sister-group relationship of *Kurmademys* and *Sankuchemys* becomes unresolved at two steps in the MPC (fig. 288). The most serious problem is the flattened *Sankuchemys* skull, preventing nearly all quadrate characters from being determined. The two taxa are united only on the basis of the temporal emargination and the exposure of the quadrate-pterygoid-basisphenoid contact, both of which appear a number of times within pleurodires. Nonetheless, when the tribe Kurmademydini becomes unresolved, these two genera are still sister taxa to the subfamily Bothremydinae (consisting of the tribes Cearachelyini, Bothremydini, and Taphrosphyini), which holds together for three steps. Table 6 compares the two genera *Sankuchemys* and *Kurmademys*.

The phylogenetic analysis of the tribe Kurmademydini (essentially just *Kurmad-*

emys, as *Sankuchemys* is poorly preserved) shows it as the sister group to the remaining Bothremydidae. In geographic and stratigraphic terms, this is surprising, as the Kurmademydini is Asian and Maastrichtian, while the oldest bothremydids (*Cearachelys*) are South American and Albian and the next oldest (*Galianemys*) are African and Cenomanian. Furthermore, the tribe Cearachelyini, which contains these bothremydids, also has skull morphology that seems more plesiomorphic for bothremydids than for the kurmademydines. However, the emarginated skull and the deep fossa precolumellaris of *Kurmademys* are primitive for Pelomedusoides, and the Cearachelyini have such subfamily Bothremydinae synapomorphies as the anteriorly opening foramen stapediotemporale (fig. 309), large postorbital, maxilla-vomer contact, as well as slight temporal emargination and small or absent fossa precolumellaris. So at the present time, the Kurmedemydini are relatively well-supported as sister taxa to all remaining bothremydids. This indicates that the biogeographic history of the bothremydids is more complex than some recent workers would suggest (e.g. Lapparent and Werner, 1998). The senior author hopes to provide a biogeographic hypothesis for bothremydids in the near future that reflects the cladogram presented here.

Kurmademys Gaffney, Chatterjee, and Rudra, 2001

Type and Only Included Species: *Kurmademys kallamedensis* Gaffney, Chatterjee, and Rudra, 2001.

Distribution: Maastrichtian of southern India.

Etymology: *Kurma*, "turtle" in Sanskrit, in allusion to the second-stage incarnation of Lord Vishnu as a turtle in Hindu mythology.

Revised Diagnosis: Bothremydid of the tribe Kurmademydini with extensive temporal emargination seen also in *Sankuchemys* but absent in all other Bothremydidae; differing from *Sankuchemys* in having a smooth, expanded triturating surface rather than a narrower one with an accessory ridge; foramen posterius canalis carotici interni in basisphenoid unique among Bothremydidae; foramen stapedio-temporale visible in dorsal view in contrast to all other bothremydids (unclear in *Sankuchemys*). Carapace low and oval; shell surface texture weak granulated polygons; six neurals, sixth to eighth costals meeting on the midline; plastron with anterior lobe longer than in Bothremydini and Taphrosphyini; bridge longer than anterior and posterior plastral lobes; posterior plastral lobe short; humeropectoral sulcus posterior to epihyoplastral suture, crossing entoplastron; pectoroabdominal sulcus far anterior to mesoplastron, as in *Araiochelys*; pubic and ischiac scars as in Bothremydini.

Discussion: *Kurmademys* is well known from a series of skulls and postcrania, including a shell (figs. 255–257) that provides most of the characters for the tribe Kurmademydini in the dataset. The other postcrania have not yet been studied. Comparison with *Sankuchemys* is given in table 6.

Kurmademys kallamedensis Gaffney, Chatterjee, and Rudra, 2001

Type Specimen: ISI R152 (figs. 56, 57, 63, 64, 282B), a nearly complete skull lacking the dorsal part of the prefrontals, the posterior part of the crista supraoccipitalis, and part of the left quadratojugal.

Type Locality: Near the village of Kallamedu, Tamil Nadu, southern India. Map of locality is in Sastry et al. (1972) (fig. 12).

Horizon: Kallamedu Formation of the Ariyalur Group. Formation named and described by Sastry et al. (1972), who correlated it with the uppermost Maastrichtian; the Cretaceous–Tertiary boundary is its upper limit (Sastry et al., 1972). Dinosaurs have been described from other exposures of the Kallamedu (Matley, 1929; Yadagiri and Ayyasami, 1987). The *Kurmademys* locality is a small pocket of fine-grained sandstone and clay, about 6 in. thick. It also contained crocodiles, gar scales, and freshwater gastropods and bivalves and is interpreted as a freshwater pond deposit (Gaffney, Chatterjee, and Rudra, 2001).

Depositional Environment: Interpreted as a freshwater pond deposit (Gaffney, Chatterjee, and Rudra, 2001).

Diagnosis: As for genus.

Etymology: For the Kallamedu Formation.

REFERRED MATERIAL: ISI R155A, partial skull (fig. 60C); ISI R155B, partial skull (fig. 58C); ISI R155C, partial skull; ISI R158, partial skull (fig. 58A); ISI R159, partial skull (fig. 60A); ISI R155D, lower jaws; ISI R155E, lower jaws (fig. 233); ISI R155F, right ramus; ISI R152, 20 shell elements; ISI R153, 8 shell elements; ISI R157, 74 shell elements; ISI R278, partial shell (figs. 255, 256). See specimen list in Shell Description section for individual shell elements.

Sankuchemys Gaffney, Sahni, Schleich, Singh, and Srivastava, 2003

TYPE AND ONLY INCLUDED SPECIES: *Sankuchemys sethnai* Gaffney, Sahni, Schleich, Singh, and Srivastava, 2003.

DISTRIBUTION: Maastrichtian of Bombay, India.

ETYMOLOGY: *Sankuch*, "compressed" in Sanskrit, in allusion to the truck that ran over the type specimen.

REVISED DIAGNOSIS: Bothremydid of the tribe Kurmademydini with extensive temporal emargination also seen in *Kurmademys*, but absent in all other Bothremydidae; differing from *Kurmademys* in having a narrow triturating surface with an accessory ridge parallel to the labial ridge (unique among Bothremydidae except for some *Foxemys*); foramen posterius canalis carotici interni formed by basisphenoid and pterygoid; foramen stapedio-temporale not visible in dorsal view, as in all other bothremydids except *Kurmademys*.

DISCUSSION: Although many characters are visible in the type skull of *Sankuchemys*, one important area completely wrecked in SDS/VPL 1125 is the cavum tympani. This region has many characters important in bothremydid systematics that are not determinable for this taxon. The occiput is also reduced to two dimensions, completely obscuring foramina and features in that area. Nonetheless, SDS/VPL 1125 does have enough characters to show its distinctness from all other taxa and to test its relationships. Table 6 compares it with *Kurmademys*.

"*Carteremys*" *leithii* is also from the Intertrappean beds in Mumbai; although its age is unclear, it could be Cretaceous or Paleogene. This taxon, originally consisting of shells and skull material apparently unavailable for 150 years and presumably lost, is considered a nomen dubium (see below). The similarity of age and locality between *Sankuchemys* and "*Carteremys*" suggests that the two may be the same taxon. However, the "*Carteremys*" figures seem to show a broad rather than a narrow skull, suggesting that they are not the same taxon. In any case, there is no material available for this taxon.

Sankuchemys sethnai Gaffney, Sahni, Schleich, Singh, and Srivastava, 2003

TYPE SPECIMEN: SDS/VPL 1125, a complete skull (figs. 66, 67) completely smashed flat.

TYPE LOCALITY: Amboli Quarry, Jogeshwari, Mumbai, India (map and faunal discussion in Singh et al., 1998) (fig. 12).

HORIZON: Green tuff bed of Amboli, Intertrappean beds, late Maastrichtian (discussion in Singh et al., 1998).

DIAGNOSIS: As for genus.

DEPOSITIONAL ENVIRONMENT: Presumed to be fresh water (Singh et al., 1998).

ETYMOLOGY: "In honor of the discoverer of the holotype skull, Prof. S. F. Sethna, known for his pioneering work on the geology of the Mumbai region" (Gaffney, Sahni, Schleich, Singh, and Srivastava, 2003:3).

DISCUSSION: See above.

SUBFAMILY BOTHREMYDINAE BAUR, 1891, NEW RANK

TYPE GENUS: *Bothremys* Leidy, 1865.

INCLUDED GENERA: *Cearachelys* Gaffney, Campos, and Hirayama, 2001; *Galianemys* Gaffney, Tong, and Meylan, 2002; *Foxemys* Tong, Gaffney, and Buffetaut, 1998; *Polysternon* Portis, 1882; *Elochelys* Nopcsa, 1931; *Zolhafah* Lapparent de Broin and Werner, 1998; *Rosasia* Carrington da Costa, 1940; *Araiochelys*, n. gen.; *Bothremys* Leidy, 1865; *Chedighaii*, n. gen.; *Taphrosphys* Cope, 1869a; *Labrostochelys*, n. gen.; *Phosphatochelys* Gaffney and Tong, 2003; *Ummulisani*, n. gen.; *Rhothonemys*, n. gen.; *Azabbaremys* Gaffney, Moody, and Walker, 2001; *Nigeremys* Broin, 1977; *Arenila* Lapparent de Broin and Werner, 1998.

DIAGNOSIS: Bothremydidae with this unique character: foramen stapedio-temporale opens anteriorly not dorsally on otic chamber (possibly present in *Sankuchemys*); other distinguishing characters are: a relatively large postorbital (except in some Taphrosphyini), in contrast to Kurmademydinae; maxilla-vomer contact present (except in *Chedighaii* and *Azabbaremys*), in contrast to Kurmademydinae and Podocnemididae; very small to absent fossa precolumellaris, unique among pleurodires except for some Podocnemididae; condylus mandibularis posterior to or on level of basioccipital-basisphenoid suture, in contrast to all other Eupleurodira (except for *Polysternon* and some Taphrosphyini); condylus occipitalis formed only by exoccipitals (except in *Galianemys*), in contrast to all other pleurodires except Pelomedusidae; ventral outline of basisphenoid usually triangular; where known, iliac scar on costals 7, 8, and suprapygal.

DISCUSSION: The subfamily Bothremydinae consists of the tribes Cearachelyini, Bothremydini, and Taphrosphyini (figs. 1, 2; table 5). It is relatively well supported in figure 288, with a decay value of 3. The alternate possible relationship of Kurmademydini + Taphrosphyini + Bothremydini is discussed under Kurmademydini.

INFRAFAMILY **CEARACHELYODDA**, NEW

TYPE GENUS: *Cearachelys* Gaffney, Campos, and Hirayama, 2001.

INCLUDED GENERA: *Cearachelys* Gaffney, Campos, and Hirayama, 2001; *Galianemys* Gaffney, Tong, and Meylan, 2002.

DIAGNOSIS: Same as for tribe Cearachelyini.

TRIBE **CEARACHELYINI**, NEW

TYPE GENUS: *Cearachelys* Gaffney, Campos, and Hirayama, 2001.

INCLUDED GENERA: *Cearachelys* Gaffney, Campos, and Hirayama, 2001; *Galianemys* Gaffney, Tong, and Meylan, 2002.

DISTRIBUTION: Early Cretaceous of Brazil and Late Cretaceous of Morocco.

DIAGNOSIS: Member of the subfamily Bothremydinae with the following unique characters: jugal nearly or completely retracted from orbital margin; fenestra postotica open and formed as a short slit; foramen jugulare posterius open (also in *Foxemys* and *Polysternon*); other differentiating characters are: temporal emargination greater than in Bothremydini and Taphrosphyini but less than in Kurmademydini; fossa precolumellaris absent, in contrast to Kurmademydini; preorbital skull narrow, in contrast to Bothremydini; jugal-quadrate contact absent, in contrast to Taphrosphyini; shelf below cavum tympani absent, in contrast to Bothremydodda; supraoccipital-quadrate contact present; exoccipitals do not completely form neck of condylus occipitalis; foramen stapedio-temporale not visible dorsally; foramen stapedio-temporale and foramen nervi trigemini not very close, in contrast to Bothremydodda; condylus mandibularis anterior to condylus occipitalis but not as anterior as in Kurmademydini; palatine forms greater part of triturating surfaces than it does in Taphrosphyini; triturating surfaces wider than in Taphrosphyini but not as wide as in Bothremydini. Six-sided first neural with short posterolateral sides; four-sided second neural not contacting the first costal; plastron with longer anterior lobe than in other bothremydids; pectoral scale posterior to entoplastron.

DISCUSSION: The tribe Cearachelyini unites *Cearachelys* (Albian, Brazil) and *Galianemys* (Cenomanian, Morocco) by a number of unreversed characters. The three species included are similar in morphology but distinguishable by a number of characters (table 7), although *Galianemys* probably has a much larger shell, if the suggested association with AMNH 30550 and 30551 proves to be correct. These two genera, found on either side of the early Atlantic Ocean, seem to be a vicariant pair, divided by the opening of the Atlantic, possibly comparable to the situation for *Hamadachelys* and *Brasilemys*, and for *Euraxemys* and *Dirqadim*.

See table 5 for comparison of Cearachelyini with other tribes, and table 7 for comparison of the members of the Cearachelyini.

Cearachelys Gaffney, Campos, and Hirayama, 2001

TYPE AND ONLY INCLUDED SPECIES: *Cearachelys placidoi* Gaffney, Campos, and Hirayama, 2001.

TABLE 7
Genera of Cearachelyini

	Cearachelys	*Galianemys whitei*	*Galianemys emringeri*
Jugal retracted from orbit	nearly	widely	widely
Incisura columellae auris	open	closed	closed
Fossa pterygoidea	moderate	shallow or absent	deep
Fenestra postotica open, formed as a short slit	yes	yes	yes
Basisphenoid-quadrate contact	narrow	narrow	broad
Cheek emargination	slight indentation at QJ	QJ forms straight cheek	QJ forms straight cheek
Postorbital-maxilla contact	slight or absent	extensive	extensive
Trough on incisura columellae auris ridge	absent	present	present
Small part of prootic visible in ventral view with foramen nervi facialis	no	no	yes
Interorbital distance	narrower	wider	wider
Sulcus olfactorius ridge	shallower	deeper	deeper
Parietal wider posterolaterally	no	yes	yes
Labial ridge	thin	thick[a]	thick to very thick
Antrum postoticum	larger	smallest	smaller
Tuberculum basioccipitale	smaller, blunt	larger, shelflike	larger, shelflike
Prefrontal-frontal suture convex anteriorly	yes	no	yes
Jugal-palatine contact	extensive	present, intermediate	small or absent
Jugal exposed on triturating surface	yes	yes	no
Foramen nervi vidiani exposed ventrally	no	no	yes

[a] But thinner than in *G. emringeri.*

DISTRIBUTION: Albian of Brazil.

ETYMOLOGY: In allusion to the type locality that is in Ceará State, Brazil, and to *chelys*, turtle in Greek.

REVISED DIAGNOSIS: Bothremydid pleurodire of the tribe Cearachelyini with the following unique character: jugal nearly or completely retracted from orbital margin but not widely separated from orbit by broad postorbital-maxilla contact, as in *Galianemys*; other differentiating characters are: incisura columellae auris open not closed, in contrast to *Galianemys*; fossa pterygoidea present, as in *Galianemys emringeri*, not absent, as in *G. whitei*; cheek with slight emargination not straight, as in *Galianemys*; interorbital distance narrower than in *Galianemys*; labial ridge thin in contrast to thick in *Galianemys*; sulcus olfactorius ridge shallower than in *Galianemys*; antrum postoticum larger than in *Galianemys*; tuberculum basioccipitale small and blunt not larger and shelflike, as in *Galianemys*; jugal-palatine contact more extensive than in *Galianemys*.

Carapace moderately domed as in *Pelomedusa*, oval in outline, with eight neurals completely separating all eight costals, in contrast to at least one pair of costals meeting in midline as in most other bothremydids; second neural does not contact first costals. Plastron with anterior lobe rounded and broader than in other Santana Pelomedusoides; pectoral scales do not extend anteriorly onto entoplastron, but do extend posteriorly onto mesoplastra; mesoplastron small and laterally placed, as in *Podocnemis*.

DISCUSSION: Do the three skulls of *Cearachelys* (table 8) represent more than one species? It could be argued that the swollen triturating surfaces, jugal depression, pinched snout, deep fossa pterygoidea, and more medial foramen posterius canalis carotici interni sufficiently differentiate BSP 1976 I 160 from THUg 1798 to make them separate taxa. However, we interpret these differences as individual variation, possibly growth related, and recognize the three skulls as belonging to one species, *Cearachelys placidoi*.

Among recent taxa, intraspecific variation, including maxillary swelling and snout pinching, has been reported in emydids, trionychids, and chelids (Cann, 1998; Carr, 1952; Dalrymple, 1977; Lindeman, 2000). Maxillary swellings typically occur in larger indi-

TABLE 8
Comparison of *Cearachelys placidoi* Specimens

	MPSC	THUg 1798	BSP 1976 I 160
Relative size (width at quadrates)	88%	73%	100%
Pinched snout	—	no	yes
Labial ridge	—	straight	convex laterally
Depression on triturating surface formed by maxilla and jugal	shallower	shallower	deeper
Degree of jugal exposure on triturating surface	intermediate	least	most
Fossa pterygoidea	slight	slight	deep
Fenestra postotica subdivided	no	no	yes (right) no (left)
Prootic exposure on ventral surface	yes/no	very narrow	yes
Position of foramen posterius canalis carotici interni	opens ventrally	opens ventrally	opens laterally
Distance across condylus mandibularis	34.6 (88%)	26.6 (73%)	39.0 (100%)
Midline length	—	31.3 (73%)	42.3 (100%)

viduals and have been associated (sometimes ambiguously) with age, sex, and dietary differences. Similarly, muscle attachment sites can be exaggerated in any vertebrate, and some individuals show greater ridging, thicker or thinner bone, and deeper concavities. The three *Cearachelys* skulls show a size progression (table 8). If BSP 1976 I 160 is placed at 100%, then MPSC is 88% of BSP 1976 I 160 and THUg 1798 is 73% of BSP 1976 I 160. This suggests an age correlation with BSP 1976 I 160 as oldest, but it may also be due to gender, as in some living emydids (Carr, 1952; Dalrymple, 1977; Lindeman, 2000). Nonetheless, the three *Cearachelys* skulls form a series showing degrees of variation that we interpret as representing a single species.

The swollen maxilla, triturating surface depression, and pinched snout occur in other taxa, but the difference in position of the foramen posterius canalis carotici interni does not occur outside the Bothremydidae. To a certain extent, this may be due to the unusual juxtaposition of a thin-walled canalis caroticus internus within a muscle attachment depression. As described in the Cranial Morphology section (*Cearachelys*, Pterygoid), an older or larger individual often has better defined muscle attachments, and it is likely that the difference in foramen position is related to the increase in depth of the fossa pterygoidea. At present, it seems best to include all the *Cearachelys* skulls in the same taxon and to interpret their differences as intraspecific variation.

Cearachelys placidoi Gaffney, Campos, and Hirayama, 2001

TYPE SPECIMEN: MPSC, a partial skull (figs. 70, 71), shell, cervicals, and limb elements.

TYPE LOCALITY: Probably Santana do Cariri, Ceara, Brazil (fig. 13).

HORIZON: Probably Romualdo Member of the Santana Formation, probably Albian in age (ca. 110 mya; Maisey, 1990, 1991).

DEPOSITIONAL ENVIRONMENT: Near-shore marine (Maisey, 1990) with freshwater episodes (Maisey, 2000). See *Araripemys* for more discussion.

DIAGNOSIS: Same as for genus.

ETYMOLOGY: In honor of Dr. Placido Nuvens, Director of the Museu Paleontologico de Santana do Cariri, Ceara, Brazil.

REFERRED MATERIAL: THUg 1798, nearly complete skeleton with skull (figs. 72, 73), lower jaw, shell (fig. 258C–E), cervicals, and limb elements, near Santana do Cariri, Romualdo Member, Santana Formation, Albian, purchased from von Leonhardt, 1993; BSP 1976 I 160, nearly complete skeleton with damaged skull (figs. 74–76), lower jaws (fig. 234), shell (fig. 258A, B), cervicals and limb elements, Juazeiro do Norte, Ceará, Brazil, Santana Formation, probably Albian.

Galianemys Gaffney, Tong, and Meylan, 2002

TYPE SPECIES: *Galianemys whitei* Gaffney, Tong, and Meylan, 2002.

INCLUDED SPECIES: *G. whitei, G. emringeri.*

DISTRIBUTION: Late Cretaceous of Morocco.

ETYMOLOGY: For Henry Galiano, who assisted in obtaining specimens of this and other turtles for the AMNH, and for his lifelong interest and support of paleontology at the AMNH.

REVISED DIAGNOSIS: Bothremydid pleurodires of the tribe Cearachelyini with the unique character of jugal widely retracted from orbital margin by broad contact of postorbital and maxilla. Other differentiating characters are: incisura columellae auris closed not open as in *Cearachelys*; cheek with no emargination, not even the slight one seen in *Cearachelys*; interorbital distance wider than in *Cearachelys*; labial ridge thicker than in *Cearachelys*; sulcus olfactorius ridge deeper than in *Cearachelys*; antrum postoticum smaller than in *Cearachelys*; tuberculum basioccipitale large and shelflike in contrast to small and blunt in *Cearachelys*; jugal-palatine contact less extensive than in *Cearachelys*.

PREVIOUS WORK: Gaffney, Tong, and Meylan (2002) named and described *Galianemys*, while Lapparent de Broin and Werner (1998) and Lapparent de Broin (2000) referred to an undescribed taxon from Erfoud that is probably *Galianemys* (see below).

DISCUSSION: Two shells from the Kem Kem beds (described below in the shell section) probably belong to *Galianemys*. The shells are not identical and may represent the two species seen in the skulls. We have left the shells out of the phylogenetic analysis until associated material becomes available.

The two species of *Galianemys* are the best known bothremydids, with a number of skulls available for each species (table 9). CT scans of one of the skulls are available online at the University of Texas Digital Imaging website: <http://www.digimorph.org/specimens/Galianemys emringeri/>. The two species of *Galianemys* are united by the retracted jugal and other characters that separate them from *Cearachelys*. However, in the MPC the genus collapses in one step because most of these characters are gradational, hard to determine in the more advanced Bothremydini, and not entered into the dataset. Evidence for the union of the two *Galianemys* species is actually stronger than expressed in the MPC. See table 7 for comparison of the species of the Cearachelyini.

Galianemys emringeri Gaffney, Tong, and Meylan, 2002

TYPE SPECIMEN: AMNH 29985, a skull (figs. 85, 86, 278) lacking most of the right triturating area, both cheeks, and the left otic chamber; donated by Henry Galiano.

TYPE LOCALITY: Near al Taouz, province de Kasr-es-Souk, Morocco (figs. 14, 15).

HORIZON: Cenomanian, Kem Kem beds.

DEPOSITIONAL ENVIRONMENT: Deltaic or fluvial (Sereno et al., 1996; Cavin et al., 2001), found with dinosaurs and other freshwater/terrestrial fauna.

DIAGNOSIS: A species of *Galianemys* differing from *Galianemys whitei* by having a prefrontal-frontal suture convex anteriorly rather than straight; small or absent jugal-palatine contact; jugal not exposed on triturating surface; triturating surface flat; labial ridge relatively thicker; antrum postoticum relatively larger; prootic exposed ventrally containing foramen nervi facialis; deep fossa pterygoidea; foramen nervi vidiani exposed ventrally; and foramen posterius canalis carotici interni formed mostly by basisphenoid with only slight or no contribution from pterygoid (Gaffney, Tong, and Meylan, 2002).

ETYMOLOGY: In recognition of Gilles Emringer for helping obtain Kem Kem specimens.

REFERRED MATERIAL: AMNH 30026, partial braincase, Kem Kem, Morocco, donated by Henry Galiano; AMNH 30035, nearly complete skull (figs. 83, 84, 87, 284B), Kem Kem, Morocco, donated by Gilles Emringer and François Escuillié; AMNH 30037, skull lacking right cheek (fig. 88), Kem Kem, Morocco, donated by Michael Hammer; AMNH 30040, nearly complete skull, donated by Michael Hammer; MDEt 46, partial braincase, Kem Kem, Morocco.

DISCUSSION: See table 7 for comparison with *Galianemys whitei* and table 9 for variation among *Galianemys* specimens.

TABLE 9
Comparison of *Galianemys* Specimens

	Galianemys emringeri						*Galianemys whitei*						
	AMNH 29985	AMNH 30037	AMNH 30035	AMNH 30040	AMNH 30026	MDEt 46	AMNH 29987	AMNH 29986	AMNH 30028	AMNH 30027	AMNH 30036	MDEt 45	AMNH 30555
Prefrontal/frontal suture convex anteriorly	yes	yes	yes	no	?	?	no	no	yes[a]	no	no	no	no
Jugal/palatine contact	no	yes but small	yes but small	yes	?	?	yes	yes	yes	yes	yes	yes	yes
Jugal exposed on triturating surface	no	no	no	yes	?	?	yes	yes	yes	yes	yes	yes	yes
Small depression on posterolateral part of triturating surface	no	no	no	no	?	?	yes	yes	yes	yes	yes	no	no
Premaxilla concave	?	yes	yes	?	?	?	?	?	?	?	?	no	no
Labial ridge	thick	thick	very thick	very thin	?	?	thin	thin	thin	thin	thin	very thin	thin
Pinched snout	slight	slight	slight	?	?	?	yes[c]	absent	absent	?	absent	absent	absent
Antrum postoticum	larger	larger	larger	?	?	smaller	smaller	smaller	smaller	?	larger	?	smaller
Prootic exposed ventrally	yes	yes	yes	yes	yes	yes	no	no	no	no	no	?	no
Fossa pterygoidea deep	yes	yes	yes	yes	yes	yes	no	no	no	no	no	?	no
Fully enclosed foramen jugulare posterius	no	yes	yes/no	?	no	no	no	no	yes	yes	no	?	no
Subdivided fenestra postotica	no	yes[b]	no	?	no	?	no	no	no	yes[b]	no	?	no
Foramen nervi vidiani exposed	yes	yes	yes	yes	yes	yes	no	no	yes	no	yes	?	yes
Pterygoid and basisphenoid form foramen posterius canalis carotici interni	no	no	no	no	no	no	yes	yes	yes	yes	yes	?	yes
Basisphenoid alone forms foramen posterius canalis carotici interni	yes	yes	yes	yes[b]	yes	yes	no	no	no	no	no	?	no

[a] Entire suture asymmetric.

[b] Damaged.

[c] Pronounced.

Galianemys whitei Gaffney, Tong, and Meylan, 2002

TYPE SPECIMEN: AMNH 29987, nearly complete skull (figs. 91, 92, 99, 284A), donated by Mr. Richard White.

TYPE LOCALITY: Near Al Taouz, Province de Kasr-es-Souk, Morocco (figs. 14, 15).

HORIZON: Cenomanian, Kem Kem beds.

DEPOSITIONAL ENVIRONMENT: Deltaic or fluvial (Cavin et al., 2001; Sereno et al., 1996), found with dinosaurs and other freshwater/terrestrial fauna.

DIAGNOSIS: A species of *Galianemys* differing from *Galianemys emringeri* by having a straight rather than curved prefrontal-frontal suture; a relatively larger jugal-palatine contact; jugal exposed on triturating surface; small depression on posteroventral part of triturating surface; labial ridge relatively thinner; antrum postoticum usually relatively smaller; prootic not exposed ventrally; shallow or absent fossa pterygoidea; foramen nervi vidiani not exposed; and foramen posterius canalis carotici formed by basisphenoid and pterygoid equally (Gaffney, Tong, and Meylan, 2002).

ETYMOLOGY: For Richard S. White, who brought a number of specimens to our attention and aided our work.

REFERRED MATERIAL: AMNH 29986, skull lacking left orbital region and palate (figs. 93, 94, 98), near Al Taouz, Province de Kasr-es-Souk, Morocco, donated by Richard S. White; AMNH 30027, skull lacking left orbital region and palate (figs. 100, 284C), "Kem Kem", Morocco, donated by François Escuillié; AMNH 30028, nearly complete skull, "Kem Kem", Morocco, donated by François Escuillié; AMNH 30036, nearly complete skull (fig. 280), "Kem Kem", Morocco, donated by Michael Hammer; MDEt 45, skull lacking basicranium with quadrate incorrectly attached, Kem Kem, Morocco; AMNH 30555, nearly complete skull (figs. 95, 96), Kem Kem, Morocco, donated by François Escuillié.

DISCUSSION: A specimen of what appears to be *Galianemys whitei* was figured in Lapparent de Broin and Werner (1998: fig. 4a, e) as "new bothremydid form, Hammada [sic] du Guir, East of Erfoud, Morocco, Albian, MNHN (P) MRS 2098, Fectay coll." In the text (Lapparent de Broin and Werner, 1998: 10) it is characterized as "A new bothremydid form, Albian of Morocco (that can be positioned early in the family development) …". No other information is provided, but the general shape and retracted jugal indicate *Galianemys*. The jugal on the triturating surface and the thin labial ridge suggest *Galianemys whitei*, but the area around the foramen posterius canalis carotici interni is too roughly drawn to determine the extent of the fossa pterygoidea or the exposure of the prootic, if any.

See table 7 for comparison with *Galianemys emringeri* and table 9 for variation among *Galianemys* specimens.

INFRAFAMILY BOTHREMYDODDA BAUR, 1891, NEW RANK

TYPE GENUS: *Bothremys* Leidy, 1865.

INCLUDED GENERA: *Foxemys* Tong, Gaffney, and Buffetaut, 1998; *Polysternon* Portis, 1882; *Elochelys* Nopcsa, 1931; *Zolhafah* Lapparent de Broin and Werner, 1998; *Rosasia* Carrington da Costa, 1940; *Araiochelys*, n. gen.; *Bothremys* Leidy, 1865; *Chedighaii*, n. gen.; *Taphrosphys* Cope, 1869a; *Labrostochelys*, n. gen.; *Phosphatochelys* Gaffney and Tong, 2003; *Ummulisani*, n. gen.; *Rhothonemys*, n. gen.; *Azabbaremys* Gaffney, Moody, and Walker, 2001; *Nigeremys* Broin, 1977; *Arenila* Lapparent de Broin and Werner, 1998.

DIAGNOSIS: Members of the subfamily Bothremydinae with the following unique characters within the Bothremydidae: quadrate shelf formed below cavum tympani (unique among all turtles); foramen stapedio-temporale and foramen nervi trigemini very close on anterior face of otic chamber (unique among all turtles); and condylus occipitalis and neck formed only of exoccipitals (also occurs in Pelomedusidae). Other differentiating characters are: fenestra postotica closed (also in *Kurmademys*); plastron with anterior margin posterior to the carapace margin; and short and wide anterior lobe.

DISCUSSION: The sister-group relationship of the Bothremydini and the Taphrosphyini is well supported in the phylogenetic analysis with a number of unambiguous characters (fig. 288). The principal weakness in this grouping is *Foxemys* and *Polysternon*, which have an open incisura columellae auris and cause a collapse of resolution in the Bothremydini and Bothremydodda with increased decay steps. The removal of these genera from the Bothremydodda to a sister-group relationship with the remaining "higher" bothremydids is a possibility that should be kept in mind. If some of the characters uniting the Bothremydini, particularly those related to the expanded snout and large triturating surfaces, were considered as plesiomorphic, then the Bothremydodda would partially collapse, resulting in a cladogram like that in figure 289.

TRIBE **BOTHREMYDINI**, NEW

TYPE GENUS: *Bothremys* Leidy, 1865.

INCLUDED GENERA: *Foxemys* Tong, Gaffney, and Buffetaut, 1998; *Polysternon* Portis, 1882; *Elochelys* Nopcsa, 1931; *Zolhafah* Lapparent de Broin and Werner, 1998; *Rosasia* Carrington da Costa, 1940; *Araiochelys*, n. gen.; *Bothremys* Leidy, 1865; *Chedighaii*, n. gen.

DIAGNOSIS: Bothremydid pleurodires with the following unique characters: preorbital part of skull very broad (except in *Araiochelys*); fenestra interorbitale low; other differentiating characters are: temporal emargination moderate, in contrast to slight to absent in Taphrosphyini and deep in Kurmademydini and Cearachelyini; jugal-quadrate contact absent; supraoccipital-quadrate contact present (except in *Zolhafah*), in contrast to Taphrosphyini; palatine forms greater part of triturating surfaces than it does in Taphrosphyini; triturating surfaces very wide (except in *Araiochelys*); shell surface with "pelomedusoid ornamentation" consisting of fine forking and irregular vascular grooves; humeropectoral sulcus on epihyoplastral suture (*Foxemys* and *Polysternon*) or posterior to it (*Rosasia*, *Araiochelys*, *Chedighaii*), and crossing entoplastron (except *Rosasia*); pectoroabdominal sulcus near or on mesoplastron (except *Araiochelys*); pubic scar oval and wider than in *Taphrosphys*; ischiac scar triangular and not near the xiphiplastral edge.

DISCUSSION: This tribe is roughly equivalent to the "*Bothremys* group" (also "Groupe *Bothremys*," "*Bothremys* Leidy 1865 group") of Antunes and Broin (1988), Lapparent de Broin and Werner (1998), Lapparent de Broin and Murelaga (1999), and Lapparent de Broin (2000a), an informal assemblage consisting of *Zolhafah, Rosasia*, and *Bothremys*. Other authors (Gaffney, Campos, and Hirayama, 2001; Gaffney, Chatterjee, and Rudra, 2001; Gaffney, Tong, and Meylan, 2002) have used this informal grouping and expanded it to include newly described taxa. However, Lapparent de Broin (2000b) also used the term "pre-*Bothremys* group" for *Polysternon* plus what we refer to as *Foxemys* ("*Polysternon mechinorum*" in the usage of Lapparent de Broin 2000b). The "pre-*Bothremys* group" would be the same as our subtribe Foxemydina.

A lower jaw, AMNH 29989 (figs. 245, 246), is probably a tribe Bothremydini based on its close similarity to the lower jaws of *Bothremys*. This specimen is from the Ypresian phosphates of couche 1, Ouled Abdoun Basin, Morocco. It probably represents a different genus from the bothremydines described here because of its very deep processus coronoideus.

Most members of the tribe have distinctive pits on the triturating surfaces (figs. 237–246). Gaffney and Zangerl (1968: 235–236) discussed the possible function of these pits in *Bothremys cooki*:

> The function of the large palatal and mandibular pits in *Bothremys* has been commented on by earlier authors. Leidy (1865, p. 111) wrote, 'The function of the latter (the pit) … is difficult to comprehend. It does not appear to be an alveolus for a tooth; but probably it may have accommodated a corneous tooth-like process springing from a corresponding hollow of the lower jaw." Baur (1891, pp. 423–424) suggested the presence of "a large tusk" in the pits. Hay (1908, p. 104) believed that the tooth idea was improbable and made another suggestion: "The whole construction of the skull of *Bothremys* indicates that it was accustomed to crush hard objects as food. Probably these objects were of such a nature that economy of force demanded that they should be brought to a particular spot on the jaw for crushing. To provide for the rapid reproduction of the horn beneath these areas for crushing, these pits became developt in a way analogous to the human 'nailbed.'"

Before discussing the merits of these ideas, the morphology of the structures involved should be summarized. There are two pits in the palate, principally formed by the jugals, but all of the surrounding bones including the cheek are modified to form the pits. Each pit is thickest (see cross-section) about midway in the cone. The triturating surfaces occupy most of the palate and have an overall form of two funnels opening ventrally. The lower jaws have matching structures which, however, do not open directly upward into the jugal pits, but open dorso-anteriorly.

Hay was almost certainly right in thinking that *Bothremys* was toothless. The "corneous tooth-like process" of Leidy has a somewhat greater possibility; however, the horny covering of recent turtles rarely forms a structure that is not present in the underlying bone. Thicknesses vary, but whole structures, like a large tusk, are not known to occur independent of an osseous core. Therefore, it seems likely that the whole triturating surface was covered by horny material, thickest in the tips of the pits but not forming tusk-like structures.

This inference is most like the suggestion of Hay previously quoted. However, Hay also thought that the pits were areas of rapid horn production and were not expressed on the external surface. It would be difficult to disprove this, but it is more probable that the pits were expressed as depressions in the external horny covering as in living turtles.

If this latter suggestion were correct, the pits might function to crack hard objects, slightly larger than the pits, which otherwise would be difficult to grasp or hold onto by means of a "normal" triturating surface. Certain ovoid mollusks (gastropods?) might comprise the food of *Bothremys*. There is a disadvantage to this hypothesis since it seems to mean that a particular individual of *Bothremys* would be limited to objects of a certain size range, because larger or smaller ones could not fit the pits. The crushing function of the pits is substantiated by other structural evidence. High and well-developed coronoid processes, as in *Bothremys* …, are characteristic of turtles with crushing habits (see Stejneger, 1944, plate 30, for an example in *Amyda*). The posterior position of the articulation and the position of the pits immediately adjacent to the coronoid processes result in an efficient crushing mechanism with the adductor musculature attached close to the object to be crushed, but far from the fulcrum.

This discussion, suggesting that the pits served for grasping and crushing slippery mollusks, still seems the best guess at present. The recent discovery that the pit morphology is much more widespread taxonomically than known in 1968 only serves to reinforce the general utility of the pit structure, whatever it was, despite the fact that no living turtle still has the pits.

See table 5 for a comparison of the tribes of the Bothremydidae and table 10 for a comparison of the genera in the tribe Bothremydini.

SUBTRIBE **FOXEMYDINA**, NEW

TYPE GENUS: *Foxemys* Tong, Gaffney, and Buffetaut, 1998.

INCLUDED GENERA: *Foxemys* Tong, Gaffney, and Buffetaut, 1998; *Polysternon* Portis, 1882; *Elochelys* Nopcsa, 1931.

DIAGNOSIS: Members of the tribe Bothremydini with the following characters contrasting with Bothremydina: maxilla-quadrate contact absent; triturating surface without maxillary pits (also in *Chedighaii*); dentary pits absent; jugal not exposed on triturating surface (also in *Chedighaii*); stapes not contained in bony canal; fossa pterygoidea deep and narrow; foramen jugulare posterius only partially closed; basisphenoid ventral outline pentagonal; pectoral scales extending onto epiplastron.

DISCUSSION: We have chosen *Foxemys* as the type genus for this taxon, as it is skull based, in contrast to *Polysternon*, in which the skull is not definitely associated with the type shell. This subtribe is essentially the same as the "pre-*Bothremys* group" of Lapparent de Broin (2000b).

Foxemys Tong, Gaffney,
and Buffetaut, 1998

TYPE AND ONLY INCLUDED SPECIES: *Foxemys mechinorum* Tong, Gaffney, and Buffetaut, 1998.

DISTRIBUTION: Late Cretaceous Late Campanian–Early Maastrichtian of France.

ETYMOLOGY: From the name of the locality, Fox Amphoux, in southern France (Tong et al., 1998).

REVISED DIAGNOSIS: A bothremydid pleurodire of the subtribe Foxemydina with

TABLE 10
Genera of Bothremydini

	Foxemys	*Polysternon*	*Zolhafah*	*Rosasia*	*Araiochelys*	*Bothremys*	*Chedighaii*
Anterior projection of prefrontal	absent	absent	indet.	absent	present	present	present
Preorbital part of skull broad	yes	yes	yes	yes	no	yes	yes
Apertura narium externa figure 8 shaped	no	no	indet.	no	yes	yes	indet.
Prefrontal-premaxilla in contact dividing apertura narium externa	no	no	no	no	yes	yes, no	no
Apertura narium externa orientation	faces anteriorly	faces anteriorly	probably faces anterodorsally	faces anteriorly	faces anterolaterally	faces anterodorsally	faces anterodorsally
Size of orbital margin	intermediate	intermediate	indet.	very large	intermediate	small, intermediate	small
Orbits face upwards strongly	no	no	no	no	no	yes	yes
Dorsal process on premaxilla tip	no	no	yes	no	yes	yes	probably no
Premaxilla extends anteriorly well beyond prefrontals	no	no	indet.	no	yes	yes	yes
Dorsal plate of parietal	wider	wider	indet.	indet.	narrower	wider	narrower
Prefrontal-palatine contact	no	indet.	no	no	no	yes	yes
Dorsal process of maxilla	narrower	narrower	narrower	narrower	narrower	wider	narrower
Postorbital-palatine contact in posterior surface of postorbital wall	indet.	indet.	yes	no	indet.	yes, no	no
Maxilla with dorsomedial process	no	no	no	no	no	yes, no	no
Apertura narium interna	oval	indet.	indet.	oval	oval	circular, oval	oval
Sulcus palatinopterygoideus	high	indet.	indet.	high	indet.	low	low
Parietal-pterygoid contact on lateral side of sulcus palatinopterygoideus	no	indet.	indet.	no	indet.	yes	yes
Fossa orbitalis enlarged posteriorly	no	indet.	no	yes	yes	yes	yes
Ridge forming lower orbital rim	low	present	present	present	present	absent or low	present
Suborbital maxillary plate deep	no	no	no	no	no	yes	yes/no
Midline depression on premaxilla on ventral surface	wide	wide	wide	narrow	narrow	narrow, wide	wide
Very wide triturating surfaces	yes	no	yes	yes	no	yes	yes/no
Triturating surface pits	absent	absent	partial	partial	complete	complete	absent
Jugal exposure in triturating pit	none	none	present	present	present	present	absent
Maxilla-palatine contact behind pit	no	no	no	no	no	present, absent	no
Lateral edge of maxilla	curved	straight	curved	curved	straight	curved	straight
Thickness of maxillary plate	thick	thin	thick	thick	thin	thick	thick
Vomer elongate anteriorly	yes	indet.	no	yes	no	yes, no	no

TABLE 10
Continued

	Foxemys	*Polysternon*	*Zolhafah*	*Rosasia*	*Araiochelys*	*Bothremys*	*Chedighaii*
Maxilla-vomer contact	yes	indet.	absent or small	yes	yes	yes	no, widely separated
Pocket on posterior surface of quadrate	no	no	no	indet.	yes	no	indet.
Large ridge on otic chamber	no	no	no	no	no	yes, no	no
Fossa pterygoidea	deeper than in *Polysternon*	deep	absent	shallow	absent	absent	absent
Antrum postoticum	larger	larger	larger	indet.	smaller	smaller, larger	larger, smaller
Incisura columellae auris	open	open	closed	closed	closed	closed	closed
Condylus mandibularis close to level of condylus occipitalis	yes	no, anterior to most of BS	yes	yes	yes	yes	yes
Quadrate-maxilla contact	absent	absent	indet.	present	present	present	indet.
Foramen chorda tympani inferius hidden in posterior view	no	indet.	no	no	yes	no	no
Foramen posterius canalis carotici interni	PT-BS	PT-BS	PT-BS-QU	PT-BS	PT-QU	PT-QU, PT-QU-BS	PT-QU
Supraoccipital-quadrate contact	yes	yes	no	yes	yes	yes	yes
Crista supraoccipitalis with ventral thickening	no	indet.	indet.	indet.	no	yes	yes
Basisphenoid-quadrate contact	broad	broad	narrow	narrow	narrow	very narrow	very narrow
Basisphenoid pentagonal	yes	yes	no	no	no	no	no
Processus clinoideus	indet.	indet.	present	present	indet.	absent	indet.
Canalis nervi abducentis a groove	indet.	indet.	no	no	indet.	yes	indet.
Pinched snout	yes	yes	no	yes	no	yes, no	no
Sulcus eustachii constricted into channel	no	no	no	no	no	yes, no	no
Posteroventral surface of exoccipital concave	yes	no	no	indet.	no	yes, no	yes

the following characters differentiating it from *Polysternon*: fossa pterygoidea deeper than in *Polysternon*; orbital rim low, as in *Bothremys*, not high, as in *Polysternon*; triturating surfaces very wide, as in *Bothremys* and *Chedighaii*, in contrast to narrower, as in *Polysternon*; condylus mandibularis close to level of condylus occipitalis, as in most Bothremydini but in contrast to *Polysternon*; shell similar to *Polysternon* but lacking the parallel striations and nuchal emargination seen in *Polysternon*; relatively large intergular scale; straight lateral border of posterior lobe of the plastron and a wide anal notch, in contrast to *Polysternon*.

DISCUSSION: Lapparent de Broin (2001: 169) synonymized the genus *Foxemys* with the genus *Polysternon* while recognizing the distinctness of the species *Foxemys mechinorum*. Her rationale seemed to be that the shells are very similar and therefore belong in the same genus. Our phylogenetic analysis shows *Foxemys* and *Polysternon* as sister taxa and belonging in the same monophyletic group, whether it is a genus or other higher category. The recognition of genera is subjective, as long as they are monophyletic, so it is basically a matter of convention and taste, not science. Interestingly, Lapparent de Broin and Werner (1998) erected a new genus, *Arenila*, for a skull very similar to a previously known taxon, *Nigeremys*, both of which could be included in the same genus. We choose to take a more split view of the situation and recognize *Foxemys* as well as *Arenila*. In our subjective view, this is more consistent with most other genera in pleurodires, as things stand at present. Furthermore, recognition of both *Foxemys* and *Polysternon* allows the expression of the sister-group relationship of these species without resorting to subgenera. In any case, other than monophyly, there are no objective criteria for the recognition of genera, and it is a matter of taste and consent.

Botfalvai (2005) announced in an abstract the discovery of two skulls and other elements from the Santonian of Hungary as new but unnamed bothremydids similar to *Foxemys*.

See table 10 for a comparison of genera of the tribe Bothremydini.

Foxemys mechinorum Tong, Gaffney, and Buffetaut, 1998

TYPE SPECIMEN: MDEt 10, a dorsoventrally crushed skull with right half of carapace and complete plastron (figs. 105, 106; Tong et al., 1998: figs. 1, 2).

TYPE LOCALITY: Fox Amphoux, southern France (fig. 14).

HORIZON: Late Campanian–Early Maastrichtian, Late Cretaceous.

DEPOSITIONAL ENVIRONMENT: The Massecaps locality, Cruzy, Hérault, France, has yielded very abundant *Foxemys* and other vertebrate remains, and it appears to be freshwater in origin. "The vertebrates are scattered through a thickness of about 1 m of variegated clays which sometimes contain iron oxide nodules, and are cut by unfossiliferous sandy channels. It would appear to be a floodplain deposit" (Buffetaut et al., 1999).

DIAGNOSIS: Same as for genus.

ETYMOLOGY: For discoverers of the material, Patrick and Annie Méchin.

REFERRED MATERIAL: From the Fox Amphoux locality: an almost complete skull (figs. 103, 104, 107, 281; PAM 511A, Tong et al., 1998: figs. 3–6); an incomplete lower jaw (figs. 235, 236; PAM 511B, Tong et al., 1998: figs. 7, 8); an almost complete and well-preserved shell in which the plastron is complete and only the posterior part of the carapace is missing (lacking right sixth to eighth costal and part of seventh and eighth left costal bones, eighth to eleventh right peripheral and eleventh left peripheral bones, suprapygal and pygal bones; PAM 548, Tong et al., 1998: figs. 9, 10); a partial shell consisting of the anterior third of the carapace in poor condition and a complete plastron (MDEt 09, Tong et al., 1998: fig. 11); a right scapula-coracoid (MDEt 11); and several isolated plates, an almost complete shell, MHNM uncataloged; Late Campanian–Early Maastrichtian, Var, France.

From the Massecaps locality: MC M2114–M2118, all lower jaws; MC M1734, nearly complete skull; MC M2119, a partial skull, Late Campanian–Early Maastrichtian, Cruzy, Herault, France (*Foxemys* is the most abundant form among vertebrates from this locality, including one complete and one

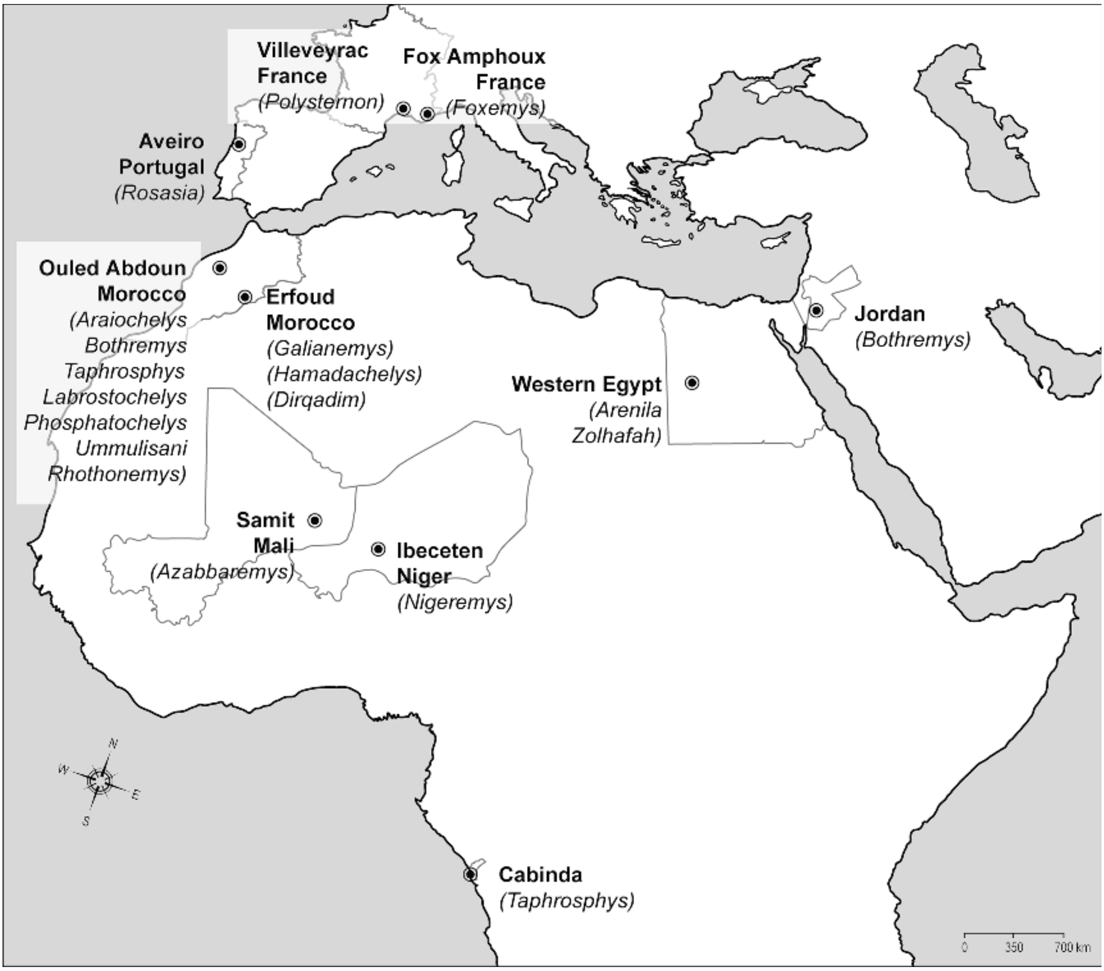

Fig. 14. Map showing localities of the family Bothremydidae, tribes Cearachelyini, Bothremydini, Taphrosphyini; family Euraxemydidae (*Dirqadim*); and *Hamadachelys* in Africa and Europe. Only generically identifiable specimens are indicated. [A. Venjara, del.]

partial skull, several lower jaws, hundreds of disarticulated and isolated plates, vertebrae, girdles and limb bones; Buffetaut et al., 1999).

From the Montplo locality: MC uncataloged, shell, Cruzy, France, Late Campanian–Early Maastrichtian.

From the Bellevue locality: MDEt C3 774, partial skull and shell fragments, Campagne sur Aude, Aude, France, Late Campanian–Early Maastrichtian.

PREVIOUS WORK: *Foxemys* has been described and figured in Tong et al. (1998), in which they described the skull and shell.

DISCUSSION: The Fox Amphoux vertebrates come from sandstones and clays similar to those known in the Aix-en-Provence Basin, farther west, as the lower part of the Rognacian. This local stage is probably a nonmarine equivalent of the type Maastrichtian stage on the basis of magnetostratigraphy (Westphal and Durand, 1990). The Fox Amphoux vertebrate assemblage is thus probably of early Maastrichtian age (Buffetaut and Le Loeuff, 1991). This is in agreement with the composition of its fauna, in which the dominant dinosaurs are titanosaurids and the ornithopod *Rhabdodon*. As shown by Le Loeuff et al. (1994), such assemblages characterize the early part of the Maastrichtian in southern France, whereas late Maastrichtian assemblages are dominated by hadrosaurid dinosaurs, which have not been reported from Fox Amphoux.

Besides turtles, the Fox Amphoux vertebrate assemblage includes hybodont sharks, a *Lepisosteus*-like actinopterygian, alligatorid and crocodylid crocodilians, theropods (including a dromaeosaurid and a possible abelisaurid), titanosaurid sauropods, ornithopods (*Rhabdodon*), ankylosaurs, and large flightless birds (Buffetaut et al., 1997).

In addition to *Foxemys*, two pleurodires are known from Late Cretaceous localities in southern France. *Polysternon provinciale* (Matheron, 1869) is known from a large series of shells and a skull, while *Elochelys perfecta* (Nopcsa, 1931) and *E. convenarum* Laurent, Tong, and Claude, 2002 are known only from a few shells. *Elochelys* differs from *Foxemys* in its smaller size (carapace length of 20–25 cm for *E. perfecta* and 35 cm for *E. convenarum*), the apparent lack of a suprapygal bone (in *E. perfecta* only), and an intergular scute that completely separates the humeral scutes (Nopcsa, 1931; Broin, 1977; Laurent et al., 2002). The shell of *Foxemys* is similar to that of *Polysternon provinciale*, although there are significant differences (Tong and Gaffney, 2000: table 1). The recently described skull of *Polysternon provinciale* (Tong and Gaffney, 2000) is also similar to the skull of *Foxemys*, but again there are significant differences, particularly in the relative positions of the mandibular and occipital condyles.

According to the description of *Polysternon atlanticum* (Lapparent de Broin and Murelaga, 1996), this species from the Late Cretaceous of northern Spain differs from *Foxemys* in being much smaller and in having a narrow first vertebral scute.

Another skull that appears to be *Foxemys mechinorum*, MC M1734, agrees with PAM 511A and MDEt 10 except that it has a well-developed accessory ridge extending from the anterior midline concavity on the premaxilla, posterolaterally along the maxilla paralleling the labial ridge. Accessory ridges are nearly absent in bothremydids, being found only in *Sankuchemys* and the undescribed CNRST-SUNY 199. MC M1734 does not seem to have other differences from the two described *Foxemys* skulls, so it is unclear whether it is best interpreted as individual variation or a new taxon. It also could be the skull of *Elochelys*, a shell-only genus similar to *Foxemys*.

Polysternon Portis, 1882

Elochelys Nopcsa, 1931, in part (only the species "*E. major*").

TYPE SPECIES: *Pleurosternon provinciale* Matheron, 1869.

INCLUDED SPECIES: *P. provinciale, P. atlanticum.*

DISTRIBUTION: Late Cretaceous, Europe.

ETYMOLOGY: Not specified by original author. Translated it could mean "many, chest".

REVISED DIAGNOSIS: A bothremydid pleurodire of the subtribe Foxemydina with the following characters differentiating it from *Foxemys*: fossa pterygoidea present but not as deep as in *Foxemys*; condylus mandibularis anterior to main body of basisphenoid and well anterior to condylus occipitalis; orbital rim high in contrast to *Foxemys*; triturating surfaces triangular and wider than in Taphrosphyini but narrower than in *Foxemys*, *Bothremys*, and *Chedighaii*; shell similar to *Foxemys* but with parallel striations on the carapace, nuchal emargination present, round lateral borders of posterior lobe of plastron, and a narrow anal notch.

PREVIOUS WORK: The genus *Polysternon* was erected by Portis in 1882 on the basis of the posterior portion of a shell from the Late Cretaceous of the Fuveau Basin, southeastern France. Portis (1882) also referred two shell fragments, including an anterior portion of carapace, to the genus *Polysternon*, as well as material earlier described as *Pleurosternon provinciale* by Matheron (1869) from the same basin. Unfortunately, Matheron did not figure any specimens. The material described by Portis (1882) is now housed in the Musée Cantonal de Géologie de Lausanne, Switzerland. In 1931, Nopcsa studied four turtle shells from the Late Cretaceous of southern France in the Musée d'Histoire Naturelle de Marseille, and reviewed Matheron's and Portis' materials. He recognized *Polysternon* and erected a new genus, *Elochelys*, including two species, *E. major* and *E. perfecta* (Nopcsa, 1931). Later, Broin (1977) studied the Late Cretaceous and Tertiary continental turtle faunas of France and synonymized *Elochelys major* Nopcsa, 1931 and *Polysternon provinciale* (Matheron, 1869). All these are based on shell material. *Foxemys mechinorum* (Tong et al., 1998) was the first pleurodiran turtle from the Late Cretaceous of southern France described on the basis of both skull and shell material. The skull figured and referred to *Polysternon provinciale* in Buffetaut et al. (1996) and Lapparent de Broin and Werner (1998: fig. 4) was described in detail by Tong and Gaffney (2000).

DISCUSSION: The separation of *Polysternon* from *Foxemys* is discussed above. See table 10 for a comparison of genera of the tribe Bothremydini.

Polysternon provinciale (Matheron, 1869)

Pleurosternon provinciale Matheron, 1869.
Polysternon provinciale Portis, 1882.
Polysternum provinciale (Matheron, 1869) in Nopcsa, 1931.
Elochelys major Nopcsa, 1931.

TYPE SPECIMEN: MHNM 1982-853, collection Matheron, anterior portion of carapace, designated as a lectotype in Broin (1977: 37, fig. 1; pl. 1, fig. 3).

TYPE LOCALITY: "Lignite de la Grande Mène, Bassin de Fuveau, France" (Broin, 1977).

HORIZON: Campanian, Late Cretaceous.

DEPOSITIONAL ENVIRONMENT: The best *P. provinciale* material (complete skull and shell) is from the Villeveyrac quarries, located about 20 km southwest of Montpellier (Hérault, France). The vertebrate fauna comes from the lower series of the Late Cretaceous beds, which are Early Campanian dark clays. It includes fishes (Ginglymodi and Teleostei), frogs, turtles, lizards, crocodiles, and dinosaurs (theropods, iguanodonts, and ankylosaurs). Turtle remains are mainly abundant shell fragments; they include both the bothremydid *Polysternon provinciale* and the cryptodire *Solemys*. The paleoecology of the vertebrate-bearing Late Cretaceous beds of Villeveyrac has been reconstructed on the basis of sedimentological and paleontological studies that indicate an estuarine landscape combining freshwater and brackish environments (see Buffetaut et al., 1996).

DIAGNOSIS: As for genus.

ETYMOLOGY: Not specified by original author, but presumably the reference is to Provence, France.

REFERRED MATERIAL: AE 28 (Costa Collection), skull (figs. 110–112) described by Tong and Gaffney (2000), figured by Buffetaut et al. (1996: fig. 5) and Lapparent de Broin and Werner (1998), Villeveyrac locality, Hérault, France; a complete shell uncataloged, Costa Collection (Buffetaut et al., 1996: fig. 4), Villeveyrac, Hérault, France; MDEt collection: shell fragments, same locality; partial plastron and isolated plates (Tong et al. 1993: figs. B–D), Monséret locality, France; MHNM collection: two shell fragments including an anterior portion of carapace, Fuveau Basin, Campanian, from "lignite de la grande Mène", Fuveau Basin, France (MHNM 1982-853, Matheron collection; Matheron, 1869; Broin, 1977: fig. 1, pl. 1, fig. 3a, b; the other specimen was lost by the time Broin reviewed the material in 1977); partial shell (collection of the "Musée Cantonal de Géologie de Lausanne", Portis, 1882); holotype of "*Elochelys major*" (MHNM 1982-857; Nopcsa, 1931: pl. XIII; Broin, 1977: fig. 2, pl. 1, fig. 1); internal cast showing the plastron with pubic and ischiac scars (MHNM 1982-855, collection Comte de Gérin-Ricard; Nopcsa, 1931: fig. 1; Broin, 1977: pl. 1, fig. 2); from "Valdonne", Fuveau Basin, France.

DISCUSSION: The identification of the skull from Villeveyrac as *Polysternon provinciale* is based solely on the occurrence of the skull in the same formation and geographic region as shells of *P. provinciale* (Buffetaut et al., 1996). However, we follow Buffetaut et al. (1996), Lapparent de Broin and Werner (1998), and Tong and Gaffney (2000) who all identified this skull as *Polysternon provinciale*. It is of course possible that further discoveries will alter this provisional identification. Nonetheless, we think that this course is preferable to naming a new taxon or to not identifying the skull at all. In any case, both skull and shells are bothremydids.

Pleurodiran shell fragments are frequent in the Late Cretaceous localities of southern France. They are usually referred to *Polysternon* (Broin, 1977; Lapparent de Broin and Murelaga, 1999; Lapparent de Broin, 2001). However, as several genera of Pleurodira are present in the Late Cretaceous of that region, some of them might belong to *Foxemys* or *Elochelys*.

Polysternon atlanticum Lapparent de Broin and Murelaga, 1996

TYPE SPECIMEN: Museo de Ciencias Naturales de Alava, Vitoria: Gasteiz number 6316 (Lapparent de Broin and Murelaga, 1996: fig. 2C; 1999: pl. 5, fig. 1), an isolated nuchal bone.

TYPE LOCALITY: Laño, Condado de Treviño, Spain (Lapparent de Broin and Murelaga, 1996, 1999).

HORIZON: Late Campanian (Lapparent de Broin and Murelaga, 1996, 1999).

DEPOSITIONAL ENVIRONMENT: Alluvial (Lapparent de Broin and Murelaga, 1996, 1999).

DIAGNOSIS: "Differs from the type species *P. provinciale*, from Fuveau, by the smaller shell (11 to 32 cm long), the vertebral 1 narrowest (not covering all the nuchal posterior border or slightly wider than the nuchal posterior border, not much wider) and the absence of the very thin striation of parallel streaks on the dorsal carapace" (Lapparent de Broin and Murelaga, 1996).

ETYMOLOGY: From the Atlantic area (Lapparent de Broin and Murelaga, 1996).

REFERRED MATERIAL: Over 200 shell fragments, some described in Lapparent de Broin and Murelaga (1999).

PREVIOUS WORK: Two papers describe *P. atlanticum*: Lapparent de Broin and Murelaga (1996) and Lapparent de Broin and Murelaga (1999).

DISCUSSION: This species seems to be more similar to *Foxemys* than to *Polysternon* by the absence of obvious parallel striations on the carapace, the less rounded lateral margins of the posterior lobe of the plastron, and the wider anal notch. The type is a nuchal; it is (barely) diagnosable because it consists of a large number of other disarticulated shell elements, presumed to be from the same taxon.

Elochelys Nopcsa, 1931

TYPE SPECIES: *Elochelys perfecta* Nopcsa, 1931.

INCLUDED SPECIES: *E. perfecta, E. convenarum.*

DISTRIBUTION: Late Cretaceous of southern France.

ETYMOLOGY: Not indicated in Nopcsa, 1931. *Elos*, Greek for swamp, and *chelys*, Greek for turtle.

REVISED DIAGNOSIS: Carapace without nuchal notch, with "pelomedusoid" surface texture (weak granulated polygons), in contrast to strong granulated polygons of *Taphrosphys*; six or seven neurals; short and broad anterior plastral lobe and small anal notch; large intergular scale completely separating gulars and humerals, reaching pectorals as in *Taphrosphys* and *Ummulisani*, but in contrast to all other bothremydids; humeropectoral sulcus mainly anterior to the epihyoplastral suture except the lateral end in contrast to other bothremydids, and crossing entoplastron, as in *Taphrosphys*, *Araiochelys*, *Chedighaii*, *Polysternon*, and *Foxemys*, in contrast to *Cearachelys* and *Rosasia*; pectoroabdominal sulcus anterior to mesoplastron, as in *Araiochelys* and *Kurmademys*, in contrast to *Chedighaii*.

PREVIOUS WORK: The genus *Elochelys* was erected by Nopcsa in 1931 on the basis of shell materials from the Campanian of Fureau Basin in southern France, and included originally two species: *E. major* and *E. perfecta* (Nopcsa, 1931). Later, Broin (1977) synonymized *E. major* with *Polysternon provinciale*. *Elochelys* is discussed in Antunes and Broin (1988), Lapparent de Broin and Werner (1998), and Lapparent de Broin and Murelaga (1999).

DISCUSSION: *Elochelys* includes two species, both consisting only of shells. According to Broin (1977), Antunes and Broin (1988), Lapparent de Broin and Werner (1998), and Lapparent de Broin and Murelaga (1999), *Elochelys* is closely related to *Taphrosphys*. This is mainly based on the large intergular scale reaching the pectoral scales, the character shared only with *Taphrosphys* and *Ummulisani* among the Bothremydidae. Despite the numerous missing data for *Elochelys*, our analysis identifies three characters that support placement of *Elochelys* in the subtribe Polysternina: narrow peripheral 1–costal 1 contact, pectoral scales reach epiplastra, and pectoral scales anterior to mesoplastra. Nonetheless, this taxon is not well established, and its phylogenetic position might need to be revised if more material, particularly cranial, becomes available.

In addition to *E. perfecta* and *E. convenarum*, some shell fragments from the Late Campanian–earliest Maastrichtian of Laño (northern Spain) and the Early Maastrichtian of Fox Amphoux (southern France) have been referred to ?*Elochelys* sp. (Lapparent de Broin and Murelaga, 1999).

Elochelys perfecta Nopcsa, 1931

TYPE SPECIMEN: MHNM 1982-852, Gérin-Ricard collection; Nopcsa, 1931: pl. XII.

TYPE LOCALITY: Fureau Basin, southern France.

HORIZON: Campanian, Late Cretaceous.

DEPOSITIONAL ENVIRONMENT: Freshwater (Broin, 1977).

REVISED DIAGNOSIS: A species of *Elochelys* differing from *E. convenarum* in smaller size of shell, nuchal bone with longer anterior margin; first peripheral with longer posterior margin; suprapygal absent; first marginal scale wider than long; first vertebral scale narrower than the second vertebral and with nearly parallel lateral margins; second and third vertebral scales wider than long; plastron wide with rounded anterior margins; intergular narrower posteriorly.

ETYMOLOGY: Not known.

REFERRED MATERIAL: An anterior part of a shell (MHNM 1982-851, Matheron collection; Nopcsa, 1931; Broin, 1977).

PREVIOUS WORK: The genus *Elochelys* was erected by Nopcsa in 1931 on the basis of shell materials from the Campanian of Fureau Basin in southern France, and originally included two species: *E. major* and *E. perfecta* (Nopcsa, 1931). *E. perfecta* was based on two specimens, one complete shell (holotype, MHNM 1982-852, Gérin-Ricard collection; Nopcsa, 1931: pl. 12) and an anterior part of a shell (MHNM 1982-851, Matheron collection) (Nopcsa, 1931; Broin, 1977).

Elochelys convenarum Laurent, Tong, and Claude, 2002

TYPE SPECIMEN: A nearly complete shell (MDEt Cas2-259).

TYPE LOCALITY: Cassagnau 2, Marignac-Laspeyres, Haute-Garonne, Petites Pyrénées, southern France.

HORIZON: Marnes d'Auzas Formation, Late Maastrichtian, Late Cretaceous.

DEPOSITIONAL ENVIRONMENT: Fluvio-lagoonal.

DIAGNOSIS: A species of *Elochelys* differing from *E. perfecta* in having a larger shell; nuchal plate wider than long with very short anterior margin and strongly expanded posterior part; first peripheral plate with very short posterior margin; suprapygal plate present; first marginal scute square-shaped, covering more than half length of nuchal plate; first vertebral scute wider anteriorly with lateral margin lying on lateral part of first peripheral; second and third vertebral scutes roughly as long as wide; anterior lobe of the plastron with nearly straight anterior margin; intergular very wide posteriorly; shorter intergulo-humeral sulcus and longer intergulo-pectoral sulcus (Laurent et al., 2002).

ETYMOLOGY: From the Convenes, an ancient people of Gaul who lived in the region (Laurent et al., 2002).

REFERRED MATERIAL: None.

PREVIOUS WORK: Laurent et al. (2002) described a nearly complete shell as the type specimen of *E. convenarum*, which is the only specimen of this species.

DISCUSSION: Although there are differences from *Elochelys perfecta*, the validity of this species should be considered in light of the fact that there is only one specimen and the characters are likely to be subject to individual variation.

SUBTRIBE **BOTHREMYDINA**, NEW

TYPE GENUS: *Bothremys* Leidy, 1865.

INCLUDED GENERA: *Zolhafah* Lapparent de Broin and Werner, 1998; *Rosasia* Carrington da Costa, 1940; *Araiochelys*, n. gen.; *Bothremys* Leidy, 1865; *Chedighaii*, n. gen.

DIAGNOSIS: Members of the tribe Bothremydini with the following characters contrasting with Foxemydina: maxilla-quadrate contact present (except in *Chedighaii*); triturating surface with maxillary pits (except *Chedighaii*); dentary pits present; jugal widely exposed on triturating surface (except *Chedighaii*); incisura columellae auris closed and stapes contained in bony canal; fossa pterygoidea absent or shallow; foramen jugulare posterius completely closed; basisphenoid ventral shape triangular; pectoral scales not extending onto epiplastron; anterior plastral lobe does not reach carapace anterior margin.

DISCUSSION: The "*Bothremys* group" (also "Groupe *Bothremys*," "*Bothremys* Leidy, 1865 group") of Antunes and Broin (1988), Lapparent de Broin and Werner (1998), Lapparent de Broin and Murelaga (1999), and Lapparent de Broin (2000a) is an informal assemblage consisting of *Zolhafah, Rosasia*, and *Bothremys*. However, Lapparent de Broin (2000b) added the term "pre-*Bothremys* group" for *Polysternon* plus what we refer to as *Foxemys* (*Polysternon mechinorum* in the usage of Lapparent de Broin, 2000b). In this usage the "pre-*Bothremys* group" would be the same as our subtribe Foxemydina, and the "*Bothremys* group" would be equivalent to our subtribe Bothremydina.

Zolhafah Lapparent de Broin and Werner, 1998

TYPE AND ONLY INCLUDED SPECIES: *Zolhafah bella* Lapparent de Broin and Werner, 1998.

DISTRIBUTION: Late Cretaceous, Egypt.

ETYMOLOGY: *zolhafah*, Arabic for turtle (Lapparent de Broin and Werner, 1998).

REVISED DIAGNOSIS: A bothremydid pleurodire of the tribe Bothremydini with the following unique characters among Bothremydini: foramen posterius canalis carotici interni formed by pterygoid, basisphenoid, and quadrate (also occurs in *Taphrosphys*); supraoccipital-quadrate contact absent (also absent in Taphrosphyini); other differentiating characters: dorsal process of premaxilla present, as in *Araiochelys* and *Bothremys*, in contrast to *Foxemys* and *Polysternon*; fossa orbitalis not enlarged posteriorly, as in *Rosasia*, *Bothremys*, and *Chedighaii*, but similar to *Foxemys*; ridge forming lower orbital rim present, in contrast to *Bothremys*; midline depression on ventral surface of premaxilla wide and very shallow; triturating surfaces triangular and very wide, as in *Bothremys*; triturating surface pit without complete posterior wall, as in *Rosasia*, in contrast to completely walled pit seen in *Bothremys* and *Araiochelys*; jugal forms tip and posterior part of pit, as in *Rosasia*; lateral edge of maxilla curved but without anterior pinching seen in *Foxemys, Rosasia,* and *Bothremys*; labial ridge relatively thick in contrast to *Araiochelys*; fossa pterygoidea absent, as in all other Bothremydini except *Foxemys* and *Polysternon*; incisura columellae auris closed, as in all Bothremydini except *Foxemys* and *Polysternon*; vomer-maxilla contact absent or very small, in contrast to extensive vomer-maxilla contact in *Rosasia* and *Bothremys cooki*.

DISCUSSION: See table 10 for a comparison of genera of the tribe Bothremydini.

Zolhafah bella Lapparent de Broin and Werner, 1998

TYPE SPECIMEN: TUB Vb-173, a nearly complete skull (figs. 115–117).

TYPE LOCALITY: Ammonite Hill, 37 km W of Conoco Channel 20, interdunal channel 31, loc. 271080/1, southwestern Egypt (Lapparent de Broin and Werner, 1998: 138) (fig. 14).

HORIZON: Dakla Formation, Ammonite Hill Member, Maastrichtian (Lapparent de Broin and Werner, 1998).

DEPOSITIONAL ENVIRONMENT: Near-shore marine (Lapparent de Broin and Werner, 1998).

DIAGNOSIS: Same as genus.

ETYMOLOGY: *bella*, Latin for beautiful (Lapparent de Broin and Werner, 1998).

REFERRED MATERIAL: None.

PREVIOUS WORK: *Zolhafah* is described only in Lapparent de Broin and Werner (1998). The six photographs of the skull (pls. I and II) are of good quality. Lapparent de Broin and Werner (1998) identified *Zolhafah* as a Bothremydidae and member of the "*Bothremys* group", an informal taxon containing *Zolhafah, Rosasia*, and *Bothremys*, fide Lapparent de Broin and Werner (1998). We include *Zolhafah* in the tribe Bothremydini, roughly equivalent to the "*Bothremys* group".

DISCUSSION: Although we differ with Lapparent de Broin and Werner (1998) in the identification of some parts of the skull of *Zolhafah* (discussed in the Cranial Morphology section), we agree substantially with their assessment of its relationships.

Rosasia Carrington da Costa, 1940

TYPE AND ONLY INCLUDED SPECIES: *Rosasia soutoi* Carrington da Costa, 1940.

DISTRIBUTION: Late Cretaceous, Europe.

ETYMOLOGY: For Prof. Rosas da Silva (Carrington da Costa, 1940).

REVISED DIAGNOSIS: A bothremydid pleurodire of the tribe Bothremydini with the following unique feature within the Bothremydini: unusually large orbital margin (possibly also in *Zolhafah*); other differentiating characters: apertura narium externa oval without prefrontal and premaxillary projections, in contrast to *Zolhafah*, *Bothremys*, *Araiochelys*, and *Chedighaii*; dorsal process of maxilla narrow, in contrast to *Bothremys*; fossa orbitalis enlarged posteriorly, in contrast to *Zolhafah* and *Foxemys*, but as in *Bothremys* and *Chedighaii*; midline depression on ventral surface of premaxilla narrow, as in *Bothremys*, not wide, as in *Zolhafah*, *Polysternon*, *Foxemys*, and *Araiochelys*; triturating surfaces triangular and very wide, as in *Zolhafah*, *Foxemys*, and *Bothremys*; triturating surface pit present, as in *Zolhafah*, without complete posterior wall, in contrast to complete pit seen in *Bothremys* and *Araiochelys*; ridge forming lower orbital rim present, in contrast to *Bothremys*; jugal forms tip and posterior part of triturating pit, as in *Zolhafah*; lateral edge of maxilla curved, in contrast to *Araiochelys*; snout pinched, in contrast to *Zolhafah*; vomer-maxilla contact extensive, as in *Foxemys* and *Bothremys cooki* but in contrast to *Zolhafah* and other Bothremydini; fossa pterygoidea shallow, in contrast to deep in *Foxemys* and *Polysternon*; incisura columellae auris closed, as in all Bothremydini except *Foxemys* and *Polysternon*; condylus mandibularis at level of condylus occipitalis, in contrast to *Polysternon* and *Araiochelys*; quadrate-maxilla contact present, in contrast to *Foxemys*, *Polysternon*, and *Chedighaii*, but as in *Bothremys* and *Araiochelys*; foramen posterius canalis carotici interni formed by pterygoid and basisphenoid, in contrast to *Chedighaii*, *Araiochelys*, and *Bothremys*; carapace rounder than in *Cearachelys*, with nuchal embayment (see Carrington da Costa, 1958: fig. 1); seven neural bones; costals 7 and 8 meet on midline; plastron with rounded anterior lobe; pectoral scale not reaching entoplastron; gular scale small and restricted to anterior part of epiplastron; pectoral scale reaches mesoplastron; posterior lobe tapering, not parallel-sided.

DISCUSSION: See table 10 for a comparison of genera of the tribe Bothremydini.

Rosasia soutoi Carrington da Costa, 1940

TYPE SPECIMEN: Holotype not designated by Carrington da Costa (1940, 1958), but lectotype designated by Antunes and Broin (1988: 163) as the carapace in plates I and III of Carrington da Costa (1940), uncataloged, Porto, Portugal.

TYPE LOCALITY: Quarry operated as "Empresa Ceramica do Vouga", Quinta do Vilar, Aveiro, Portugal (Carrington da Costa, 1940) (fig. 14).

HORIZON: "Une formation gréseuse aturienne, trés probablement du Maestrichtian saumatre" (Carrington da Costa, 1940: 17). Late Campanian to Maastrichtian (Antunes and Broin, 1988).

DEPOSITIONAL ENVIRONMENT: "Tropical to subtropical climate in an area constituted by a low coastal plain only occasionally linked to the sea, saturated with fresh water" (Antunes and Broin, 1988).

DIAGNOSIS: Same as genus.

ETYMOLOGY: For Dr. Alberto Souto (Carrington da Costa, 1940).

REFERRED MATERIAL: Uncataloged skull (figs. 120, 121) in the Universidade Nova de Lisboa, Portugal, described and figured in Antunes and Broin (1988: figs. 3–8, pl. 3, fig. 3, pl. 4, fig. 3, pl. 5, figs. 1–4), associated with a peripheral bone; three femoral fragments; four cervical vertebrae (Antunes and Broin, 1988); shells in this same collection are: MTA 1 (Antunes and Broin, 1988: pl. 3, figs. 1, 2), MTA 2 (Antunes and Broin, 1988: pl. 4, figs. 1, 2, pl. 1, fig. 1); two shells (only one figured) in the Serviços Geológicos de Portugal de Lisbonne (Carrington da Costa, 1958: pls. 3, 4); one shell in the Faculdade de Ciências e Tecnologia, Universidade de Coimbra (Carrington da Costa, 1958: pls. 5, 6).

PREVIOUS WORK: Sauvage (1898) seems to have been the first to describe a specimen of what Carrington da Costa (1940) named *Rosasia soutoi*. Sauvage based his taxon on a carapace, and later (Carrington da Costa, 1958) described more complete shells. Antunes and Broin (1988) described a skull identified as this taxon, although only a shell fragment was associated with the skull. The association is supported by the fact that the shells and the skulls all belong to the same group and were found in the same area and horizon, in the absence of other pleurodires.

DISCUSSION: Lapparent de Broin and Werner (1998) rejected the Antunes and Broin (1988) identification of some cervicals as belonging to *Rosasia* and identified them as varanoid instead. We have seen these cervicals and agree that they are very different from the few other known bothremydid cervicals, but strange things happen, and we do not think they are lizard vertebrae. In any case, these cervicals are not included in our dataset.

Araiochelys, new genus

TYPE AND ONLY INCLUDED SPECIES: *Araiochelys hirayamai*, n. sp.

DISTRIBUTION: Paleocene of Morocco.

ETYMOLOGY: *Araios*, Greek for narrow, in allusion to narrow triturating surfaces; *chelys*, Greek for turtle.

DIAGNOSIS: A bothremydid pleurodire of the tribe Bothremydini with the following unique features within Bothremydini: preorbital part of skull narrower than in all other Bothremydini; triturating surfaces narrower than in all other Bothremydini; and apertura narium externa facing anterolaterally in contrast to anteriorly; other differentiating characters: dorsal process of maxilla (orbitonarial bar) narrow in contrast to *Bothremys*; fossa orbitalis enlarged posteriorly as in *Bothremys*, *Rosasia*, and *Chedighaii* and in contrast to *Foxemys* and *Zolhafah*; ridge forming lower rim of orbit relatively distinct in contrast to *Bothremys*; midline depression on ventral surface of premaxilla narrow, as in *Rosasia* and *Bothremys*, not wide, as in *Zolhafah*, *Polysternon* and *Foxemys*; triturating surface pit present and completely developed, as in *Bothremys*, not partial, as in *Zolhafah* and *Rosasia*; jugal forms tip and posterior part of pit; lateral edge of maxilla relatively straight, in contrast to *Bothremys*, *Rosasia*, and *Zolhafah*; anterior part of vomer short, with narrow maxilla contact, in contrast to broad contact in *Bothremys cooki*, *Rosasia*, and *Foxemys*; fossa pterygoidea absent; incisura columellae auris closed, as in all Bothremydini except *Foxemys* and *Polysternon*; condylus mandibularis anterior to level of condylus occipitalis but not far anterior, as in *Polysternon*; quadrate-maxilla contact present in contrast to *Foxemys*, *Polysternon*, and *Chedighaii*, but as in *Bothremys* and *Rosasia*; foramen posterius canalis carotici interni formed by pterygoid and quadrate, in contrast to *Rosasia*, *Zolhafah*, *Polysternon*, and *Foxemys*; lower jaw with triturating pits and long processus retroarticularis; carapace with discontinuous neural series; narrow vertebral scutes, very long second vertebral; plastron with narrow posterior lobe and wide bridge; posterior lobe with parallel lateral margins; mesoplastron wider than long; pointed xiphiplastral ends with wide anal notch; humeropectoral sulcus posterior to the epihyoplastral suture, crossing entoplastron; pectoroabdominal sulcus anterior to the mesoplastron.

DISCUSSION: *Araiochelys* is a member of the Bothremydini, on the basis of skull features. The shell characters of this taxon differ from those of the tribe Taphrosphyini (which also occur in this unit) as follows: (1) finer ornamentation on the shell surface; (2) xiphiplastron much longer than wide; and (3) ischiac scar triangular and more anteriorly placed, not as close to the posterior margin of the plastron, as in *Taphrosphys*.

See table 10 for a comparison of genera of the tribe Bothremydini.

Araiochelys hirayamai, new species

TYPE SPECIMEN: THUg 3338, skull (figs. 124, 125), lower jaws (figs. 237, 238), partial disarticulated shell (figs. 262, 263), including a few carapace fragments (left first and fifth costals, left third, seventh, and eighth peripherals and other fragments), nearly complete plastron, and limb bones.

TYPE LOCALITY: Ouled Abdoun phosphate basin, Morocco (figs. 14–16). The Ouled Abdoun Basin is about 100 km southeast of Casablanca, Morocco. The basin, extending some 100 km from east to west and 80 km from north to south, is the largest phosphate basin in Morocco. The

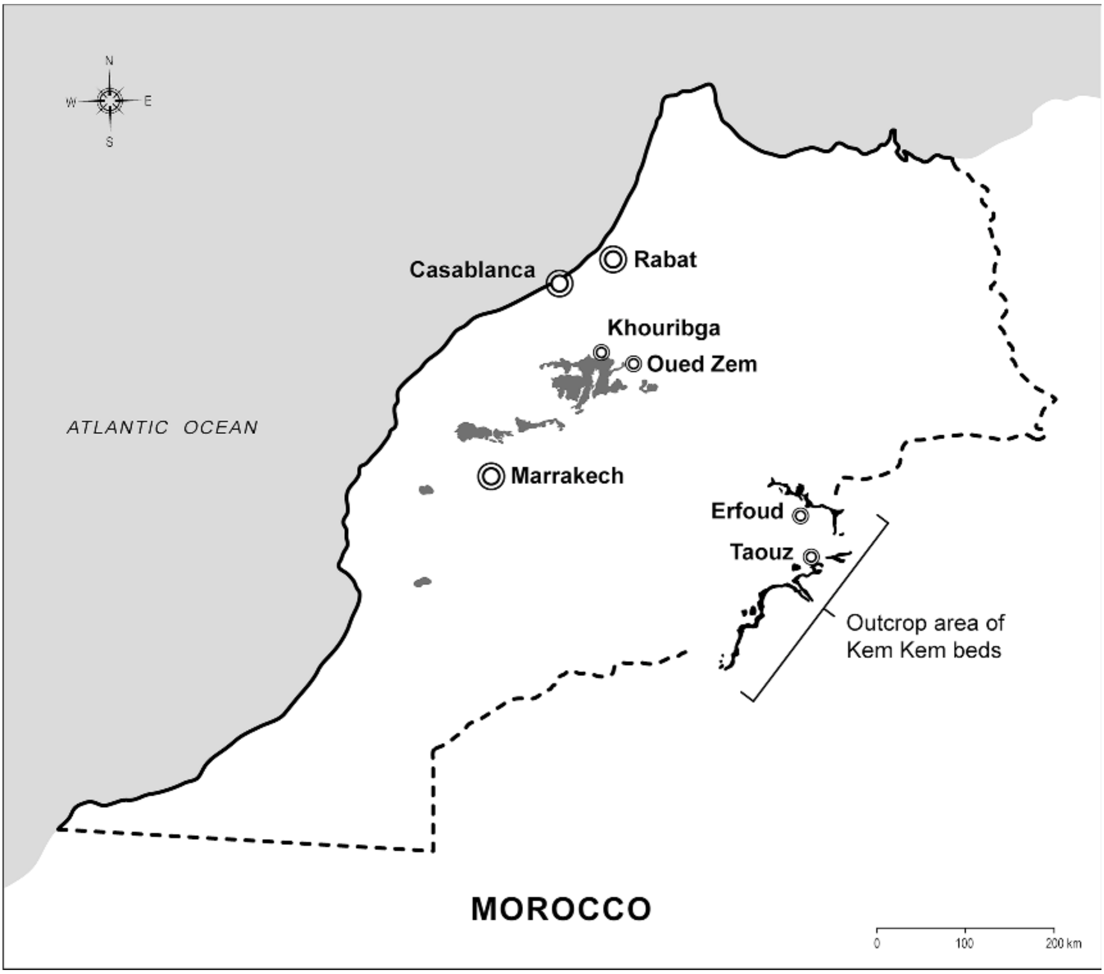

Fig. 15. Map of Morocco showing main outcrops yielding turtles. Near the coast are the late Cretaceous–Paleogene phosphate exposures, and southeast along the border are the Cenomanian Kem Kem exposures (after Dutheil, 1999a, 1999b; and Noubhani and Cappetta, 1997). [A. Venjara, del.]

stratigraphy of the phosphates in this region (fig. 17) has been developed by Arambourg (1935, 1952), primarily on the basis of the selachians. The fossiliferous deposits range in age from the Maastrichtian to the Ypresian (Arambourg, 1952; Noubhani and Cappetta, 1997).

Vertebrate remains from the phosphates of Morocco are abundant. Surprisingly, there are no turtles reported in the phosphates of Morocco by Arambourg (1952). The first turtle remains from the Moroccan phosphates were reported by Ambroggi and Arambourg (1951) from the Maastrichtian of Oued Erguita, some 200 km southwest of the Ouled Abdoun Basin. They indicated abundant turtle remains as “chelonian indet.” (Ambroggi and Arambourg, 1951). More than 20 years later, Moody (1976) reported a large “pelomedusid turtle” shell from the Paleocene of Benguerir in the Cantour Basin. Gmira (1995) mentioned a large skull of a cheloniid sea turtle from the presumed Maastrichtian of Benguerir. More extensive turtle remains have been reported from the Ouled Abdoun Basin only recently (Karl et al., 1998; Lapparent de Broin, 2000a; Gaffney and Tong, 2003; Hirayama and Tong, 2003; Tong and Hirayama, 2002, 2004).

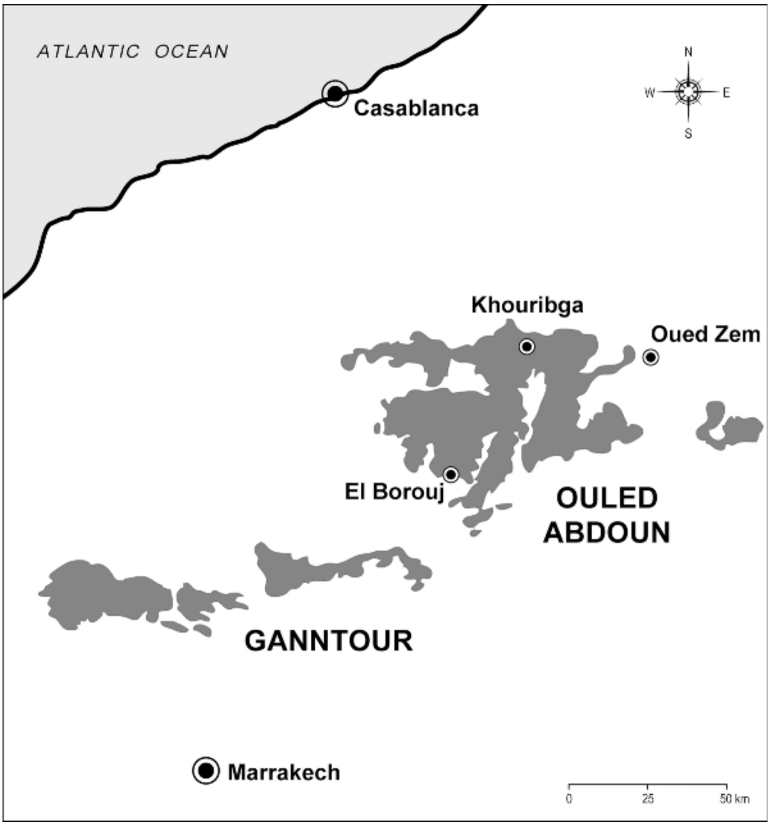

Fig. 16. Map of the late Cretaceous–Paleogene phosphate basins in Morocco yielding turtles (after Noubhani and Cappetta, 1997). [A. Venjara, del.]

The turtle remains from the Ouled Abdoun Basin are very abundant and diversified. Most specimens were collected by local people for commercial purposes (Osborne, 2000); their exact location and stratigraphic level are therefore often unknown. However, some specimens have been collected in situ during fieldwork for the present project, and some have the original locality information obtained from the local collectors. The specimens from the Maastrichtian deposits are easily distinguished from those from the Paleogene since they are contained in soft yellow phosphates, which are different from the overlying gray-white Tertiary sediments. The turtle remains are further dated, when possible, by the shark teeth included in the original matrix around the specimen.

The phosphate deposits of the Ouled Abdoun Basin contain both articulated skeletons and isolated elements. The fact that most specimens are skulls is due to selective collecting by the local people. The abundance of the fossils collected also depends a great deal on the extent and position of phosphate exploration. The Danian beds have yielded the most abundant and diverse turtles, partly because the upper part of the Danian is a hard limestone layer that is not removed by the miners. The free surface left behind by the excavating machines makes the collection of fossils easier. The reptile remains from the Maastrichtian layers were rather fragmentary; the abundant and more complete specimens from these beds have been reported only recently, since this layer was rarely excavated in the past.

DEPOSITIONAL ENVIRONMENT: Near-shore marine. The phosphate deposits of the Ouled Abdoun Basin, as well as the other phosphate basins of Morocco, were formed in long, narrow gulfs opening to the Atlantic margin

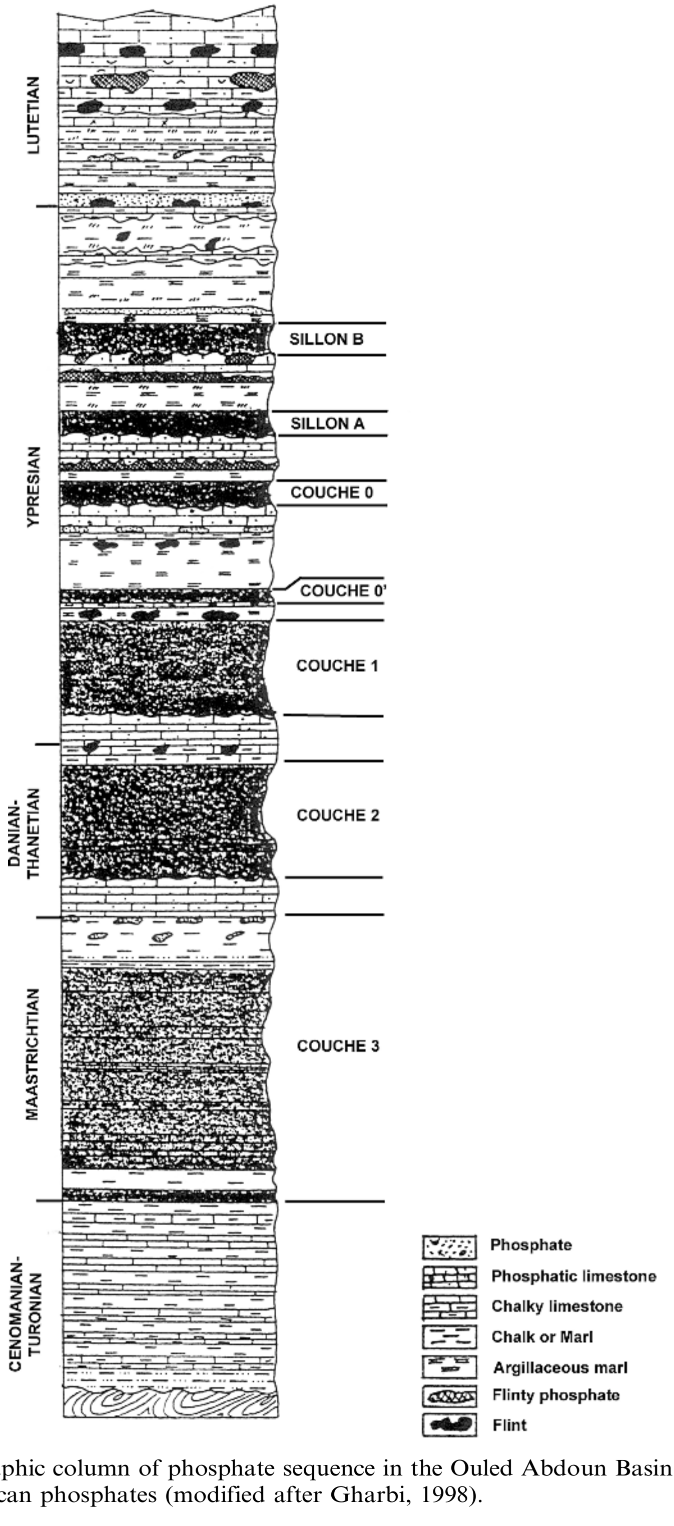

Fig. 17. Stratigraphic column of phosphate sequence in the Ouled Abdoun Basin, the main source of turtles in the Moroccan phosphates (modified after Gharbi, 1998).

in a tropical climate (Arambourg, 1952; Lucas and Prévot-Lucas, 1996). A bathymetric study (Arambourg, 1952) based on the fish fauna of Maghreb indicated deposition in a near-shore marine basin of shallow water during both the Maastrichtian and Eocene. The Maastrichtian deposits, however, have been formed in deeper water than those of the Eocene (Arambourg, 1952). The presence of some selachians, such as *Alopias*, *Heptranchias*, *Hexanchus*, and *Echinorhinus* in the Ypresian deposits, indicates a bathyal influence, which might indicate deeper water than previously thought. The upwelling currents, which are responsible for the phosphatogenesis, are probably related to the presence of these bathyal forms in the Ouled Abdoun Basin, which was situated more than 100 km from the opening of the gulf during that period (Cappetta, 1981).

The vertebrate assemblage from the Ouled Abdoun Basin consists mostly of marine species. All turtle remains from that basin (table 11) are marine, which include cheloniids (Karl et al., 1998; Tong and Hirayama, 2002; Hirayama and Tong, 2003), dermochelyids (Tong and Hirayama, 2004), and bothremydid side-necked turtles (Gaffney and Tong, 2003). A very specialized trionychoid turtle (AMNH 30001, 30558, 30001) with broad secondary palate and pits similar to those in *Bothremys* was presumably also marine. Besides turtles, selachians (Arambourg, 1935, 1952; Cappetta, 1981, 1983, 1984, 1986, 1988; Noubhani and Cappetta, 1992, 1994, 1997), bony fishes (Cavin et al., 2000), and crocodiles (Arambourg, 1952; Buffetaut and Wouters, 1979) were reported from both Maastrichtian and Tertiary beds. In addition, the Maastrichtian beds have yielded mosasaurs and plesiosaurs (Arambourg, 1952; Bardet et al., 2001), dinosaurs (Pereda Suberbiola et al., 2004; Buffetaut et al., 2005), and pterosaurs (Pereda Suberbiola et al., 2003). The nonmarine taxa, assumed to be floated bodies, include a few dinosaurs from the Maastrichtian and mammals from the Tertiary beds (Gheerbrant et al., 1996, 1998, 2001, 2002, 2003).

HORIZON: Danian, Paleocene, based on shark teeth in matrix (Cappetta, personal commun.) (fig. 17, table 11).

DIAGNOSIS: Same as genus.

ETYMOLOGY: In recognition of the work on turtles by Dr. Ren Hirayama, Waseda University. His lifelong contributions to turtle systematics and his consistent support of this project are gratefully recognized.

REFERRED MATERIAL: MDEt 25, an incomplete and disarticulated shell, collected by H. Tong, L. Cavin, and S. Xerri during January 1999; Danian, Early Paleocene, collected on the surface of Dalle Couche 2 (Danian, Paleocene), Recette 4, Ouled Abdoun Basin, Morocco, consists of neurals 1–2, left costals 1–4 (the fourth is incomplete), right costals 2–5 (costals 3 and 5 are incomplete), left 10th and 11th peripherals, one peripheral of bridge region, right hypoplastron and xiphiplastron, and other fragments.

MDEt 25 is identified as *Araiochelys hirayamai* because of the similar size, the shape and structure of the first and fifth costal plates, the similar development of the axillary and inguinal buttress scars, the shape of the posterior lobe of the plastron, and the shape and position of the pubic and ischiac scars. In the context of the known fauna, this identification is likely, but the diversity of bothremydids in the fauna must be kept in mind when considering this identification. The carapace length of MDEt 25 is estimated at 300 mm. Both MDEt 25 and THUg 3338 are from the Danian beds of the Ouled Abdoun Basin, Morocco. None of the plastron and only part of the carapace restoration (fig. 263) are dependent on the identification of MDEt 25 as *Araiochelys*.

PREVIOUS WORK: None.

DISCUSSION: *Araiochelys* is unique among the tribe Bothremydini in having a relatively narrow skull, narrow triturating surfaces, and narrow lower jaw. If its distinctions from the other tribe Bothremydini are interpreted as minor, the question can be asked: Is *Araiochelys* a narrow-jawed morph of another already-recognized species? It is found in the same locality and units as *Bothremys maghrebiana*, and it makes sense to examine the possibility that *Araiochelys hirayamai* and *Bothremys maghrebiana* might be the same species.

The existence of five skulls identified as *B. maghrebiana* provides at least some chance of assessing the range of variation in that

TABLE 11

Moroccan Phosphate Specimens with Original Data and/or Dated by Shark Teeth

Specimens are named and described in this paper unless another reference is given.

Ypresian

Phosphatochelys tedfordi

MDEt 26, skull
AMNH 30008, skull, Gaffney and Tong, 2003

Bothremys kellyi

AMNH 30553, skull

Bothremydini indet.

AMNH 29989, lower jaw, Ouled Abdoun basin, couche 1, specimen purchased with original information from the collector or dealer.

Ummulisani rutgersensis

AMNH 30569, skull

Thanetian

Tasbacka ouledabdounensis

AMNH 30033, skull, recette 4, Tong and Hirayama, 2002, specimen purchased with original information from the collector or dealer.
AMNH 30032, skull

Danian

Pitted cryptodire, undescribed

AMNH 30001, skull, in prep.
AMNH 30558, skull & lower jaw
AMNH 30554, skull

Osteopygis emarginatus

MDEt 27, skull, Hirayama and Tong, 2003
MDEt 28, lower jaw, recette 4, Dalle couche 2, specimen purchased with original information from the collector or dealer.
MDE 29, lower jaw
"*Osteopygoides*" type, skull, Karl et al., 1998
"Osteopygoides", skull
MDEt 34, hyoplastron, recette 4, Dalle couche 2, specimen collected during the fieldwork in January 1999.

Labrostochelys galkini

AMNH 29984, skull

Bothremys maghrebiana

AMNH 30234, skull
AMNH 30561, skull, recette 4, Dalle couche 2, specimen purchased with original information from the collector or dealer.
AMNH 30041, skull, recette 4, Dalle couche 2, specimen purchased with original information from the collector or dealer.
MHNL 20-268370, skull

Taphrosphyini indet.

AMNH 30559, post. part of plastron + humerus

Taphrosphys ippolittoi

AMNH 30500, including skull
AMNH 30042, skull

Araiochelys hirayamai

THUg 3338, skull + shell
MDEt 25, partial shell, recette 4, Dalle couche 2, specimen collected during the fieldwork in January 1999.

Maastrichtian

Dermochelyid indet.

MDEt 06, hyoplastron, couche 3, Tong and Hirayama, 2004

Chelonioidea indet.

MDEt 39, lower jaw, couche 3, specimen purchased with original information from the collector or dealer.
MDEt 40, 2 peripherals, Oued Zem, couche 3, specimen collected during the fieldwork in January 1999.

species. Some characters can be measured (appendix 5), and others are judged by observation, which is not necessarily less objective. Nonetheless, the available material is insufficient for a well-founded answer to this question, and this analysis must be considered in that context. Although all six skulls have postmortem damage, none seems to be conspicuously distorted by dorsoventral or mediolateral crushing.

Modern studies of infraspecific variation of living turtles show that a few trionychid (Dalrymple, 1977) and emydid (Lindeman, 2000) species do develop broad-jawed and narrow-jawed morphs. Chelids are known to have broad-jawed morphs (Cann, 1998), but these have not been studied in detail. These recent species with variations in the size of the triturating surfaces are usually interpreted as size-related, with large, older females developing the widest surfaces, although this is not consistent in all reported taxa. While the six skulls examined here do vary in size, the single *Araiochelys* skull is only slightly larger than the smallest *B. maghrebiana* skull (AMNH 30041). The *Araiochelys* skull is about the same size as two of the *B. maghrebiana* skulls (AMNH 30522, AMNH 30561), and it is about 20% smaller than the two largest *B. maghrebiana* skulls. This comparison shows that the single *Araiochelys* skull falls at the small end of the size range among these specimens. For the ratios detailed below, see figure 315 and appendix 5 for measurements.

1. Skull width: The skull of *Araiochelys* is longer than wide and is narrower than any of the *B. maghrebiana* skulls. The width/length (B/A) ratio of *Araiochelys* is 0.96. All of the *B. maghrebiana* skulls are wider than long; the width/length ratio of *B. maghrebiana* varies from 1.04 to 1.16. It is hard to judge the significance of this difference with such a small sample, but the senior author's measurements of recent *Podocnemis* suggest that such variation is common within a population.
2. Preorbital skull width: By observation, it is apparent that the snout of *Araiochelys* is narrower than those in the five *B. maghrebiana* skulls. Skull width at midorbit (H) gives a ratio relative to the basicranial length (H/A) of 0.67 for *Araiochelys* and a range of 0.77–1.0 for the *B. maghrebiana* skulls. Comparing this width with available trionychids and emydids suggests that these differences are well within the range of narrow- and broad-jawed morphs seen in these species.
3. Width of triturating surfaces: This measurement (M/A) gives ratios of 0.20 for *Araiochelys* and a range of 0.26–0.35 for *B. maghrebiana*. An unusually wide triturating area is a nearly universal characteristic of the Bothremydini, except for *Araiochelys*. The phylogenetic analysis is based on many characters, but the MPC still puts *Araiochelys* as sister taxon to *Bothremys* + *Chedighaii*, even when maxilla width and related characters are excluded. In chelids, trionychids, and emydids, most of the taxa within each family are predominantly narrow-jawed, with the broad-jawed forms being variations from the norm. *Araiochelys* would oppose this pattern, with a narrow-jawed variant from the wide-jawed norm. Nonetheless, it would still be possible to interpret *Araiochelys* as a young, narrow-jawed male, and *Bothremys maghrebiana* as the older females.
4. Depth of maxilla (labial ridge) below orbit: The maxilla in *Araiochelys* is shallower than those in *B. maghrebiana*. However, the range of variation (labial ridge depth/basicranial length A) within *B. maghrebiana*, 0.20–0.27, includes an extreme that is close to the ratio for *Araiochelys*, which is 0.18.
5. Thickness of orbitonarial bar: This character does not seem to be related to the width of the triturating surface. It is the distance between the aperture narium externa and the orbit (orbitonarial bar/basicranial length A). In *Araiochelys*, the ratio is 0.11, and in *B. maghrebiana*, the range is 0.15–0.17. This seems to be a consistent character differentiating these possible taxa.
6. Apertura narium externa faces more anterolaterally, and orbits face more laterally: These characters may be related to the large triturating surfaces in that they reflect the angle of the skull surface to the horizontal plane. However, when looking at chelids, emydids, and trionychids, there are no significant differences in the orientation of these openings between broad- and narrow-jawed morphs.
7. Dorsal maxillary process reaches onto skull roof: This character is the position and shape of the prefrontal-maxilla suture. In *Bothremys*, the suture is more dorsomedial and trends anteromedially, in contrast to the straight suture of *Araiochelys*. However, the suture is clear in only two *B. maghrebiana* specimens, and in one of these it is not bilaterally symmetrical, making it a weak distinguishing feature.

8. Ventral rim of orbit forming distinct ridge: None of the *B. maghrebiana* skulls has a well-defined ridge marking the lower orbital margin, as seen in *Araiochelys*. This does not seem to be related to the triturating surface size.
9. Structure of triturating surface pit: The triturating surface is formed differently in the two taxa. The triturating pit in *Bothremys maghrebiana* has the jugal forming its tip, and the maxilla and palatine broadly meeting posterior to the pit. In *Araiochelys* the jugal extends posteriorly to separate the maxilla and palatine.

Araiochelys does not fall within the range of morphologic or size variation shown by *B. maghrebiana*, but it is not very far from the extremes of that variation in some characters. The significance of this is hard to judge. A mathematical analysis more sophisticated than a simple ratio could be performed on these measurements, but it would be unlikely to produce definitive conclusions given the very small sample sizes. *Araiochelys* could still be interpreted as a narrow-jawed morph and synonymized with *B. maghrebiana*, but the other characters are inconsistent with this interpretation. The phylogenetic analysis shows that *Araiochelys* consistently falls outside the monophyletic group *Bothremys* + *Chedighaii*, even when the maxilla width and associated characters are deleted. Examining the MPC shows that no matter where *Araiochelys* is placed within the Bothremydini, its narrow skull and jaws are a homoplasy. If THUg 3338 were a variant of one of the *Bothremys* species, it would be expected to fall within *Bothremys* or at least within the *Bothremys* + *Chedighaii* clade, based on the other characters. Given the limits of the available material, it is not possible to completely exclude the interpretation that THUg 3338 should be included in *B. maghrebiana*, but at present, the evidence is much more in favor of recognizing it as a separate taxon outside *Bothremys* + *Chedighaii*.

Bothremys Leidy, 1865

Karkaemys Zalmout, Mustafa, and Wilson, 2005.

Type Species: *Bothremys cooki* Leidy, 1865.

Included Species: *B. cooki*, *B. maghrebiana*, *B. kellyi*, and *B. arabicus*.

Distribution: Presumed Late Cretaceous of the eastern United States, Late Cretaceous of Middle East, and Paleocene to Early Eocene of Morocco.

Etymology: *Bothros*, Greek for pit, and *emys*, Latin for turtle.

Revised Diagnosis: A bothremydid pleurodire of the tribe Bothremydini with the following unique features: dorsal process of maxilla broad, separating apertura narium externa and orbital rim more than in any other Bothremydini; differs from *Chedighaii* in having well-developed maxilla-jugal pits on triturating surface; suborbital depth of maxilla deeper than in other Bothremydini except *Chedighaii hutchisoni*; orbits face strongly upward, in contrast to all other Bothremydini except *Chedighaii*; basisphenoid-quadrate contact very narrow, in contrast to all other Bothremydini except *Chedighaii*; lower jaw with deep pit on triturating surface.

Discussion: Zug (2001) identified a series of shell elements and a humerus from the Pliocene Lee Creek Mine of North Carolina as *Bothremys*, species unspecified. The external surface texture of the shell elements is generally smooth or randomly rugose, agreeing with *Chedighaii barberi* and many Pelomedusoides. The humerus is unknown in most taxa, but diagnostic differences, if any, between bothremydids and podocnemidids are not apparent. The nuchal bone, USNM 186773 (Zug, 2001: fig. 2A, B), is not emarginate, as in *Chedighaii* (formerly *Bothremys barberi*), so there is evidence that the Lee Creek pelomedusoid is not *Chedighaii*. The Lee Creek nuchal could be from a bothremydid or podocnemidid; its morphology is consistent with the extinct *Bairdemys* and *Shweboemys* group podocnemidids. The Lee Creek Pliocene "*Bothremys*" is incertae sedis at the level of Pelomedusoides.

Hutchison and Weems (1998) identified fragmentary shell elements as ?*Bothremys* (and *Taphrosphys*; see this genus for discussion below) from the Paleocene Williamsburg Formation of South Carolina. The specimens are not represented by complete entoplastra, xiphiplastra, or nuchals, which would be diagnostic for *Taphrosphys*, but they are clearly Pelomedusoides. The absence of a shell for the redefined *Bothremys* as used here would make shell identifications difficult in any case. The ?*Bothremys* fragments show a smooth surface texture very similar to what was called *Bothremys barberi* in the past and what is here referred to the genus *Chedighaii*. Unfortunately, the smooth surface texture is common in Pelomedusoides and does not even allow differentiation of Bothremydidae from Podocnemididae. Thus, this material is incertae sedis at the level of Pelomedusoides. Nonetheless, it is interesting to note the occurrence of two distinct pelomedusoid species, at least one of which is a bothremydid, in the same Late Paleocene unit of the Atlantic Coastal Plain.

Garcia and Reynoso (2002) reported "*Bothremys*" from both shells and skulls from the Campanian of Coahuila State, Mexico. We have been unable to see these specimens and cannot definitively comment on the identifications, but thanks to Don Brinkman and Rubén Armando Rodriguez de la Rosa, we have been able to examine photographs of some of this material. The shells are Pelomedusoides and are consistent with a bothremydid like *Chedighaii*. The skull specimens look bothremydid and also seem to be similar to *Chedighaii*, but sutures, presence/absence of pits, and other diagnostic features are not clear in the photographs. For the present, we cannot substantiate the identification, but it is a likely bothremydid.

See table 10 for a comparison of genera of the tribe Bothremydini.

Bothremys cooki Leidy, 1865

Type Specimen: AMNH 2521, skull and jaws (figs. 129, 130, 239, 279). Originally Rutgers University 1.KV-6 141, 142.

Type Locality: "The Green-sand near Barnsboro, Gloucester County, New Jersey" (Leidy, 1865: 110) (fig. 18).

Horizon: At this locality, the most likely source of the specimen is the Maastrichtian Navesink Formation (thanks to Neil Landman for helping with this assessment).

Depositional Environment: Near-shore marine; see Gallagher (1993) for discussion of the New Jersey sequence.

Diagnosis: A member of the genus *Bothremys* with the following unique features: triturating pit formed entirely by widely exposed jugal; small jugal exposure in orbital rim; elongate vomer with wide maxilla contact; midline concavity formed by premaxilla and vomer elongate and narrow; apertura narium interna opens more posteriorly than in other species. Other distinguishing features: ventral rim of orbit without distinct margin, in contrast to *B. kellyi* and *B. arabicus*; postorbital-palatine not in contact in posterior surface of septum orbitotemporale, in contrast to *B. maghrebiana*; jugal prevents maxilla-palatine contact posterior to pit, in contrast to *B. maghrebiana*; lower jaws wider than in *B. maghrebiana*.

Etymology: "The species is dedicated to Prof. George H. Cook, of Rutger's College, New Brunswick, New Jersey, by whom the specimen was obtained, and through whose explorations our knowledge of the vertebrate fauna of the Green-sand formations of New Jersey has been greatly enriched" (Leidy, 1865: 113). See Sidar (1976) for a biography of Cook, who also collected specimens of *Taphrosphys sulcatus*.

Referred Material: AMNH 29444, right otic chamber (figs. 131, 132, 135), Elizabethtown, North Carolina, Campanian, Black Creek Formation (see Baird and Horner, 1979, for map and discussion of the Black Creek Formation), collected by R. Jerry Britt, Jr., 1983–1984.

Previous Work: In 1865, Joseph Leidy recognized *Bothremys* as a pleurodire and compared it with *Podocnemis*: "Of all recent turtles with which I am acquainted, the fossil skull, in general physiognomy and structure, resembles most that of the great turtle of the Amazon, *Podocnemis expansa*. From this, and all others, however, it differs in several striking peculiarities" (Leidy, 1865: 110). Leidy went on to describe and figure (pl. 18, figs. 4–7, reproduced here as fig. 19) the skull and jaws. Leidy's identification of his new skull as a form related to *Podocnemis* was quite astute for the time. Pleurodires were poorly represented in collections and their diagnostic characters were not easily determinable from the literature. As in many of his other discoveries, Leidy's work stands the test of time.

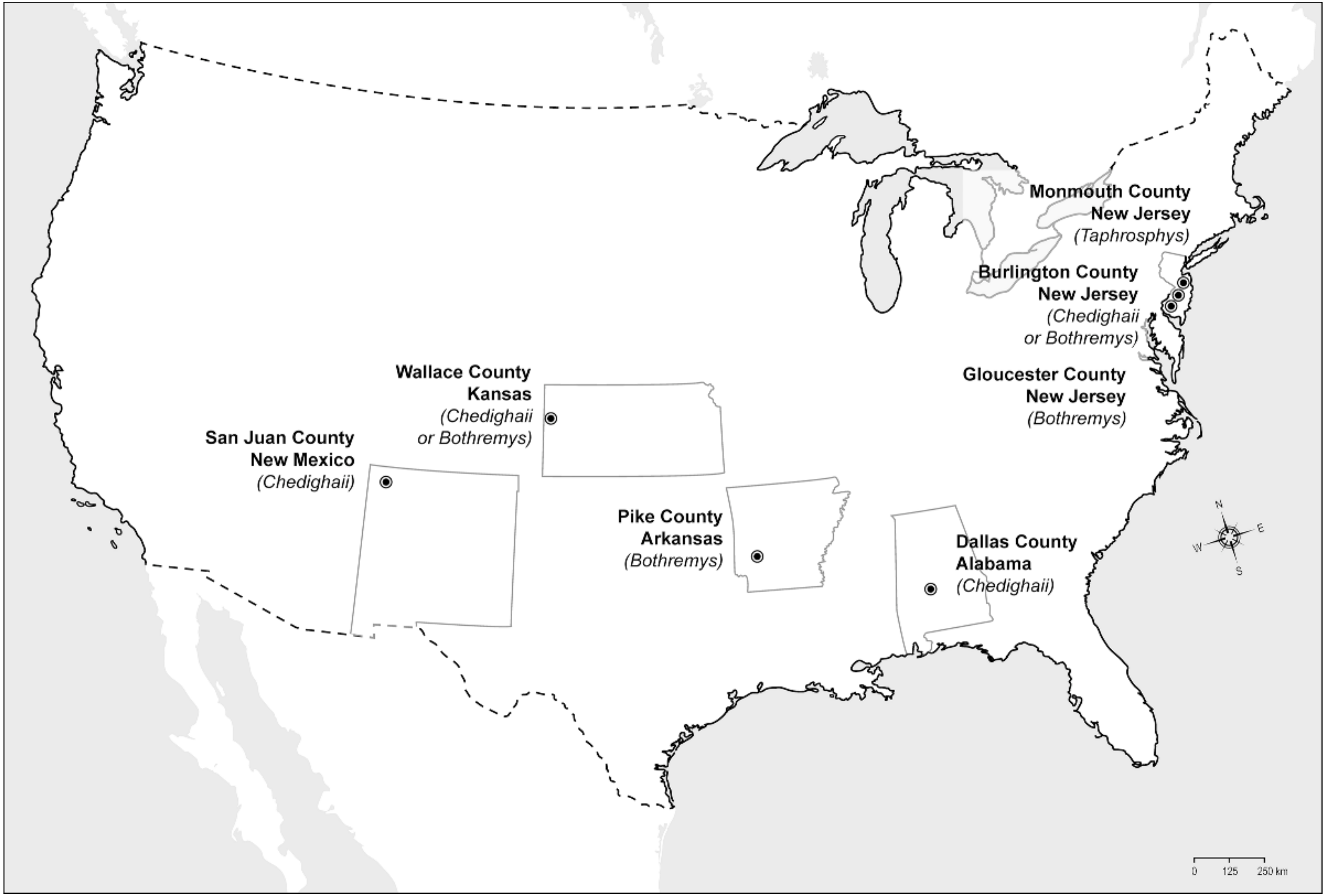

Fig. 18. Map showing localities of the family Bothremydidae, tribes Bothremydini and Taphrosphyini, in North America. See Note Added in Proof for explanation of generic distributions [A. Venjara, del.]

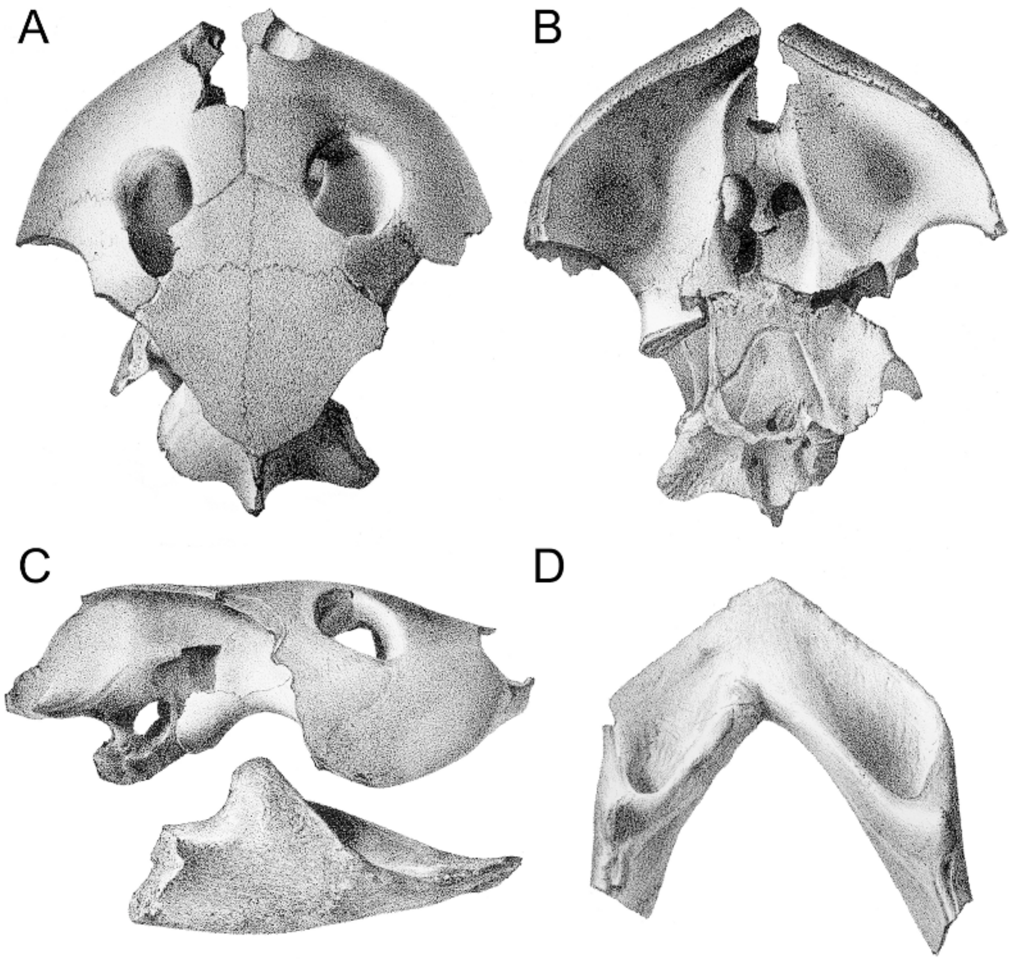

Fig. 19. *Bothremys cooki* Leidy, 1865. Original figures of type skull, AMNH 2521, from Leidy (1865: pl. 18).

George Baur examined the skull of *Bothremys* and, in 1891, erected the family Bothremydidae for *Bothremys* and *Taphrosphys* and included the family in the Pleurodira. Oliver Perry Hay (1908) also examined the skull and redescribed and figured (pl. 23, figs. 2, 3, figs. 96, 97) it, also using the family Bothremydidae. Gaffney and Zangerl (1968) published the most extensive and completely illustrated (figs. 13–16, 19A, B, 20, 21C, D, 22A–C) redescription of *Bothremys cooki* to date. They followed the then-current inclusion of bothremydids in the family Pelomedusidae. Gaffney and Zangerl (1968) included the species "*Podocnemis*" *barberi* Schmidt in *Bothremys* on the basis of the pitted lower jaws and the enclosed stapedial canal. This species is placed in the genus *Chedighaii* (q.v.) here. Many identifications of *Bothremys* in the literature (e.g., Robb, 1989) are based on "*Bothremys*" (= *Chedighaii*) *barberi* and no longer represent age and geographic distributions of *Bothremys* as here conceived.

DISCUSSION: As *Bothremys cooki* is now based primarily on the type skull from Barnsboro, New Jersey, its age is of some interest. The region around Barnsboro includes the Danian Hornerstown Formation, as well as the late Maastrichtian Navesink Formation. However, the West Jersey Marl Company had pits just south of Barnsboro that were almost entirely in the Cretaceous, and they have yielded a series of dinosaur and other fossils (Gallagher, 1993). Close examination of the type skull of *Bothremys cooki*, AMNH 2521, has shown glauconite grains and glauconitic clay remaining as matrix, consistent with either Hornerstown or Navesink Formations. However, the bone of the specimen is dark brown, not the greenish-gray of typical Hornerstown bone. Furthermore, Gallagher (1993) suggested that the bone-producing horizon at Barnsboro was in the Navesink. At present, it seems likely that the type of *Bothremys cooki* is Maastrichtian rather than Paleocene.

The identification of a right otic chamber, AMNH 29444, as *Bothremys cooki* is based on the very limited overlap area of the basisphenoid, the agreement in size (*B. cooki* is significantly smaller than all known specimens of *Chedighaii*), and the close agreement with *B. maghrebiana*. These are not overwhelmingly compelling reasons, and the otic chamber has been added to the restoration only as an additional side view (fig. 127D). Although described in the skull morphology section under *Bothremys cooki*, it is quite possible that this specimen is not *Bothremys cooki*, and information from it has not been used in the dataset.

See table 12 for a comparison of the species in *Bothremys*.

Bothremys maghrebiana, new species

TYPE SPECIMEN: AMNH 30561, nearly complete skull (figs. 142, 143, 145), field number A8 of H. Tong.

TYPE LOCALITY: Recette 4, Ouled Abdoun Basin, Morocco (figs. 14–16).

HORIZON: Dalle Couche 2, Danian, Early Paleocene (fig. 17, table 11). Information about the stratigraphic level and age of the locality of this specimen are from the Moroccan collector via H. Tong.

DEPOSITIONAL ENVIRONMENT: Near-shore marine; discussion of Moroccan phosphates is under *Araiochelys hirayamai*.

DIAGNOSIS: A member of the genus *Bothremys* with the following unique features: postorbital-palatine contact on posterior surface of septum orbitotemporale (unknown in *B. kellyi* and *B. arabicus*); jugal exposed only in tip of triturating pit, allowing broad contact of palatine and maxilla; midline concavity formed by premaxilla and maxilla short and narrow; other distinguishing features: very narrow vomer-maxilla contact, in contrast to *B. cooki*; ventral rim of orbit without distinct margin, in contrast to *B. kellyi* and *B. arabicus*; lower jaws narrower than in *B. cooki*.

ETYMOLOGY: From "Maghreb", Arabian name for the three countries (Tunisia, Algeria, and Morocco) in northwest Africa.

REFERRED MATERIAL: AMNH 30234, skull (figs. 140, 141), Danian phosphates based on shark teeth in matrix (Cappetta, personal commun.), Oued Zem, Ouled Abdoun Basin, from F. Escuillié; AMNH 30041, skull (figs. 138, 139, 278B), Ouled Abdoun Basin, Danian phosphates based on shark teeth in matrix (Cappetta, personal commun.), from B. Segaoui; AMNH 30522, skull (fig. 144) and jaws (figs. 240, 241), Paleogene, Ouled Abdoun phosphates, Morocco, based on matrix; MHNL 20-268370, skull, Danian phosphates, Ouled Abdoun Basin, Morocco.

PREVIOUS WORK: None.

DISCUSSION: The discovery of a series of well-preserved skulls in the Moroccan phosphates has significantly improved knowledge of variation in the cranial morphology in the genus *Bothremys*. The Moroccan skulls are similar to *Bothremys cooki* in shape and size, although the American species seems to be Late Cretaceous and the African species Paleocene in age.

See table 12 for a comparison of the species in *Bothremys*.

Bothremys kellyi, new species

TYPE SPECIMEN: AMNH 30553 (figs. 148, 149, 285), a nearly complete skull, from F. Escuillié.

TYPE LOCALITY: Ouled Abdoun Basin, Morocco (figs. 14–16).

HORIZON: Early Ypresian, Early Eocene, Phosphates (Cappetta, personal commun., from shark teeth) (fig. 17).

DEPOSITIONAL ENVIRONMENT: Near-shore marine; discussion of Moroccan phosphates is under *Araiochelys hirayamai*.

DIAGNOSIS: A member of the genus *Bothremys* with the following unique features: dorsal process of premaxilla contacts prefrontals to separate apertura narium externa; sulcus eustachii constricted into narrow channel formed by squamosal and

TABLE 12
Species of *Bothremys*

	Bothremys cooki	*Bothremys maghrebiana*	*Bothremys kellyi*	*Bothremys arabicus*
Postorbital-palatine contact in posterior surface of septum orbitotemporale	no	yes	indet.	indet.
Jugal completely forms triturating pit	yes	no	yes	yes
Jugal widely exposed on triturating surface	yes	no	no	no
Jugal prevents maxilla-palatine contact posterior to pit	yes	no	yes	yes
Jugal exposure in orbital rim	smaller	larger	larger	indet.
Vomer elongate anteriorly	yes[a]	no[b]	indet.	no[b]
Midline concavity formed by premaxilla and vomer anterior to apertura narium interna	elongate, narrow	short, narrow	short, wide	short, wide
Apertura narium interna	more posterior	more anterior	more anterior	more anterior
Labial ridge very thick and blunt	no	no	yes	yes
Anterior end of vomer widely expanded	no	no	no	yes
Ventral rim of orbit with distinct margin	no	no	yes	yes
Foramen posterius canalis carotici interni	indet.	PT + QU	PT + QU + BS	PT + QU
Midline premaxilla dorsal process contacts prefrontal	no	no	yes	indet.
Large ridge on dorsal surface of squamosal and opisthotic	indet.	no	yes	no
Anterior margin of otic chamber swollen into overhanging ridge	indet.	no	yes	no
Sulcus eustachii constricted into narrow channel formed by squamosal and quadrate	indet.	no	yes	no
Skull size	smaller	smaller	larger	larger

[a] Wide MX contact.
[b] Narrow MX contact.

quadrate; anterior margin of otic chamber swollen into overhanging ridge; large ridge on dorsal surface of squamosal and opisthotic; basisphenoid as well as pterygoid and quadrate forming foramen posterius canalis carotici interni.

ETYMOLOGY: For Jeanne Kelly, in recognition of her skill and efforts in preparing turtle skulls and her years of service to the Department of Paleontology, American Museum of Natural History.

REFERRED MATERIAL: None.

PREVIOUS WORK: None.

DISCUSSION: This Eocene *Bothremys* is larger than *B. cooki* and *B. maghrebiana*, and nearly the size of *B. arabicus*. The unique ear morphology, with a very deep channel for the eustachian tube (fig. 285), is unique among turtles and is a good autapomorphy for this species.

See table 12 for a comparison of the species in *Bothremys*.

Bothremys arabicus (Zalmout, Mustafa, and Wilson, 2005)

Karkaemys arabicus Zalmout, Mustafa, and Wilson, 2005.

TYPE SPECIMEN: YUP-HUS 100, a partial skull lacking most of skull roof (figs. 152–154), associated with a plastron, caudal vertebral fragments, and some limb elements (Zalmout et al., 2005).

TYPE LOCALITY: Wadi Falqa, near El-Huseiniyah and El-Hashimiyah, Jordan (Zalmout et al., 2005) (fig. 14).

HORIZON: Wadi Umm Ghudran Formation, Santonian, Late Cretaceous (Zalmout et al., 2005).

DEPOSITIONAL ENVIRONMENT: Near-shore marine (Zalmout et al., 2005).

DIAGNOSIS: A member of the genus *Bothremys* with the following unique feature: anterior end of vomer widely expanded where it contacts premaxilla and maxilla; other distinguishing features: jugal prevents maxilla-palatine contact posterior to triturating pit, in contrast to *B. maghrebiana*; midline concavity formed by premaxilla and vomer much wider than in *B. cooki* and *B. maghrebiana*; sulcus eustachii not constricted into deep channel by squamosal and quadrate, in contrast to *B. kellyi*.

ETYMOLOGY: For "Arabia," source of the specimen (Zalmout et al., 2005).

REFERRED MATERIAL: None.

PREVIOUS WORK: Zalmout et al. (2005) provided useful stereophotographs and line drawings of the skull (Zalmout et al., 2005: figs. 4, 5) and a photograph and line drawing of the internal surface of the associated plastron (Zalmout et al., 2005: fig. 7).

DISCUSSION: Zalmout et al. (2005) named this skull a new genus, *Karkaemys*. Our analysis shows it to be nested within other species that we are limiting to the genus *Bothremys*, and we therefore place this species within *Bothremys* as well. The discovery of the species *kellyi* and *maghrebiana*, unknown to Zalmout et al. (2005), has made the erection of a separate genus for *arabicus* less necessary.

See table 12 for a comparison of the species in *Bothremys*.

Chedighaii, new genus

TYPE SPECIES: *Chedighaii hutchisoni*, n. sp.

INCLUDED SPECIES: *C. barberi*, *C. hutchisoni*.

DISTRIBUTION: Late Cretaceous, eastern and central United States.

ETYMOLOGY: *Ch'ééh digháhii*, Navajo for turtle, in reference to the locality of the type species on Navajo Tribal Lands. We are very grateful to Steve Semken for help with the Navajo language.

DIAGNOSIS: A bothremydid pleurodire of the tribe Bothremydini with the following unique feature within Bothremydini: vomer widely separated from maxilla, associated with large apertura narium interna, in contrast to vomer-maxilla nearly or in contact, as in all other Bothremydini; other differentiating characters: anterior projection of prefrontal present, in contrast to *Foxemys*, *Polysternon*, and *Rosasia*; apertura narium externa facing anterodorsally to a greater extent than in *Bothremys* and other Bothremydini (except possibly the incomplete *Zolhafah*); orbit small, as in *Bothremys* and in contrast to all other Bothremydini; orbits face strongly upward, as in *Bothremys* and in contrast to other Bothremydini; prefrontal-palatine contact present, as in *Bothremys* and *Araiochelys* and in contrast to all other Bothremydini; dorsal process of maxilla narrow, in contrast to *Bothremys* but in common with all other Bothremydini; sulcus palatinopterygoideus low, as in *Bothremys* but in contrast to all other Bothremydini; fossa orbitalis enlarged posteriorly, as in *Bothremys*, *Araiochelys*, and *Rosasia* and in contrast to *Foxemys* and *Zolhafah*; ridge forming lower margin of orbital rim high, as in *Bothremys arabicus*, *Polysternon*, *Zolhafah*, *Rosasia*, and *Araiochelys* but in contrast to other *Bothremys* species; suborbital maxillary plate deep, as in *Bothremys* and in contrast to all other Bothremydini; triturating surface pit absent; no exposure of jugal on triturating surface; midline depression on ventral surface of premaxilla very wide, as in *Bothremys arabicus* and *Zolhafah* and in contrast to other *Bothremys*, *Rosasia*, and *Araiochelys*; fossa pterygoidea absent; incisura columellae auris closed; foramen posterius canalis carotici interni formed by pterygoid and quadrate; basisphenoid-quadrate contact very narrow, as in *Bothremys* and in contrast to all other Bothremydini; lower jaws with triturating surface pits; shell (known only from *C. barberi*) typical of Bothremydina, pectoral scales well posterior to epiplastra, in contrast to Foxemydina; pectoral scales in contact with mesoplastra, in contrast to Foxemydina and *Araiochelys*; peripheral 1 contact to costal 1 wide, as in *Rosasia* and in contrast to narrow in Foxemydina and *Araiochelys*; anterior lobe of plastron does not reach anterior carapace margin, as in *Rosasia* and the Foxemydina and in contrast to the Cearachelyini.

DISCUSSION: The recognition of this new genus of North American pleurodire is an attempt to reflect the degree of diversity shown by the newly discovered species in the subtribe Bothremydina. The basic cladogram (fig. 288) shows *Bothremys cooki* from the Cretaceous of New Jersey as belonging in an African/Middle Eastern clade of four species that is characterized by maxillary pits, a more rounded skull, and other features differentiating it from the two species here placed in the new genus *Chedighaii*, which lacks pits in the maxilla and has a more pointed skull. Although the recognition of genera is based only on taste and monophyly, this generic division is consistent with the subjective formation of other generic groups in pleurodires, reflecting phylogeny and morphology.

We have chosen to base the new genus on the species *C. hutchisoni* because that species is in turn based on a well-preserved skull, in contrast to the partial skulls of *C. barberi.* Although two of the partial skulls of *C. barberi* are associated with shells, we are not confident that the type specimen of *C. barberi*, a shell without skull, is complete enough to allow future resolution of the possibility that more bothremydid taxa are included in *Chedighaii barberi* (discussed under *C. barberi* below). The conservative nature of bothremydid shells may not reflect the diversity seen in skull morphology.

See table 10 for a comparison of genera of the tribe Bothremydini, table 13 for a comparison of the species in *Chedighaii*, table 14 for a comparison of the lower jaws in *C. barberi*, and table 15 for a comparison of the shells in *C. barberi.*

Chedighaii hutchisoni, new species

TYPE SPECIMEN: KUVP 14765, skull (figs. 157–159), field no. MJW 45, collected by Jack Whetstone, 1963.

TYPE LOCALITY: "New Mexico #35 Hunters (sic) Wash" (label). NW1/4, SW1/4, sec. 34, T24N, R13W, San Juan County, New Mexico (Spencer Lucas, personal commun.; Sullivan and Lucas, 2003) (fig. 18).

HORIZON: Lowermost part of the Kirtland Formation (Scott et al., 1979). Hunt and Lucas (1992) have named this the Hunter Wash Member of the Kirtland Formation, and Clemens (1973) referred to it as the Hunter Wash local fauna. It is Late Campanian in age based on Hunt and Lucas (1992) and the dating of the nearby magnetozones as roughly 73–74 mya (Fassett and Steiner, 1997).

DEPOSITIONAL ENVIRONMENT: Freshwater rivers and deltas with other turtle species, gars, and dinosaurs common (Sullivan and Lucas, 2003).

DIAGNOSIS: A member of the genus *Chedighaii* differing from the only other species, *Chedighaii barberi*, in the following characters: suborbital maxillary plate deeper; triturating surfaces wider; preorbital part of skull wider.

ETYMOLOGY: In honor of Dr. Howard Hutchison, for his lifelong contributions to vertebrate paleontology; and who recognized this skull as a bothremydid after the senior author had misidentified it as a trionychid.

REFERRED MATERIAL: None; however, some specimens should be kept in mind when thinking of Rocky Mountain region pleurodires. "*Naiadochelys*" *ingravata* Hay, 1908 is a distal fragment of xiphiplastron (Hay, 1908: figs. 125, 126) "brought to [F. W. Putnam] by Indians, at Chaco Canyon, New Mexico" in 1900, without any clear locality data. However, using guilt by association, the skull of *Chedighaii hutchisoni* was found not too far away, and it is possible that they belong to the same taxon. They are in the same size range, and "*Naiadochelys*" is smooth, lacking surface texture, as in specimens of *Chedighaii barberi.*

Another suspicious shell is YPM 3608, Niobrara Formation, Wallace Co., Kansas, described and figured in Gaffney and Zangerl (1968: figs. 9–12) as "*Bothremys barberi*, subspecies C" (Gaffney and Zangerl, 1968: 206). Although there is extensive pitting and pathologic erosion on much of the shell surface, the shell texture is basically smooth or bald, as in "*Naiadochelys*" and *Chedighaii barberi.* Both have a crescentic ischiac scar on the xiphiplastron, but that is common in Pelomedusoides. Although YPM 3608 was found in marine rocks, its preservation is very different from typical Niobrara Formation specimens. It might also prove to be referable to *Chedighaii hutchisoni.*

DISCUSSION: See table 13 for a comparison of the species in *Chedighaii.*

Chedighaii barberi (Schmidt, 1940)

Podocnemis barberi Schmidt, 1940.
Podocnemis alabamae Zangerl, 1948.
Bothremys barberi Gaffney and Zangerl, 1968.

TYPE SPECIMEN: FMNH P26055, a nearly complete shell (Schmidt, 1940: figs. 2–5).

TYPE LOCALITY: A gully on the SW1/4 of NE 1/4 of section 29, T8S, R23W, E. L.

TABLE 13
Species of *Chedighaii*

	Chedighaii hutchisoni	*Chedighaii barberi*
Suborbital maxillary plate	deeper	shallower
Triturating surfaces	wider	narrower
Preorbital part of skull	wider	narrower
Antrum postoticum	larger	smaller
Condylus mandibularis	slightly more posterior	slightly more anterior
Anterior median concavity	wide	probably narrow
Palatine contribution to triturating surface	wider	narrower
Fenestra postotica divided by bone	no	yes

Presley Farm, near Delight, Pike Co., Arkansas (Schmidt, 1940) (fig. 18).

HORIZON: Brownstone Marl, Campanian, Late Cretaceous (Gaffney and Zangerl, 1968).

DEPOSITIONAL ENVIRONMENT: Near-shore marine (Zangerl, 1948).

DIAGNOSIS: A member of the genus *Chedighaii* differing from the only other species, *Chedighaii hutchisoni*, in the following characters: suborbital maxillary plate shallower; triturating surfaces narrower, preorbital part of skull narrower; other differentiating features: premaxilla protuberant, unique among Bothremydini (but not known in *C. hutchisoni*); apertura narium externa faces strongly anterodorsally, more than in any other Bothremydini (not known for *C. hutchisoni*); labial ridge straight, relatively thin and acute, in contrast to *Bothremys*; carapace low, more round than oval, broader posteriorly; nuchal notch present; six or seven neurals; plastron with short and wide anterior lobe; posterior lobe with lateral margins tapering posteriorly; humeropectoral sulcus posterior to the epi-hyoplastral suture, crossing entoplastron; pectoroabdominal sulcus crossing mesoplastron; first vertebral tapered posteriorly to lie in part on nuchal bone, unique among bothremydids; costal bones 2–4 short in relation to width, as in *Taphrosphys* but in contrast to *Cearachelys*; xiphiplastral notch broad and U-shaped, xiphiplastra end in rounded projections; pubic scar short and wide, ischiac scar triangular to curved, separated from xiphiplastral edge.

ETYMOLOGY: In recognition of Mr. Charles M. Barber, who collected the type as well as many other Arkansas and Alabama specimens (Schmidt, 1940; Zangerl, 1948).

REFERRED MATERIAL: Schmidt (1940) referred a series of paratypes to this species: FMNH P26058, neural one, John Humphreys farm (0.5 mile SW of type locality, fide Schmidt, 1940); FMNH P26060, hyoplastron fragment, near Delight, Arkansas; FMNH P26059, peripherals 1 and 2, John Humphreys farm.

In 1968, Gaffney and Zangerl synonymized "*Podocnemis*" *barberi* Schmidt, 1940 with "*Podocnemis*" *alabamae* Zangerl, 1948. The following material is described and figured in Zangerl (1948): FMNH P27370, type of "*Podocnemis*" *alabamae*, a nearly complete shell with pelvis; collected by C. M. Barber, May, 1946; FMNH P27369, nearly complete carapace, most of the plastron and other skeletal fragments; FMNH P27372, most of the carapace and part of the plastron; FMNH P27331, posterior portion of the carapace of a very small individual; FMNH P27405, fragmentary, badly weathered specimen, about the size of P27369, includes a humerus and parts of both carapace and plastron; FMNH P27419, two peripherals of a very small individual, about the size of P27331; horizon and locality: Mooreville Chalk member of the Selma Formation, Late Cretaceous Campanian/Santonian. All specimens were collected in exposures of the Harrell Station area (see Zangerl, 1948: pl. 3 for localities), southeast of Marion Junction, Dallas County, Alabama.

FMNH PR 247, partial skull (figs. 162, 163; Gaffney and Zangerl, 1968: figs. 17, 18, 19D), lower jaws (figs. 242, 244; Gaffney and Zangerl, 1968: fig. 22D, E), and shell (Gaffney and Zangerl, 1968: figs. 2, 3), described in Gaffney and Zangerl (1968), from Mooreville Chalk member, Selma

Formation, 1 mile E of Harrell, Dallas Co., Alabama; ALAB PV 2001.2 (field no. 00-5-9), partial skull (figs. 164, 165), lower jaws (figs. 242–244), nearly complete plastron, and anterior section of carapace, Gaston Pond, near Harrell, Dallas Co., Alabama, Mooreville Chalk member, Selma Formation, collected by Ed Hooks; YPM PU 12951, natural endocast of skull (figs. 166, 167; Gaffney, 1977a; a cast of this endocast and its mold are AMNH 30567), ?Magothy Clay, ?Turonian, Cliffwood, New Jersey; ANSP 15902, shell (Gaffney and Zangerl, 1968: figs. 4–8), Graham Brick Yards, Maple Shade, Burlington Co., New Jersey, Merchantville Formation, Campanian (Gallagher, 1993, see also for section and faunal list); YPM 3608, shell (Gaffney and Zangerl, 1968: figs. 9–12), Wallace Co., Kansas, B. F. Mudge and Party, 1876, Niobrara Formation, Santonian/Coniacian; CSU-K-85-7-4, right otic chamber and basisphenoid, Blufftown Formation, Campanian, Hannahatchee Creek "longwalk" outcrop, Stewart Co., Georgia (see Schwimmer, 1986, for geology); CSU-BRK-83-1-2, costals 1 and 2 (Schwimmer, 1986: pl. 2, fig. E), Blufftown Formation, Hannahatchee Creek, Stewart Co., Georgia; CSU-SSK-81-7-1, neural bone (Schwimmer, 1986: pl. 2, fig. F), Blufftown Formation, Hannahatchee Creek, Stewart Co., Georgia; NJSM 12704–12707, 12718 (Gallagher, Parris, and Spamer, 1986: 25), Marshalltown Formation, Campanian, Ellisdale locality, Monmouth Co., New Jersey; CSU K-90-6-2, jaw symphysis, Blufftown Formation, Campanian, Hannahatchee Creek, 200 m below "longwalk" outcrop, 3.8 km W of Union, Stewart Co., Georgia; NJSM 12704–12707, 12718, shell fragments, Marshalltown Formation, Campanian, Ellisdale, New Jersey (Gallagher, Parris, and Spamer, 1986).

In the collections of the North Carolina State Museum are some bothremydid specimens being described by Gaffney and Schneider (ms in prep.). This material includes a series of otic chambers from the Campanian Tar Heel Formation of North Carolina that are indistinguishable from the *Chedighaii barberi* ear regions from the Selma Formation skulls, but that are too incomplete to be identified with certainty as *C. barberi.* The quadrate of one of these, NCSM 12766, is figured here (fig. 286D). We list this material although we do not describe it at this time. NCSM 12766, otic chamber, Tar Heel Formation, Phoebus Landing, North Carolina; NCSM 14102, 14103, 14226, 14227, all otic chambers, NCSM 14228, parietals, Tar Heel Formation, Elizabethtown, North Carolina; NCSM 14577, 19721 14598, all quadrates, Bladen Co. annex, North Carolina.

Miller (1967: 225–226, pl. 1, fig. 12; ANSP 15304) reported "*Taphrosphys dares*" from the Campanian Black Creek Formation of Phoebus Landing, North Carolina. As described, the material is consistent with *Chedighaii barberi*. The senior author has seen this material, but no elements containing strictly diagnostic characters seem to be present, and the material must be considered Pelomedusoides incertae sedis.

Although the "?*Bothremys*" specimens described by Hutchison and Weems (1998) are here considered to be Pelomedusoides incertae sedis, to the extent they are known, they agree with *Chedighaii barberi*. Paleocene Williamsburg Formation of South Carolina, St. Stephen locality: ChM PV3735, PV3774, PV3805, PV3816, right costal fragments; ChM PV3883, hyoplastron fragment; ChM PV3747, PV3927, hypoplastron fragment; ChM PV3887, left xiphiplastron fragment; ChM PV3770, PV3897, peripheral fragments; ChM PV3801, PV4303, costal fragments; SCSM 83.78.15, costal fragment.

PREVIOUS WORK: "*Podocnemis*" *barberi* was erected by K. P. Schmidt in 1940 for a shell and other fragments found in Arkansas by an amateur collector, Charles Barber, who had a long relationship with the Field Museum of Natural History, where he deposited a large collection of turtles and other fossils. Schmidt put the species in *Podocnemis*, which has been, like *Trionyx*, *Testudo*, and *Chelone*, a wastebasket designation, closer to a family name. Barber continued collecting in Alabama, finding many turtles that were described by Zangerl, including the pleurodire "*Podocnemis*" *alabamae* (Zangerl, 1948). Zangerl (1948) presented a phylogeny of pelomedusids (sensu lato, now equal to Pelomedusoides) based on plastron morphology that did not distinguish between podoc-

TABLE 14
***Chedighaii* Lower Jaws**

	FMNH PR 247	ALAB 2001.2	CSU K-90-6-2	NJSM 12704 (cast)
Specimen	nearly complete lower jaw	articulations and symphysis missing	symphysis only	articulation missing
Age and locality	Campanian, Alabama	Campanian, Alabama	Campanian, Alabama	Campanian, New Jersey
Associated skeletal elements	shell, partial skull	partial skull, partial shell	none	none
Jaw width	wider	narrower	?	wider
Triturating pit	deeper	shallower	?	deeper
Symphyseal depression well defined by lingual ridge	no	yes	yes	no
Triturating pits in skull	?	no	?	?
Coronoid forms nearly all of pit	no	yes	?	?

nemidid and bothremydid groups, which is not surprising considering that there are almost no shell characters distinguishing these groups. Barber's discovery of a skull-shell association for "*Podocnemis*" *alabamae* in 1949 caused Zangerl to realize that the species *alabamae* belonged to *Bothremys*, resulting in the Gaffney and Zangerl (1968) combination, *Bothremys barberi*, for the material previously included in both "*Podocnemis*" *barberi* and "*Podocnemis*" *alabamae.*

Schwimmer (1986: 116) noted the presence of "*Bothremys*" *barberi* in the Campanian Blufftown Formation of western Georgia: "The most abundant reptiles are the 'pavingstone turtle' *Bothremys barberi* and, surprisingly, the giant crocodile *Deinosuchus.* At least one hundred kilograms of *Bothremys* material have been recovered, apparently derived from several dozen individual animals." The senior author has examined some of this material and finds that it is most similar to the large Merchantville shell described in Gaffney and Zangerl (1968) in size and bone thickness. A skull roof fragment from the same area is very similar to *Chedighaii barberi*, ALAB PV 2001.2.

DISCUSSION: The recent discovery by R. Hooks in the Campanian Selma Chalk of a partial skull and jaws in articulation with shell elements identifiable as *Chedighaii barberi* has prompted a reassessment of this taxon. The skull, ALAB 2001.2 (figs. 164, 165; table 14), has no pits in the maxillary triturating surface, and it is therefore like that of *Chedighaii hutchisoni* rather than *Bothremys*. The only previous skull material of "*Bothremys*" *barberi* associated with a shell is FMNH PR 247 (figs. 162, 163; Gaffney and Zangerl, 1968), which lacks the triturating surfaces in the skull. Both of these specimens have lower jaws, and these jaws have pits. ALAB 2001.2 has shallower pits than does FMNH PR 247, but both seem to be within the bounds of individual variation. Still, it is possible that FMNH PR 247 had pits in the skull and represents a different taxon from ALAB 2001.2. Shells in the Pelomedusoides are morphologically conservative, and one shell morphotype might include a number of different species, which will become apparent only when the skulls are known.

There is certainly a large (70–75 cm carapace length, as in ANSP 15902), smoothly textured ("bald" or "pavingstone"), bothremydid found in near-shore marine, Campanian sediments from New Jersey to Kansas (this includes the species *Chedighaii barberi*, which is known from mostly smaller shells, but some individuals, e.g., FMNH P 27406, reached the size of ANSP 15902). Sometimes referred to in scrap fauna accounts as the "pavingstone turtle" (Schwimmer, 1986: 115; see also Lehman, 1997), there is at present no basis for recognizing more than one species among these shell specimens, although more than one may exist. Furthermore, in the absence of a shell for *Chedighaii hutchisoni*, it is possible that some of the shells now referred to *C. barberi* may belong to *C. hutchisoni*, despite the fact that *C. hutchisoni* is found in freshwater sediments, and that all

TABLE 15
***Chedighaii barberi* Geographic Variation in Shells**

	Merchantville Fm	Selma Fm	Niobrara Fm
Content	1 shell	2 skulls, > 6 shells	1 shell
Midline length of plastron	635 mm (est.)	485–540 mm	630 mm (est.)
Nuchal	indet.	wider	narrower
Mesoplastra	width > length	width > length	width = length
Epiplastral symphysis	indet.	shorter	longer
Gular lip	no	yes, no	yes
Ischiac scar	triangular	triangular to curved	curved
Neurals	6	6 or 7	probably 7

the *C. barberi* specimens are near-shore marine (table 15). Until there is evidence to the contrary, we consider these widespread records a single taxon, *Chedighaii barberi*.

In their revision of the genus *Bothremys*, Gaffney and Zangerl (1968) recognized three subspecies of "*Bothremys*" (= *Chedighaii*) *barberi* corresponding to three supposed paleogeographic provinces. The subspecies A includes one specimen from New Jersey (the Atlantic coastal province), the subspecies B includes Alabama and Arkansas specimens (the Gulf coastal province), and the subspecies C includes one specimen from Kansas (the epicontinental province). The distinction of these subspecies is mainly geographical rather than morphological. As shown in table 15, all these shells are very similar to one another, with some minor variations. One of the two specimens with an associated skull and shell (FMNH PR 247) is not particularly closer in morphology to the type shell than it is to the other specimens. There is no morphological evidence to distinguish the New Jersey specimen from the Alabama and Arkansas specimens, while the Kansas specimen (YPM 3608) differs from the others in having a narrower nuchal, equidimensional mesoplastra, and longer epiplastral symphysis. YPM 3608 might belong to *C. hutchisoni*, as mentioned in the systematic section, or it may simply reflect intraspecific variation. We do not recognize the subspecies of Gaffney and Zangerl (1968).

The two specimens, YPM PU 12951 (endocast) and ALAB PV 2001.2 (partial skull), show that *Chedighaii barberi* did not have a pit on the triturating surfaces, as in *Bothremys*. This is clear from ALAB PV 2001.2 alone, because it is the posterior part of the triturating surface on the maxilla that is preserved. In the endocast, YPM PU 12951, it is less obvious, but the jugal and maxilla form a deep rim below the orbital margin, as in *C. hutchisoni*, which is very different from the absent rim of *Bothremys cooki*. The pit itself would not be seen in the endocast, but the floor of the fossa orbitalis is clearly very similar in *C. hutchisoni* and *C. barberi* and distinct from the floor in *Bothremys*. The pitted bothremydids all have at least some of the jugal significantly altered from the primitive condition to form part of the pit. Enough of the jugal and maxilla is preserved in *C. barberi* to show that a pit was absent and that the jugal has no exposure on the triturating surface.

See table 14 for a comparison of the lower jaws and table 15 for a comparison of the shells in *C. barberi*.

TRIBE **TAPHROSPHYINI**, NEW

TYPE GENUS: *Taphrosphys* Cope, 1869a.

INCLUDED GENERA: *Taphrosphys* Cope, 1869a; *Labrostochelys*, n. gen.; *Phosphatochelys* Gaffney and Tong, 2003; *Ummulisani*, n. gen; *Rhothonemys*, n. gen.; *Azabbaremys* Gaffney, Moody, and Walker, 2001; *Nigeremys* Broin, 1977; *Arenila* Lapparent de Broin and Werner, 1998.

DIAGNOSIS: Members of the subfamily Bothremydinae with the following unique characters: jugal-quadrate contact present; supraoccipital-quadrate contact absent (except in unnamed taxon CNRST-SUNY 199); small palatine contribution to triturating surfaces; dorsally arched palate (except in *Labrostochelys*, but unknown for *Taphrosphys* and *Rhothonemys*); maxilla-quadratojugal contact absent. Other differentiating characters are: preorbital part of skull usually narrower than in Bothremydini; fenestra interorbitale high, in contrast to Bothremydini; temporal emargination slight or absent, in contrast to Kurmademydini and Cearachelyini; fossa precolumellaris absent, in contrast to Kurmademydini; shelf below cavum tympani present, as in Bothremydini; foramen jugulare posterius closed, as in Kurmademydini and Bothremydini; exoccipitals completely form neck and condylus occipitalis, in contrast to Kurmademydini and Cearachelyini; foramen stapedio-temporale not visible in dorsal view; foramen stapedio-temporale and foramen nervi trigemini very close together; fenestra postotica closed; jugal not retracted from orbit; pectoral scales on plastron reach entoplastron; neurals do not reach suprapygal; (following characters known only for *Taphrosphys*): shell surface covered by strong texture consisting of irregular raised polygons delimited by network of deep furrows; nuchal notch absent; seven neurals, costals 7 and 8 meeting on midline; first costal length greater than twice length of second costal; first marginal scale about equidimensional, pleural scales extending well onto peripheral bones; (following characters known only for *Taphrosphys* and *Ummulisani*): shell surface covered by strong texture consisting of irregular raised polygons delimited by network of deep furrows; posterior plastral lobe broad, in contrast to *Chedighaii*, and possessing a semicircular anal notch; intergular scale large, separating small gulars, humerals, and part of pectorals; pubic scar long and narrow, ischiac scar round and near edge of xiphiplastron.

DISCUSSION: This tribe is roughly equivalent to the "*Taphrosphys* group" plus the "*Nigeremys*" group of Antunes and Broin (1988), Lapparent de Broin and Werner (1998), Lapparent de Broin and Murelaga (1999), and Lapparent de Broin (2000a). Other authors (Gaffney, Moody, and Walker, 2001; Gaffney, Tong, and Meylan, 2002; Gaffney and Tong, 2003) have used the term "*Nigeremys* group" and expanded it to include *Taphrosphys* and newly described taxa.

A lower jaw from the Late Cretaceous of Syria that probably belongs in the tribe Taphrosphyini was described by Bardet et al. (2000: 281, fig.7d, e) as "Chelonioidea gen. and sp. indet." Tong and Hirayama (2004:58) suggested that this jaw is a dermochelyid. In addition to chelonioids, in the same fauna with this jaw are shell elements (Bardet et al., 2000: 281, fig.7a–c, g), one of which (fig. 7a) has the iliac scar small, round, and at the shell margin, features probably diagnostic for the tribe Taphrosphyini. The lower jaw is very similar to those of *Rhothonemys* and *Taphrosphys congolensis* (see figs. 248–250).

See table 5 for comparison of the tribes in the Bothremydidae.

SUBTRIBE **TAPHROSPHYINA**, NEW

TYPE GENUS: *Taphrosphys* Cope, 1869a.

INCLUDED GENERA: *Taphrosphys* Cope, 1869a; *Labrostochelys*, n. gen.; *Phosphatochelys* Gaffney and Tong, 2003; *Ummulisani*, n. gen.; *Rhothonemys*, n. gen.; *Azabbaremys* Gaffney, Moody, and Walker, 2001; CNRST SUNY 199 (Gaffney, Roberts, Sissoko, Bouré, Tapanila, and O'Leary, in press).

DIAGNOSIS: Members of the tribe Taphrosphyini with the following characters contrasting with Nigeremydina: labial ridge thinner; septum orbitotemporale at least partially open; condylus mandibularis anterior to condylus occipitalis; fossa pterygoidea absent or small (except in CNRST SUNY 199); basisphenoid ventral outline triangular or pentagonal, not V-shaped.

Taphrosphys Cope, 1869a

Platemys Leidy, 1856 (in part).
Prochonias Cope, 1869b.
Podocnemis Schmidt, 1931 (in part).
Amblypeza Hay, 1908 (as restricted by Gaffney, 1975a).
Bantuchelys Dollo, 1924.

TYPE SPECIES: *Platemys sulcatus* Leidy, 1856.

INCLUDED SPECIES: *T. sulcatus*, *T. ippolitoi*, *T. congolensis*.

DISTRIBUTION: Paleocene of New Jersey; Paleocene of Morocco; Paleocene of Cabinda.

ETYMOLOGY: Unknown (*taphros*, Greek for trench, possibly in reference to surface texture of shell).

DIAGNOSIS: A bothremydid pleurodire of the tribe Taphrosphyini with these unique characters among Taphrosphyini: pentagonal basisphenoid; foramen posterius canalis carotici interni formed by basisphenoid, pterygoid, and quadrate; sulcus eustachii with dorsal and ventral process; sulcus eustachii opens more ventrally than in any other Taphrosphyini; other differentiating characters: narrow jugal, as in *Labrostochelys* and in contrast to *Phosphatochelys* and *Azabbaremys*; squamosal with vertical flange, as in *Labrostochelys* and *Phosphatochelys* in contrast to *Azabbaremys*; skull length to height about intermediate between *Labrostochelys* and *Azabbaremys*; triturating surfaces a curved trough, as in *Labrostochelys* and in contrast to all other Taphrosphyini; labial ridge on maxilla thin, as in *Labrostochelys* and in contrast to all other Taphrosphyini; palate not dorsally arched; posteroventrally opening pocket on posterior surface of quadrate, as in *Labrostochelys* and in contrast to all other Taphrosphyini; ventrally opening channel at back of skull, as in *Labrostochelys*; condylus mandibularis well anterior to condylus occipitalis, as in *Labrostochelys*; fossa pterygoidea absent.

DISCUSSION: Although in the past *Taphrosphys* has been recognized primarily on the basis of its plastral morphology and surface texture, we propose a more rigorous definition based primarily on cranial morphology. The discovery of another distinctive genus of Taphrosphyini, *Ummulisani*, with plastral characters very similar to *Taphrosphys*, has significantly altered the scope of the characters previously thought to be diagnostic for the genus. These shell characters may very well be at the level of the Taphrosphyini.

According to Gaffney (1975a), one of the synonyms of *Taphrosphys* is *Amblypeza entellus* Hay (1908; lectotype NJSM 6614, xiphiplastron fragment), which is based on a mixed type specimen. The unique nature of this taxon as diagnosed by Hay was the presence of a nuchal scute in a pelomedusid pleurodire where previously such a scute had never been reported. There were no data concerning the locality or conditions of association of the fragments, and the portions of the shell bearing the nuchal scale (NJSM 11342 and 11343, Hay, 1908: fig. 125) are identifiable as the chelonioid sea turtle, *Osteopygis*. The xiphiplastron (NJSM 6614, Hay, 1908: fig. 132) is identifiable as *Taphrosphys sulcatus* on the basis of the circular ischiac scar and shape of the xiphiplastral projections. Other fragments (not the figured elements and bearing the group number NJSM 6613) include some pieces with the ornamentation seen in the adocid *Adocus*. Gaffney (1975a) chose the xiphiplastral fragment as the lectotype and synonymized it with *Taphrosphys sulcatus*, with which we concur.

Partial shells and shell fragments described and figured by Lapparent de Broin and Werner (1998: pp. 41–43, pls. 3 and 4) from the late Cretaceous of Egypt were identified by them as *Taphrosphys*, in some cases "*Taphrosphys* cf. *sulcatus*". The basis for these identifications is the very close similarity to the (now Paleocene) shells of *Taphrosphys sulcatus* from New Jersey. The specific shell characters are the "typical very marked decoration of small prominent polygons and granulations and rounded crests" (Lapparent de Broin and Werner, 1998: 41) and the somewhat elongate nuchal. The surface texture of these shells is similar to that in *Taphrosphys sulcatus*, but this texture occurs elsewhere, and the other similarities are not diagnostic of *Taphrosphys* in our analysis. It is possible that these specimens belong to the genus *Taphrosphys*, because skulls of *Taphrosphys ippolitoi* do occur in North Africa, but the shell material alone is inadequate to support this assertion. Therefore we do not consider these records a valid range or stratigraphic extension of *Taphrosphys* but they are probably bothremydids.

"*Taphrosphys*" *miocenica* Collins and Lynn, 1936 could be a podocnemidid and is incertae sedis at the level of Pelomedusoides (see below).

Hutchison and Weems (1998) identified *Taphrosphys* (and ?*Bothremys*, see genus for further discussion) from the Paleocene Williamsburg Formation of South Carolina. The *Taphrosphys* material does not contain diagnostic complete xiphiplastra or entoplastra, but the surface texture of the identified elements is very similar to that of *Taphrosphys sulcatus* from New Jersey. This distinctive surface texture also occurs in *Ummulisani* from Morocco and is probably diagnostic for the tribe Taphrosphyini. The South Carolina Paleocene record is amended to tribe Taphrosphyini incertae sedis.

Bardet et al. (2000: 281, fig.7a–c) identified as "*Taphrosphys sulcatus*" shell elements, one of which (fig. 7a) has the small, round, iliac scar placed at the shell margin, with the shell texture found in *Taphrosphys*; features probably diagnostic for the tribe Taphrosphyini. Other elements are identified as "*Nigeremys* group". An associated lower jaw (Bardet et al., 2000: 281, fig. 7d, e) is very similar to those of *Rhothonemys* and *Taphrosphys congolensis* (see figs. 248–250). Although more than one bothremydid taxon seem to be included, all are best referred to as tribe Taphrosphyini incertae sedis.

See table 16 for a comparison of the genera in the tribe Taphrosphyini and table 17 for a comparison of the species in *Taphrosphys*.

Taphrosphys sulcatus (Leidy, 1856)

Platemys sulcatus Leidy, 1856.
Taphrosphys molops Cope, 1869a.
Prochonias sulcatus (Leidy) Cope, 1869b.
Taphrosphys molops var. *enodis* Cope, 1870.
Prochonias longinuchus Cope, 1870.
Taphrosphys leslianus Cope, 1870.
Prochonias enodis Cope, 1870.
Taphrosphys longinuchus Cope, 1870.
Prochonias leslianus Cope, 1870.
Amblypeza antellius Hay, 1908.

TYPE SPECIMEN: AMNH 2522, fifth, sixth, and seventh left peripherals and left xiphiplastron (Leidy, 1865: pl. 19, fig. 4; repeated here as fig. 20). Although only the peripherals were figured by Leidy, it is the xiphiplastron that has the diagnostic features of the genus. All the elements have the characteristic surface texture. If future workers doubt the association of these elements (which I do not), then the peripherals must be designated as the lectotype.

LOCALITY AND HORIZON: "Tinton Falls, N.J." (Leidy, 1865: 109) (fig. 18). No further information is available. The locality has not been relocated and the horizon of the type is not known. However, as Gallagher (1993: 141) has discussed:

> In the AMNH collections there are several interesting vertebrate specimens recorded from Tinton Falls, including the type of *Taphrosphys sulcatus* (AMNH 2522), the type of *Adocus parvus* (AMNH 2528), a specimen of *Hyposaurus rogersii* (AMNH 2545), and a specimen of *Thoracosaurus neocesariensis* (AMNH 2548). This fauna has a distinctively Hornerstown Formation cast to it, and it is more likely from that unit rather than from the Tinton Formation. While the Hornerstown Formation is not to be seen at this section, it is likely that it is present in the vicinity and was perhaps mined for greensand marl. If so, these vertebrate remains may represent a northeastern-most extension of the basal Main Fossiliferous Layer (MFL) that has produced so many specimens from pits elsewhere further to the southwest.

The Hornerstown MFL appears to be Danian (Landman et al., 2004). If the type of *Taphrosphys sulcatus* is from the Hornerstown Formation, then it is Danian as well.

The age of *Taphrosphys sulcatus* depends on the age of the basal Hornerstown Formation where all of the well-substantiated specimens have come from. In 1975, Gaffney described two skull/shell associations (ANSP 15544, YPM PU 18706) from the MFL (Gallagher, 1993) at the Inversand Co. greensand pit at Sewell, New Jersey. He was able to figure *Taphrosphys* specimens, YPM PU 18706 and YPM PU 18707, in situ before collection, showing that although disarticulated and "shingled", the skeletons could not have been reworked from older units. More than a dozen ammonites of three genera have been found at the same horizon in the MFL at Sewell, specimens of *Sphenodiscus* occurring directly with YPM PU 18706 and ANSP 15544 (Gaffney, 1975a). These observations were consistent with the view that the lower few feet of the Hornerstown Formation, the MFL, is latest Maastrichtian (Olsson, 1963; Koch and Olsson, 1974, 1977; summarized in Gallagher, 1993, and references) in contrast to the view that all of the Hornerstown is Tertiary (Minard et al., 1969; Owens and Sohl, 1969), down to the contact with the Navesink. Vertebrate paleontologists working on the MFL have adopted the idea that the MFL is Maastrichtian, primarily due to the association of typically Cretaceous invertebrates with fragile, partially articulated vertebrate skeletons, such as noted above.

TABLE 16
Genera of Taphrosphyini

	Taphrosphys	*Labrostochelys*	*Azabbaremys*	*Phosphatochelys*	*Nigeremys*	*Arenila*	*Rhothonemys*	*Ummulisani*
Prefrontal extremely long, narrow	no	yes	no	no	no	no	no	no
Apertura narium externa at least partly divided	no	yes	no	no	no	no	yes	yes
Frontal in orbital margin	yes	yes	yes	no	yes	yes	yes	no
Jugal	narrow	narrow	broad	broad	?	?	broad	?
Squamosal with vertical flange	yes	yes	no	yes	?	?	yes	yes
Squamosal elongated posteriorly	no	yes	no	no	no	?	?	no
Quadratojugal-jugal contact	present	present	present	absent	?	?	?	absent
Skull long, narrow	no	yes	no	no	no	no	no	no
Skull short	no	no	yes	yes	no	no	no	yes
Premaxilla projects past labial ridge	no	yes	yes	no	yes	?	yes	yes
Triturating surface on maxilla thin curved trough	yes	yes	no	no	no	no	no	no
Labial ridge on maxilla	thin	thin	thick	thick	very thick	very thick	thick	thin
Maxilla-vomer contact	?	yes	no	indet.	yes	yes	?	?
Dorsally arched palate	no	no	yes	yes	yes	yes	?	no
Cavum tympani	wider	wider	narrower	narrower	narrower	?	?	narrower
Sulcus eustachii with dorsal process	yes	yes	no	yes	?	?	yes	no
Sulcus eustachii with ventral process	yes	no	no	no	?	?	no	yes
Foramen posterius canalis carotici interni formed by	PT, BS, QU	PT, QU	PT, QU	PT, QU	?	BS, PT	?	QU, QU+PT
Fenestra postotica	more vertical	more horizontal	more vertical	more vertical	more vertical	?	?	more horizontal
Posteroventrally opening concavity on quadrate	yes	yes	no	no	no	?	?	no
Processus trochlearis pterygoidei very small	?	yes	no	no	no	no	?	no
Postorbital lacking medial process	?	no	yes	yes	no	no	yes	yes
Sulcus palatinopterygoideus	?	wide	wide	wide	narrow	narrow	?	narrow
Ventrally opening channel at back of skull	yes	yes	no	no	no	?	?	no
Basisphenoid V-shaped	no	no	no	no	yes	yes	?	no
Basisphenoid pentagonal	yes	no	no	no	no	no	?	yes
Basisphenoid triangular and elongate	no	yes	no	no	no	no	?	no
Vomer robust	?	no	no	?	yes	yes	?	?
Condylus mandibularis position in relation to condylus occipitalis	anterior	anterior	anterior	posterior	posterior	posterior	?	anterior
Fossa pterygoidei	absent	absent	absent	absent	deep, narrow	deep, narrow	?	absent
Septum orbitotemporale at least partially open	open	?	open	open	closed	closed	open	open

TABLE 16
Continued

	Taphrosphys	*Labrostochelys*	*Azabbaremys*	*Phosphatochelys*	*Nigeremys*	*Arenila*	*Rhothonemys*	*Unmulisani*
Prominent crenellations on triturating surface	no	no	yes	no	no	no	no	no
Prefrontal extends to anterior edge of premaxilla	no	no	yes	no	no	?	no	no
Cheek emargination	yes & no	no	no	yes	no	no	?	no
Preorbital region very short	no	no	no	yes	no	no	no	no
Very large quadrate covering half of cheek	no	no	no	yes	?	?	?	yes
Foramen nervi trigemini trough	no	no	no	yes	?	no	?	yes
Antrum postoticum	small	small	absent	small	absent	?	small	absent
Sulcus eustachii open more ventrally	yes	no	no	no	no	?	no	no
Interorbital width	narrow	very narrow	wide	wide	wide	wide	narrow	wide
Parietal enters orbital margin	no	no	no	yes	no	no	yes	yes
Parietal forms postorbital wall and pocket	yes	?	no	yes	?	?	yes	yes
Medial process of jugal	?	?	small	small	?	?	small	small
Maxilla deep	no	no	yes	yes	no	no	yes	yes
Apertura narium externa	small	small	small	large	small	?	large	large
Prefrontal horn	no	no	no	no	no	no	no	yes
PF-PAR contact	no	no	no	yes	no	no	no	yes

Recent stratigraphic work by Olsson and others (Olsson et al., 1997, 2000, 2002), however, has significantly altered this picture. They have found more complete sequences with asteroid impact features and better microfossil preservation in well cores spanning the Cretaceous/Tertiary (K/T) boundary. Surface exposures, such as at Sewell, usually leach out calcareous foraminifera. The new borehole sequences show a spherule layer, shocked minerals, and an iridium anomaly that presumably mark the impact of the Chicxulub asteroid, followed by tsunami-caused sedimentologic features. The foraminifera sequence is consistent with these events and shows evidence for continuous deposition. The Hornerstown–New Egypt/Navesink formational boundary corresponds closely with the newly interpreted K/T boundary. The updip surface exposure at Sewell, however, is harder to interpret. The absence of foraminifera, inconsistent radiometric dating results (Gallagher, 1993, 2002; see also Gallagher, 1991), and the presence of undoubted Maastrichtian invertebrates in the MFL (Landman et al. 2004) require the ad hoc reworking hypothesis to be invoked for mosasaurs, ammonites, and some microfossils if the MFL is Danian in age. There is also rare earth element evidence (Staron et al., 2001; see also Gallagher, 1992) that the more fragmentary mosasaur bones in the MFL are contemporaneous with the partially articulated specimens, arguing against reworking. However, the multiple lines of evidence for the K/T impact being aligned with the Hornerstown–Navesink/New Egypt lithologic boundary seem to be dominant at present. Landman et al. (2004) also argued for ammonite reworking at the K/T boundary, and their extensive fossil and sedimentologic analysis of the New Jersey K/T boundary and Hornerstown MFL argues for reworking of the ammonites and Cretaceous elements in the MFL. Therefore, we accept the conclusion that the partially articulated vertebrates in the MFL, including *Taphrosphys sulcatus*, are Danian and not Maastrichtian, as concluded earlier.

DEPOSITIONAL ENVIRONMENT: *Taphrosphys sulcatus* is known to occur with certainty only in the lower Hornerstown Formation, MFL (Parris, 1974; Gallagher, 1993). Fossils from this unit have been collected

TABLE 17
Species of *Taphrosphys*

	T. sulcatus	*T. congolensis*	*T. ippolitoi*
Snout expanded	?	no	yes
Premaxilla labial ridge	shallow	deep	shallow
Expanded quadrate shelf	no	no	yes
Sulcus eustachii	opens ventrally	opens ventrally	opens posteroventrally
Lateral surface of maxilla	?	slightly convex	slightly concave
Fossa precolumellaris	absent	absent	present
Cavum tympani	shallow	shallow	deep
Sulcus eustachii with lateral process	no	no	yes
Skull roof surface texture	smooth	smooth	corrugated
Premaxilla wider anteriorly	no	no	yes
Fenestra postotica separated into two foramina	no	no	yes
Tuberculum basioccipitale	smaller	smaller	larger
Rostrum basisphenoidale	short, flat, barely defined	long, lat. compressed, prominent	indet.
Sella turcica	very shallow, wide	deep, narrow	indet.
Dorsum sellae	very low	high	indet.
Processus clinoideus	missing (small if present)	high, large	indet.
Processus inferior parietalis	farther from midline	closer to midline	indet.
Prefrontal	thick	thin	thick

and studied for more than 150 years, and there is an extensive literature relevant to it. The most thorough studies of the MFL are Landman et al. (2004) for the invertebrates and Gallagher (1993) for the vertebrates. Gallagher (1993) reviewed the literature, listed and revised the vertebrate records, and presented a regional analysis of the Maastrichtian–Paleocene deposits in New Jersey. Gallagher (1993) interpreted the MFL as being deposited in a mid-to-outer-shelf environment, with extremely low rates of deposition and almost no clastic input. However, Landman et al. (2004) argued that the preservation of delicate, semiarticulated vertebrates in the MFL may be a consequence of relatively rapid burial by the very active burrowing infauna, evidenced by the many burrows preserved. In addition to the presumably reworked mosasaurs (Gallagher, 2002), there are a number of turtles represented by partially articulated skeletons: *Peretresius* (Baird, 1964), *Osteopygis* (Fastovsky, 1985), *Adocus* and *Agomphus* (Gallagher, 1993), and *Dollochelys* (Parris et al., 1986), as well as *Taphrosphys* (Gaffney, 1975a). The *Bothremys* referred to by Gallagher (1993 and references) is based on shell fragments that are smooth textured and could be any bothremydid, including *Chedighaii*, since the shell of *Bothremys* is not known. Crocodiles, particularly *Hyposaurus*, *Bottosaurus*, and *Thoracosaurus*, are also known from skulls or partial skeletons (Gallagher, 1993). No dinosaurs or pterosaurs are known from the MFL.

It is likely that *Taphrosphys sulcatus* was an offshore, almost pelagic, element of the fauna, living in 400–600 feet of water, the presumed depositional environment of the Hornerstown Formation. It is possible that if all the known specimens of *T. sulcatus* are from the MFL (possible but far from documented), then it is the most common vertebrate fossil in the MFL. If the base of the MFL is the K/T impact horizon, it is possible that all these turtles fell victim to the consequences of the big Mexican Boom (Robertson et al., 2004).

DIAGNOSIS: A bothremydid pleurodire of the genus *Taphrosphys* distinguished from the other two species as follows: from *T. congolensis*: premaxilla labial ridge shallow not deep; rostrum basisphenoidale short and flat, barely defined; sella turcica shallow and

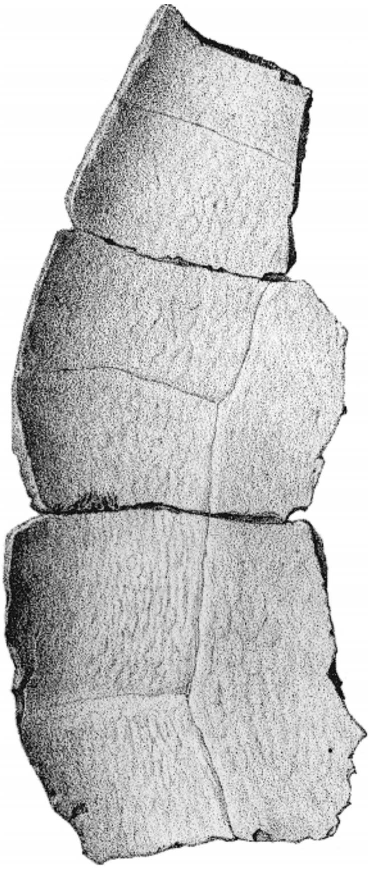

Fig. 20. *Taphrosphys sulcatus* (Leidy), 1865. Original figure of type specimen (described as *Platemys sulcatus*), left peripherals 5–7, AMNH 2522, from Leidy (1865: pl. 19).

wide; dorsum sellae low; processus clinoideus small; processus inferior parietalis farther from midline than in *T. congolensis*. Distinguished from *T. ippolitoi*: quadrate shelf not expanded laterally; sulcus eustachii opens ventrally rather than posteroventrally; fossa precolumellaris absent; sulcus eustachii without lateral process; premaxilla narrow; fenestra postotica not subdivided; tuberculum basioccipitale smaller; cavum tympani shallow rather than deep.

Shell distinguished from "*Taphrosphys*" *olssoni* by plastron relatively narrower than in "*T.*" *olssoni*; xiphiplastral notch shallower and not as circular as in "*T.*" *olssoni*; anterior plastral lobe relatively longer than in "*T.*" *olssoni*; xiphiplastral points more lateral compared with "*T.*" *olssoni*.

ETYMOLOGY: Unknown from original author, possibly from *sulcus*, Latin for furrow or groove, in reference to the ornamentation.

REFERRED MATERIAL: YPM PU 18706, partial shell (described below) collected by Regensburg and Dilkes, August 1960, form the lowermost portion of the Hornerstown Formation, Sewell, New Jersey; YPM PU 18707, partial shell with associated limb and skull fragments (figs. 171, 175), same data as in YPM PU 18706; YPM PU 18708, left xiphiplastron, same data as in YPM PU 18706; ANSP 15544, carapace with partial skull (figs. 170, 176) and limb elements, collected by Keith Madden and James Maddox from the "bone bed" at the Inversand pits, Sewell, New Jersey (Richards and Gallagher, 1974; White, 1972); NJSM 11362, posterior part of skull (figs. 172–174, 176, 177), MFL Hornerstown Formation, Inversand pit, Sewell, New Jersey, coll. January 1975, R. Karpiej; NJSM 10410; a plastron, no data; NJSM 11340, skull fragments collected by D. Parris, 1973, from the lowest foot of the Hornerstown Formation, Inversand pit, Sewell, New Jersey; AMNH 1347, nuchal and first peripheral, "Cretaceous, New Jersey" (label), Cope Collection; AMNH 1343 (Hay, 1908: 118), plastral fragments, "Cretaceous, upper Marl" (label), Cope Collection; AMNH 1129 (Hay, 1908: 119), fragments of shell, "Birmingham, 10–21, 1868, EDC" (label), Cope Collection; AMNH 1470 (Hay, 1908: 119, fig. 119), neural bones, nuchal, carapace fragments, "Barnsboro, 9/8 1870" (label), Cope Collection; AMNH 1472 (type of *Taphrosphys molops* Cope, figured in Cope, 1870: pl. 7, fig. 16, text-figs. 43, 44; Hay, 1908: figs. 112–116), shell fragments, West Jersey Marl Company pits, Barnsboro, New Jersey, August 25, 1868, Cope Collection; AMNH 1474 (Hay, 1908: figs. 117, 118), xiphiplastron and other fragments, Birmingham, New Jersey, Cope Collection; AMNH 1477 (Hay, 1908: fig. 120), shell fragments, West Jersey Marl Company pits, Barnsboro, New Jersey, 1855, Cope Collection; AMNH 1471 (Hay, 1908: fig. 106), anterior plastral bones, mixed with AMNH 1470 (label), Cope Collection; AMNH 1467 (type of *Taphrosphys leslianus* Cope, figured in Hay, 1908: figs. 103–105), partial shell, Hornerstown, New Jersey, collected by Dr. S. Lockwood, Cope Collection; AMNH 1124 (type of *Taphrosphys longinuchus* Cope, figured in Hay, 1908: figs. 101, 102), partial shell with limb fragments (this specimen was apparently mixed with the type of *Adocus agilis* Cope, AMNH 1135), David Haine's marl pit, Medford, New Jersey, March 15, 1870, Cope Collection; AMNH 1468, posterior carapace, Cope Collection (Hay, 1908: figs. 99, 100), Barnsboro, New Jersey, Cope Collection; AMNH 1469, shell fragments, West Jersey Marl Company pits, Barnsboro, New Jersey, 1869, Cope Collection; AMNH 2524 (Cope, 1870: 165, fig. 45), nuchal bone, Barnsboro, New Jersey, in the Rutgers University Cook Collection until 1970; NJSM 12507, possible *Taphrosphys*, Marshalltown Formation, Campanian, Ellisdale, New Jersey (Gallagher et al., 1986).

Hutchison and Weems (1998) identified *Taphrosphys* from the Late Paleocene Williamsburg Formation of South Carolina. Although we identify this material as Taphrosphyini incertae sedis, it should be considered when dealing with Atlantic Coastal Plain *Taphrosphys*, and we list it here. Kingstree locality: ChM PV4763, plastral fragment. St Stephen locality: ChM PV4304, anterior part of right xiphiplastron; ChM PV4159, medial fragment of left hyoplastron; ChM PV4203, anterior fragment of nuchal; ChM PV4200, peripheral 11; ChM PV3060, PV4307, left peripheral 1; ChM PV3881, fragment of right hyoplastron; ChM PV3034, PV4192, peripheral 3 fragments; ChM PV3035, PV3037, PV4301, proximal costal fragments; ChM PV3872, proximal left costal 7; ChM PV3749, PV3789, PV3799, PV3808, PV3849, PV4189, PV4199, PV4306, costal fragments; ChM PV4289, PV4305, bridge peripheral fragments; ChM PV3031, PV3884, xiphiplastron fragment; ChM PV 3058, PV3809, PV3838, PV3842, PV3858, PV 4141, PV4194, PV4302, peripheral fragments; ChM PV3009, PV3776, costal 1 fragments; ChM PV3013, right costal 8 fragment; ChM PV3697, PV3891, PV3925, PV4190, plastral fragments; ChM PV3848, epiplastron fragment; ChM PV3698, PV3728, PV3810, PV3827, PV3928, PV4162, PV4208, shell fragments; SCSM 83.78.14, 83.78.38, peripheral fragments; SCSM 83.78.23, plastron fragment; SCSM 83.78.24, peripheral 1; SCSM 83.78.18, costal 1 fragment.

PREVIOUS WORK: In 1856, Joseph Leidy first recorded the presence of a pleurodire in the fossil record of North America. Consisting of three peripherals and a xiphiplastron, he named the specimen *Platemys sulcatus*, placing it in a genus that was somewhat broadly conceived and that implied that it was a chelid, the modern assignment for this genus. When Cope studied it, he was so enthusiastic about putting this species in a new genus that he created two genera for it, at almost the same time:

> Hay (1908: 104) noted that Cope named two new genera, *Taphrosphys* and *Prochonias*, for the same species (*Platemys sulcatus* Leidy) in the same year, 1869. "Which of these names has precedence depends on which was issued first to the public, the April number of the American Naturalist or Cook's *Geology of New Jersey*. Investigations not wholly satisfactory seem to show that the latter was first publisht [sic] probably some time about the first of March, 1869" Hay (1908: 104). I accept Hay's conclusion that *Taphrosphys* was published (Cope, 1869a) earlier than *Prochonias* (Cope, 1869b). (Gaffney, 1975a: 3).

Cope (1869a, 1869b, 1870) named seven species for *Taphrosphys* (or *Prochonias*) over the next few years, all based on partial shells from the New Jersey greensands. Hay (1908) recognized five of Cope's species and added one, *T. dares*, here considered to be a nomen nudem.

Collins and Lynn (1936) named an anterior plastral lobe from the Miocene Calvert Formation as *Taphrosphys miocenica*. This species was reassigned to *Bothremys* by Gaffney and Zangerl (1968), because it lacks the plastral scale morphology diagnostic of *Taphrosphys*. This species could be either a bothremydid or podocnemidid and is currently considered Pelomedusoides incertae sedis.

Zangerl (1947) assigned to *Taphrosphys* a shell named by Schmidt (1931), *Podocnemis olssoni*, from the Eocene of Peru. Zangerl (1947) also reviewed the species recognized by Hay (1908), saying "the validity of some of the features here listed as 'distinguishing' characters is definitely doubtful" (Zangerl, 1947: 39). In his 1948 Selma paper on "*Podocnemis*" *alabamae*, Zangerl used plastral characters to place *Taphrosphys* within his Pelomedusinae.

Gaffney (1975a) described new shells of *Taphrosphys sulcatus* and either synonymized or reassigned all of Hay's species, recognizing only *sulcatus* and *olssoni*. Broin (1977) reassigned the French Paleocene *Tretosternum ambiguum* (Gaudry, 1890) to *Taphrosphys* as *T. ambiguus*, and suggested that *Taphrosphys* may also occur elsewhere in Europe

DISCUSSION: This, the first described bothremydid (Leidy, 1856, as *Platemys sulcatus*), is still known only from three incomplete skulls, as well as from a great deal of partial shell material. *Taphrosphys sulcatus* is weakly supported as the sister taxon to *T. ippolitoi* with *T. congolensis* (fig. 288). *Taphrosphys* itself is the sister group to *Rhothonemys*, *Phosphatochelys*, and *Ummulisani*.

USNM 357714, identified as *Taphrosphys sulcatus* by Weems (1988), is a pygal, suprapygal, and eleventh left peripheral from the Brightseat Formation, Danian, Hampton Mall, Prince Georges Co., Maryland (Weems, 1988: fig. 3D, E). This fragment is probably from a pleurodire and could very well belong to *Taphrosphys*, but it lacks diagnostic features and is too incomplete to extend the temporal and geographic range on its basis. It is Pelomedusoides incertae sedis.

See table 17 for a comparison of the species in *Taphrosphys*.

Taphrosphys ippolitoi, new species

TYPE SPECIMEN: AMNH 30042, a nearly complete skull (figs. 180, 181).

TYPE LOCALITY: Moroccan phosphates (figs. 14–16), probably Ouled Abdoun, purchased from M. Hammer, 1998.

HORIZON: Danian, based on shark teeth in matrix (Cappetta, personal commun.) (fig. 17, table 11).

DEPOSITIONAL ENVIRONMENT: Near-shore marine (discussion of Moroccan phosphates is under *Araiochelys hirayamai*).

DIAGNOSIS: A bothremydid pleurodire of the genus *Taphrosphys* distinguished from the other two species by these unique characters: expanded rather than narrow snout; quadrate shelf expanded laterally; sulcus eustachii opens posteroventrally rather than ventrally; lateral surface of maxilla slightly concave rather than convex (not known in *T. sulcatus*); deep fossa precolumellaris present; cavum tympani deep rather than shallow; sulcus eustachii with ventral process; skull roof with corrugated surface texture absent in *T. congolensis* and *T. sulcatus*; premaxilla wider than in other species; fenestra postotica divided into two foramina rather than one.

ETYMOLOGY: For Frank Ippolito, Senior Artist in the Department of Paleontology, AMNH, in recognition of his skill and years of service drawing turtles.

REFERRED MATERIAL: AMNH 30500, partial skull lacking palate (figs. 182–184), Danian, based on shark teeth in matrix (Cappetta, personal commun.), Ouled Abdoun phosphates, Morocco, purchased from M. Hammer.

PREVIOUS WORK: None.

DISCUSSION: The skull in *Taphrosphys ippolitoi* is the best known of the species in the genus. The other two species have shell material as well as skulls, but this species does not. It is possible that some of the many shells known from the North African Paleogene (see Dubious Taxa) do belong to *Taphrosphys*, but so far there are no associations.

See table 17 for a comparison of the species in *Taphrosphys*.

Taphrosphys congolensis (Dollo, 1913)

Podocnemis congolensis Dollo, 1912.
Podocnemis congolensis Dollo, 1913.
Bantuchelys congolensis Dollo, 1924.

TYPE SPECIMEN: Uncataloged specimen in the MRAC, consisting of the first right costal, peripherals 2–4, and fragments of peripheral 1 and the nuchal, figured in Wood (1975: fig. 1) and Dollo (1913: pl. 7, figs. 1, 2). As discussed by Wood (1975), Dollo (1924) designated a new type for *Bantuchelys congolensis*, but this is preceded by the Dollo (1913) specimen.

TYPE LOCALITY: Presumably (Dollo, 1913; Wood, 1975) cliff exposures near Landana, Cabinda, a formerly Portuguese colony on the north side of the Congo River (fig. 14).

HORIZON: Presumed to be the sequence consisting of mostly Paleocene sediments (Dollo, 1913; Wood, 1975). Darteville and

Casier (1943, 1959) described 32 beds at Landana, the lower 29 as Paleocene with turtles commonly found in most of them. Most of the turtles come from beds identified as Montian in age (Darteville and Casier, 1959; Wood, 1973, 1975).

DEPOSITIONAL ENVIRONMENT: The *Taphrosphys congolensis* material is thought to have come mostly from near-shore marine beds (Cahen, 1954) and is associated with rarer cheloniid specimens (Wood, 1973) and crocodiles (Dollo, 1914). The fish from these units have been described by Darteville and Casier (1943, 1949, 1959).

DIAGNOSIS: A bothremydid pleurodire of the genus *Taphrosphys* with these unique characters: premaxilla labial ridge deep not shallow; prefrontal thin and short; distinguished from the other two species as follows: from *T. sulcatus*: rostrum basisphenoidale a long and prominent, laterally compressed rod; sella turcica deep and narrow; dorsum sellae high; processus clinoideus high and large; processus inferior parietalis closer to midline than in *T. sulcatus*; from *T. ippolitoi*: snout not expanded; quadrate shelf not expanded laterally; sulcus eustachii opens ventrally rather than posteroventrally; fossa precolumellaris absent; sulcus eustachii without lateral process; premaxilla narrow; fenestra postotica not subdivided; tuberculum basioccipitale smaller; lateral surface of maxilla convex rather than concave; cavum tympani shallow rather than deep.

ETYMOLOGY: Presumably in allusion to the Congo River, adjacent to the type locality.

REFERRED MATERIAL: Uncataloged skull (figs. 187–189) in the MRAC collections, "Landana" presumably Paleocene. Although there is a report (Wood, personal commun.) that shell material was found with this skull, we have not seen it. The identification of this skull with the type shell material is based only on their common occurrence at the same locality.

The following specimens described in Wood (1975), all from the Montian Paleocene, Landana cliffs, Cabinda: Uncataloged MRAC: an eighth cervical vertebra, parts of the carapace including the nuchal, first and second neurals, the pygal, the first and fifth pleurals, and various peripherals (first through third, eighth, ninth, and eleventh) and a pelvis (Wood, 1975: pl. 6; all listed, without numbers, in Dollo, 1924); MRAC 3086A, two adjacent peripherals; MRAC 4794 (Wood, 1975: pls. 3, 4), a nearly complete plastron lacking the right xiphi- and hypoplastron, the lateral portion of the right hyoplastron, and medial parts of the left hypo- and hyoplastron; MRAC 4795 (Wood, 1975: pls. 1, 2), the posterior third of a carapace; MRAC 6316, fragment of a peripheral; MRAC 6320 (Wood, 1975: pl. 6), posterior portion of a pair of xiphiplastra with associated left pelvis; MRAC 6322, nearly complete left xiphiplastron; MRAC 6323, fragment of a right xiphiplastron; MRAC 6328, fragment of the proximal end of a pleural; MRAC 6329, fragment of a peripheral; MRAC 6337 (Wood, 1975: pl. 6), complete pair of xiphiplastra; and MRAC 6340, fragment of a peripheral. Wood (1975) also referred the following undeterminable shell fragments to this species on the basis of their size and surface texture: MRAC 6295, 6313–6315, 6317, 6319, 6321, 6324–6326, 6331–6335, 6338, 6339, 6341–6344, 16024, and 16025.

MRAC 3090, lower jaw (fig. 250; Dollo, 1924: fig. 1; Wood, 1973: pl. 3), bed 12, Landana, Cabinda (Wood, 1973), originally identified as *Bantuchelys congolensis* by Dollo (1924), then redescribed as a lophochelyine toxochelyid by Wood (1973). However, in light of the narrow triturating surfaces of the lower jaw in the only other Taphrosphyini known with a jaw, *Rhothonemys*; we think that there is a good basis for identifying MRAC 3090 as *Taphrosphys congolensis* (see below).

PREVIOUS WORK: First named *Podocnemis congolensis* by Dollo in 1912, without a specimen or diagnosis. The actual description dates from Dollo (1913), the first time the name was used legally (Wood, 1975). Dollo (1913) provided figures of shell pieces and a rudimentary description. Dollo was correct in relating the form to *Podocnemis*-like Pelomedusoides, but he apparently did it on the basis of an axillary musk duct, a character also found in cryptodires. Dollo (1924) identified a lower jaw as belonging to his new genus *Bantuchelys*, which he created for *congolensis*. Wood (1973) identified the lower jaw as a toxochelyid (which we do not agree). Wood (1975) considerably increased knowledge of *congolensis* by describing the plastron, much of the carapace, and reassigning the species to *Taphrosphys* on the basis of plastral morphology (with which we agree).

DISCUSSION: The skull identified here as *Taphrosphys congolensis* (MRAC uncataloged) was originally associated with a shell fragment (Wood, personal commun.) having the typical *Taphrosphys* surface texture. The skull is clearly very similar to skulls of *Taphrosphys sulcatus*, and the most common shells in the Landana sequence are very similar to *Taphrosphys sulcatus*, which is the basis for the identification.

The lower jaw described by Dollo (1924) as the pleurodire "*Bantuchelys congolensis*" and by Wood (1973) as a possible toxochelyid is probably the lower jaw of *Taphrosphys congolensis*. We agree with Dollo's identification and corroborate it with new evidence. The association of the jaw in the same beds as the skull and shell of *Taphrosphys congolensis* supports this idea as argued by Dollo (1924), but as Wood (1973) demonstrated, there are also sea turtles in these units. The discovery of a lower jaw of a closely related member of the tribe Taphrosphyini, the Moroccan *Rhothonemys brinkmani*, adds new support to Dollo's contention. The very narrow lower jaw, MRAC 3090, inconsistent with African pleurodires then known to Wood (1973), was a reason for Wood to reject Dollo's assertion. The discovery of the *Rhothonemys* lower jaw, however, shows that at least one Taphrosphyini also has very narrow lower jaws. Furthermore, MRAC 3090 has a large processus retroarticularis, absent in chelonioids. We have not directly examined MRAC 3090 and cannot present a detailed description of it, but based on figures in Dollo (1924) and Wood (1973) (reproduced here as fig. 250) we can list the following similarities between these specimens: very narrow triturating surface; narrow jaw rami; symphyseal hook; processus retroarticularis present; and V-shaped sulcus cartilaginis meckelii. These similarities are consistent with MRAC 3090 being identified as a Taphrosphyini, but they are not conclusive. We think that Dollo's original identification is well enough supported to include this jaw in the dataset for the few characters that it provides. Exclusion of it does not alter the MPC.

Another lower jaw that may belong to the tribe Taphrosphyini was described by Bardet et al. (2000: 281, fig.7d, e) as a "Chelonioidea gen. and sp. indet." Associated with this jaw are shell elements also described and figured (Bardet et al., 2000: 281, fig.7a–c, g), one of which (fig. 7a) has the iliac scar small, round, and at the shell margin, features probably diagnostic for the tribe Taphrosphyini. The lower jaw is very similar to those of *Rhothonemys* and *Taphrosphys congolensis* (see figs. 248–250).

See table 17 for a comparison of the species in *Taphrosphys*.

Labrostochelys, new genus

TYPE AND ONLY INCLUDED SPECIES: *Labrostochelys galkini*, n. gen. et sp.

DISTRIBUTION: Paleocene of Morocco.

ETYMOLOGY: *Labrostos*, Greek for rushing furiously, in allusion to its sharply pointed head.

DIAGNOSIS: A bothremydid pleurodire of the tribe Taphrosphyini with these unique characters among Taphrosphyini: skull very long and narrow with an elongate, tapering preorbital region; extremely long prefrontal, maxilla, and premaxilla; premaxilla with anterior projection extending anterior to labial ridge unique among turtles; apertura narium externa partially or completely divided by prefrontal and premaxilla; long squamosal projection extending posteriorly to an extent unique among turtles (except for some trionychoids); large, triangular basisphenoid nearly separating pterygoids; interorbital distance relatively shorter than in any other Taphrosphyini; fenestra postotica more horizontal than in other Taphrosphyini; processus trochlearis pterygoidei parasagittal and very small; other differentiating characters are: narrow jugal, in contrast to *Azabbaremys* and *Phosphatochelys*; squamosal with vertical flange, as in *Taphrosphys* and *Phosphatochelys* and in contrast to *Azabbaremys*; triturating surface a broadly curved trough, as in *Taphrosphys* and in contrast to all other

Taphrosphyini; labial ridge on maxilla thin, as in *Taphrosphys* and in contrast to all other Taphrosphyini; sulcus eustachii with dorsal process; foramen posterius canalis carotici interni formed almost completely by quadrate with small contribution of pterygoid; posteroventrally opening pocket on posterior surface of quadrate, as in *Taphrosphys*; postorbital with medial process; sulcus palatinopterygoideus wide; ventrally opening channel at back of skull, as in *Taphrosphys*; condylus mandibularis well anterior to condylus occipitalis, as in *Taphrosphys*; fossa pterygoidea absent.

DISCUSSION: See table 16 for a comparison of the genera in the tribe Taphrosphyini.

Labrostochelys galkini, new species

TYPE SPECIMEN: AMNH 30043, a nearly complete skull (figs. 192, 193, 195, 287) purchased from M. Hammer, 1998.

TYPE LOCALITY: Phosphates near Oued Zem, Ouled Abdoun Basin, Morocco (figs. 14–16).

HORIZON: Presumed to be Tertiary based on matrix.

DEPOSITIONAL ENVIRONMENT: Near-shore marine; discussion of Moroccan phosphate deposits is under *Araiochelys hirayamai.*

DIAGNOSIS: As for genus.

ETYMOLOGY: For Judy Galkin, in appreciation of her years of efforts in the Department of Vertebrate Paleontology, AMNH, on behalf of this project.

REFERRED MATERIAL: AMNH 29984, a nearly complete skull (fig. 194), Danian based on shark teeth in matrix (Cappetta, personal commun.), near Khouribga, Ouled Abdoun Basin, Morocco, donated by H. Galiano, 1995.

PREVIOUS WORK: None.

DISCUSSION: This very narrow-jawed turtle differs considerably from the other bothremydids, resembling trionychids instead. It illustrates the remarkable degree of diversity present in the pleurodires, particularly in the near-shore seas of the African margin. This unusual species is known from two skulls, collapsed dorsoventrally but relatively well preserved. *Labrostochelys* is the sister taxon to *Taphrosphys, Rhothonemys, Ummulisani,* and *Phosphatochelys* (fig. 288).

Phosphatochelys Gaffney and Tong, 2003

TYPE AND ONLY INCLUDED SPECIES: *Phosphatochelys tedfordi* Gaffney and Tong, 2003.

DISTRIBUTION: Eocene of Morocco.

ETYMOLOGY: In allusion to its discovery in the phosphate beds of Morocco.

REVISED DIAGNOSIS: A bothremydid pleurodire of the tribe Taphrosphyini with these unique characters among Taphrosphyini: preorbital region very short with extremely narrow dorsal process of maxilla; wide figure 8-shaped apertura narium externa lying above a premaxilla that slopes posterodorsally to anteroventrally; frontal small and widely separated from orbital margin; broad prefrontal-parietal contact; large quadrate extending anteriorly to cover half of cheek; labial ridge of maxilla deeper than in other Taphrosphyini except *Rhothonemys*; quadratojugal widely separated from jugal, as in *Rhothonemys*; anterolaterally facing trough developed on pterygoid, parietal, and quadrate extending anterodorsally from foramen nervi trigemini ventrolaterally to condylus mandibularis. Other differentiating characters are: squamosal with vertical flange in contrast to *Azabbaremys*; palate dorsally arched, in contrast to *Taphrosphys* and *Labrostochelys*; sulcus eustachii with dorsal process, in contrast to *Azabbaremys* and *Labrostochelys*; foramen posterius canalis carotici interni formed by pterygoid and quadrate; postorbital lacks medial process and postorbital wall open, in contrast to *Arenila* and *Nigeremys*; condylus mandibularis anterior to condylus occipitalis; fossa pterygoidea absent.

DISCUSSION: See table 16 for a comparison of the genera in the tribe Taphrosphyini.

Phosphatochelys tedfordi Gaffney and Tong, 2003

TYPE SPECIMEN: AMNH 30008, complete skull without lower jaws (figs. 198, 199, 203, 279A, 286), gift from François Escuillié.

TYPE LOCALITY: Oued Zem, Ouled Abdoun Basin, Morocco (Gaffney and Tong, 2003) (figs. 14–16).

HORIZON: Ypresian phosphates, Eocene, based on shark teeth in matrix (Cappetta, personal commun.) (fig. 17; see *Araiochelys*

TABLE 18
Comparisons of Two Specimens of *Phosphatochelys tedfordi*

	AMNH 30008	MDEt 26
Premaxilla	shorter, more vertical	longer, less vertical
Triturating surface	narrower, deeper, more vertical	wider, shallower, more horizontal
Orbit	larger	smaller
Cheek emargination	probably present	present
Skull length	67.2 mm	102.9 mm

hirayamai for discussion of Moroccan phosphates; see also table 11). The original description of AMNH 30008 stated that it was Paleocene based on shark teeth analysis. Further study of the shark teeth has shown this to be in error and that the age, again based on shark teeth (Cappetta, personal commun.), is Eocene.

DEPOSITIONAL ENVIRONMENT: Near-shore marine; discussion of Moroccan phosphate deposits is under *Araiochelys hirayamai*.

DIAGNOSIS: As for genus.

ETYMOLOGY: For Dr. Richard H. Tedford, in recognition of his lifelong contributions to vertebrate paleontology in general and to the American Museum of Natural History in particular.

REFERRED MATERIAL: MDEt 26, a nearly complete skull (figs. 200, 201), Ypresian phosphates, based on shark teeth (Cappetta, personal commun.), Ouled Abdoun Basin, Morocco.

PREVIOUS WORK: The species was named and described by Gaffney and Tong (2003). All the figures from that paper, plus new ones, are repeated here. The description and diagnosis have also been revised and updated with the addition of new taxa.

DISCUSSION: It is possible that the two skulls now known for *Phosphatochelys* represent two species. A list of differentiating characters is in table 18 and features are discussed in the descriptive section. However, in the absence of more material and the probability that at least some of these features are individual variation, we have shown restraint and not created a second species.

Ummulisani, new genus

TYPE AND ONLY INCLUDED SPECIES: *Ummulisani rutgersensis*, n. gen. et sp.

DISTRIBUTION: Eocene of Morocco.

ETYMOLOGY: *Ummu-'lIhsan*, Arabic, "mother of integrity". The senior author is very much indebted to Mark Stephen Caponigro of Columbia University for suggesting this name.

DIAGNOSIS: A member of the tribe Taphrosphyini with the unique feature of a hornlike, anterodorsal process on each prefrontal. Other distinguishing features are septum orbitotemporale open and reduced to low ridge on postorbital and parietal, as in *Phosphatochelys*, *Taphrosphys*, and *Azabbaremys*, but in contrast to *Nigeremys* and *Arenila*; apertura narium externa smaller than in *Rhothonemys*, but similar in size to *Phosphatochelys*; preorbital part of skull short, in contrast to *Taphrosphys* and *Labrostochelys*; triturating surface unique in having very deep labial ridge beneath orbit with very low to absent labial ridge beneath apertura narium externa; labial ridge and maxilla very thin, as in *Labrostochelys* and in contrast to *Phosphatochelys* and *Rhothonemys*; wide quadrate-basisphenoid contact, as in *Taphrosphys* and in contrast to all other Taphrosphyini; foramen posterius canalis carotici interni formed entirely by quadrate, as in *Labrostochelys*, but in contrast to all other pleurodires.

DISCUSSION: This genus, now known from three skulls, one with a plastron, is one of the more unusual pleurodires. *Ummulisani* has small hornlike processes on the prefrontals, and these may have borne a scale that would make the process larger in life, as in the squamosal horns of meiolaniids. This is clear evidence for intense mating battles and burrowing. The phylogenetic analysis resolves *Ummulisani* as the sister taxon to *Phosphatochelys*.

See table 16 for a comparison of the genera in the tribe Taphrosphyini.

Ummulisani rutgersensis, new species

TYPE SPECIMEN: AMNH 30563, skull, lacking palate (figs. 206, 207), purchased from Adam Aaronson.

TYPE LOCALITY: "Mrah Iaresh, 20 km south east of Ouled Boali" (from Adam Aaronson), Morocco (figs. 14–16).

HORIZON: "Eocene Phosphates, Upper Ypresian, Couche O" (from Adam Aaronson); see figure 17 and *Araiochelys hirayamai* for discussion of Moroccan phosphates (see table 11).

DEPOSITIONAL ENVIRONMENT: Near-shore marine (see *Araiochelys hirayamai* for discussion of Moroccan phosphates).

DIAGNOSIS: As for genus.

ETYMOLOGY: For Rutgers, the State University of New Jersey, in gratitude to the faculty of the Department of Geology, Rutgers College, New Brunswick, who from 1961 to 1965 provided the senior author with inspiration, encouragement, and friendship, as well as with an education.

REFERRED MATERIAL: AMNH 30562, skull and plastron (figs. 268, 269), Paleogene phosphates, Mrah Iahresh, Morocco; AMNH 30569, skull, Ypresian (based on shark teeth; Cappetta, personal commun.), phosphates, Oued Zem, Ouled Abdoun Basin, Morocco.

PREVIOUS WORK: None.

DISCUSSION: See above.

Rhothonemys, new genus

TYPE AND ONLY INCLUDED SPECIES: *Rhothonemys brinkmani*, n. gen. et sp.

DISTRIBUTION: Paleogene of Morocco.

ETYMOLOGY: *Rhothon*, Greek for nose, beak, in allusion to the gigantic apertura narium externa.

DIAGNOSIS: A bothremydid pleurodire of the tribe Taphrosphyini with these unique characters among Taphrosphyini: apertura narium externa larger than in any other bothremydid; maxilla deeper and longer than in any other bothremydid; anterior half of skull deeper with respect to rest of skull than in any other bothremydid; labial ridge thick in cross section with broadly curved outer surface and slightly concave inner surface. Other differentiating features are: parietal enters orbital margin, in contrast to all bothremydids except *Phosphatochelys* and *Ummulisani*; squamosal with vertical flange, in contrast to *Azabbaremys*; frontal shorter than prefrontal (also in *Phosphatochelys*), enters orbit for its full length; interorbital width narrower than in other Taphrosphyini except in *Labrostochelys*; parietal forms major part of postorbital ridge and pocket, as in *Taphrosphys* and *Phosphatochelys*.

DISCUSSION: See table 16 for a comparison of the genera in the tribe Taphrosphyini.

Rhothonemys brinkmani, new species

TYPE SPECIMEN: AMNH 30521 (figs. 209–211), partial skull, lacking palate and basicranium, and lower jaw.

TYPE LOCALITY: Ouled Abdoun Basin, Morocco, based on matrix composition and included fossils.

HORIZON: Within the Paleogene phosphate sequence, based on matrix composition and included fossils (see table 11).

DEPOSITIONAL ENVIRONMENT: Near-shore marine: discussion of Moroccan phosphate deposits is under *Araiochelys hirayamai.*

DIAGNOSIS: As for genus.

ETYMOLOGY: In recognition of the contributions of Dr. Donald Brinkman, Royal Tyrrell Museum of Palaeontology, to the field of chelonian paleontology and evolution.

REFERRED MATERIAL: None.

PREVIOUS WORK: None.

DISCUSSION: Although the only known specimen of this taxon is an incomplete skull, lacking most of the palate and basicranium, the preserved areas are so different from other pleurodires that it is easily diagnosed. There are also sufficient characters to resolve it in the cladogram (fig. 288) as the sister taxon to *Phosphatochelys* + *Ummulisani.*

Azabbaremys Gaffney, Moody, and Walker, 2001

TYPE AND ONLY INCLUDED SPECIES: *Azabbaremys moragjonesi* Gaffney, Moody, and Walker, 2001.

DISTRIBUTION: Paleocene of eastern Mali.

ETYMOLOGY: *Azabbar*, a monster in popular Mali folk stories in the Tamasheq language. Thanks to Mr. Ibrahim Litny for suggesting this reference.

Revised Diagnosis: A bothremydid pleurodire of the tribe Taphrosphyini with these unique characters among Taphrosphyini: triturating surfaces covered with prominent toothlike crenellations forming a corrugated surface; prefrontal extending anteriorly to anterior edge of premaxilla; deep premaxilla with anterior surface sloping anterodorsal to posteroventral; skull roof broadly convex to a greater degree than in any other Taphrosphyini. Other differentiating characters are: short, wedge-shaped skull higher than in *Arenila* and *Nigeremys*, differing from the short skull of *Phosphatochelys* by the presence of a prominent skull roof convexity; broad jugal exposure in orbit, as in *Phosphatochelys* and *Arenila* but in contrast to *Taphrosphys* and *Labrostochelys*; squamosal without vertical flange in contrast to *Taphrosphys*, *Labrostochelys*, and *Phosphatochelys*; labial ridge thicker than in *Taphrosphys* and *Labrostochelys* but thinner than in *Arenila* and *Nigeremys*; no maxilla-vomer contact; dorsally arched palate in contrast to *Taphrosphys* and *Labrostochelys*; foramen posterius canalis carotici interni formed by pterygoid and quadrate; postorbital lacking medial process; sulcus palatinopterygoideus wide; vomer narrow; condylus mandibularis anterior to condylus occipitalis; basisphenoid solid triangular not excavated posteriorly; postorbital wall open; fossa pterygoidea absent.

Previous Work: See species for Previous Work.

Discussion: See table 16 for a comparison of the genera in the tribe Taphrosphyini.

Azabbaremys moragjonesi Gaffney, Moody, and Walker, 2001

Type Specimen: BMNH R 16370, a complete skull lacking lower jaws (figs. 214–218, 280, 281C, 286A).

Type Locality: North of In Fargas near Samit, eastern Mali (see Moody and Sutcliffe, 1990, 1991, 1993).

Horizon: Teberemt Formation, Paleocene (see Moody and Sutcliffe, 1990, 1991, 1993, 1995).

Depositional Environment: Shallow marine (Moody and Sutcliffe, 1993).

Diagnosis: As for genus.

Etymology: For Ms. Morag Jones, a student who participated in the discovery of this specimen; she died tragically on the first Mali expedition (Gaffney, Moody, and Walker, 2001).

Referred Material: None.

Previous Work: This taxon was named and described by Gaffney, Moody, and Walker (2001); the diagnosis and description is updated and revised here.

Discussion: *Azabbaremys* is the sister taxon to another Mali form, the undescribed CNRST-SUNY 199. Together they are weakly supported as the sister group to the remaining Taphrosphyina.

UNDESCRIBED TAXON: CNRST SUNY 199

Specimen: CNRST SUNY 199, a nearly complete skull, figured in Gaffney, Roberts, Sissoko, Bouré, Tapanila, and O'Leary (in press).

Locality: South of the Adrar des Iforas Mountains, between Saguirilidad and In Fargas, Mali.

Horizon: Middle to upper portion of the Paleocene Teberemt Formation.

Depositional Environment: Near shore marine.

Revised Diagnosis: A bothremydid pleurodire of the subtribe Taphrosphydina with these unique characters among the tribe Taphrosphyini: small pit formed by jugal, maxilla, and palatine on triturating surface; jugal exposed on triturating surface; accessory ridge present on anterior triturating surface; wide palatine-basisphenoid contact separating pterygoids on midline; supraoccipital-quadrate contact present; basioccipital narrowly enters condylus occipitalis; palatine-jugal contact in small septum orbitotemporale; other distinguishing characters: skull relatively long and narrow in contrast to all Taphrosphyini except *Labrostochelys*; fossa pterygoideus deep and narrow as in Nigeremydina but in contrast to all other Taphrosphydina; foramen posterius canalis carotici interni formed by pterygoid, basisphenoid, and quadrate in contrast to all Taphrosphyini except *Taphrosphys*; small remnant of septum orbitotemporale present consisting of ventral parietal process as in *Phosphatochelys* but in contrast to other Taphrosphyini.

TABLE 19
Comparison of *Arenila* and *Nigeremys*

	Arenila	*Nigeremys*
Orbits	larger	smaller
Suborbital maxillary plate	shallower	deeper
Labial ridge	acute	blunt

REFERRED MATERIAL: None.

PREVIOUS WORK: Possibly Gaffney, Roberts, Sissoko, Bouré, Tapanila, and O'Leary (in press), if it is published before the present work.

DISCUSSION: This skull is named and described in a paper that will have a publication date close to the publication date of the present paper, that is, it may be published before or after the present paper. The actual dates of publication are not under the control of the authors. Therefore, we are not mentioning the name of this new taxon here, it is referred to only by its catalogue number, CNRST SUNY 199. Although the description and figures of this skull appear in Gaffney, Roberts, Sissoko, Bouré, Tapanila, and O'Leary (in press), the taxon has been entered into the data set analysed here. The taxon appears as CNRST SUNY 199 in the cladograms in figures 288–292, 294, 296–314, 317.

SUBTRIBE **NIGEREMYDINA**, NEW

TYPE GENUS: *Nigeremys* Broin, 1977.

INCLUDED GENERA: *Nigeremys* Broin, 1977; *Arenila* Lapparent de Broin and Werner, 1998.

DIAGNOSIS: Member of tribe Taphrosphyini with the following characters contrasting with subtribe Taphrosphyina: labial ridge thicker; septum orbitotemporale completely closed; antrum postoticum completely closed (also in *Azabbaremys* and *Ummulisani*); condylus mandibularis posterior to condylus occipitalis; fossa pterygoidea deep and narrow (also in CNRST SUNY 199); basisphenoid ventral outline V-shaped.

DISCUSSION: See table 19 for a comaparison of the genera in the Nigeremydina.

Nigeremys Broin, 1977

Potamochelys Bergounioux and Crouzel, 1968.

TYPE AND ONLY INCLUDED SPECIES: *Potamochelys gigantea* Bergounioux and Crouzel, 1968.

DISTRIBUTION: Maastrichtian of Niger, ?Eocene of Mali.

ETYMOLOGY: Presumably in allusion to the country of Niger.

REVISED DIAGNOSIS: A bothremydid pleurodire of the subtribe Nigeremydina; differs from *Arenila* in these characters: smaller orbits; suborbital maxillary plate deeper; labial ridge blunt.

PREVIOUS WORK: See species Previous Work.

DISCUSSION: See table 16 for a comparison of the genera in the tribe Taphrosphyini.

Nigeremys gigantea (Bergounioux and Crouzel, 1968)

TYPE SPECIMEN: MNHN (P) NIR 1 (label), a nearly complete skull (figs. 221–223) lacking lower jaws with its surface badly eroded. However, Bergounioux and Crouzel (1968: 183) gave its number as "Muséum de Paris … 1964-27".

TYPE LOCALITY: "Niger" (Bergounioux and Crouzel, 1968: 179). "East of Ibeceten, Niger" (Lapparent de Broin and Werner, 1998: 145) (fig. 14).

HORIZON: "Maastrichtian" (Bergounioux and Crouzel, 1968: 183).

DEPOSITIONAL ENVIRONMENT: Specimen found with: "*Mosasaurus nigeriensis* Swinton, *Stratodus apcalis* Cope, *Onchosaurus pharao* Dames …" (Bergounioux and Crouzel, 1968: 183), suggesting a near-shore marine burial environment.

DIAGNOSIS: As for genus.

ETYMOLOGY: Unknown, presumably referring to the large size of the skull.

REFERRED MATERIAL: BMNH R 10927, articulated right and left premaxillae and maxillae, partial quadrate, "loc 3, In Fargas, Samit limestone" (label), Eocene, Mali. The specimen as preserved is almost identical with *Nigeremys*, but it is too incomplete to be certain, so we extend the range of *Nigeremys* with doubt.

PREVIOUS WORK: *Nigeremys* Broin, 1977 began life as *Potamochelys* Bergounioux and Crouzel, 1968. Bergounioux and Crouzel (1968) named what they thought was a new genus for a large, battered skull from Niger. They thought that in the absence of a carapace it was difficult to place their "*Potamochelys*" taxonomically, but they concluded that it was a cryptodire, possibly related to chelydrids. F. M. Bergounioux, a Catholic priest in Lyon, was infamous for his other work on fossil turtles (see section on Dubious Taxa). Bergounioux and Crouzel (1968) gave a brief description with dorsal and ventral photographs of the skull (Bergounioux and Crouzel, 1968: figs. 1, 2) and a dorsal line drawing (fig. 1b). The dorsal line drawing is in error; there are no nasals and we have interpreted other sutures differently, although sutures are very difficult to see on this specimen. Later, Broin (1977: 83) recognized that *Potamochelys* Bergounioux and Crouzel, 1968 was preoccupied by *Potamochelys* Fitzinger, 1843 (a synonym of *Trionyx* according to Romer, 1956: 514), and created the new genus, *Nigeremys*, for the species *gigantea*.

Bergounioux and Crouzel (1968) had referred their "*Potamochelys*" to the Chelydridae with doubt, and Broin (1977) was the first to recognize its pleurodiran affinities. Antunes and Broin (1988) identified *Nigeremys* as a bothremydid, but unfortunately allied it with the undiagnosable "*Sokotochelys*" Halstead, 1979b in a "Groupe *Nigeremys*", which was in a larger group containing *Bothremys* and *Rosasia*, but not *Taphrosphys*. In the description and discussion sections, there was new information about *Nigeremys*.

Lapparent de Broin and Werner (1998) provided the most complete previous description of *Nigeremys*. They argued for the close relationship of *Arenila* with *Nigeremys*, a conclusion supported by us, and provided a comparative description for the two taxa, line drawings for *Nigeremys* (fig. 4b, f) and measurements of the type skull, MNHN(P) NIR 1. Lapparent de Broin and Werner (1998) showed the "phyletic Group *Nigeremys*" containing *Nigeremys*, "*Sokotochelys*", and *Arenila*, along with more fragmentary material.

DISCUSSION: *Nigeremys* is based on a nearly complete, but poorly preserved and badly prepared, skull. Painted sutures and repair materials obscure important areas. Although we disagree with some of the Lapparent de Broin and Werner (1998) sutures, we agree with their conclusion that *Nigeremys* is closely related to *Arenila*. In fact, our reconstruction of *Arenila* shows it to be very similar to *Nigeremys*. Both could be placed in the same genus as separate species, as they are a strictly monophyletic group, but we keep the genera separate here for old times' sake.

Arenila Lapparent de Broin and Werner, 1998

TYPE AND ONLY INCLUDED SPECIES: *Arenila krebsi* Lapparent de Broin and Werner, 1998.

DISTRIBUTION: Late Cretaceous, Egypt.

ETYMOLOGY: *Arena*, Latin for sand (Lapparent de Broin and Werner, 1998).

DIAGNOSIS: A bothremydid pleurodire of the subtribe Nigeremydina; differs from *Nigeremys* in these characters: larger orbits; suborbital maxillary plate shallower; labial ridge acute.

DISCUSSION: See table 16 for a comparison of the genera in the tribe Taphrosphyini.

Arenila krebsi Lapparent de Broin and Werner, 1998

TYPE SPECIMEN: TUB Vb-641, a partial skull (figs. 226–230).

TYPE LOCALITY: "Ammonite Hills, interdunal channel 28, loc. 291080/2" (Lapparent de Broin and Werner, 1998: 174) (fig. 14).

HORIZON: "Dakla Formation, Ammonite Hill Member, Maastrichtian" (Lapparent de Broin and Werner, 1998: 174).

DIAGNOSIS: Same as for genus.

ETYMOLOGY: In honor of Dr. Bernard Krebs (Lapparent de Broin and Werner, 1998: 174).

REFERRED MATERIAL: Lapparent de Broin and Werner (1998) identified a partial carapace, TUB Vb-648, lacking peripherals, nuchal, and pygal, as "? cf. *Arenila krebsi*". The "cf." is an abbreviation of the Latin, *confere*, meaning to compare, but there is no shell associated with the type skull to be used for comparison. The reasons for identifying this shell as *Arenila* are not specifically stated, but it occurs in the same unit as the type skull, is of an appropriate size, and is excluded from their "*Bothremys* Group" and "*Taphrosphys* Group" by Lapparent de Broin and Werner

(1998). It is too incomplete to be included in the dataset presented here, and is considered Pelomedusoides incertae sedis.

PREVIOUS WORK: *Arenila* has been described only in Lapparent de Broin and Werner (1998). The photographs, plates VI and VII (Lapparent de Broin and Werner, 1998), are of good quality but lack line drawings identifying elements, and only partial restorations of the palate and lateral views are shown (Lapparent de Broin and Werner, 1998: fig. 12). Here we provide line drawings for these photographs (figs. 227, 229) as well as new photographs in the same orientation.

DISCUSSION: Lapparent de Broin and Werner (1998) identified *Arenila* as a bothremydid and a member of the "*Nigeremys* Group". They identified a separate "*Taphrosphys* Group". Here, we argue that *Arenila* is closely related to *Nigeremys* and agree with Lapparent de Broin and Werner.

Examinations of the type skull and associated material in the Technische Universität Berlin revealed that two skull elements, not identified by Lapparent de Broin and Werner, are part of the type skull, TUB Vb-641. These elements are included in the line drawings. They are: a partial right maxilla, premaxilla, and vomer; and a partial right pterygoid consisting of the processus trochlearis pterygoidei. These elements articulate with the type skull directly, so there is little doubt of the association.

Our restoration of the skull of *Arenila* (fig. 224) differs from that of Lapparent de Broin and Werner (1998: fig. 12) in some details in ventral view and in overall shape in lateral view. These differences result from the newly added elements, different interpretation of some sutures, and a different interpretation of postmortem crushing. Considering the poor state of preservation of the type skull, the new restoration does not differ greatly from the original one.

DUBIOUS TAXA

A congenital disease of paleontology is the naming of poorly preserved specimens as new taxa. No doubt many of these are actually organic remains, although the published descriptions often do not demonstrate this unequivocally. Nonetheless, many names in the literature are based on inadequate specimens, and much effort is spent repeating them, usually to no positive effect. We have essentially divided the names into those with hope for future workers (incertae sedis) and those without hope of further identifications (nomina dubia). We have chosen these designations, which are commonly used to categorize poorly known taxa. We use "incertae sedis" (= "of uncertain position") to designate taxa that preserve enough characters to be usefully diagnosed at the alpha level, but do not have enough characters to test their wider relationships at the present time. In our opinion, these taxa are complete enough so that there is hope for future material to be found and indentified with the type specimens. For incertae sedis the degree of uncertainty is always indicated.

The incertae sedis designation is not used for taxa that cannot be diagnosed adequately on the basis of the type specimen. Rather, the designation "nomen dubium" is used in the sense of Mayr (1969: 347), "an available name which cannot be assigned to a definite taxon owing to shortcomings in the original diagnosis or the type material." The decision on what are an adequate diagnosis and type specimen is subjective, but we are of the opinion that a more restricted view serves systematists and other researchers better than a more lax one. Certainly many of these fragmentary specimens may represent unique taxa, but once they are named and become referred to in the literature, they are often used as the basis for studies in biogeography, diversity, and evolution, when the original material is completely inadequate for such work.

TAXA INCERTAE SEDIS

Apodichelys lucianoi Price, 1954

TYPE SPECIMEN: DNPM 418-R, a steinkern.

DISCUSSION: This taxon is from the Late Cretaceous Apodi Formation of Rio Grande del Norte, Brazil, and is described by Price (1954). It is clearly a pleurodire, showing a sutured pelvis, and study of the type supports the presence of laterally placed mesoplastra. Antunes and Broin (1988) placed it in the Bothremydidae because the internal mold shows "une morphologie et des rapports de dimensions conformes a ceux de *Bothremys*" (Antunes and Broin, 1988: 179). Presumably this refers to the short, broad, anterior plastral lobe seen in both *Apodichelys* and "*Bothremys*" (now *Chedighaii*) *barberi*. However, while this taxon may be a bothremydid, a wide anterior lobe is not sufficient to objectively identify *Apodichelys* as such. The podocnemidid, *Bairdemys venezuelensis* (fig. 275) also has a short, wide anterior lobe. Nonetheless, *Apodichelys* is diagnosable; the wide, nearly horizontal epiplastra are distinct from other Pelomedusoides. However, it has too many missing data to be analyzed in our dataset.

CURRENT STATUS: Pelomedusoides incertae sedis.

"*Chrysemys*" *montolivensis* Roman, 1897

TYPE SPECIMEN: University of Lyon 92839.

DISCUSSION: This record consists of a shell with carapace and plastron from the Oligocene of Montoulieu, France. First described by Roman (1897) as an emydid, it was questionably identified as the podocnemidid *Neochelys* by Broin (1977). Roman has photographs (Roman, 1897) and Broin has line drawings showing sutures, sulci, and a dorsal view of the xiphiplastron (Broin, 1977: fig. 66). Later, Lapparent de Broin and Werner (1998) and Lapparent de Broin (2001) identified this taxon as a bothremydid, but without giving any reasons. The shell is nearly complete, but unfortunately lacks the anteromedial region, so that the nuchal bone, entoplastron, and most of the epiplastra, all areas with useful characters, are missing. The relatively short anterior plastral lobe is typical of bothremydids, but also occurs in podocnemidids (i.e., *Bairdemys*). The pectoral scale barely reaches the mesoplastron, also found in both bothremydids and podocnemidids. The surface ornamentation appears to be smooth. There are seven neurals, with the seventh and eighth costals meeting on the midline, again found in both podocnemidids and bothremydids. The pubic articulation scar is small, also not unique to either family. At present, this form, while probably a member of the Pelomedusoides, could be either a bothremydid or a podocnemidid. It is inadequate to extend the range of the Bothremydidae into the Oligocene, as claimed by Lapparent de Broin and Werner (1998). While we accept it as diagnosable, it is only marginally so.

CURRENT STATUS: Pelomedusoides incertae sedis.

Palaeaspis conybearii (Owen, 1849)
Gray, 1870

Palaeaspis bowerbanki (Owen, 1842)
Gray, 1870

TYPE SPECIMEN: There may be more than one taxon involved in this series of names, as suggested by Broin (1977: 49), although Williams (1954a) synonymized them all as *Palaeaspis conybearii*. The oldest of the species is *Platemys bowerbanki* Owen, 1842, with a type that is apparently lost (Williams, 1954a), but the genus *Palaeaspis* was named by Gray (1870) for *Emys conybearii* Owen, 1849 (*in* Owen and Bell, 1849) with BMNH R39449 as a type. Both are partial shells.

DISCUSSION: The Early Eocene London Clay of England has yielded a series of shells (Clouter et al., 2000) identifiable as Pelomedusoides, which were reviewed by Williams (1954a), who concluded that there was one species, correctly named *Palaeaspis conybearii* (Owen). Broin (1977: 48–49) commented on the material and compared it with *Taphrosphys*, noting that the surface texture and position of the pectoral/abdominal sulcus were similar. However, she concluded that the shell material was poorly described and probably included more than one taxon. A partial skull, BMNH 38953 (Owen, 1850: pl. 29, figs. 1, 2) from Sheppy, Kent, figured and described by Owen (1850) as *Platemys bowerbanki*, was suggested by Broin (1977: 49) as possibly *Erymnochelys*. However, Ren Hirayama has recently noted (personal commun.; we are also grateful to Sandra Chapman for assistance) that the skull has a processus trochlearis oticum and appears to be a carretochelyid. Broin (1988: 138) placed "*Palaeaspis bowerbanki* (Owen, 1842)" as possibly being part of *Neochelys* Bergounioux, 1954 without comment. Lapparent de Broin (2001: 169) placed *Palaeaspis* Gray, 1970 in the Bothremydidae, also without comment, and we cannot find a previous reference explaining either of these attributions. On the basis of the described shell material (and the BMNH material that we have seen), it is not possible to assign any of the separate (or synonymized) species of the London Clay pleurodire/pleurodires to a family.

CURRENT STATUS: Pelomedusoides incertae sedis.

"*Podocnemis*" *somaliensis* Walker, 1966

TYPE SPECIMEN: Partial shell, Sedgwick Museum, Cambridge, C 54.276 (Walker, 1966).

DISCUSSION: This nearly complete shell from the Eocene of Somalia has the sutural pattern preserved, but apparently lacks sulci impressions. Entering it in our dataset produces a whopping 87% missing data, but the miracle of our ability to analyze meager information resolves "*Podocnemis*" *somaliensis* with the Bothremydidae, a conclusion apparently consistent with that of Lapparent de Broin (2000a), who listed it as "*Bothremys somaliensis* (Walker, 1966)." It is not possible to assign this shell to a genus, however, and its recognition as a bothremydid must be considered tenuous at best.

CURRENT STATUS: Bothremydidae incertae sedis.

"*Podocnemis*" *parva* Haas, 1978a

TYPE SPECIMEN: A nearly complete shell, Hebrew University of Jerusalem, Israel, Department of Zoology collection, HUJP-Testudinata-3 (Haas, 1978a).

DISCUSSION: See "*Podocnemis*" *judea.*

"*Podocnemis*" *judea* Haas, 1978b

TYPE SPECIMEN: A nearly complete shell, Hebrew University of Jerusalem, Israel, Department of Zoology collection, HUJP 3664.

DISCUSSION: Haas (1978a, 1978b) described a series of small shells from the Cenomanian of Israel. The criteria differentiating two species among these shells seem to be within the variation seen in some recent pleurodire species. Apparently Broin (1988) and Lapparent de Broin and Werner (1998) came to the same conclusion, as they only list the older species as valid. They also place *parva* in *Bothremys*. When *parva*/*judea* is entered in the dataset (83% missing data) and analyzed in the larger dataset, it resolves as the sister taxon to *Foxemys* + *Polysternon*. This is a little surprising considering the large amount of missing data, but the few characters available produce this single cladogram. However, this material has not been reexamined in recent years, and a new assessment of the character distributions is needed to clarify some of the characters that are inconsistent in the figures. It is necessary to leave *parva*/*judea* without a generic assignment and place it incertae sedis within the Bothremydini until it is better known.

CURRENT STATUS: Bothremydini incertae sedis.

"*Taphrosphys*" *olssoni* (Schmidt, 1931)

TYPE SPECIMEN: FMNH P14172, partial shell (fig. 267).

DISCUSSION: This partial shell was described by Schmidt (1931) from the Eocene of Peru as *Podocnemis olssoni.* Zangerl recognized its similarities to *Taphrosphys* and changed it to *Taphrosphys olssoni.* This was accepted by Gaffney (1975a), who provided comparative diagnoses for *T. olssoni* and *T. sulcatus* (table 24). When entered into the dataset, this taxon comes out in a multichotomy with all members of the Taphrosphyini. We remove the species *olssoni* from *Taphrosphys.*

CURRENT STATUS: Taphrosphyini incertae sedis.

"*Taphrosphys*" *ambiguus* (Gaudry, 1890)

TYPE SPECIMEN: MNHN-MTA1, a plastron (fig. 267).

DISCUSSION: A plastron from the Paleocene of France was named *Tretosternum ambiguum* by Gaudry (1890:) 251, fig. 355 and reassigned to *Taphrosphys* by Broin (1977), who redescribed and figured it (Broin, 1977: fig. 4, pl. 4, figs. 9, 10). "*Taphrosphys*" *ambiguus* has enough characters to enter into the dataset, which, when analyzed, shows it in a multichotomy with all Taphrosphyini. The available material is insufficient to place in a genus (table 24).

CURRENT STATUS: Taphrosphyini incertae sedis.

"*Taphrosphys*" *miocenica* Collins and Lynn, 1936

TYPE SPECIMEN: USNM 13784, anterior lobe of a plastron.

Discussion: This partial plastron from the Miocene Calvert Formation of Camp Roosevelt, Maryland, was named *Taphrosphys miocenica* (Collins and Lynn, 1936: pl. 1). The assignment to *Taphrosphys* was rejected by Gaffney and Zangerl (1968: 208) because *Taphrosphys* is characterized by a large intergular scale separating the gular scales, humeral scales, and part of the pectoral scales. In "*Taphrosphys*" *miocenica* the intergular separates only the gulars and part of the humerals, as in *Bothremys*. Gaffney and Zangerl therefore assigned "*T.*" *miocenica* to *Bothremys*. However, Gaffney (1975a) rejected this generic assignment, because the *Bothremys* scale pattern also occurs in *Podocnemis* and other taxa and is inadequate for a generic determination. "*Taphrosphys*" *miocenica* was therefore made a nomen dubium. The *Bothremys* scale pattern, in fact, occurs widely in Pelomedusoides, within Bothremydidae as well as Podocnemididae. It is notable that *Bairdemys* (fig. 275; Gaffney and Wood, 2002; Wood and Díaz de Gamero, 1971) has an anterior plastral lobe nearly identical in size, shape, and scale arrangement to that in "*Taphrosphys*" *miocenica*. *Bairdemys* has a short, rounded, anterior plastral lobe (fig. 275), as in many bothremydids. *Bairdemys* occurs in the Miocene of Venezuela and Puerto Rico. However, the group that it belongs to within the Podocnemididae, the *Shweboemys* Group, is known throughout the Caribbean (Domning and Clark, 1993 [this record contains the posterior end of a lower jaw that is a podocnemidid]; Domning et al., 1997; Sánchez-Villagra et al., 2000; Gaffney and Wood, 2002). Furthermore, an undescribed lower jaw in the South Carolina State Museum (SCSM SC90.16.24) from the Oligocene of South Carolina is very similar to the lower jaw of *Bairdemys* from Venezuela (we are very grateful to Dr. R. Weems for bringing this specimen to our attention). The fact that *Bairdemys* and its near relatives are now known to occur in the mid-Tertiary of the Atlantic coast as well as the Caribbean, and that the morphology of "*Taphrosphys/Bothremys*" *miocenica* is so similar to that group, suggests that this specimen could easily be a podocnemidid and should not be used as a mid-Tertiary record of the Bothremydidae. The anterior plastral lobe is too incomplete to enter into the dataset.

Current Status: Pelomedusoides incertae sedis.

Taquetochelys decorata Broin, 1980

Type Specimen: MNHN-GDF 847, a right hypoplastron (Broin, 1980: pl. 3, fig. 10).

Discussion: These shell fragments from the Aptian of Gadoufaoua, Niger (Broin, 1980), have a surface texture similar to that of *Araripemys*. The texture is not unique to *Araripemys*, however. The type alone is not diagnosable as a distinct taxon. It is unique only if locality and age are considered. The described fragments are inadequate to show a sister-group relationship to *Araripemys*. There are too many missing data to enter into our dataset. If new articulated specimens from the same locality become available, this taxon might become diagnosable.

Current Status: Pleurodira incertae sedis.

TAXA NOMINA DUBIA

Apertotemporalis baharijensis Stromer, 1934

Type Specimen: BSP uncataloged, now lost (Crumly, 1984).

Discussion: This partial skull from the Late Cretaceous of Egypt was described and figured by Stromer (1934: plate 1, fig. 1a–c) but was apparently later destroyed in World War II (Crumly, 1984) with much of the Munich collection. The figures show a turtle skull, which Antunes and Broin (1988), Broin (1988), Lapparent de Broin and Werner (1998), and Lapparent de Broin (2000a) assigned to the Bothremydidae. Antunes and Broin (1988) based this on "Le dessin du reste de crâne montre une morphologie et les dimensions compatibles avec *Bothremys* et *Rosasia* …" (Antunes and Broin, 1988: 179). In the absence of the original, the only information on "*Apertotemporalis*" is the description and figures in Stromer (1934), which show a badly eroded and damaged partial skull of something that would probably be difficult or impossible to objectively diagnose even if the original were available. Even if new, complete material were to be found at the type locality, identifying it with the type figures would be very argumentative. The only apparent feature of the skull from the figures is a fully enclosed incisura columellae auris, consistent with the Bothremydidae, but also found in other groups. In fact, an Egyptian bothremydid skull, *Arenila*, has been found and it could very well be the same species as "*Apertotemporalis*," but this is impossible to determine given the absence of a type specimen. The figures alone are inadequate to diagnose the taxon, and in the absence of a type specimen, the taxon should be ignored.

CURRENT STATUS: Nomen dubium.

Carteremys leithi (Carter, 1852) Williams, 1953

TYPE SPECIMEN: None designated in original description of species (Carter, 1852); no specimens seen by subsequent authors; present whereabouts unknown. Williams (1953) based his diagnosis of a new genus on the figures of Carter (1852), which consist of two plates showing a reconstruction based on nine partial specimens. The material figured shows a carapace, plastron, partial skull, and partial lower jaws. If available, this material would presumably allow an adequate diagnosis, but there is no evidence that this material has been available since 1852.

LOCALITY AND HORIZON: Possibly Maastrichtian or Paleocene Intertrappean beds of Bombay (Mumbai), India (Wood, 1970).

DISCUSSION: "*Testudo*" *leithii* Carter was originally recognized as a pleurodire by its author, despite being referred to "*Testudo*". Subsequently, Gray (1871) assigned the species to the chelid genus, *Hydraspis*, which was questioned by Williams (1953), who suggested that the original figures showed a mesoplastron and that the skull looked like *Stereogenys*, a podocnemidid. However, the original description and Williams' diagnosis of the genus are inadequate to diagnose this taxon. The original figures are reconstructions. No figure of the original material exists, so that there is no possibility of designating a lectotype on the basis of the figures, as the original figures are reconstructions. If at some future date Carter's original, properly labeled material becomes available, then this taxon might be resurrected.

Wood (1970) added further arguments that *C. leithii* is a pelomedusid (sensu lato, now equals Pelomedusoides) and concurred in recognizing *Carteremys* as a diagnosable genus. Jain (1977) added another species, *C. pisdurensis*, an undoubted Pelomedusoides later reassigned to the genus *Shweboemys* (Jain, 1986). We concur that this species is a podocnemidid and not a bothremydid. Singh et al. (1998), in the initial announcement of the skull that was later named *Sankuchemys*, also considered *Carteremys* a nomen dubium.

Williams (1953) also figured a carapace from the Intertrappean beds of Worli Hill, Bombay (Mumbai), that he identified as *Carteremys leithii*, and which was apparently found in the 1940s by Dr. R. N. Sukheswala. This carapace was figured and described by Singh et al. (1998), along with a plastron anterior lobe. Williams (1953) apparently identified this carapace as *Carteremys* on the basis of its locality, small size, and surface texture. The association of the plastron with the carapace may not be original, as Williams (1953) specifically stated that the plastron and skull were missing. However, the plastral lobe is of the right size and apparently is from the same locality. The plastron shows very small gular scales with a large pair of intergular scales completely separating the humerals, similar but not identical to the figure in Carter (1852). Therefore, it is quite possible that this shell material could be the same species that Carter (1852) described, and that this is the shell of the skull described as *Sankuchemys*. However, even if the new shell material were accepted as the shell of *Sankuchemys*, tenuous at best, it is even harder to argue that these shell specimens are the same species as those described by Carter in 1852.

CURRENT STATUS: Nomen dubium.

Crassachelys neurirregularis (Bergounioux, 1952)

TYPE SPECIMEN: None designated by original author of *Gafsachelys neurirregularis* Bergounioux, 1952. A neotype designated by Moody (1972) is a carapace fragment in plate 46, figure 2 of Bergounioux (1952).

DISCUSSION: In 1972, Moody used the neural number to recognize three genera in the Tunisian Eocene Pelomedusoides. Two of these, *Gafsachelys* and *Eusarkia*, had been named, so he added a third for *Gafsachelys* *neurirregularis*. In Moody's scheme, *Gafsachelys* Stefano, 1903 is restricted to seven neural bones in contact (Moody, 1972: pl. 16); *Crassachelys* Moody 1972 is characterized by smaller neurals, five in number, some separated by costals meeting on the midline (Bergounioux, 1952: pl. 46, figs. 4, 5; 1956: figs. 22, 23, pl. 10, fig. 2, pls. 11–13; Moody, 1972: pl. 16, fig. 2, pl. 17); and *Eusarkia* Bergounioux, 1952 is characterized by an absence of neurals (Bergounioux, 1952: pl. 46, figs. 1–3; 1956: fig. 20; Moody, 1972: fig. 3). Broin (1977) and Antunes and Broin (1988) have disputed the use of this character, ascribing it to individual variation and lumping all three genera into *Taphrosphys*. Broin (1988) and Lapparent de Broin (2000a) also synonymized *Crassachelys* with *Taphrosphys*. However, the neotype designated by Moody (1972) consists only of a central part of a carapace showing discontinuous neurals and a *Taphrosphys*-like texture. Given the variations in the neural pattern in North African Paleogene Pelomedusoides, this neotype must be considered inadequate for a diagnosable taxon.

When dealing with this large suite of Tunisian shells, the Moroccan specimens must be kept in mind. Broin (1988) and Lapparent de Broin (2000a) synonymized all these Tunisian taxa as *Taphrosphys phosphaticus*. Aside from the designation of *phosphaticus* as a nomen dubium, there is a problem using shell characters alone to diagnose *Taphrosphys* in light of the new discoveries in Morocco. The Moroccan fauna has yielded a diverse group of taxa related to *Taphrosphys*. The discovery of a skull-shell association for *Ummulisani* shows that many shell characters used by earlier authors to diagnose *Taphrosphys* have a wider distribution, perhaps wider than the tribe Taphrosphyini. Although there are a number of shells known from the Tunisian phosphates, most are steinkerns. Complete shells with extensive bone preserved are relatively rare, so analyzing the possible correlation of neural number with other characters is difficult. Therefore, the identification of alpha taxa among the Tunisian shells is problematic, especially in the absence of any skull-shell associations. It might be possible to recognize some of the best preserved specimens as tribe Taphrosphyini incertae sedis, but unfortunately this excludes most of the type specimens.

CURRENT STATUS: Nomen dubium.

Euclastochelys interrupta Bergounioux, 1955a

TYPE SPECIMEN: None designated. Moody (1972) did not mention this taxon. We designate the shell figured in Bergounioux (1956: pl. 14, figs. 1, 2), TU G1, in the collection of the Service Géologique du Ministere des Travaux Publique de Tunisie, Tunisia, as lectotype.

DISCUSSION: This taxon was named in Bergounioux (1955a) without diagnosis or description. Bergounioux (1956: pls. 14, 15) described and figured it, but did not designate a type. No subsequent author has designated a lectotype, and we do so here. Bergounioux (1956) described and figured a second shell, TU G2, and these are the only specimens ascribed to this species. Antunes and Broin (1988), Broin (1988), and Lapparent de Broin (2000a) synonymized this taxon with *Taphrosphys*.

This species has, if Bergounioux (1956: figs. 26, 27) is to be believed, a more complete series of neurals than do *Crassachelys* and *Eusarkia*, as delimited by Moody (1972), but is very similar to *Gafsachelys*. Both described specimens are primarily steinkerns, lack carapacial bone, and have an incomplete plastron preserved. We agree with Lapparent de Broin (2000a) that none of these Tunisian taxa can be objectively distinguished from each other, including this one. Like the others, it could be *Taphrosphys*, but that assemblage of shell characters has a wider distribution than does *Taphrosphys*. It is apparent from the fact that following the discovery of more specimens from this area, there is still no consensus on what can be diagnosed and identified, that these shells are inadequate for a taxon diagnosis, even though they can be placed in the Taphrosphyini.

CURRENT STATUS: Nomen dubium.

Eusarkia rotundiformis Bergounioux, 1952

TYPE SPECIMEN: MNHN 1969-1, most of a carapace and plastron, formerly in the Institut National Agronomique de Paris.

DISCUSSION: Bergounioux (1952) created this genus and species on the basis of a partial shell and steinkern and placed it in his new pleurodiran family Eusarkiidae. It is characterized by the absence of the neurals (Bergounioux, 1952). In 1956, the same author redescribed the species, said to be based on additional specimens, but the figures are the same as the type specimen. Bergounioux and Crouzel (1968) described a very poor specimen as *Eusarkia* sp. Moody (1972) recognized this genus and species and added to it a shell in the Metlaoui Museum. Broin (1977:45) reexamined the holotype of this species housed in the MNHN in Paris and noted that "the neurals are absent dorsally and ventrally on the anterior part. On the posterior part where only the internal mold is preserved, the 6th and 7th neurals appear ventrally posterior to the midline meeting of the 5th costals." She suggested therefore that *Eusarkia rotundiformis* and *Crassachelys neurirregularis* (Bergounioux, 1952) may be individual variation in a single species. In addition, these two taxa have the same neural morphology. *Eusarkia* was synonymized with *Taphrosphys* by Antunes and Broin (1988), Broin (1988), and Lapparent de Broin (2000a), but the relevant characters have a wider distribution than the genus *Taphrosphys*. It is unlikely that any of these possible taxa can be distinguished solely on the basis of a steinkern and probably not even a complete shell. The considerable skull diversity now known in the North African Pelomedusoides is not reflected in the more conservative shells (see above discussion under *Crassachelys*). The type of *Eusarkia rotundiformis* is resolved in a multichotomy with Taphrosphyini.

CURRENT STATUS: Nomen dubium.

Gafsachelys moularensis Bergounioux, 1955a

TYPE SPECIMEN: "G1", probably in the collection of the Mines de Moularès, Tunisia, a partial shell figured in Bergounioux (1956: pl. 10, fig. 1).

DISCUSSION: Bergounioux (1956: fig. 21) did provide some comic relief for hard-pressed paleontologists when he named a new species *Gafsachelys moularensis* by describing a turtle shell backwards (Bergounioux, 1956: fig. 21; see also *G. neurrirregularis*, fig. 24), with the pygal labeled nuchal and vice versa (showing that all turtle shells look alike, no matter what direction they are going). This was only to be expected from the author of the world's oldest turtle, *Archaeochelys pougeti* Bergounioux, 1938, a Permian concretion.

CURRENT STATUS: Nomen dubium.

Gafsachelys phosphatica Stefano, 1903

TYPE SPECIMEN: A partial shell steinkern in the MNHN, formerly in L'Ecole Nationale Supérieure des Mines de Paris.

DISCUSSION: Stefano (1903) was the first to study turtle remains from the Ypresian of Gafsa, Tunisia. In 1903 he created *Gafsachelys phosphatica* on the basis of a partial shell in the collection of "Ecole Nationale Supérieure des Mines de Paris" and placed it in the Chelydridae. Bergounioux (1952) correctly rejected the species *phosphatica* (but illegally) and created *neurirregularis* as the replacement "type species" of the genus *Gafsachelys*. He placed this genus in "Family Incertae sedis" in Cryptodires. Bergounioux (1956) erected another species of *Gafsachelys*, *G. moularensis*, and included *Gafsachelys* in the family Eusarkiidae, created by the same author in 1952 (Bergounioux, 1952, 1955b, 1956). Moody (1972) rehabilitated *Gafsachelys phosphatica* Stefano, 1903 and characterized it by seven continuous neurals. He assigned four more shells in the Metlaoui Museum, Tunisia, to this species. Broin (1977) reexamined the type specimen of *Gafsachelys phosphatica* and confirmed that it does have the continuous series of neurals. She pointed out, however, that this specimen cannot even be assigned to Pelomedusoides with certainty since cheloniids are also present in the same locality, and the latter also have narrow neurals. She rejected *Gafsachelys phosphatica* since it is based on an indeterminate specimen. Moody and Buffetaut (1981) reaffirmed their recognition of the three monotypic genera, *Gafsachelys*, *Crassachelys*, and *Eusarkia*. *Gafsachelys* (and *Eusarkia* and *Crassachelys*) have been synonymized with *Taphrosphys* by Antunes and Broin (1988), Broin (1988), and Lapparent de Broin (2000a).

Examination of the holotype of *Gafsachelys phosphatica* Stefano by us supports

Broin's original (1977) assessment that the holotype is not diagnosable. The dubious assignment of better specimens to this taxon by later authors does not make the holotype any more diagnosable or the name any more available.

CURRENT STATUS: Nomen dubium.

Naiadochelys ingravata Hay, 1908

TYPE SPECIMEN: AMNH 6078.

DISCUSSION: The type and only known specimen of this taxon is the posterior part of a left xiphiplastron, AMNH 6078 (Hay, 1908: fig. 133). It was given to an AMNH archeologist working at Chaco Canyon, New Mexico, in 1900 by Native Americans and is presumably from the San Juan Basin, Late Cretaceous–Eocene. It agrees closely in size, shape of the ischiac scar, and smooth external surface with YPM 3608 *Chedighaii* (formerly *Bothremys*) *barberi*. Unfortunately, these features are widespread in Pelomedusoides and inadequate to objectively identify AMNH 6078. This taxon is considered to be incertae sedis at the level of Pelomedusoides, as these features occur in both Bothremydidae and Podocnemididae. However, if this fragment did come from the San Juan Basin, it is possible that it belongs to *Chedighaii hutchisoni*, presently known only from a skull.

Broin (1988) synonymized *Naiadochelys ingravata* with *Taphrosphys sulcatus*, but *Taphrosphys* is unique among pleurodires in having a small, circular ischiac scar, quite different from the large triangular scar in *Naiadochelys* and in most other pleurodires. *Naiadochelys ingravata* also has a smooth external surface texture, different from the pebbled surface of *Taphrosphys*.

CURRENT STATUS: Nomen dubium.

"*Najadochelys*" (sic) *patagonica* Staesche, 1929

"*Najadochelys*" (sic) *major* Staesche, 1929

TYPE SPECIMEN: Unclear.

DISCUSSION: In keeping with the tradition of naming useless fragments, Staesche (1929) described a collection of fragments from the Late Cretaceous (now Paleocene) of Argentina as containing the new taxa "*Najadochelys*" *patagonica* and "*N.*" *major*. The reasons for identifying these (and misspelling the generic name) with Hay's fragment are unclear, but presumably one unidentifiable taxon deserves a few more. Broin (1977: 31) suggested that these were "restes d'un ancien Chélidé" (Broin, 1977: 31), which was repeated in Broin and Fuente (1993). The Staesche material, as figured, is nearly identical with fossil chelids in the Museo de la Plata seen by one of us (E.S.G.), and we concur with this identification.

CURRENT STATUS: Nomen dubium for both species.

"*Podocnemis*" *lata* Ristori, 1895

TYPE SPECIMEN: A partial carapace plus some fragments, uncataloged, supposedly in a museum in Italy, current whereabouts unknown.

DISCUSSION: The type and only known specimen is from the Miocene of Malta, described and figured by Ristori (1895). The carapace is unusual, but not unique, in having costals 6–8 meeting on the midline, but otherwise it has no distinguishing features. Lapparent de Broin and Werner (1998) and Lapparent de Broin (2001) identified it as a bothremydid, but gave no reasons, nor did they indicate if they had seen, or even found, the specimen, which we have not. The figured carapace is similar to bothremydids like *Rosasia* and *Chedighaii barberi* in having (probably) a posterolaterally expanded shell and a similar shell margin. However, these features are not unique to bothremydids. This shell could be a podocnemidid or a bothremydid, but it is inadequate as a basis for extending the range of the Bothremydidae into the Miocene, as claimed by Lapparent de Broin and Werner (1998). The original description is detailed and there is a good figure, but the specimen consists only of the posterior two-thirds of a carapace and is not sufficient to distinguish it as a unique taxon.

CURRENT STATUS: Nomen dubium.

Sokotochelys umarumohammedi Halstead, 1979b

TYPE SPECIMEN: "Sokoto State Government Palaeontological Collection" SOSG no. 1. Probably no longer exists.

DISCUSSION: See below.

Sokotochelys lawanbungudui Halstead, 1979b

TYPE SPECIMEN: "Sokoto State Government Palaeontological Collection" SOSG no. 2. Probably no longer exists.

DISCUSSION: Although the naming of these Maastrichtian fossils from Nigeria (Halstead, 1979b) would seem to be more of a satire on paleontological practice than a serious study, I am persuaded by some of the people involved that it was an attempt to legitimize and help establish paleontological research in Nigeria. The two type specimens, "Sokoto State Government Palaeontological Collection" no. 1 and no. 2 (Halstead, 1979a: figs. 26, 27; Walker, 1979: figs. 5, 6), are unprepared partial skulls that seem to be turtles, and could very well be pleurodires, although no diagnostic pleurodiran characters are apparent in the figures or description. The diagnosis (Halstead, 1979b) listed characters commonly found throughout turtles, cryptodires, as well as pleurodires. Four shells, not collected and not associated with the skulls, were apparently found in the same place showing sutured pelves and are arguably pleurodires. Although there is no evidence that the skulls still exist or that the "Sokoto State Government Collection" exists, if they became available after preparation, at least one might be diagnosable. As it stands, however, the genus and its two species are undiagnosable. Unfortunately, Antunes and Broin (1988), Broin (1988), Lapparent de Broin and Werner (1998), and Lapparent de Broin (2000a) chose to recognize "*Sokotochelys*" as a bothremydid and include it in comparisons with other bothremydids, based apparently on imaginative interpretations of the figures in Halstead (1979a) and Walker (1979). There is no objective basis for including these taxa in the Bothremydidae.

CURRENT STATUS: Nomen dubium for both species.

"*Taphrosphys*" *dares* Hay, 1908

TYPE SPECIMEN: AMNH 1127 (Hay, 1908: figs. 121–124). As this is apparently a mixed specimen, we here designate the entoplastron as the lectotype (Hay, 1908: fig. 123).

DISCUSSION: In 1908, Hay described some unassociated shell fragments (including lateral portions of the left fifth costal, incomplete right eighth peripheral, entoplastron, two fragments of xiphiplastra) and named them "*Taphrosphys dares*". The origin of the material is unknown, but "The matrix adhering to the bones shows that the fossil did not come from the greensand of New Jersey", and they were thought "to have been secured in the same locality and formation as the carapace of *Peritresius ornatus*; this is, on Bonnahachee Creek, Stewart County, Georgia, in the Ripley formation, of the Upper Cretaceous" (Hay, 1908: 120, 122).

The specimens are numbered with paint 1–5. Hay (1908) gave detailed descriptions, but made some misinterpretations. The costal plate was determined as a right fifth costal by Hay; it is in fact the left side since the inguinal scar is placed nearer the anterior margin and directed anteromedially. The plate numbered as 5 was thought to be a fragment of xiphiplastron with the ischiac scar. The plate is a right xiphiplastron as mentioned by Hay, but the scar on the inner surface is the pubic scar because it is oval. The ischiac scar is more triangular. In addition, this xiphiplastron is clearly smaller and thinner than the other xiphiplastron and cannot belong to the same individual. Hay was not certain whether the peripheral was the seventh or eighth. It is the eighth peripheral based on the wide shape and half-opened medial part for the bridge. The seventh peripheral is entirely opened medially. The supposedly unique arrow shape of the entoplastron seems to be due to damage. These shell fragments are very thick, about 17 mm thick for the anterior margin of the costal plate. The sculpture is visible on the costal and peripheral plates and consists of the more common Pelomedusoides ornamentation, as in *Chedighaii barberi*, different from the *Taphrosphys* pattern. Both xiphiplastron fragments bear the pubic scar. The inguinal buttress extends far medially on the fifth costal, as in many bothremydids. The fragments in "*T.*" *dares* are not *Taphrosphys* since the shell-surface sculpture is different in *Taphrosphys*.

Because Hay expressed the entoplastron shape (Hay, 1908: 105, fig. 123) as a particularly unique feature of this species; we designate it as the lectotype. This element is AMNH 1127 and has Hay's number 2 painted on it. The excavated posterolateral margin is, in our opinion, due to postmortem damage, and the thickness and smooth external surface texture occur in other taxa, such as *Chedighaii*. The "*T.*" *dares* specimens are consistent with *Chedighaii barberi* and could belong to that species. Nonetheless, the material is insufficient for a diagnosis and is best considered a nomen dubium.

Miller (1967: 225–226, pl. 1, fig. 12; ANSP 15304) reported "*Taphrosphys dares*" from the Campanian Black Creek Formation of Phoebus Landing, North Carolina. As described, the material is consistent with the "pavingstone turtle" of the Gulf Coast sediments of other authors (see discussion under *Chedighaii barberi* above) and could be *Chedighaii barberi*.

CURRENT STATUS: Nomen dubium.

Platycheloides nyasae Haughton, 1928

TYPE SPECIMEN: A partial shell, no. 7860, in the South African Museum.

DISCUSSION: This poorly preserved shell from the Early Cretaceous of Malawi has much of the plastron and little of the carapace preserved (Haughton, 1928). Lapparent de Broin (2000a) listed it as "Pelomedusidae Cope 1868, Plesions to still extant genera of Pelomedusidae" (Lapparent de Broin, 2000a: 67). No reasons are given for this assignment. Entered into our dataset, it shows 97% missing data. After analysis, it does resolve within Pelomedusoides, showing no particular relationship to the Pelomedusidae. However, in view of the extensive missing data, it would be very hard to objectively diagnose.

CURRENT STATUS: Nomen dubium.

INTRODUCTION TO PLEURODIRE SKULL MORPHOLOGY

Nearly all of the anatomical terms used in this paper, as in other papers by the senior author, are defined and described in Gaffney (1972b, 1979a). A few new terms are added to aid in the description of pleurodire skulls, and these are defined under the bones indicated: septum orbitotemporale (figs. 23, 25; Jugal), sulcus palatinopterygoideus (fig. 23; Pterygoid), cavum pterygoidei (Gaffney, 1979a: figs. 84, 86, "pterygoideus muscle chamber"; Pterygoid), fossa pterygoidea (fig. 81; Pterygoid), sulcus eustachii (figs. 282, 286; Quadrate), and fossa precolumellaris (fig. 282; Quadrate, also called "precolumellar fossa" in earlier works). The figures of pelomedusids (figs. 21–25) are intended to be used while reading the following section. This introductory section and the following descriptions are all organized on a common plan of topics that is summarized as an outline in appendix 1. The Character Descriptions sections are also organized by bone in the same order as in the taxon descriptions and this introductory section.

One of the handy things about studying pleurodires is that a couple of groups found low in the cladogram ("basal"), pelomedusids and chelids, still exist in the living fauna and are known from well-preserved specimens. The Pelomedusidae (in the sense used here, i.e., *Pelusios* and *Pelomedusa*) are chosen as examples in this introduction because they are both relatively generalized and available in many collections as skeletons and preserved specimens.

The reader is also referred to the website of DigiMorph, the University of Texas at Austin Digital Library (http://www.digimorph.org/specimens/Pelusios_sinuatus/) for a computed tomographic (CT) scan of *Pelusios*, done with the participation of the senior author, which forms an important adjunct to this introductory section. The same site also has CT scans of the bothremydid *Galianemys* and other pleurodires, *Hamadachelys, Podocnemis, Elseya*, and *Chelus*, as well as cryptodires. We are grateful to Tim Rowe and his UT colleagues for this work.

PREFRONTAL (figs. 21, 25)

The prefrontal in the Pelomedusoides is the most anterior skull-roofing element, as nasal bones, found in chelids, are absent. The prefrontal is a curved plate forming the roof of the fossa nasalis and the dorsal margin of the apertura narium externa. It also forms the anterior margin of the orbit and the anterior part of the interorbital skull roof, which seems to be narrow in the primitive condition. The prefrontal also forms the anterior part of the sulcus olfactorius.

FRONTAL (figs. 21, 25)

The frontal in the Pelomedusoides is a flat bone that forms the more posterior part of the interorbital roof and the orbital margin. On its ventral surface it continues the sulcus olfactorius from the fossa nasalis of the prefrontal. Ventral to the paired sulcus olfactorius ridges is the foramen interorbitale, a space lying between the two fossae orbitalis. The orbit in the Pelomedusoides is usually formed by the prefrontal anterodorsally, the frontal posterodorsally, the postorbital posteriorly, the jugal posteroventrally, and the maxilla ventrally.

PARIETAL (figs. 21, 25)

Dorsal plate: The dorsal plate of the parietal in the Pelomedusoides (figs. 6–8) varies from a very emarginate condition, which is probably primitive for the group, such as in pelomedusids, to an extensively roofed condition as seen in bothremydids like *Bothremys* and podocnemidids like *Dacquemys* (Gaffney, DeBlieux, Simons, Sánchez-Villagra, and Meylan, 2003)

Processus inferior parietalis: This parasagittal plate runs anteroposteriorly and forms the side wall of the braincase or cavum cranii (figs. 22, 43A). The anterior margin of the processus inferior parietalis forms the posterior edge of the foramen interorbitale (fig. 22). The ventral edge contacts the crista pterygoidea of the pterygoid (fig. 22; Gaffney, 1979a: fig. 21). The foramen nervi trigemini, the exit for the trigeminal nerve from the cavum cranii, is formed by the processus inferior parietalis anterodorsally, the prootic dorsolaterally, and the pterygoid ventrally.

JUGAL (figs. 21, 23–25)

The jugal has a flat lateral plate forming part of the cheek and a more complex medial pro-

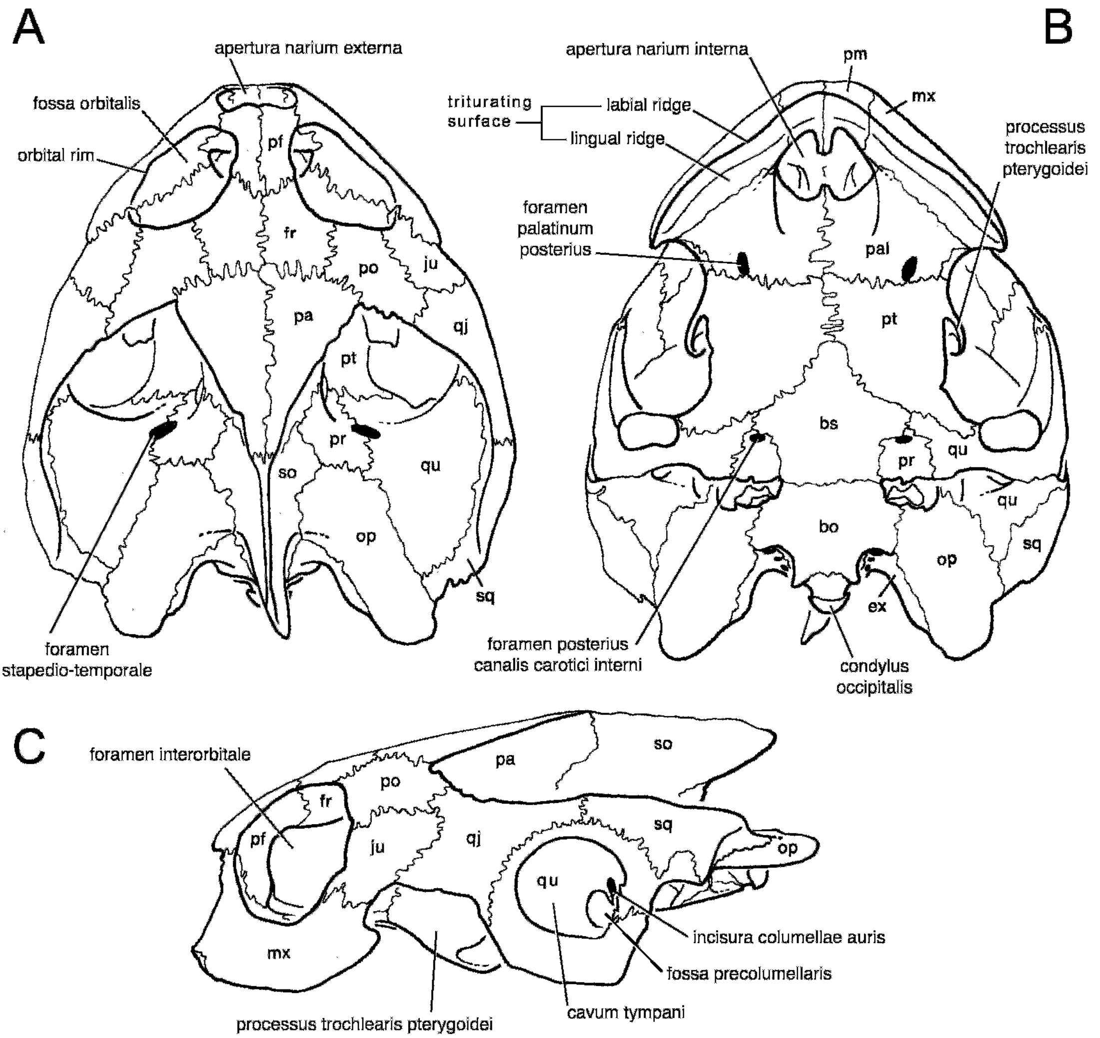

Fig. 21. *Pelomedusa subrufa*, MCZ 134434 (modified from Gaffney, 1979a). **A**, dorsal; **B**, ventral; **C**, left lateral. [L. Meeker, del.]

cess forming part of the wall behind the orbit (the septum orbitotemporale) and, in some bothremydids, part of the triturating surface.

Structures of lateral plate: The lateral plate of the jugal may form part of a ventral cheek emargination, and usually forms the posteroventral margin of the orbit.

Structures of medial process: Pleurodires are characterized by a wall between the orbital cavity, the fossa orbitalis, and the large space containing the adductor musculature, the fossa temporalis. This wall is the septum orbitotemporale (figs. 23, 25). The medial process of the jugal forms the ventral part of the septum and contacts the maxilla anteriorly and ventrally, the palatine medially and ventrally, and the pterygoid posteromedially at the base of the processus trochlearis pterygoidei. There is usually a postorbital contact dorsomedially as well. This complex formation of the septum orbitotemporale is found in nearly all pleurodires, although some (e.g., Taphrosphyini) may reduce or lose the septum entirely.

QUADRATOJUGAL (fig. 21)

The quadratojugal is a flat bone lying anterior, anterodorsal, or dorsal to the

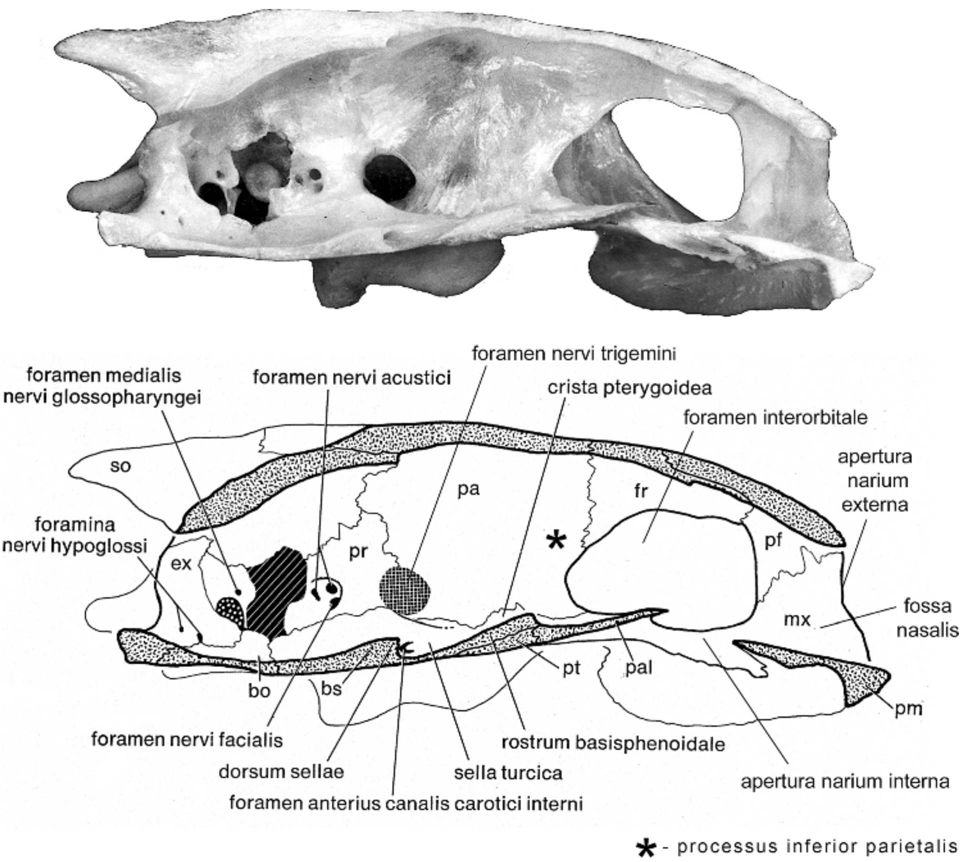

Fig. 22. *Pelusios subniger*, AMNH 71188 (modified from Gaffney, 1979a). Sagittal section of skull. [L. Meeker, del.]

quadrate that forms much of the posterior cheek and temporal roof. The quadratojugal is absent in chelids.

SQUAMOSAL (fig. 21)

The squamosal is a conical bone forming a cap covering the antrum postoticum, a hollow space extending posterodorsally from the quadrate. Within pleurodires, the antrum postoticum (figs. 281, 283) and the squamosal covering it may vary from relatively large (e.g., Pelomedusidae, figs. 23–25) to small and completely filled with bone (e.g., *Azabbaremys*; fig. 281C).

POSTORBITAL (fig. 21)

The postorbital, like the jugal below it, consists of a flat, dorsolateral plate on the temporal roof and a ventromedial process forming part of the septum orbitotemporale.

Structures of lateral plate: The postorbital forms the posterior margin of the orbit and the anterior margin of the temporal emargination, if present.

Structures of medial process: The postorbital forms the dorsal part (fig. 25) of the septum orbitotemporale (see Jugal). It also forms the lateral part of the roof and lateral wall of the sulcus palatinopterygoideus (see Pterygoid for discussion, fig. 23).

PREMAXILLA (figs. 21, 23, 24)

The premaxilla is a wedge-shaped bone forming on its dorsal surface the floor of the fossa nasalis and the ventral margin of the apertura narium externa. On its ventral surface, the premaxilla bears the triturating surface with a vertical, labial ridge anteriorly and a horizontal plate posteriorly.

MAXILLA (figs. 21, **23**, **24)**

The maxilla may be roughly divided into a more lateral, vertical plate, and a more medial, horizontal plate.

Structures of vertical plate: The vertical plate of the maxilla forms the ventral margin of the orbit, the lateral margin of the apertura narium externa, and the lateral walls of the fossa nasalis. It also forms the labial ridge and usually part of the cheek.

Structures of horizontal plate: The dorsal surface of the maxilla forms much of the floor of the fossa orbitalis, the lateral margin of the foramen orbitonasale, and, along with the premaxilla, the anterior part of the choanal passage. On its ventral surface it bears the triturating surface with the vertical labial ridge laterally and the horizontal plate medially.

VOMER (fig. 136)

The vomer is a single element lying between the premaxillae anteriorly and the palatines posteriorly. It separates the paired apertura narium interna. The vomer is absent in the Pelomedusidae and some Podocnemididae.

PALATINE (figs. 21, 23**,** 24)

The palatine is a relatively flat, horizontal bone in the roof of the mouth.

Structures on dorsal surface: The palatine forms the more medial part of the fossa orbitalis floor, part of the foramen orbitonasale, and most of the apertura narium interna and its associated choanal groove. The palatine forms the anterior floor of the sulcus palatinopterygoideus (see Pterygoid) and some of its adjacent walls, meeting the jugal laterally and the postorbital medially (figs. 23, 24).

Structures on ventral surface: The palatine forms most of the apertura narium interna and may extend laterally to form part of the triturating surface. The foramen palatinum posterius lies near the palatine/pterygoid suture and penetrates dorsally into the floor of the sulcus palatinopterygoideus (figs. 21, 23).

QUADRATE (figs. 21, 281)

The quadrate is a large, complex element, forming the middle and outer ear laterally, and containing structures associated with the cranioquadrate space medially (Gaffney, 1979a: figs. 10, 16, 17).

Structures formed by lateral portion: The principal feature of the quadrate is the cavum tympani, a large, funnel-shaped cavity that opens laterally. The stapes or columellae auris enters near the center of the cavum tympani via the incisura columellae auris. The incisura (figs. 281, 283) may be a V-shaped cleft opening posteroventrally, an oblong opening containing both stapes and eustachian tube, or a completely closed canal containing only the stapes.

Just anterior to the incisura columellae auris there may be a variably developed depression, the fossa precolumellaris (fig. 282). Above and behind the incisura is a cone-shaped extension of the cavum tympani, the antrum postoticum (figs. 23–25, 281–284), which is formed by both quadrate and squamosal. In Pelomedusoides the antrum varies from large to moderate to absent.

Structures formed by medial portion: The medial end of the quadrate in turtles is tightly sutured to the braincase elements, obliterating the cranioquadrate space (Gaffney, 1975b, 1979a). Anteriorly, the quadrate contacts the prootic with the stapedial artery between them, causing the formation of the canalis stapedio-temporalis and the foramen stapedio-temporale (fig. 21). The foramen primitively lies on the anterodorsal part of the otic chamber in the quadrate-prootic suture, but in bothremydids it lies on the anterior surface of the otic chamber, near the foramen nervi trigemini (fig. 132F).

The former cranioquadrate space also contains the lateral head vein as well as the stapedial artery. The quadrate forms the lateral part of the canalis cavernosum and sulcus cavernosum, which house the lateral head vein (Gaffney, 1979a: figs. 10, 17). Posteriorly, the stapedial artery and lateral head vein enter the skull via the fenestra postotica (fig. 135), which is variably ossified (figs. 46, 135, 177). The quadrate forms the lateral part of this opening, and the opisthotic and prootic form the more medial parts.

Ventrally in pleurodires, the quadrate contacts the prootic, but this contact is

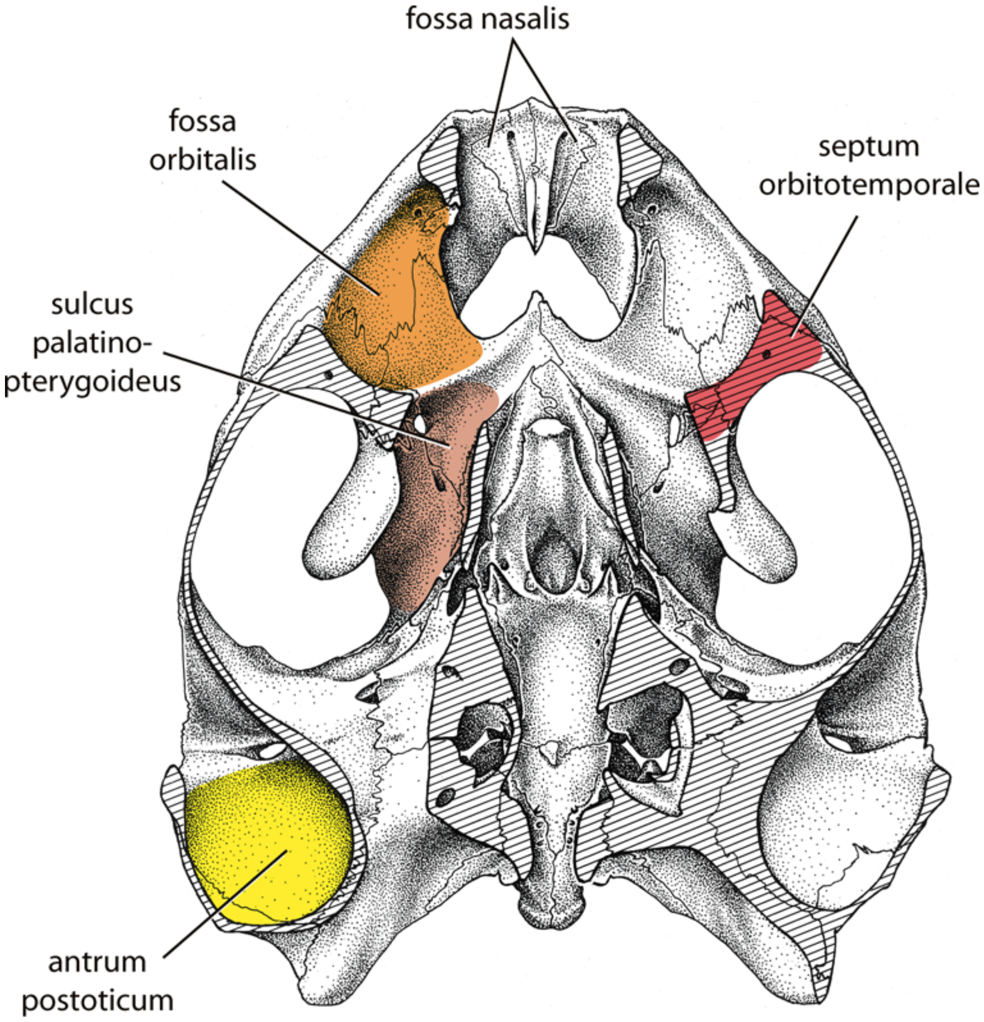

Fig. 23. *Pelusios castaneus*, AMNH 10062 (modified from Gaffney, 1979a). Dorsal view of horizontally sectioned skull. [L. Meeker, del.]

variably covered by a basisphenoid-quadrate contact so that in bothremydids, but not in chelids and pelomedusids, the prootic-quadrate contact is no longer visible ventrally, although it is still present dorsally. In euraxemydids the prootic is only partially covered. In podocnemidids, the prootic is not visible in ventral view but it is exposed inside the cavum pterygoidei (see Pterygoid).

The quadrate along with the pterygoid may form a depression in bothremydids, the fossa pterygoidea (figs. 81, 82), which marks an attachment area for a division of the M. pterygoideus (Schumacher, 1954, 1955a, 1955b, 1956, 1973). In podocnemidids, *Hamadachelys*, and *Brasilemys*, a much deeper concavity, the cavum pterygoidei, with overhanging edges anteriorly and medially, is present, formed by the basisphenoid, pterygoid, and quadrate (Gaffney, 1979a: fig. 86).

Pterygoid (figs. 21, 23, 24)

The pterygoid in pleurodires is roughly horizontal, with a curled lateral process, the processus trochlearis pterygoidei, and a thin ventrolateral flange. It forms or contributes to many of the distinctively pleurodiran structures: the processus trochlearis pterygoidei (fig. 21), the sulcus palatinopterygoideus

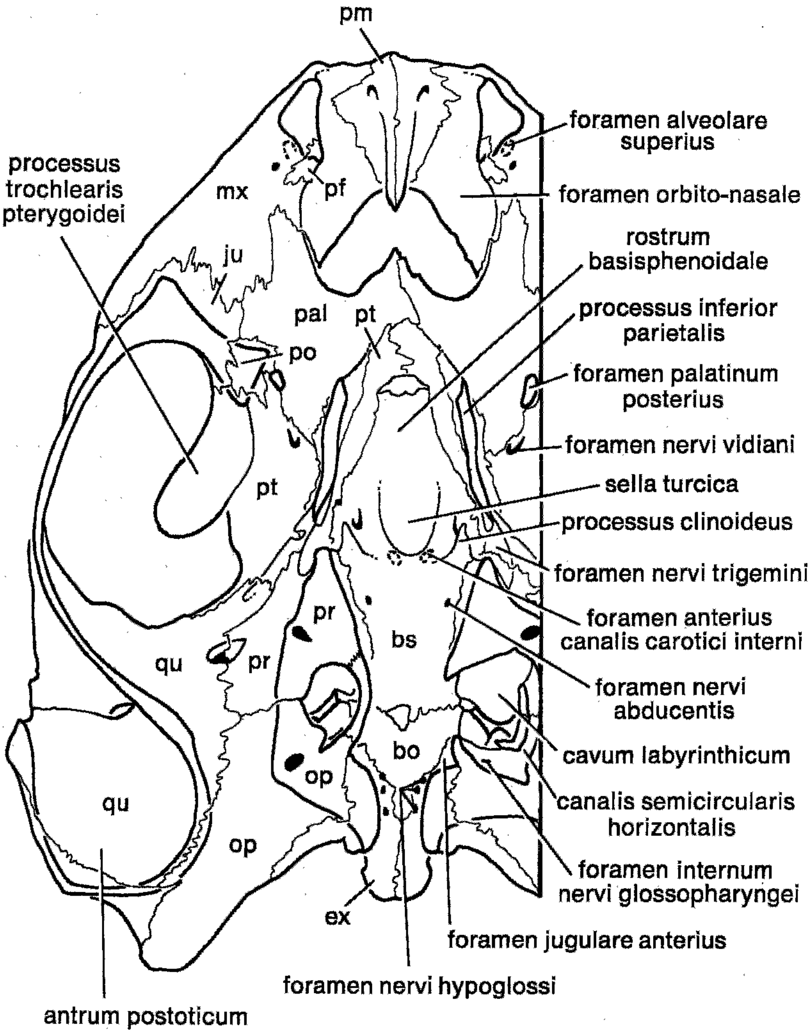

Fig. 24. *Pelusios castaneus*, AMNH 10062 (modified from Gaffney, 1979a). Dorsal view of horizontally sectioned skull. [L. Meeker, del.]

(fig. 23), and the septum orbitotemporale (fig. 23).

Structures on ventral surface: The most prominent ventral feature is the processus trochlearis pterygoidei, the trochlea for the main adductor tendon, covered in life by oral mucosa (Schumacher, 1954, 1955a, 1955b, 1956, 1973; Gaffney, 1975b, 1979a). Posteriorly, the pterygoid and quadrate may form a shallow muscle attachment area, the fossa pterygoidea (fig. 81), or a deep one having overhanging edges and involving the basisphenoid, the cavum pterygoidei of podocnemidids (see Quadrate, also Gaffney, 1979a: fig. 86). In bothremydids the pterygoid and/or quadrate may participate in forming the foramen posterius canalis carotici interni (figs. 276, 277).

Structures on dorsal surface: The processus trochlearis pterygoidei curls dorsally and medially to partially enclose a troughlike space medially, the sulcus palatinopterygoideus (figs. 23, 24, 202). The medial wall of the sulcus palatinopterygoideus is formed by a parasagittal ridge, the crista pterygoidea (fig. 174; Gaffney, 1979a: figs. 21, 54). More anteriorly, the sulcus palatinopterygoideus is formed by the palatine ventrally and it is

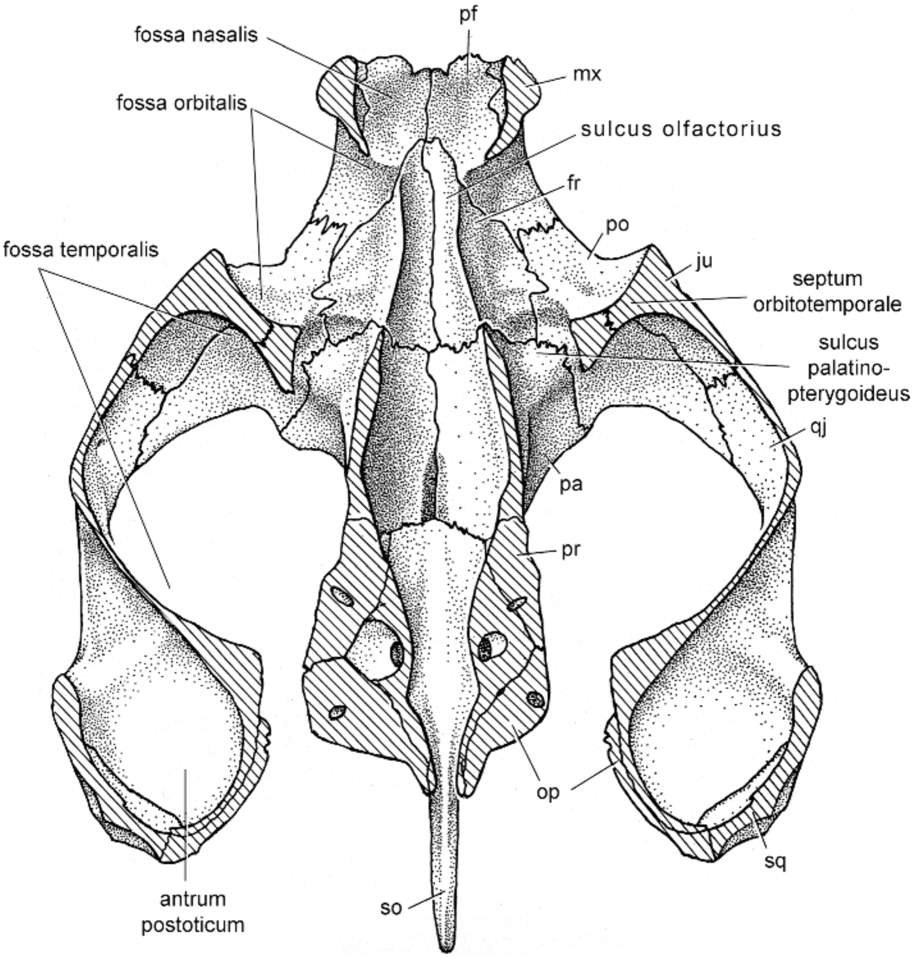

Fig. 25. *Pelusios castaneus*, AMNH 10062 (modified from Gaffney, 1979a). Ventral view of horizontally sectioned skull roof. This is the upper part of specimen in figures 23 and 24. [L. Meeker, del.]

roofed over dorsally by contact of parietal, postorbital, and frontal (fig. 25). The sulcus palatinopterygoideus contains a division of the pterygoideus musculature (Schumacher, 1954, 1955a, 1955b, 1956, 1973).

The anterior contacts of the processus trochlearis pterygoidei with the jugal, palatine, postorbital, and parietal join the processus with the posterior wall of the septum orbitotemporale (see Jugal). These three structures (figs. 23, 24), processus trochlearis pterygoidei, sulcus palatinopterygoidei, and septum orbitotemporale, form a morphology unique to pleurodires.

The crista pterygoidea separates the cavum cranii from the more external parts of the skull and forms the ventral margin of the foramen nervi trigemini and the lateral wall of the sulcus cavernosus (figs. 24, 174).

SUPRAOCCIPITAL (figs. 21, 25)

The unpaired supraoccipital bone connects the other two inner ear bones, the paired prootic and opisthotic, to house the semicircular canals, membranous labyrinth, and acoustic nerves. The supraoccipital forms the dorsal margin of the foramen magnum and has a variably developed posterodorsal process, the crista supraoccipitalis.

EXOCCIPITAL (figs. 21, 22, 46, 79)

The exoccipital is a roughly L-shaped bone that lies at the back of the skull and forms the sides and most of the floor of the foramen magnum. It forms part or all of the condylus occipitalis, with the basioccipital being present or absent in the condylus of Pelomedusoides.

The exoccipital contains a number of nerves and vessels exiting the skull. Near the base of the condylus occipitalis are the foramen nervi hypoglossi, one to three in number, extending from inside the skull to the posterior surface of the exoccipital (figs. 22, 79, 175). The jugular vein exits just anterior and lateral to these via the foramen jugulare anterius (inside the skull; Gaffney, 1979a: figs. 66–68) and the foramen jugulare posterius (lateral to the foramen nervi hypoglossi, figs. 53, 87, 135) on the posterior surface of the exoccipital (figs. 79, 99, 175). The foramen jugulare posterius may be completely formed by bone (fig. 159) mostly consisting of the exoccipital, or it may be partially or widely open laterally (fig. 46). When the foramen jugulare posterius is closed, the exoccipital forms at least part of a medial margin for the fenestra postotica.

Basioccipital (figs. 21–24, 175)

The basioccipital is an unpaired bone that lies posterior to the basisphenoid and between the paired exoccipitals. It may form the ventral part of the condylus occipitalis. There are usually paired, variably developed posterolaterally directed processes, the tuberculum basioccipitale, which form attachment sites for some of the vertebral connective tissue.

Prootic (figs. 21–24, 132, 174)

The prootic is a cubelike ossification containing a number of basicranial structures. The anterior and dorsal surface is exposed in the fossa temporalis and forms the foramen nervi trigemini anteromedially along with the pterygoid and parietal. The foramen stapedio-temporale (fig. 21A) is formed anterolaterally or anterodorsolaterally along with the quadrate. In bothremydids these foramina can be very close to each other, restricting the anterior exposure of the prootic (figs. 132, 202).

The prootic contacts the quadrate laterally to fill the cranioquadrate space (Goodrich, 1930). The cavum acustico-jugulare (Gaffney, 1979a: figs. 84, 87) is the remnant of this space and is formed by quadrate, prootic, and opisthotic in turtles. The posterior end of the stapedial artery passage is the aditus canalis stapedio-temporalis, which leads into the canalis stapedio-temporalis, which in turn opens anteriorly at the foramen stapedio-temporale, all formed laterally by the quadrate and medially by the prootic. These structures are figured in Gaffney (1979a: figs. 10, 84, 87). The canalis cavernosum and foramen cavernosum contain the lateral head vein and are formed by prootic, quadrate, and pterygoid (Gaffney, 1979a: figs. 38, 45, 46). The facial nerve (VII) and its associated hyomandibular branch are contained in the foramen nervi facialis (actually a canal as well as foramina, figs. 34, 276, 277) formed by the prootic.

The inner ear, the cavum labyrinthicum, including the semicircular canals, is formed by the prootic anteroventrally, the opisthotic posteroventrally, and the supraoccipital dorsally (figs. 23–25; Gaffney, 1979a: figs. 52, 84, 87, 105, 109). The footplate of the columella auris (fig. 46) articulates in the fenestra ovalis (fig. 36), a laterally facing opening between the cavum labyrinthicum medially and the cavum acustico-jugulare (fig. 36) laterally. All of these inner ear features are substantially the same in both cryptodires and pleurodires.

The ventral exposure of the prootic and its associated structures does vary between cryptodires and pleurodires (Gaffney, 1990: fig. 20). In cryptodires the primitive condition of the foramen posterius canalis carotici interni is within the basisphenoid, and, because this is the primitive condition for turtles (i.e., *Proganochelys*), it would also be expected to be the primitive condition for pleurodires, and this may eventually prove to be the case. However, at present the formation of the foramen posterius canalis carotici interni by the prootic seems to be primitive for pleurodires, as it occurs in chelids, pelomedusids, and euraxemydids (figs. 21, 26, 276, 277). The prootic of nearly all pleurodires contains the distal part of the canalis caroticus internus, but the ventral surface of the prootic may be variably covered by the quadrate, prootic, and basisphenoid (figs. 276, 277). The foramen nervi facialis may open into the canalis caroticus internus (fig. 34) or it may open ventrally separate from the foramen posterius canalis carotici interni (fig. 44).

Because the prootic in forms like bothremydids is underlain by thin sheets of the quadrate and pterygoid, the development of a depression in this area, the fossa pterygoidea (figs. 81, 82), may have the effect of eroding through these layers to expose a small part of the prootic as well as the foramen nervi facialis in the deepest part of the fossa pterygoidea (figs. 276, 277; see character 95 for discussion).

OPISTHOTIC (figs. 21, 23, 24, 46, 276)

The opisthotic is an irregularly shaped bone making up the posteroventral third of the inner ear, the cavum labyrinthicum, and the posterior part of the cavum acusticojugulare. The foramen jugulare posterius may be closed laterally by the opisthotic, which forms the roof and may form the medial edge of the fenestra postotica (fig. 132). Primitively, as in chelids and pelomedusids, the ventral end of the processus interfenestralis of the opisthotic is exposed in ventral view (fig. 276). However, this is covered in other Pelomedusoides by the basioccipital, quadrate, and/or exoccipital.

BASISPHENOID (figs. 21–24, 276, 277)

The basisphenoid is a triangular, unpaired bone, lying in the middle of the basicranium and forming the floor of the cavum cranii. Its ventral surface is relatively flat in pleurodires, except for the formation of the cavum pterygoidei in podocnemidids and the fossa pterygoidea in bothremydids (see Quadrate, Pterygoid). The basisphenoid may form all of the foramen posterius canalis carotici interni, as in *Kurmademys* (fig. 63), or it may form part of it, as in *Taphrosphys* (figs. 276, 277). The MPC shows that neither state is primitive for pleurodires; rather, in the primitive state the basisphenoid is separated from the foramen posterius canalis carotici interni. The dorsal surface of the basisphenoid is complex but does not vary significantly from that in cryptodires (Gaffney, 1979a).

CRANIAL MORPHOLOGY

The taxa described below are in the same order as in the Systematics section. The bones are arranged in the same order and with the same subheadings as in the Morphology Outline in appendix 1. The bone abbreviations are in the list of abbreviations and are the same as those used by the senior author in previous works. The figure references are to the best figure showing the bone or feature, not to all figures showing that bone or feature. Most figures have a photograph associated with a labeled line drawing based on the photograph. The figure references in the text are to the labeled line drawing, rather than to both. Because morphology is discussed under both the generic descriptions that follow and under the Character Description section at the end of the paper, there are morphology figures in both sections. The figures that pertain to one or two particular taxa are usually found under the genus described, while figures that compare particular areas of morphology among a large suite of taxa are found in the Character Description section.

In this section the skull figures are usually in the following order for each genus: restored three-view drawing, shaded palatal drawing, six-view photographs with associated labeled line drawing, oblique photograph with labeled line drawing. The oblique views are in the same orientation as the oblique ear views in Gaffney (1979a: figs. 85–102). Supplemental figures are usually placed between the six-view figures and the obliques. Not all taxa lend themselves to this pattern, so there are exceptions.

The reader will be aided (hopefully) by the comparative views of whole skulls at the beginning of this paper (figs. 3–11). The Character Description section at the end of this paper (figs. 276–287) has comparative figures of the basicranium and the quadrate for many taxa. The restored views are determined by rotating structures from right to left, or adding structures from other specimens where stated. There are no hypothetical additions or additions from other taxa unless specifically stated.

HYPERFAMILY PELOMEDUSOIDES

FAMILY ARARIPEMYDIDAE

Araripemys barretoi

There are four skulls of *Araripemys* that form the basis of this description. None is complete or nearly complete, but three are relatively well preserved; the best is THUg 1357. A fourth, partial skull, AMNH 24453, provides internal information. Meylan (1996) provided another description of the skull of *Araripemys*, with stereophotographs of the basicranium.

Araripemys is an interesting and important taxon that is among the oldest pleurodires known from high-quality skull material. Despite a number of autapomorphic features, it retains the generalized Pelomedusoides basicranium and other features. In the phylogenetic analysis, *Araripemys* is either the sister taxon to the Pelomedusoides or in a multichotomy with Pelomedusidae and all other Pelomedusoides.

PREFRONTAL (figs. 26, 29, 31)

Preservation: There is no complete prefrontal in any of the four skulls. However, the posterior parts of both prefrontals are preserved in THUg 1357, AMNH 24454, and THUg 1907. AMNH 24454 has the most anteriorly complete prefrontal margins, but the surfaces are damaged. THUg 1357 has the best preserved prefrontal in terms of sutures and lack of surface damage. All the prefrontal morphology, except its anteriormost limits, can be seen in one specimen or another.

Contacts: The prefrontal in *Araripemys* contacts the maxilla dorsal process anteroventrolaterally and sends a process posteroventrally along the anterior orbital margin. It approaches but does not reach the palatine. The prefrontal contacts the frontal posteriorly and the other prefrontal medially.

Structures: The missing anterior margin of the prefrontal in our skulls prevents an exact determination of the dorsal shape of the apertura narium externa in *Araripemys*. The restoration (fig. 26) shows only the maximum extent of the prefrontal as preserved; a small anterior projection could have been present.

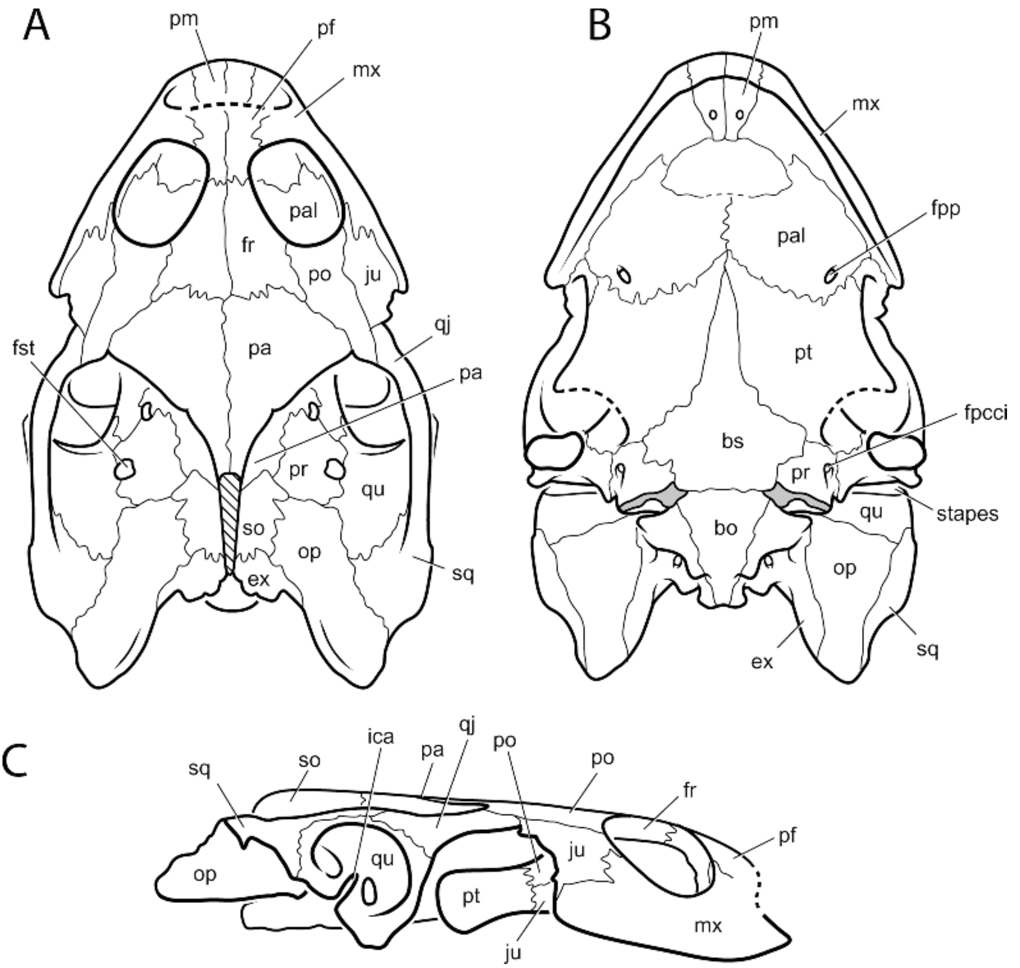

Fig. 26. *Araripemys barretoi* Price, 1973. Partially restored skull based on THUg 1357, THUg 1907, AMNH 24453, and AMNH 24454. **A**, dorsal; **B**, ventral; **C**, lateral. For more detailed view of area around foramen posterius canalis carotici interni, see figure 276D. [F. Ippolito, del.]

The interorbital distance is narrow in *Araripemys*, similar to the Euraxemydidae and some Podocnemididae (*Podocnemis*), but in contrast to the Bothremydidae (except *Kurmademys*). The Pelomedusidae vary from narrow to broad, but the narrow interorbital distance seen in *Pelomedusa* and most *Pelusios* species is the most common and may be primitive for that family. The Chelidae also vary in their interorbital distance but the broad condition occurs as the more general condition in Gaffney's (1977b) cladogram, with the narrow interorbital distance being in the more derived *Chelodina* and *Hydromedusa*.

FRONTAL (figs. 26, 29, 31, 33)

Preservation: The only complete frontal in *Araripemys* is on the right side of THUg 1357 (figs. 28, 29), although the left one is only slightly damaged. Most of both frontals are present in AMNH 24454 and THUg 1907. The ventral surface is preserved and visible in AMNH 24454. The frontal is missing in AMNH 24453.

Contacts: The frontal in *Araripemys* contacts the prefrontal anteriorly, the postorbital posterolaterally, the parietal posteriorly, and the other frontal medially. Contrary to Meylan (1996), the frontals do not

Fig. 27. *Araripemys barretoi* Price, 1973. Partially restored ventral view of skull based on all specimens, primarily THUg 1357. For more detailed view of area around foramen posterius canalis carotici interni, see figure 276D. [A. Smucker, del.]

partially separate the prefrontals. The suture is roughly transverse.

Structures: The frontal in *Araripemys* forms the posteromedial part of the orbital margin, as in most other Pelomedusoides. The bone is more triangular, due to anterior pinching, than in bothremydids, but in agreement with most pelomedusids and euraxemydids. On the ventral surface, the sulcus olfactorius is visible in AMNH 24454 and is lower than in bothremydids and chelids but similar to pelomedusids and euraxemydids.

The description in Meylan (1996: 23, fig. 4) that the frontal almost completely separates the prefrontals is incorrect, as can be seen in THUg 1907, THUg 1357, and reexamination of AMNH 24454. The frontal does underlie some of the prefrontal, and the broken bone surface produces irregular sutural expression. However, the prefrontal-frontal contact on the best preserved specimens is an irregularly transverse contact, as in pelomedusids and *Dirqadim* (the contact is poorly preserved in *Euraxemys*).

PARIETAL (figs. 26, 29, 31, 33)

Preservation: A complete parietal is probably not present in the available *Araripemys* specimens. In all the skulls at least some of the temporal margin seems to be broken. The restored dorsal view (fig. 26) is based on what is preserved in THUg 1357, which seems to be missing only a small part of the edge. In any case, it is unlikely that the temporal margin was very much greater than that shown in the restoration. At least some of the dorsal surface of both parietals is damaged in AMNH 24454 and THUg 1907, and the left parietal of THUg 1357 is badly broken. AMNH 24453 lacks the parietal.

The ventral processus inferior parietalis is present and visible in AMNH 24454. It is covered in THUg 1907 and only partially visible in THUg 1357. Some of the parietal is preserved in AMNH 24453, but due to the application of paint during illustration for Meylan (1996), its surface is partially covered.

Contacts of dorsal plate: The parietal in *Araripemys* contacts the frontal anteriorly, the postorbital laterally, and the other frontal medially. Contrary to Meylan (1996), it does not contact the quadratojugal.

Structures of dorsal plate: The degree of temporal emargination in *Araripemys* is greater than in euraxemydids and all bothremydids except Kurmademydini. However, it is similar to the extent of emargination seen in Pelomedusidae among pleurodires. An important question is whether the pelomedusid condition is homologous to that in *Araripemys*, as this character is one that allies *Araripemys* with pelomedusids. The inclusion of the poorly known *Teneremys* in the analysis (fig. 292) makes the emarginate condition primitive for Pelomedusoides. The morphology of the parietal roof and its contacts are basically indistinguishable in *Araripemys*, pelomedusids, *Teneremys*, and Kurmademydini, and it is clear that it cannot be strictly homologous in all these, so it must have evolved independently at least twice. The question remains open.

There is no ventral process of the parietal lateral to the sulcus palatinopterygoideus.

Contacts of processus inferior parietalis: The processus inferior parietalis in *Araripemys* contacts the pterygoid ventrally, the prootic posteroventrally, and the supraoccipital posteriorly. Contrary to Meylan (1996), there is no palatine contact. The anteroventral edge of the parietal is covered in AMNH 24454, and in THUg 1357 the parietal does not extend anteriorly past the pterygoid-palatine suture.

Structures of the processus inferior parietalis: The foramen nervi trigemini is formed by the parietal anteriorly, the prootic posteriorly, with the pterygoid variably entering the ventral margin, as in other pleurodires. On the right side of AMNH 24454 the pterygoid is almost completely excluded from the foramen margin by a near contact of the parietal and prootic.

JUGAL (figs. 26, 27, 31)

Preservation: The jugal is present at least partially in all four *Araripemys* skulls. The only complete or nearly complete one is on the right side of THUg 1357. All but the posterior margins of the jugal are present in AMNH 24454, and most of the right jugal is present in THUg 1907. The medial part of the right jugal is present and partially disarticulated in AMNH 24453.

Contacts of lateral plate: The jugal in *Araripemys* contacts the maxilla anteroventrally, the postorbital dorsally, and the quadratojugal posterodorsally. These contacts also occur in Euraxemydidae, Pelomedusidae, and most Bothremydidae, but not in Chelidae, which lacks a quadratojugal (fig. 3).

Structures of the lateral plate: *Araripemys* has a large cheek emargination bordered by the maxilla, jugal, quadratojugal, and quadrate. The jugal is curved to form the anterodorsal part of the margin. The degree of cheek emargination in *Araripemys* is comparable in extent to that in the Euraxemydidae and slightly more than in most Pelomedusidae. Only *Kurmademys* among bothremydids has a cheek emargination, and the jugal is not exposed in it. Chelids have a very large cheek emargination extending over the quadrate.

The jugal enters the orbit of *Araripemys*, but narrowly, as in euraxemydids, in contrast to the wide exposure of pelomedusids and chelids.

Contacts of medial process: In the orbital floor the jugal of *Araripemys* contacts the maxilla anteriorly, the palatine posteromedially, and the postorbital posterodorsally. In the septum orbitotemporale, seen in posterior view, the jugal contacts the postorbital medially and the pterygoid posteroventrolaterally. These are as in other Pelomedusoides.

Structures of medial process: Due to the shallow depth of the skull, the septum orbitotemporale in *Araripemys* is also shallow compared with many other pleurodires. The jugal is visible in ventral view and has a small portion exposed just posterior to, but not actually on, the triturating surface.

QUADRATOJUGAL (figs. 26, 29)

Preservation: Although not preserved at present, a quadratojugal fragment was originally present in AMNH 24454 adhering to the quadrate (visible in photographs in AMNH archives). A complete or nearly complete right quadratojugal is present in THUg 1357, and a nearly complete left one is present as well, lacking its anterior end. A nearly complete right quadratojugal is also present in THUg 1907, although its broken surface has obscured some of the anterior sutures. The left quadratojugal is only a fragment on the quadrate.

Contacts: The quadratojugal of *Araripemys* contacts the jugal anteriorly, the postorbital anterodorsally, the quadrate posteroventrally, and the squamosal posterodorsally. These contacts are the same as in pelomedusids, but differ from euraxemydids because the latter also have a parietal contact. The quadratojugal in bothremydids has variable contacts, but the *Cearachelys* condition is similar to that in *Araripemys* and pelomedusids. Chelids lack a quadratojugal.

Structures: The quadratojugal of *Araripemys* is a long, thin plate, smaller than in pelomedusids and euraxemydids because *Araripemys* has a more extensive cheek emargination and lacks the ventral expansion seen in those taxa. Pelomedusids and euraxemydids have a similarly shaped quadratojugal, but the temporal emargination of pelomedusids is more extensive, agreeing with *Araripemys* in this feature. The shape of the quadratojugal in Meylan (1996: fig. 4) is incorrect (see fig. 29).

SQUAMOSAL (figs. 26, 29)

Preservation: A complete squamosal is not present in the available specimens. The restoration (fig. 26) is a composite of the right side of THUg 1357, which has the most complete squamosal, and THUg 1907, which has more of the posterior part preserved. The ventral part of the squamosal is present in AMNH 24454 and AMNH 24453. Most of the right squamosal is in THUg 1907 and THUg 1357, with the left sides of both specimens preserving fragments of the bone.

Contacts: The squamosal of *Araripemys* contacts the quadrate anteriorly and anteromedially, the opisthotic medially, and the quadratojugal anteriorly in a very narrow suture.

Structures: The squamosal in *Araripemys* is relatively low and narrow compared with bothremydids, but in agreement with pelomedusids. The squamosal of euraxemydids is more expanded on the temporal roof, contacting the parietal, in contrast to the narrow one of *Araripemys*.

The antrum postoticum of *Araripemys* is large in contrast to some bothremydids, and agrees in size with that in euraxemydids, but is not as large as in pelomedusids and chelids, although assessing the relative size of this cavity can be subjective. There are no deep flanges or posterior processes on the squamosal in *Araripemys*.

POSTORBITAL (figs. 26, 29)

Preservation: The only complete or nearly complete postorbital in *Araripemys* is

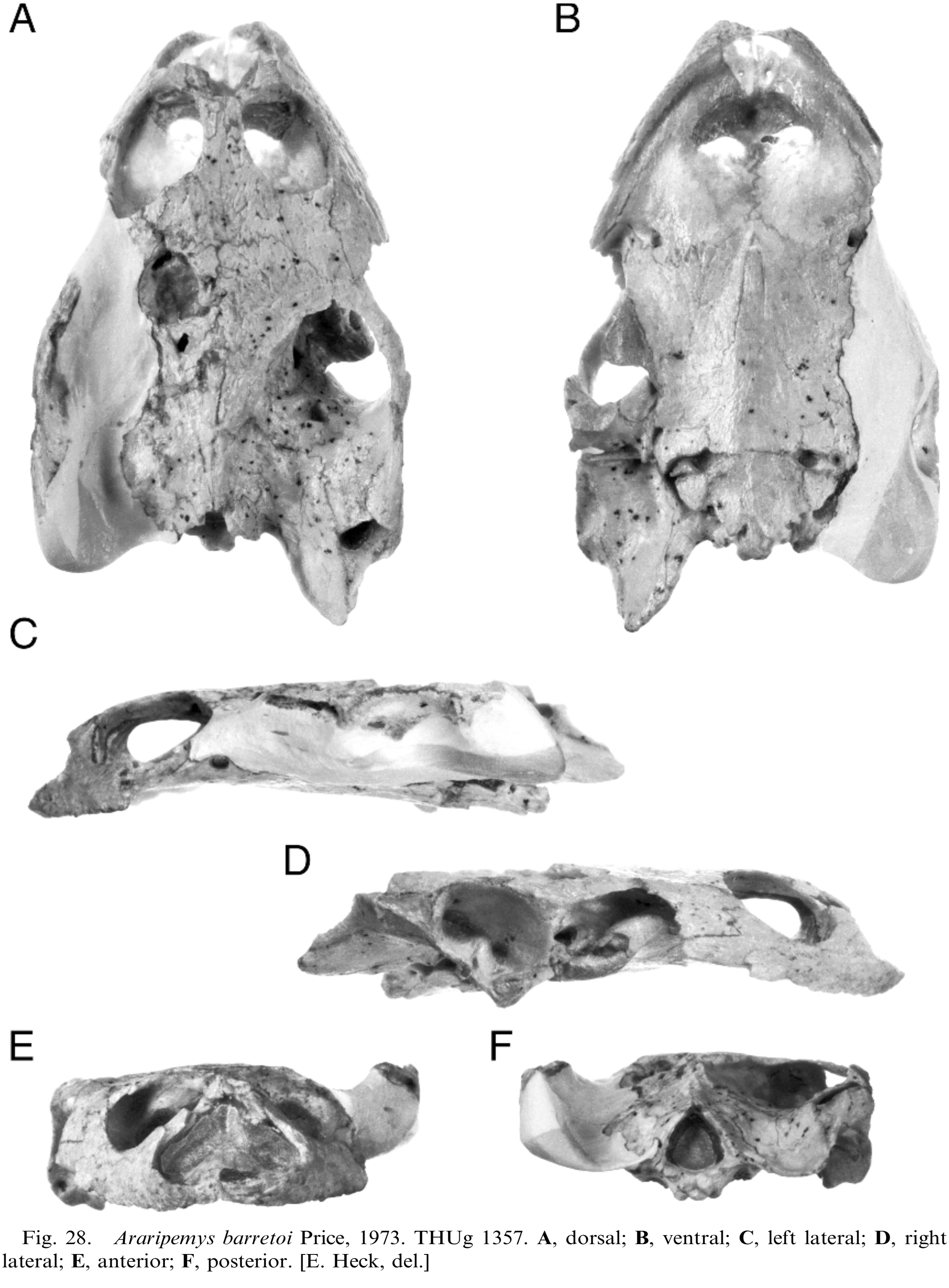

Fig. 28. *Araripemys barretoi* Price, 1973. THUg 1357. **A**, dorsal; **B**, ventral; **C**, left lateral; **D**, right lateral; **E**, anterior; **F**, posterior. [E. Heck, del.]

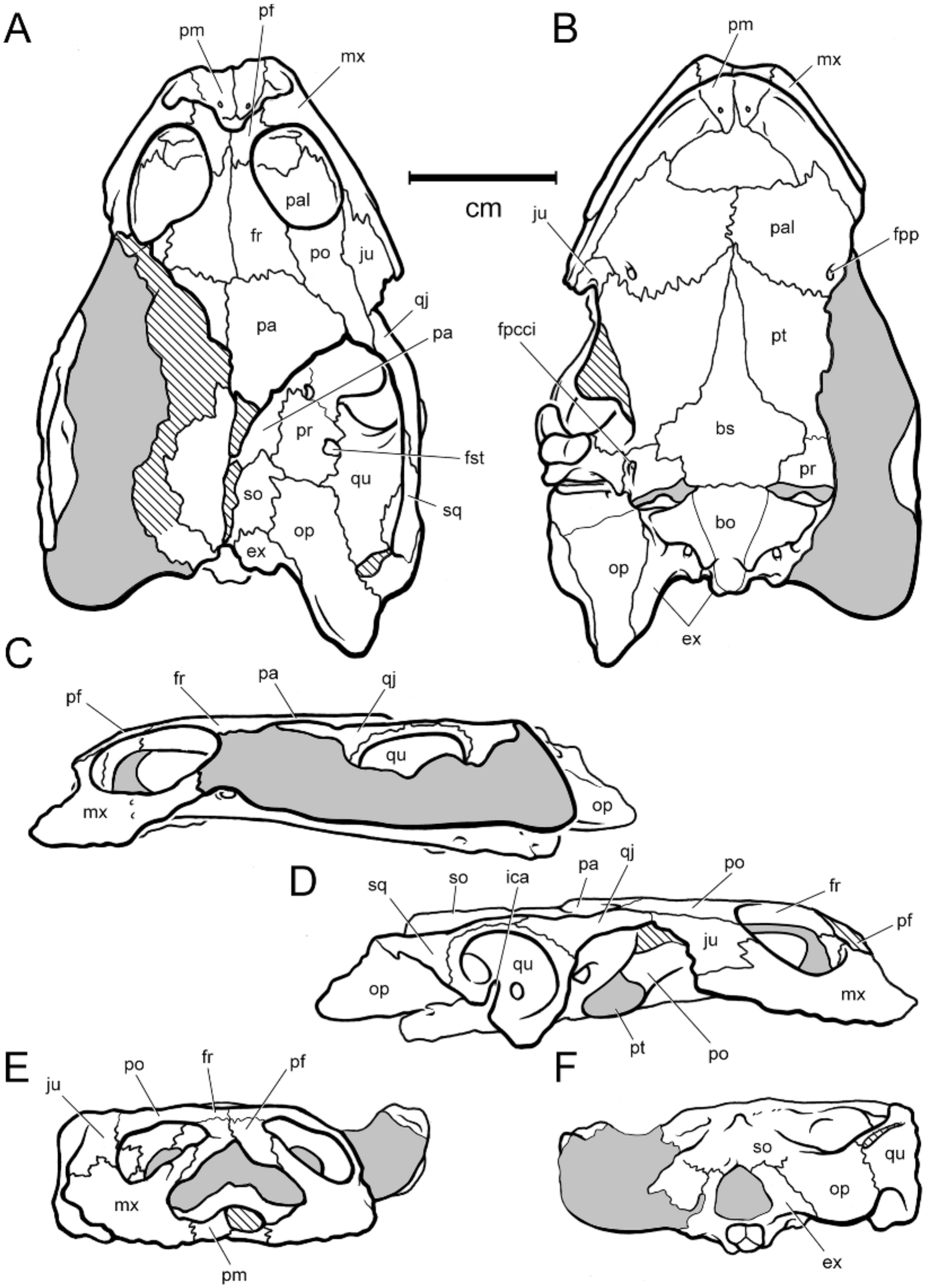

Fig. 29. *Araripemys barretoi* Price, 1973. THUg 1357. **A**, dorsal; **B**, ventral; **C**, left lateral; **D**, right lateral; **E**, anterior; **F**, posterior. [E. Heck, del.]

on the right side of THUg 1357. AMNH 24454 has a mostly complete right postorbital that has a damaged surface and lacks some of the temporal roof. The left one lacks the temporal roof. In THUg 1907 both postorbitals are present and damaged posteriorly. In AMNH 24453 the right medial process of the postorbital is present and partially disarticulated.

Contacts of lateral plate: The postorbital in *Araripemys* contacts the frontal anteromedially, the jugal ventrolaterally, the quadratojugal posterolaterally, and the parietal posteromedially. These contacts are very similar to those in pelomedusids and differ from euraxemydids in having a free posterior margin without the parietal-quadratojugal contact. Chelids differ in lacking a quadratojugal, but the other contacts are as in *Araripemys*.

Structures of the lateral plate: As in other pleurodires, the postorbital of *Araripemys* forms the posterodorsal margin of the orbit. The postorbital in *Araripemys* is longer than in pelomedusids and is exposed along the temporal margin. The report in Meylan(1996: 24) that THUg 1357 has no temporal exposure of the postorbital is incorrect. Euraxemydids have a parietal-quadratojugal contact preventing postorbital exposure.

Contacts of medial process: In the anterior view of the septum orbitotemporale, the postorbital contacts the frontal dorsomedially, the palatine ventrally, and the jugal ventrolaterally. In the posterior view of the septum, the postorbital contacts the parietal dorsomedially, the pterygoid ventromedially, the jugal ventrolaterally, and the palatine ventrally, as in other Pelomedusoides.

Structures of medial process: The postorbital forms the lateral wall and part of the roof of the sulcus palatinopterygoideus, as in most other Pelomedusoides. The sulcus is lower in *Araripemys* than in euraxemydids, chelids, pelomedusids, and most bothremydids due to the low skull. As noted by Meylan (1996: 24), there is a large foramen in the postorbital on its medial surface just dorsal to the foramen palatinum posterius in the wall of the sulcus palatinopterygoideus. There are two smaller foramina above it as well, as seen in AMNH 24454 and AMNH 24453. A similar foramen occurs variably in most chelids, pelomedusids, and bothremydids. It opens into branches inside the postorbital wall and seems to carry nutrient vessels.

The postorbital forms part of the posterior wall of the fossa orbitalis, the septum orbitotemporale. In *Araripemys* there is a relatively deep concavity formed mostly by the postorbital that does not occur in pelomedusids, chelids, euraxemydids, and primitive bothremydids like *Galianemys* and *Cearachelys*. The anterior wall of the fossa temporalis, above the processus trochlearis pterygoideus, is mostly formed by the postorbital in *Araripemys*. It has a shallow, horizontal trough above the processus, not seen in chelids, pelomedusids, euraxemydids, and bothremydids.

PREMAXILLA (figs. 26, 27, 29)

Preservation: The premaxilla is almost complete in AMNH 24453, which lacks only the posterior edges of both. In THUg 1357 the posterior edges are complete, with only a small part of the anterior edges missing. The restoration combines both of these specimens. In THUg 1907 the premaxillae are mostly covered by matrix or they are broken. In AMNH 24454 most of both premaxillae are missing.

Contacts: In *Araripemys* the premaxilla contacts the maxilla posterolaterally and the other premaxilla medially. There is no vomer preserved in any of the four *Araripemys* specimens (see Vomer).

Structures on dorsal surface: The dorsal surface of the premaxilla in *Araripemys* forms the floor of the fossa orbitalis and the ventral rim of the apertura narium externa. The apertura in *Araripemys* projects anteriorly beyond the preserved portion of the prefrontal, but this may not have been the case originally, as the prefrontal is broken. The premaxilla in *Araripemys* is flat or slightly depressed, as in *Galianemys* and most chelids, not raised into a midline projection, as in some pelomedusids and many bothremydids. The fossa orbitalis floor rises posteriorly but is flat, without midline separation of choanae.

The parasagittal groove leading into the dorsal opening of the foramen praepalatinum is deep in *Araripemys*, more so than in most chelids and pelomedusids.

Structures on ventral surface: The labial ridge in *Araripemys* is sharp, but its two surfaces meet at an obtuse angle so the labial ridge is relatively thick at its base, in contrast to *Emydura* but in common with most pelomedusids. The labial ridge on the premaxilla of *Araripemys* is also relatively shallower than in chelids and pelomedusids, but similar to some bothremydids.

There is a very shallow midline depression in *Araripemys*, similar to that in some *Emydura*, but *Araripemys* lacks the deep, well-defined midline concavity seen in bothremydids and many pelomedusids. There are no accessory ridges or troughs.

MAXILLA (figs. 26, 27)

Preservation: At least parts of both maxillae are present in all four specimens. The most complete one is on the right side of THUg 1357, but AMNH 24453 has a nearly complete right maxilla as well as a partial left one. THUg 1357 has its left maxilla damaged posteriorly. AMNH 24454 and THUg 1907 have both maxillae covered ventrally by matrix. In lateral and medial views the maxillae of AMNH 24454 are well preserved and nearly complete. In THUg 1907 only the lateral parts of the maxillae are visible, and they are damaged, more so on the left than on the right.

Contacts of vertical plate: The maxilla in *Araripemys* contacts the premaxilla anteromedially, the jugal posterodorsally, and the prefrontal anterodorsally.

Structures of vertical plate: The maxilla in *Araripemys* forms the entire lower half of the orbital margin and the lateral margin of the apertura narium externa. In *Araripemys* the maxilla beneath the orbit is shallower than in euraxemydids, most chelids, bothremydids, and some pelomedusids. The dorsal process of the maxilla is narrow in *Araripemys*, as in most pelomedusids, euraxemydids, and most chelids, and some bothremydids like the tribe Cearachelyini. The maxilla forms the anterior edge of the deep cheek emargination in *Araripemys*.

Contacts of horizontal plate: The maxilla contacts the premaxilla anteromedially, the palatine posteromedially, and the jugal posteriorly. There is no midline maxilla contact, as in some chelids, and no evidence of a vomer contact, although one was possible.

Structures of horizontal plate: The maxilla in *Araripemys* is unusually thin in ventral view, with the palatine encroaching anterolaterally toward the labial ridge. The thick labial ridge of the premaxilla narrows posteriorly as it is formed by the maxilla, so the greater part of the labial ridge in *Araripemys* is narrower in comparison to most pelomedusids but similar to *Emydura*. The labial ridge in *Araripemys* is slightly convex ventrally, similar to euraxemydids, not sharply curved, as in pelomedusids and *Emydura*. The lingual ridge is nearly absent. It is a very low ridge close to and paralleling the labial ridge, visible along the posterior part of the triturating surface. Due to the absence of a distinct lingual ridge, it is hard to be sure where the triturating surface (i.e., the area actually covered by the horny beak) ended. The triturating surface of *Araripemys* is not highly vascularized, as it is in many turtles. The palatine does not form a significant part of the triturating surface in *Araripemys*.

The dorsal surface of the medial plate of the maxilla in *Araripemys* does not form a significant part of the floor of the fossa orbitalis, as it does in bothremydids.

VOMER

Preservation: There is no vomer preserved in the four *Araripemys* specimens. THUg 1357 is the most complete in this area with no sign of damage and with both premaxillae and palatine edges preserved. If a vomer were present it would have been attached to these edges. However, the vomer is the most infrequently preserved of skull elements in Pelomedusoides. For example, only 2 of 14 *Galianemys* skulls have even fragments of a vomer present. A small vomer could have easily fallen out of THUg 1357, but it is unlikely that a large vomer with broad contacts was present.

PALATINE (figs. 26, 27)

Preservation: The palatine is present in all four *Araripemys* skulls, at least in part. The most complete one is on the right side of THUg 1357. The left one is slightly broken laterally. In AMNH 24454 and THUg 1907 the ventral surfaces are partially obscured by matrix, and in THUg 1907 the dorsal

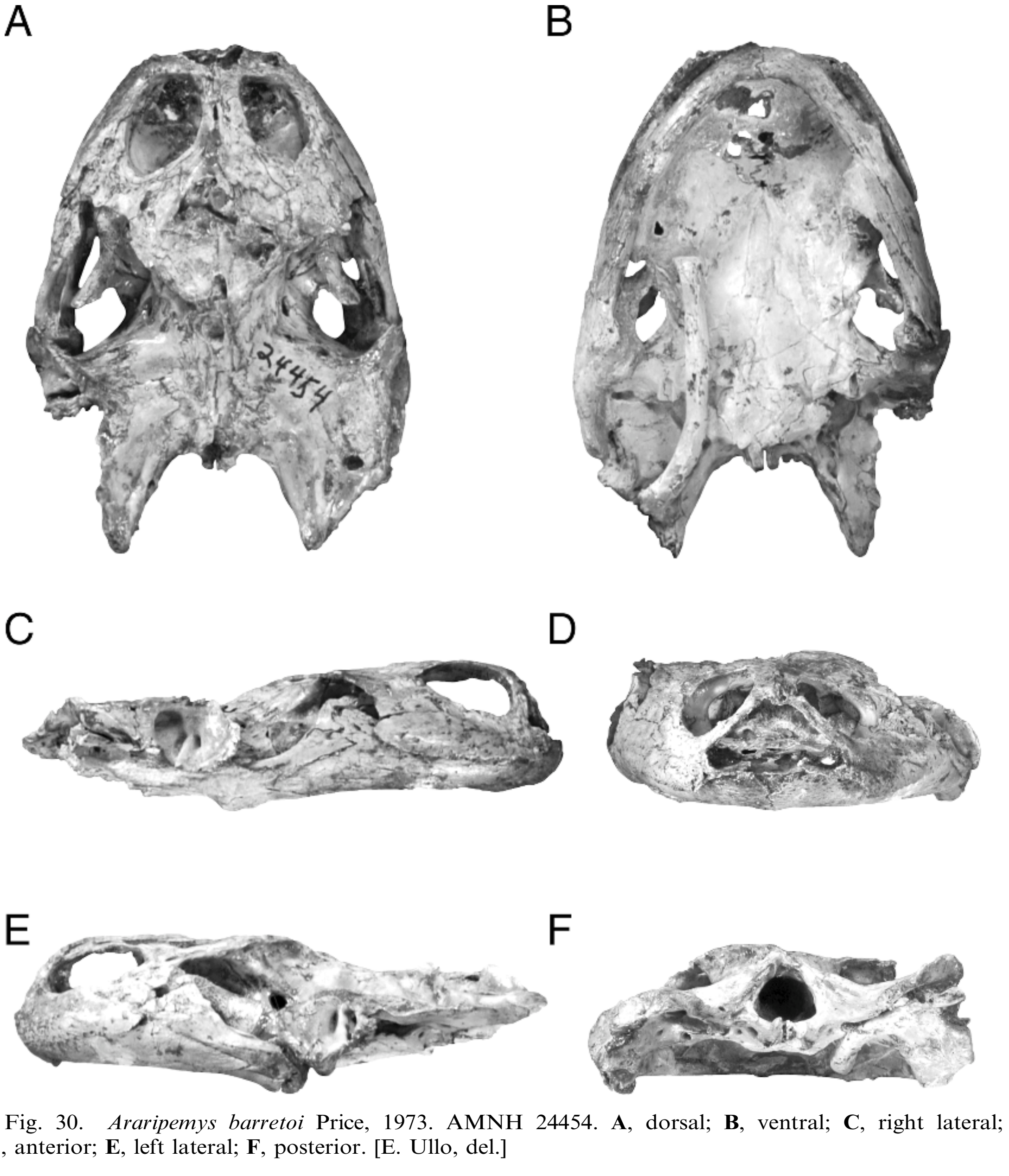

Fig. 30. *Araripemys barretoi* Price, 1973. AMNH 24454. **A**, dorsal; **B**, ventral; **C**, right lateral; **D**, anterior; **E**, left lateral; **F**, posterior. [E. Ullo, del.]

surfaces are also obscured by matrix. In AMNH 24454 the dorsal surfaces are mostly visible. In AMNH 24453 a small fragment of right palatine is present posteriorly.

Contacts: The palatine in *Araripemys* contacts the maxilla anterolaterally, the other palatine medially, the pterygoid posteriorly, and the jugal anterolaterally. On the dorsal surface it also contacts the postorbital posterolaterally and the parietal dorsally. Contrary to Meylan (1996: fig. 4), there is no palatine-basisphenoid contact on either dorsal or ventral surfaces of available specimens.

Structures on dorsal surface: The palatine forms most of the floor of the fossa orbitalis in *Araripemys*; its anterior margin is

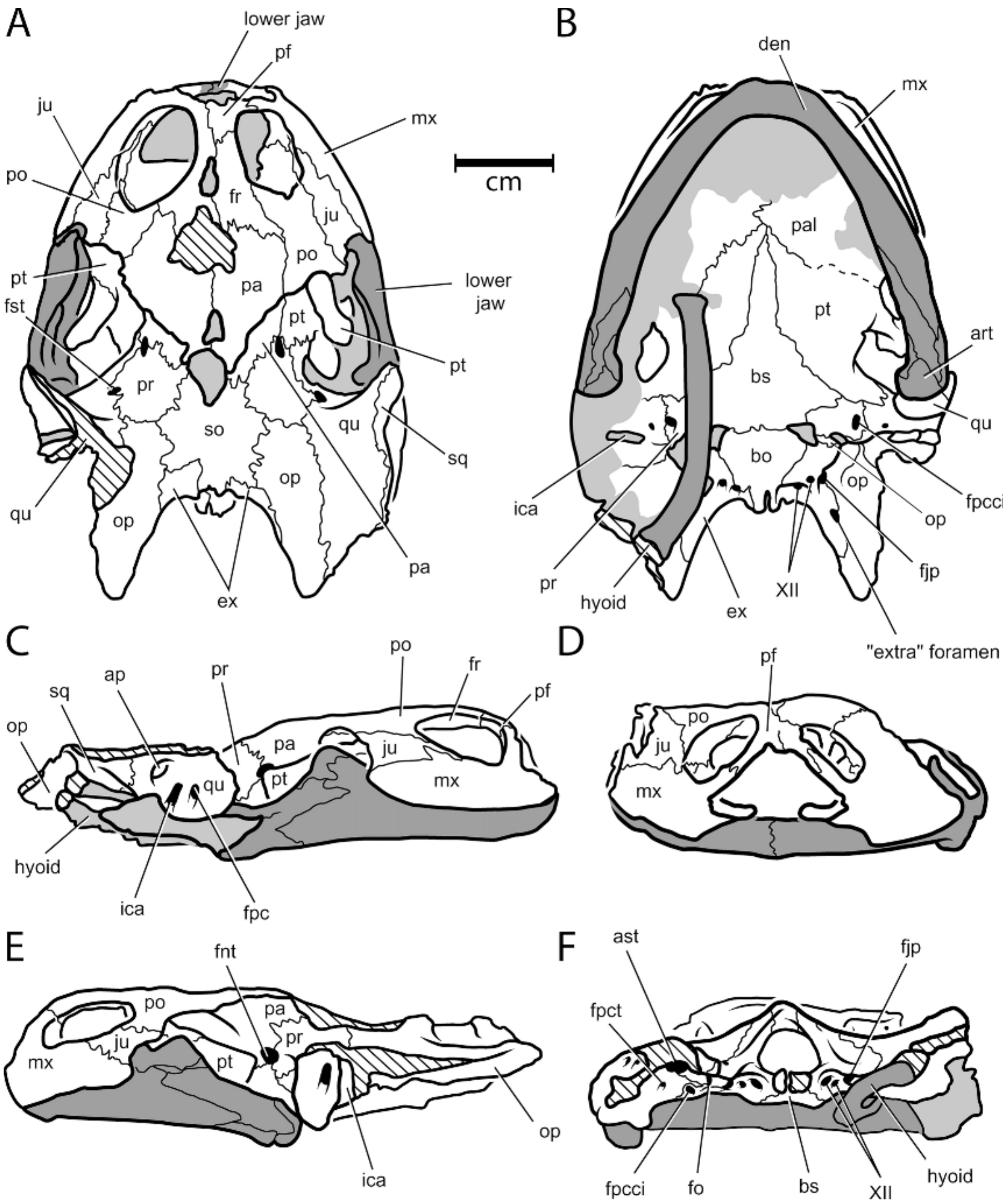

Fig. 31. *Araripemys barretoi* Price, 1973. AMNH 24454. **A**, dorsal; **B**, ventral; **C**, right lateral; **D**, anterior; **E**, left lateral; **F**, posterior. See figure 38 for another view of "extra" foramen. [E. Ullo, del.]

the posterior edge of the apertura narium interna. There is no clear vertical differentiation between the apertura and the foramen orbitonasale. There is no dorsal process of the palatine along the processus inferior parietalis. The palatine forms the anterior floor of the sulcus palatinopterygoideus, as in other pleurodires, and its contact ridge is low.

Structures on ventral surface: The palatine in *Araripemys* encroaches onto the narrow, poorly defined, triturating surface because the maxilla is so narrow. The palatine is flat in *Araripemys*; it is not arched or curved to form choanal grooves, as in euraxemydids, pelomedusids, bothremydids, and podocnemidids. In this it is similar to some chelids.

QUADRATE (figs. 26, 31, 36, 37, 282C)

Preservation: The most complete quadrate is on the right side of THUg 1357; it does not seem to be missing any bone and is not obscured by matrix. The left one is only represented by a fragment of the dorsal edge. In AMNH 24454 both quadrates are present, but they lack their dorsal surfaces. In THUg 1907 the left quadrate is well preserved ventrally, retaining the stapes, but it is damaged dorsally and obscured by matrix laterally. In AMNH 24453 the right quadrate is present but lacks its dorsal part.

Contacts on lateral surface: The quadrate in *Araripemys* contacts the quadratojugal anterodorsally and the squamosal posterodorsally.

Structures on lateral surface: The quadrate forms the posterior edge of the cheek emargination, which is relatively extensive in *Araripemys* (see Jugal). The quadrate does not enter the edge of the temporal emargination, although the squamosal-quadratojugal contact is narrow.

The cavum tympani in *Araripemys* (fig. 282C) has an open incisura columellae auris, in contrast to most Bothremydidae, but in common with the Pelomedusidae, Euraxemydidae, and Chelidae. The incisura columellae auris of *Araripemys* is oblong and nearly closed distally so that it contains both stapes and eustachian tube, also in contrast to Bothremydidae but in common with the Pelomedusidae, Euraxemydidae, and Chelidae. The cavum tympani of *Araripemys* has a deep fossa precolumellaris that is oblong and oriented vertically. The fossa is similar to that in chelids and pelomedusids, in contrast to bothremydids except the Kurmademydini. Euraxemydids have a relatively shallow fossa precolumellaris compared to *Araripemys* and pelomedusids.

The antrum postoticum of *Araripemys* is present and completely developed, in contrast to bothremydids (except *Kurmademys*), but it is distinctly smaller than in pelomedusids and chelids. The antrum of *Euraxemys* is larger than in *Araripemys*, but smaller than in chelids and pelomedusids.

Contacts on dorsal and anterior surface: The quadrate in *Araripemys* contacts the prootic anteromedially, the opisthotic posteromedially, and the squamosal posterolaterally, all as in other pleurodires. There is no supraoccipital contact, in contrast to many bothremydids.

Structures on dorsal and anterior surface: The otic chamber in *Araripemys* is relatively low and flat compared to other pleurodires, except the more derived Chelidae (Gaffney, 1977b), which also have very low skulls. Nonetheless, the foramen stapediotemporale is in about the same relative position in *Araripemys* as it is in chelids, pelomedusids, and euraxemydids. The foramen in these groups is clearly visible in dorsal view as it opens more dorsally than anteriorly, in contrast to bothremydids where it opens more anteriorly and is usually not visible in dorsal view.

Contacts on ventral surface: The quadrate in *Araripemys* contacts the pterygoid anteromedially, the prootic medially, and the opisthotic posteriorly. There is no exoccipital or basioccipital contact.

Structures on ventral surface: The quadrate in *Araripemys* does not participate in formation of the foramen posterius canalis carotici interni (fig. 276). The barely developed fossa pterygoidea is a very shallow depression mostly formed by the pterygoid, but the quadrate forms the posterior, poorly defined portion. The condylus mandibularis in *Araripemys* lies well anterior to the condylus occipitalis, as it does in pelomedusids, chelids, and euraxemydids.

Contacts on posterior surface: Due to the unusually low, flat skull of *Araripemys*, little of the quadrate is actually visible in an axially directed posterior view, so this discussion includes features visible ventrally as well. The quadrate in *Araripemys* (figs. 36, 37) contacts the squamosal dorsolaterally, the opisthotic dorsomedially, and the prootic medially. The prootic contact is primitive for pleurodires, being found also in chelids, euraxemydids, and pelomedusids. There is no exoccipital contact, also agreeing with these groups and in contrast to podocnemidids and bothremydids.

Structures on posterior surface: The fenestra postotica of *Araripemys* (figs, 36, 37) is formed laterally by the quadrate, which, as in pelomedusids and chelids, does not form any subdivisions. The specimen figured in Meylan (1996: fig. 7), AMNH 24453, is partially eroded so that the bone surface is less extensive than in the other three *Araripemys* skulls. The fenestra postotica is not as large in the other three specimens as it is in AMNH 24453, but the internal features are more visible.

The incisura columellae auris in *Araripemys* (figs. 37, 282C) is a trough that extends medially to lie below the fenestra postotica and opens into the fenestra ovalis. The trough is more open in *Araripemys* and chelids than it is in pelomedusids and euraxemydids. The aditus canalis stapediotemporalis is formed dorsally and laterally by the quadrate, with the more medial canalis cavernosus having its roof formed by quadrate. The foramen chorda tympani inferius lies on the posterior surface of the quadrate, as in other pleurodires.

PTERYGOID (figs. 26, 27, 34, 35)

Preservation: Both pterygoids are present in THUg 1907 and AMNH 24454, but they are partially obscured by hyoids. Some of the lateral and dorsal surface is visible in AMNH 24454, but not in THUg 1907. In THUg 1357 the right pterygoid lacks its lateral margin and the left one lacks more of the bone. Some of the dorsal surface in this skull is visible on the right but not on the left. AMNH 24453 has most of the right pterygoid preserved, with its dorsal and lateral surfaces visible, as described in Meylan (1996). The bone in this specimen, however, is eroded due to overzealous acid preparation.

Contacts on ventral surface: The pterygoid of *Araripemys* contacts the palatine anteriorly, the basisphenoid posteromedially, the prootic posteriorly, and the quadrate posterolaterally. Anteromedially the paired pterygoids have a short contact, found on all four skulls, so that the basisphenoid does not completely separate the pterygoids and contact the palatines.

Structures on ventral surface: The processus trochlearis pterygoidei is best preserved on both sides of AMNH 24454, where only some of the edges are damaged. The processus in *Araripemys* lies at an acute angle to the skull midline, as in chelids and pelomedusids and in contrast to most bothremydids and podocnemidids. The pterygoid flange is mostly broken in all the specimens, but its base and some of the flange persists in THUg 1907 and AMNH 24454.

The quadrate ramus in THUg 1907 forms part of a very shallow depression, not really identifiable as the fossa pterygoidea, which only has an anterior margin; posteriorly it merges with the rest of the pterygoid surface. AMNH 24454 and AMNH 24453 have even less of the fossa defined.

Contacts on dorsal surface: The base of the processus trochlearis pterygoidei contacts the postorbital anterodorsally and the jugal anterolaterally. The crista pterygoidea contacts the palatine anteriorly, the parietal anterodorsally, and the prootic posterodorsally. The basisphenoid lies along the pterygoid medially.

Structures on dorsal surface: The anterior opening of the sulcus palatinopterygoideus in *Araripemys* is slightly larger than in euraxemydids and pelomedusids, and it is distinctly larger than in bothremydids. The pterygoid forms the floor and lower wall of the sulcus. The opening into the foramen palatinum posterius is more lateral than ventral in *Araripemys*, as in most other pleurodires.

The sulcus cavernosus and the canalis cavernosus are visible in AMNH 24453 (fig. 34) as described by Meylan (1996). Beneath the sulcus cavernosus, within the pterygoid, is the canalis nervi vidiani, which begins posteriorly in the canalis caroticus internus, near the foramen nervi facialis, as in other pleurodires. The canalis nervi vidiani extends anteriorly to exit the broken, anterior edge of pterygoid, presumably on its way to the foramen palatinum posterius. The posterior margin of the foramen is covered or missing in all the specimens, so this cannot be determined definitely. In the floor of the sulcus cavernosus is a small foramen (shown as "A" in fig. 34) that communicates with the

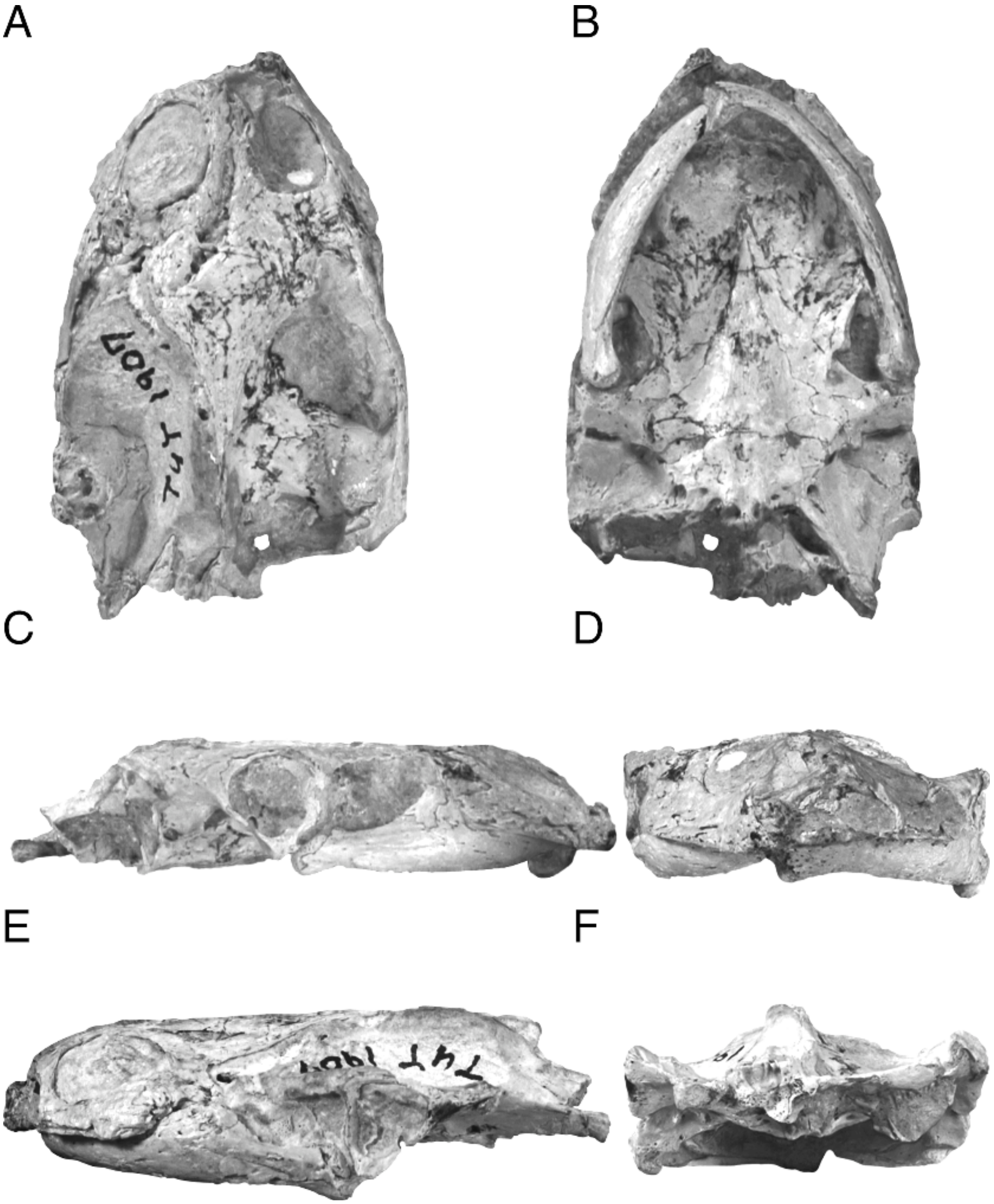

Fig. 32. *Araripemys barretoi* Price, 1973. THUg 1907. **A**, dorsal; **B**, ventral; **C**, right lateral; **D**, anterior; **E**, left lateral; **F**, posterior. [E. Ullo, del.]

canalis nervi vidiani (as described in Meylan, 1996).

The foramen nervi trigemini has the pterygoid forming its ventral edge, with the parietal dorsally and the prootic posteriorly. Contrary to Meylan (1996: fig. 5), the pterygoid extends posteriorly to meet the quadrate beneath the prootic, as in all turtles.

Araripemys has a foramen caroticum laterale that is formed by the pterygoid and

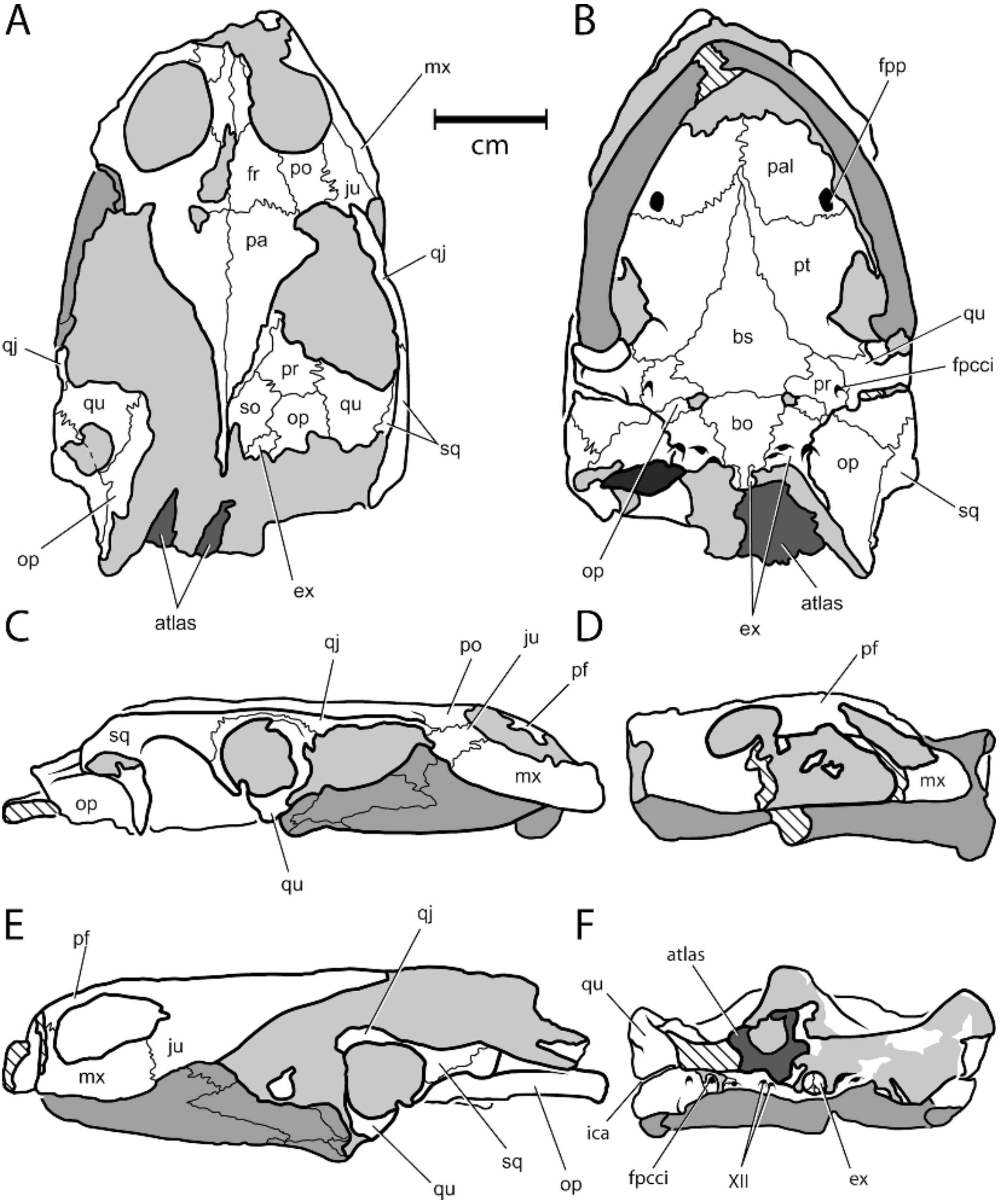

Fig. 33. *Araripemys barretoi* Price, 1973. THUg 1907. **A**, dorsal; **B**, ventral; **C**, right lateral; **D**, anterior; **E**, left lateral; **F**, posterior. [E. Ullo, del.]

basisphenoid. Although this is visible only in the damaged skull, AMNH 24453, which has some of the surface eroded, it is certainly present (fig. 34). Pelomedusids lack the foramen caroticum laterale and canalis caroticus lateralis (Albrecht, 1976; Gaffney, 1979a), while they are present in chelids and podocnemidids but not in bothremydids.

SUPRAOCCIPITAL (figs. 26, 29, 31)

Preservation: None of the skulls preserve an entire crista supraoccipitalis, but all have at least some of the anteroventral part preserved. The best preserved is in AMNH 24454, which shows sutures clearly.

Contacts: The supraoccipital in *Araripemys* contacts the parietal dorsally and anteriorly, the prootic anterolaterally, the opisthotic posterolaterally, and the exoccipital posteroventrally, as in the primitive pleurodiran condition.

Structures: The crista supraoccipitalis is not preserved except for a short distance just above the foramen magnum. The foramen magnum has its dorsal margin formed by the supraoccipital, and the cavum labyrinthicum dorsal structures are also formed by the supraoccipital, as in other pleurodires.

EXOCCIPITAL (figs. 26, 36–38, 276D)

Preservation: At least one exoccipital is preserved in each *Araripemys* skull, with both nearly complete in AMNH 24454.

Contacts: The exoccipital in *Araripemys* contacts the supraoccipital anterodorsally, the opisthotic laterally and anteroventrally, and the basioccipital anteromedially, as in pelomedusids. There is no quadrate or basisphenoid contact.

Structures: The foramen magnum in *Araripemys* is mostly formed by the exoccipital, as in most pleurodires, with the supraoccipital present in the margin dorsally. The condylus occipitalis in *Araripemys* also has the primitive pleurodire condition, with the exoccipitals forming it dorsolaterally and the basioccipital forming the ventral third. The branches of the foramen nervi hypoglossi exit in three canals, with the posterior two being much larger than the most anterior one. The exoccipital is relatively thick here, and the canals are long compared with most other pleurodires.

The exoccipital forms the foramen jugulare posterius in *Araripemys*. There is considerable variation in the degree of closure of this foramen (figs. 36, 37), more than has been documented for any other pleurodire. Of the two specimens described by Meylan (1996), AMNH 24453 has an open foramen jugulare posterius but it is missing bone due to acid erosion. AMNH 24454 is well preserved, and new preparation removing a hyoid has exposed more of the occipital area. This specimen also has a widely open foramen with no sign of abrasion, loss, or damage. THUg 1357 shows both foramina open, but the left one is damaged. The right one has an open margin, but it is not widely open; the bone extends dorsally and ventrally. It is possible that a thin process, now missing, completed the margin. This skull is also the smallest and may be a juvenile with less ossification than that in the other skulls. THUg 1907 is well preserved on both sides in the area of the foramen jugulare posterius and shows a complete closure of the foramen by thick bone on all margins, a very different condition from the other skulls. However, the foramen is not completed by dorsal and ventral extensions of the exoccipital around the foramen. Instead, the opisthotic forms the lateral wall with a broad opisthotic-exoccipital contact ventrally. THUg 1907 and AMNH 24454 are similar in size, so the difference in closure of the foramen is unlikely to be due to growth differences. Pelomedusids, podocnemidids, and chelids have a closed foramen jugulare posterius, but it is open in euraxemydids and some bothremydids (Cearachelyini, *Foxemys*, and *Polysternon*). This character is coded as polymorphic for *Araripemys* in the dataset.

The exoccipital in *Araripemys* and most Pelomedusoides has a posterolateral process extending along the posteromedial edge of the opisthotic. Chelids such as *Emydura* have a very short or absent posterolateral process. In *Araripemys* this process is long and flat because the opisthotic is unusually long and flat. On the left side of AMNH 24454 there is a foramen formed in the opisthotic-exoccipital suture, about halfway along the length of the exoccipital (fig. 38). This foramen is a short canal that extends anteroventrally to posterodorsally and is about the size of the largest foramen nervi hypoglossi. On the ventral surface, this foramen blends into the upper margin of the foramen jugulare posterius, so it is likely that the foramen contained one of the nerves or vessels that exited through the foramen jugulare posterius. The senior author has never seen a foramen in the opisthotic-exoccipital suture in any turtle, concluding that this is an anomaly caused by

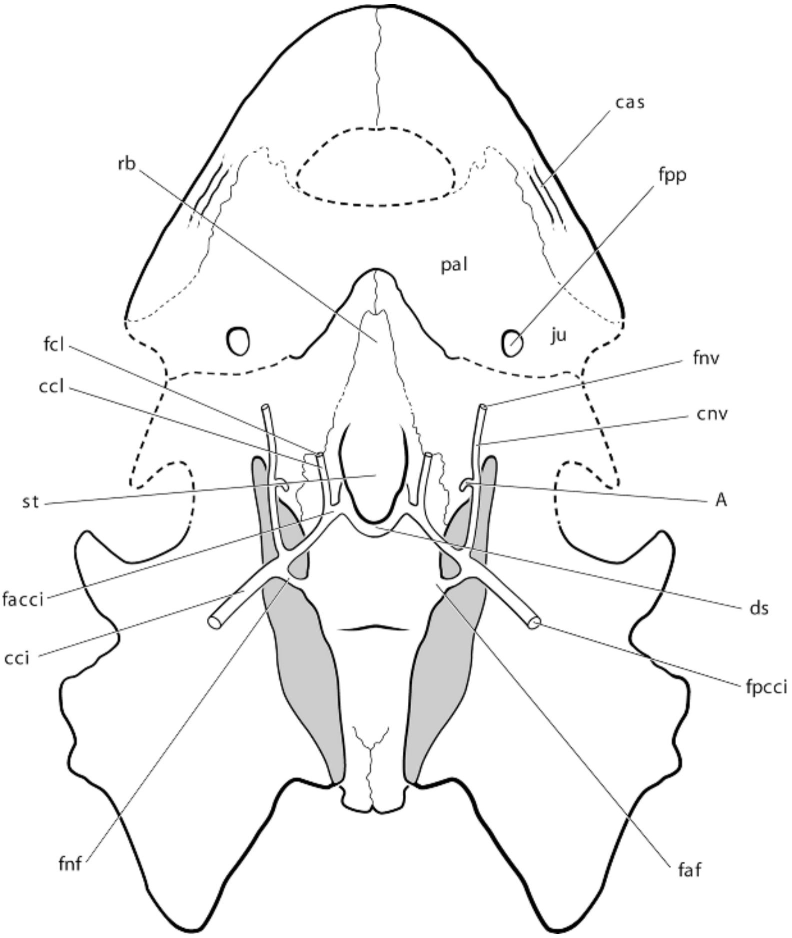

Fig. 34. *Araripemys barretoi* Price, 1973. Restored, semidiagrammatic frontal view showing canals and basicranial structures, based on AMNH 24453 seen in following figure. [A. Venjara, del.]

a soft structure, probably a nerve, being more dorsally placed when the exoccipital and opisthotic were being ossified.

Araripemys is unique in having a greatly expanded anteroventral part of the exoccipital (fig. 276D). In other pleurodires, such as chelids and pelomedusids, the exoccipital sends a ventral process to the basioccipital. The basioccipital covers most of the anteroventral part of the exoccipital. In *Araripemys* the anteroventral part of the exoccipital is expanded for nearly the length of the basioccipital and lies lateral to it so that a broad surface of exoccipital is visible in ventral view. In euraxemydids a small part of the exoccipital is visible ventrally, and some bothremydids (e.g., *Cearachelys*) have the exoccipital slightly visible in ventral view. However, in podocnemidids and most bothremydids, the anteroventral part of the exoccipital is not visible ventrally. *Araripemys* is the only pleurodire to have this anteroventral part of the exoccipital expanded to this extent. Part of this morphology is the result of the absence of a basioccipital-opisthotic contact, found in pelomedusids, chelids, and podocnemidids but not in euraxemydids and bothremydids.

BASIOCCIPITAL (figs. 26, 36, 37, 276D)

Preservation: The basioccipital is present and nearly complete in THUg 1357 and THUg 1907. Only a small part of the basioccipital area seems damaged in AMNH

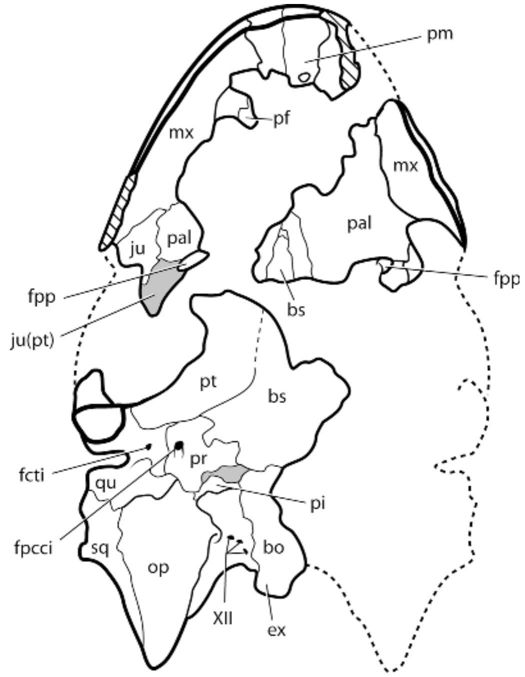

Fig. 35. *Araripemys barretoi* Price, 1973. AMNH 24453 in ventral view showing preserved skull sections. Also see preceding figure and Meylan (1996: figs. 5–7) for other views of this skull. The abbreviation ju(pt) indicates the pterygoid sutural contact area on the jugal. [A.M. Phillips, del.]

24454. In AMNH 24453 the occipital process and much of the left half is missing.

Contacts: The basioccipital in *Araripemys* contacts the basisphenoid anteriorly and the exoccipitals laterally. Due to the large exoccipital, there is no opisthotic contact. There is also no quadrate contact, in contrast to all bothremydids and podocnemidids but in agreement with chelids, pelomedusids, and euraxemydids.

Structures: The condylus occipitalis in *Araripemys* is formed equally by the two exoccipitals and the basioccipital, the presumed primitive condition for pleurodires and seen in chelids, euraxemydids, podocnemidids, and the Kurmademydini. The pelomedusids exclude the basioccipital from the condyle, as do most bothremydids. Meylan (1996: 28) stated that the basioccipital "makes a small contribution to the occipital condyle." The two skulls included in that study are damaged. The more complete skulls, THUg 1907 and THUg 1357, show that the basioccipital forms the usual third of the condyle.

The tuberculum basioccipitale is a small, acutely pointed, posterior projection in *Araripemys*, formed almost entirely by the basioccipital, as in pelomedusids. The process is wider in most chelids, smaller in euraxemydids, and nearly absent in bothremydids.

The basioccipital of *Araripemys* has a smooth ventral surface, lacking the ventral concavity seen in most bothremydids. The bone is relatively long, as in chelids, pelomedusids, and euraxemydids, not short, as in podocnemidids and bothremydids.

PROOTIC (figs. 26, 31, 36, 37, 276D)

Preservation: The prootic is present on both sides of THUg 1357, THUg 1907, and AMNH 24454. Dorsal and ventral surfaces are best seen in AMNH 24454. The right prootic is present in AMNH 24453, where it can also be seen internally, and, thanks to overpreparation, many of its internal features are also visible.

Contacts: The prootic in *Araripemys* contacts the parietal dorsomedially, the quadrate laterally, the supraoccipital posterodorsally, and the opisthotic posteriorly. Ventrally, it also contacts the basisphenoid medially and the pterygoid anteriorly. It is separated from the processus interfenestralis of the opisthotic posteriorly by a small unossified space (fig. 276D).

Structures: The prootic forms the posterior half of the foramen nervi trigemini, with the parietal forming the anterior half, and the pterygoid barely entering or not entering the margin (see Parietal, Pterygoid). The prootic forms the medial half of the foramen stapedio-temporalis with the quadrate (see Quadrate).

The internal features of the cavum acustico-jugulare are visible in AMNH 24454 and AMNH 24453 and were described in Meylan (1996). These do not differ a great deal among pleurodires, with *Araripemys* being particularly similar to pelomedusids. The cavum labyrinthicum is also relatively conservative.

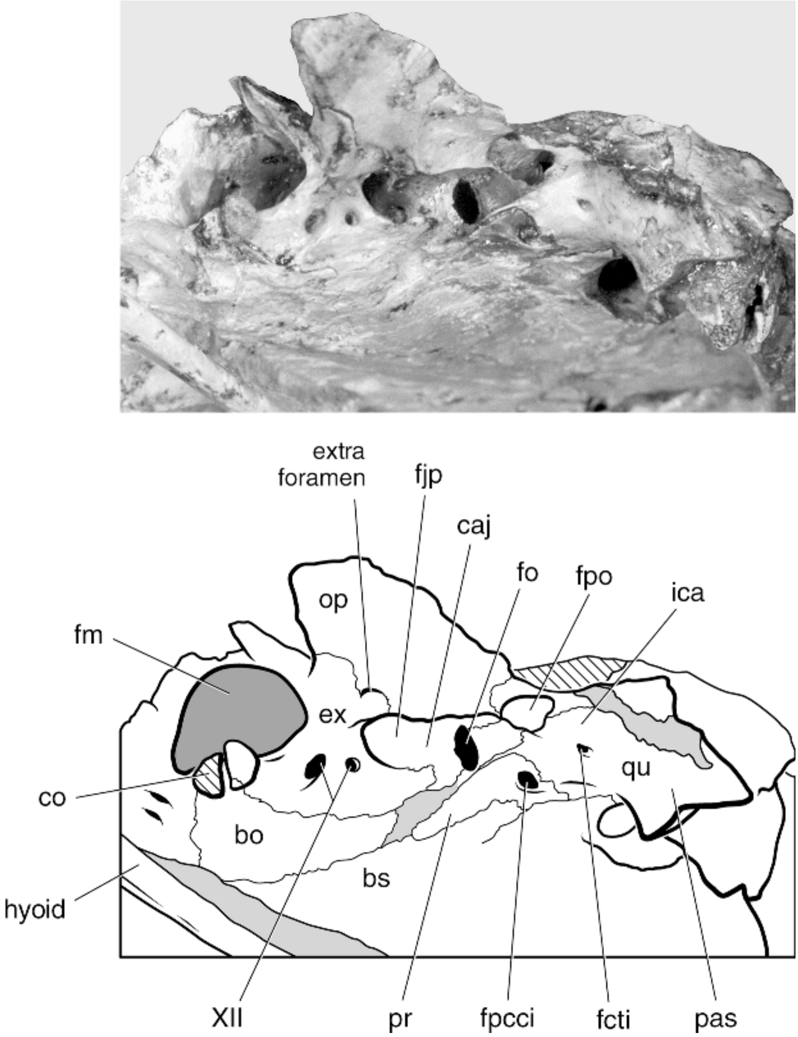

Fig. 36. *Araripemys barretoi* Price, 1973. AMNH 24454. Posterior oblique view of skull reversed from left side. [A. Venjara and E.S. Gaffney, del.]

The main difference between *Araripemys* and other pleurodires in this area is the widely open incisura columellae auris. In most bothremydids the stapes is in a bony canal.

The prootic in *Araripemys* is widely exposed on the ventral surface, the presumed primitive condition for pleurodires, as it occurs in chelids and pelomedusids (fig. 276D). Euraxemydids have a partially exposed prootic, while podocnemidids and bothremydids have the prootic completely covered or with only a small exposure. In *Araripemys* and many pelomedusids the exposure is L-shaped, with a narrow medial process. In chelids the shape of the exposure varies and is often irregular.

The prootic of pleurodires is a complex element; although roughly cube-shaped, it contains a number of soft structures (figs. 34, 276D). The internal carotid artery enters the prootic and extends anteromedially. The facial (VII) nerve enters the prootic, forms the geniculate ganglion, and branches into the vidian (palatine) branch trending anteriorly, the hyomandibular branch trending posteriorly, and the chorda tympani branching ventrally. In Gaffney (1979a) there is a discussion of these structures and the

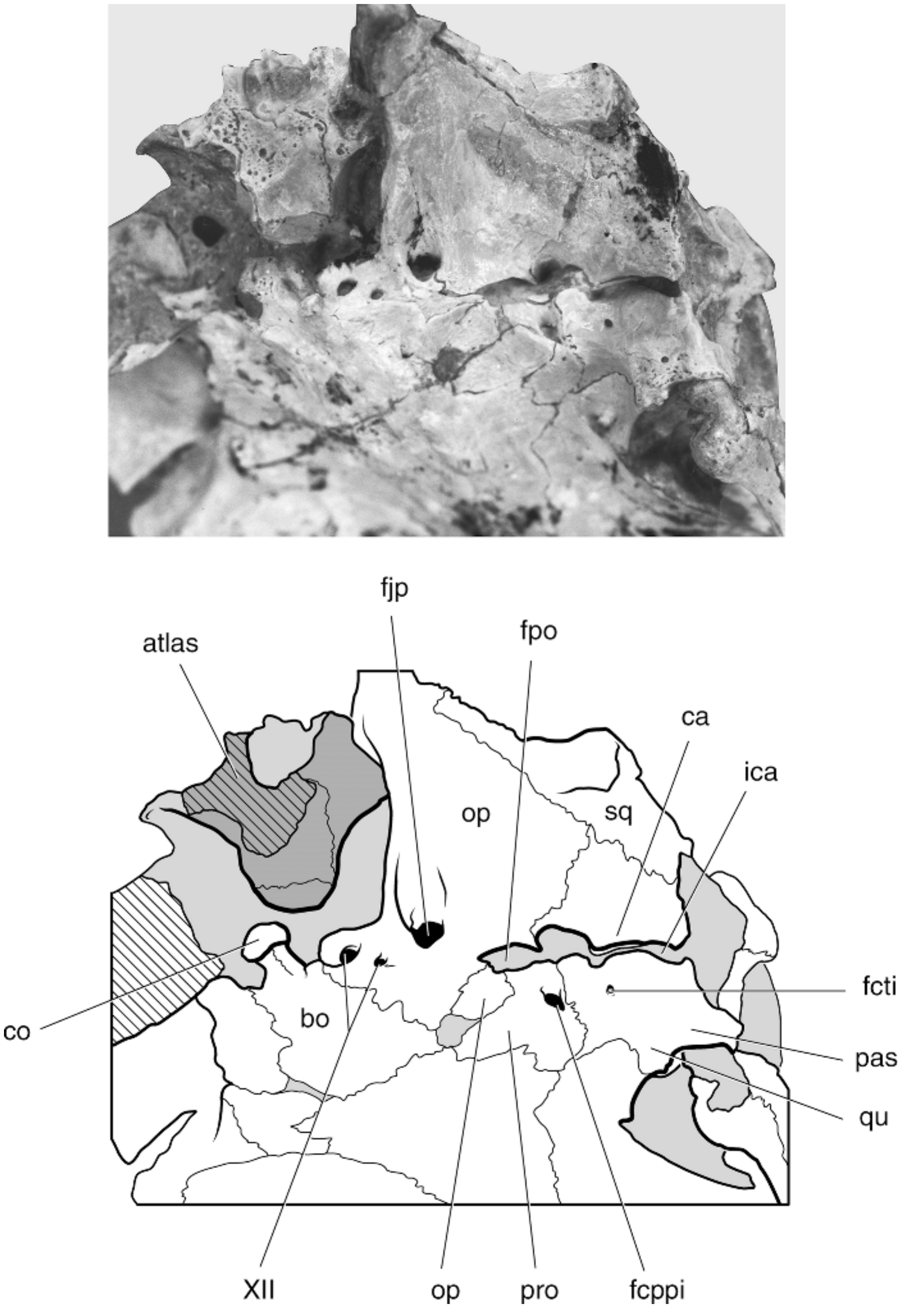

Fig. 37. *Araripemys barretoi* Price, 1973. Posterior oblique view of skull of THUg 1907 reversed from left side. [A. Venjara and E.S. Gaffney, del.]

surrounding prootic ossification in turtles generally. In *Araripemys* the prootic is similar to that in pelomedusids, which have been partially described by van der Merwe (1940) and corrected in Gaffney (1979a).

The foramen posterius canalis carotici interni in *Araripemys* lies at the anterior end of a groove formed on the ventral surface of the prootic (figs. 36, 37). This is not a preparational artifact of AMNH 24453, as it is

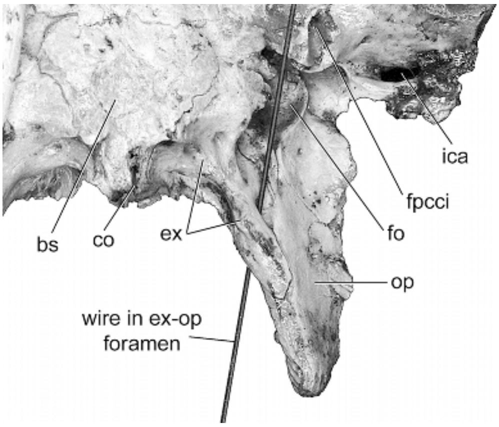

Fig. 38. *Araripemys barretoi* Price, 1973. Ventral view of left posterolateral part of skull of AMNH 24454 showing wire in unnamed foramen (see text). [E.S. Gaffney, del.]

present in all four specimens. A thin plate of quadrate extends medially to overlie the posterior margin of this groove, and it slightly enters the groove, but not the foramen posterius canalis carotici interni. The groove and medial quadrate process are variably developed in pelomedusids and some chelids, but the thin, medial quadrate process does not occur elsewhere in pleurodires.

The canalis caroticus internus in *Araripemys* extends anteromedially through the prootic and into the basisphenoid (fig. 34). In AMNH 24454 the basisphenoid portion is eroded, exposing the canal. The foramen nervi facialis enters the prootic at the fossa acustico-facialis and travels ventrally to open in the roof of the canalis caroticus internus. In chelids and pelomedusids, this opening is close to the foramen posterius canalis carotici interni, but in *Araripemys* the foramen nervi facialis, which may be used as a morphologic landmark, is separated from the foramen posterius canalis carotici interni by a length of canal. Presumably this is an extension of the canalis caroticus internus, rather than a more medial position of the foramen nervi facialis, which is extremely stable in turtles. Some pelomedusids have a slight extension of the canalis caroticus internus posteriorly, but not to the extent seen in *Araripemys*.

In the canalis caroticus internus, at the position of the foramen nervi facialis ventral opening, is the geniculate ganglion in life. The vidian or palatine branch extends anteriorly from this ganglion, and this opening can be seen at this position in AMNH 24453. The canalis nervi vidiani extends anteriorly into the pterygoid (see Pterygoid). Posteriorly the chorda tympani branches from the hyomandibular branch of the facial nerve and forms a canal extending laterally and ventrally into the quadrate (fig. 37). Only the quadrate end of this canal, the foramen chorda tympani inferius, can be seen in *Araripemys*.

Internal features of the cavum labyrinthicum are visible in AMNH 24453, and these agree with recent pelomedusids and do not vary much among turtles.

In Meylan (1996: fig. 4) the prootic is incorrectly shown as rectangular; it should be L-shaped, and there is no foramen medial to the foramen posterius canalis carotici interni.

OPISTHOTIC (figs. 26, 36–38, 276D)

Preservation: The opisthotic of *Araripemys* is present and nearly complete on the right side of AMNH 24453, the right side of THUg 1357, and the right side of AMNH 24454, but it is covered by the hyoid. In THUg 1907 both opisthotics are present, with the right being nearly complete but partially covered by matrix dorsally; the left is damaged posteriorly. In AMNH 24454 the left opisthotic is missing its lateral margin and some of the dorsal surface, but it is well preserved otherwise, with much of the internal area being visible. In AMNH 24453 the internal area is also free of matrix, but there has been some preparational erosion.

Contacts: The opisthotic in *Araripemys* contacts the supraoccipital anteromedially, the prootic anteriorly, the quadrate anterolaterally, the squamosal posterolaterally, and the exoccipital medially. Contrary to Meylan (1996: 26), there is no contact with the basisphenoid on the ventral surface. The processus interfenestralis is separated by a space in all four specimens. The bone labeled "pr" in Meylan (1996: fig. 4) is the opisthotic, but it does not touch the basisphenoid or come close to it as shown in the figure.

Structures: The opisthotic in *Araripemys* is a flat bone forming part of the cavum labyrinthicum and cavum acustico-jugulare. These features are largely visible in AMNH 24453 and AMNH 24454. In ventral view the usual chelonian landmarks can be seen: the fenestra ovalis, being formed posteriorly by the processus interfenestralis, and the curved trough containing the perilymphatic sac posterior and lateral to these structures. The ridge forming the margin of this trough varies in size among the four *Araripemys* specimens, resulting in variation of the size and shape of the foramen jugulare posterius and fenestra postotica. This ridge is lowest in AMNH 24453, probably due to preparational erosion, but it is unlikely to have been as high as it is in THUg 1907. In THUg 1907 the ridge is high but also curved ventromedially to meet the exoccipital. In AMNH 24454 the ridge is higher than in AMNH 24453, but it still does not form divisions within the fenestra postotica or between the fenestra postotica and foramen jugulare posterius. AMNH 24454 seems to be well preserved with no damage. THUg 1357 has a higher ridge than does AMNH 24454 but a smaller one than in THUg 1907. It does form a medial wall to the fenestra postotica, but the foramen jugulare posterius is open.

The foramen jugulare posterius varies considerably in *Araripemys*; it may be open (AMNH 24454) or completely closed (THUg 1907) (see Exoccipital). When closed, as in THUg 1907, the opisthotic makes up the lateral margin, in contrast to nearly all other members of the hyperfamily Pelomedusoides.

The fenestra postotica in *Araripemys* (figs. 36, 37) lies between the quadrate laterally and the opisthotic medially. The opisthotic portion is formed by the lateral margin of the perilymphatic ridges, described above. In AMNH 24453 the ridge is very low, barely visible, and there is almost no medial margin to the fenestra. The ridge is low but distinct in AMNH 24454. In THUg 1357 the ridge is high, nearly enclosing the fenestra postotica, but the more posterior part of the ridge is lower and possibly damaged. In THUg 1907 the ridge defining the fenestra postotica is low, as in AMNH 24454, which is particularly odd since the posterior part of the ridge is as high as possible, making extensive contact with the exoccipital. It all goes to show that some of this crap makes no sense at all. The morphology of the fenestra postotica region in *Araripemys* does not differ greatly from that in primitive chelids and pelomedusids, but it is different from other pleurodires. Euraxemydids have a more ossified cavum acustico-jugulare with the fenestra postotica a discrete structure. The more extensive bony walls of the cavum acustico-jugulare, particularly in the lateral and ventral parts, more fully enclose the perilymphatic system and separate the fenestra postotica from the incisura columellae auris and stapes.

The processus interfenestralis of the opisthotic forms the posterior margin of the fenestra ovalis and a posterior wall for part of the cavum labyrinthicum (Gaffney, 1979a). The processus is the anterior wall for the part of the perilymphatic system (the pericapsular recess of Wever [1978], which is around the stapedial footplate), the basis columellae basalis, and curves medially around the cavum labyrinthicum to the fenestra perilymphatica. This region is relatively conservative in all casichelydians, including *Araripemys*. What does vary in turtles is the floor that covers the processus interfenestralis as seen in ventral view. *Araripemys*, along with pelomedusids and chelids, has the primitive chelonian condition of a ventrally exposed processus interfenestralis (fig. 276D). The degree of ossification varies among the four *Araripemys* specimens. In THUg 1907 the ventral end of the processus interfenestralis is relatively large and contacts the prootic anteriorly and the exoccipital posteriorly. In AMNH 24453 and AMNH 24454 there is a small exoccipital contact. In THUg 1357 the exoccipital contact is very small, and the ventral end of the processus is smaller also.

Euraxemydids, bothremydids, and podocnemidids have processes of the exoccipital, quadrate, or basioccipital covering the processus interfenestralis. In some specimens of *Pelusios*, the processus is also covered or partially covered. Whether this is systematic and species specific or individual variation is not known.

The opisthotic contribution to the cavum labyrinthicum is relatively conservative in turtles. Meylan (1996) described this for *Araripemys*. Comparison of the cavum labyrinthicum in *Araripemys*, chelids, and pelomedusids shows that they are all similar.

The processus paroccipitalis of the opisthotic is a posterolateral process that is very wide and flat in *Araripemys*. In chelids the processus is short and deeper, but in pelomedusids it is wide and flat, similar to *Araripemys*. Podocnemidids and bothremydids have a shorter and deeper processus paroccipitalis. Although Meylan (1996) characterized *Euraxemys* (FR 4922), pelomedusids, and *Podocnemis expansa* as having a relatively large and posteriorly projecting opisthotic, a wider comparison of pleurodires leads to the conclusion that pelomedusids and *Araripemys* actually share a wider and flatter processus paroccipitalis than in other pleurodires.

BASISPHENOID (figs. 26, 34, 276D)

Preservation: The basisphenoid is present and complete in THUg 1357, THUg 1907, and AMNH 24454. In AMNH 24453 some of the right side is missing, and the anterior end is preserved in a part of the skull not connected to the rest of the basisphenoid by a definite contact. In AMNH 24453 the dorsal surface is prepared (figured in Meylan, 1996: figs. 5, 6), but it has had some of its surface eroded by acidic frenzy. Nonetheless, this is an undisguised blessing, as it reveals the paths of canals that might otherwise prove contentious.

Contacts on ventral surface: The basisphenoid in *Araripemys* contacts the pterygoids anterolaterally, separating them for almost their entire length but not reaching the palatines in any specimen, despite Meylan's (1996) figure 4. In AMNH 24453 and AMNH 24454, the only specimens available to Meylan, the pterygoids clearly meet anterior to the basisphenoid on both dorsal and ventral surfaces. The basisphenoid contacts the basioccipital posteriorly and the prootic posterolaterally.

Structures on ventral surface: The ventral surface is smooth in *Araripemys*, with a slight midline convexity. The basisphenoid forms a small part of the margin of the unossified space around the processus interfenestralis, as in primitive chelids, most pelomedusids, and euraxemydids (which cover the opisthotic but still have a space).

Contacts on dorsal surface: Only in AMNH 24453 is the dorsal surface visible, and the basisphenoid contacts the pterygoids anterolaterally, the prootics laterally, and the basioccipital posteriorly.

Structures on dorsal surface: The anterior part of the basisphenoid is the fused trabeculae cranii, the rostrum basisphenoidale in the adult. In *Araripemys* the rostrum is significantly longer than in pelomedusids, primitive chelids, and *Euraxemys*. In most pleurodires the pterygoids meet ventral to the rostrum, but in *Araripemys* the ventral exposure is nearly the same as the dorsal shape. Some of the middle of the rostrum is missing in AMNH 24453, but the other specimens show a shallow, midline concavity. The sella turcica is shallow and only partially overhung by a thin dorsum sellae, but it is likely that the dorsum sellae has been reduced in thickness by preparation. The foramen anterius canalis carotici interni lies at the lateral corner of the sella turcica overhung by the dorsum sellae. In pelomedusids and primitive chelids the sella turcica is narrower and deeper, with a more distinct anterior margin. The foramen anterius canalis carotici interni is closer to the midline as well.

The surface of the dorsum sellae is smooth, without any sign of the processus clinoideus or foramen nervi abducentis. The absence of these features is likely due to acid erosion, as the medullary cancellous part of the bone is exposed on the surface, rather than the smooth lamellar bone that usually forms an original bone surface.

It is likely that the bone erosion is what has caused the exposure of the arterial canal system in this basisphenoid. In AMNH 24453, the canalis caroticus internus can be seen (fig. 34) as a sulcus extending posterolaterally from the foramen anterius canalis carotici interni to the prootic suture, as described and figured in Meylan (1996). The canalis is covered by a small strap of bone remaining on the dorsum sellae on both sides.

A canal (now a groove due to erosion) branches off the canalis caroticus internus just lateral to the foramen anterius canalis carotici interni. This was identified in Meylan (1996) as the canalis caroticus lateralis, and the senior author agrees with this identification. It ends at the foramen caroticum laterale on the dorsal surface of the basisphenoid, and in life it contained the palatine artery. The canalis caroticus lateralis and the palatine artery are absent in the recent Pelomedusidae (Albrecht, 1976) and in the Bothremydidae. The condition is indeterminate in the Euraxemydidae and *Hamadachelys*.

FAMILY EURAXEMYDIDAE

Euraxemys essweini

Euraxemys is known from only one skull that is nearly complete, uncrushed, and was prepared by both acid and mechanical means. This skull, FR 4922, has much of the internal area free of matrix and did not suffer from overpreparation in acid. Because it is so well preserved, and because the taxon is outside the larger groups, Bothremydidae and Podocnemididae, this specimen has been described in more detail with wider comparisons. The other euraxemydid, *Dirqadim*, has a description that emphasizes comparisons between these two genera. This skull has been briefly described under its number in Gaffney and Meylan (1991). Significant corrections have been made to this earlier description.

PREFRONTAL (figs. 39, 42)

Preservation: The skull of FR 4922 is damaged in the interorbital region; only a small portion of the prefrontals remain, as well as the impression of the ventral surface in matrix. The dorsal surfaces of both prefrontals are gone, but enough of the anterior edge of the left prefrontal is present to preserve the dorsal margin of the apertura narium externa, which shows that there are no nasal bones. The anteroventral processes and contacts with the maxillae are present on both sides. Nearly all of the posterior parts of both prefrontals are missing.

Contacts: Laterally the prefrontal contacts the maxilla, but in FR 4922 the dorsal portion of this contact is missing and only the ventral part of the suture is preserved. The two prefrontals are in contact anteriorly, but their posterior limits are unclear. The earlier (Gaffney and Meylan, 1991) statement that the frontals sent processes anteriorly to partially divide the prefrontals in FR 4922 is uncertain. This is the case in the specimen as preserved, but the bone and matrix impression visible document only the ventral surface. In most Pelomedusoides the frontals underlie the prefrontals on the midline, and that is the case in *Euraxemys*. Unfortunately, whether the frontals divided the prefrontals on the dorsal surface as well is not determinable.

Structures: The prefrontal is a curved bone with a dorsal plate on the skull roof and a ventral plate separating the fossa nasalis from the fossa orbitalis, forming a margin for the large foramen orbitonasale medially. The anteroventral process of the prefrontal in *Euraxemys* extends ventrally along the posterior edge of the maxilla. This process is visible on both sides of FR 4922 but can it be seen in its entirety only on the right side. Even here the posterior margin is a thin but broken edge, so its complete extent posteromedially is not determinable. However, considering that it is very thin and close to the margin of the adjacent maxilla, it is likely that the preserved margin is close to the original margin in extent.

FRONTAL (figs. 39, 42, 43C)

Preservation: The right and left frontals in FR 4922 are complete posteriorly but broken and mostly missing interorbitally and anteriorly.

Contacts: The anterior contacts with the prefrontals are preserved as impressions on matrix and adhering bone fragments from the ventral surface. These show that the frontals extend between the orbits and partially separate the prefrontals on the ventral surface. It cannot be determined if this separation was present on the dorsal surface.

Structures: The frontal forms the interorbital portion of the skull roof, as preserved in *Euraxemys*. The interorbital area is very narrow, but most of the bone here is missing and only matrix impressions and adhering bone fragments are preserved. Nonetheless, it is likely that the interorbital area was narrow, as in *Araripemys*, because that is most consistent with the nearby areas that are preserved.

The sulcus olfactorius is preserved as a cast in the matrix. This is much narrower than the sulcus in such forms as *Pelusios* but is comparable to the size seen in *Podocnemis*.

The posterior part of the frontal in *Euraxemys* is transversely expanded, similar to *Araripemys*. There is a posterolateral contact with the postorbital and a transverse contact with the parietal posteriorly. The sutural contact as figured (fig. 42) is based on the preserved suture, not necessarily the dorsalmost expression of the suture, as some of the surface bone is eroded.

Most of the ventral surface of the frontal in FR 4922 is hidden by matrix, but a portion of it is seen in the posterior wall of the right orbit and in the roof of the sulcus palatinopterygoideus. The frontal does not send any process ventrally to make up part of the processus inferior parietalis, as it does in *Pelusios* and *Podocnemis*.

PARIETAL (figs. 39, 42, 43A)

Preservation: Both parietals are nearly complete in FR 4922; the right one has the lateral surface of the processus inferior parietalis free of matrix.

Contacts of dorsal plate: The dorsal plate of the parietal in *Euraxemys* contacts the frontal anteriorly, the postorbital anterolaterally, and the quadratojugal laterally.

Structures of dorsal plate: The posterior half of the lateral edge of the parietal borders the temporal emargination. The temporal emargination in *Euraxemys* is roughly comparable to that seen in *Podocnemis*, although it is a little more emarginate in *Euraxemys* because the foramen stapedio-temporale is visible in the latter and not in *Podocnemis*. The parietal is more extensive than in *Pelomedusa* and *Pelusios* but smaller than in *Peltocephalus* and *Erymnochelys*. Posteriorly the parietal tapers to a point. The dorsal contact with the supraoccipital figured in Gaffney and Meylan (1991) is an error. The right parietal has a short, incomplete suture at its posterior end. This may represent an injury during life or a growth anomaly.

Contacts of processus inferior parietalis: The parasagittal, ventral process of the parietal, the processus inferior parietalis (fig. 43), can be seen on its lateral surface on the right side of FR 4922. The processus begins anteriorly where the processus forms the curved posterior edge of the foramen interorbitale. The anterior part of the processus inferior parietalis contacts the palatine ventrally. Posteriorly the parietal contacts the crista pterygoidea of the pterygoid. This is similar to the condition in most other Pelomedusoides. Posteriorly the processus inferior parietalis forms the dorsal part of the margin of the foramen nervi trigemini.

Structures of processus inferior parietalis: The processus inferior parietalis in *Euraxemys* has roughly the same extent as in pelomedusids. It forms the posterior margin of the foramen interorbitalis and the lateral wall of the cavum cranii. The processus forms the medial wall and part of the roof of the sulcus palatinopterygoideus. A small foramen of unknown function is within the parietal-pterygoid suture. The foramen nervi trigemini in *Euraxemys* is similar in size and position to that in pelomedusids and is formed by the parietal anterodorsally, the prootic dorsolaterally, and the pterygoid ventrally.

JUGAL (figs. 39, 42, 43B, C)

Preservation: The jugal in FR 4922 is preserved on both sides. On the left side some of the lateral edge is missing and most of the internal features are covered by matrix. On the right side the jugal is complete and all of its morphology is visible.

Contacts of lateral plate: Posteriorly the jugal contacts the quadratojugal in a narrow suture that is less extensive than in *Pelomedusa* and *Pelusios* because they have a less extensive cheek emargination. *Araripemys* also has a narrow jugal-quadratojugal contact and its cheek emargination is similar in extent to that in *Euraxemys*. *Podocnemis* has an extensive cheek emargination similar to that in *Euraxemys* but the jugal-quadratojugal contact in that species is much more extensive, presumably related to the presence of a very small postorbital. The jugal in *Euraxemys* is smaller than that bone in most other Pelomedusoides, even *Pelusios* and *Pelomedusa*. It is possible that the condition of the jugal in *Euraxemys* is primitive for Pelomedusoides.

The jugal contacts the maxilla anteriorly where both form the ventral margin of the orbital edge. As in many other Pelomedusoides this contact in *Euraxemys* is an interfingering suture. In *Araripemys* the

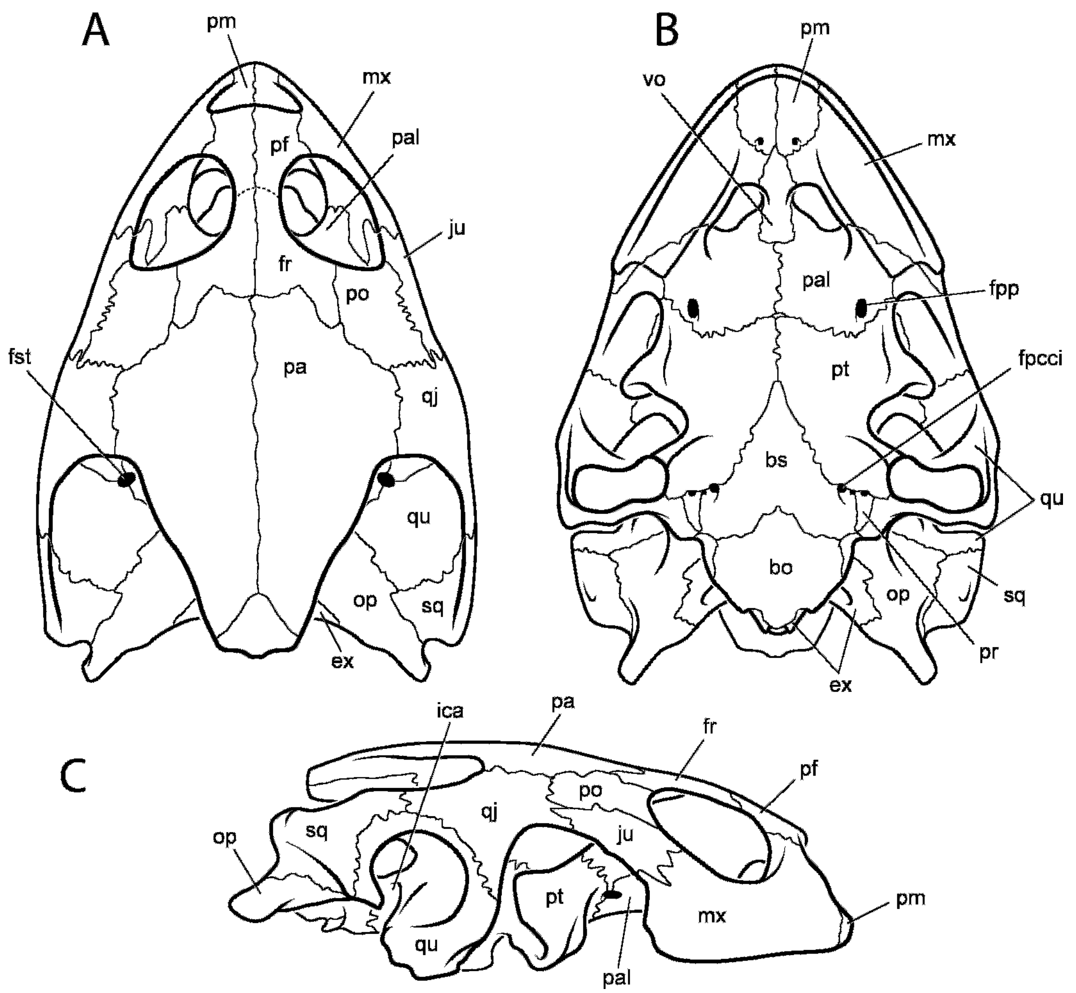

Fig. 39. *Euraxemys essweini*, n. gen. et sp. Partially restored skull based on FR 4922 holotype. **A**, dorsal; **B**, ventral; **C**, lateral. See also figure 44A for details of basicranial foramina and canals. For more detailed view of area around foramen posterius canalis carotici interni, see figure 276C. See also figure 281A for more detailed view of quadrate. [F. Ippolito, del.]

jugal-maxilla contact is placed farther anteriorly than in *Euraxemys* so that the jugal has a greater exposure along the cheek margin.

Structures of lateral plate: The jugal is a flat plate on the cheek with a medial process that participates in the characteristically pleurodiran septum orbitotemporale. The flat plate in *Euraxemys* borders the cheek emargination dorsally and the orbital margin anteriorly.

Contacts of medial process: The medial edge of the medial process contacts the postorbital, and together they make up the septum orbitotemporale. The posterior surface of this wall forms the anterior wall of the temporal muscle cavity, the fossa temporalis inferior. Both postorbital and jugal reach the pterygoid bone and form a significant brace for the processus trochlearis pterygoidei. In posteroventral view, the jugal process contacts the postorbital dorsally, the pterygoid posteriorly, the palatine ventrally, and the maxilla anteroventrally.

In the floor of the fossa orbitalis, the jugal contacts the maxilla anteriorly and the palatine medially, as in most Pelomedusoides.

Fig. 40. *Euraxemys essweini*, n. gen. et sp. Partially restored ventral view of skull based on FR 4922 holotype. See also figures 44A and 276C for more detailed view of area around foramen posterius canalis carotici interni. [B. Degner, del.]

Structures of medial process: The medial process of the jugal in *Euraxemys* and other pleurodires is a complex structure (see Gaffney [1979a, 1979c] for further description in chelids). In euraxemydids and pelomedusids, this process is at its simplest. The process is a posteroventrally curved plate with an anterior extension, which forms part of the floor of the fossa orbitalis with a V-shaped exposure tapering anteriorly. In *Euraxemys* (figs. 43B, C), lateral to this exposure the jugal lies medial to the maxilla and medial to the V shape; the jugal lies lateral to the palatine. In some *Pelusios* the V shape is not apparent and the palatine contact is much less extensive. In most pelomedusids, however, this V-shaped portion of the jugal is present on the floor of the fossa orbitalis. At the palatine-maxilla-jugal junction there is a small foramen of unknown function. There is a larger, and still unknown, foramen between the jugal and palatine more posteriorly. The curved medial process of the jugal is a C-shaped sheet (try saying that after a few swigs of turtle juice), concave posteroventrally.

QUADRATOJUGAL (figs. 39, 42)

Preservation: The right quadratojugal in FR 4922 is nearly complete, but the left one is represented only by a few fragments.

Contacts: As in pelomedusids, the quadratojugal of *Euraxemys* contacts the postorbital anterodorsally, the jugal anteroventrally, the quadrate posteroventrally, and the squamosal posteriorly. However, *Euraxemys* differs from *Pelusios* and *Pelomedusa* in having a broad medial contact with the parietal and a less extensive temporal emargination. In pelomedusids, the quadratojugal does not contact the parietal, and the postorbital enters the margin of the temporal emargination. *Podocnemis* also has a broad quadratojugal-parietal contact but it is more extensive than in *Euraxemys*. It is likely that the condition in *Euraxemys* is primitive for all Pelomedusoides.

Structures: The quadratojugal of *Euraxemys* forms the posterodorsal margin of the cheek emargination and the anterolateral margin of the temporal emargination.

SQUAMOSAL (figs. 39, 42)

Preservation: The right squamosal in FR 4922 is complete and well preserved, but the left one has its lateral surface missing.

Contacts: The cone-shaped squamosal has a narrow anterior contact with the quadratojugal in *Euraxemys*, as in pelomedusids. Anteroventrally there is the curved quadrate contact, as in many other turtles, and medially there is the opisthotic contact.

Structures: The cone-shaped squamosal fits onto the circular antrum postoticum of the quadrate, forming the dorsal part of that hollow structure. *Euraxemys* has a moderately large antrum (fig. 281A), larger than in *Podocnemis* and much larger than in bothremydids. The antrum postoticum in euraxemydids, *Araripemys*, and pelomedusids are all comparable in size to the antrum postoticum of chelids. These all have a large antrum that is presumably the primitive condition for Pelomedusoides. Pelomedusids have an antrum that extends posteriorly to a greater extent than those in euraxemydids and *Araripemys*.

POSTORBITAL (figs. 39, 42, 43)

Preservation: The postorbital of FR 4922 is preserved on both sides, but on the left side only the dorsal surface is exposed; the rest is embedded in matrix. On the right side the ventral process is completely visible and well preserved.

Contacts of lateral plate: The lateral plate of the postorbital in *Euraxemys* forms the posterior orbital margin, contacts the parietal posteromedially, the jugal laterally, the frontal anteromedially, and the quadratojugal posteriorly.

Structures of lateral plate: The postorbital is separated from the temporal margin by a broad contact of parietal and quadratojugal. In *Pelusios* and *Pelomedusa* the emargination is greater than in *Euraxemys*, and it separates these bones, exposing the postorbital along the temporal emargination. *Araripemys* also has a postorbital similar in shape to *Euraxemys*, but the parietal-quadratojugal contact is absent due to the slightly more extensive temporal emargination and a larger postorbital.

Contacts of medial process: Dorsomedially the postorbital contacts the frontal, and that bone forms the roof of the sulcus palatinopterygoideus (fig. 43C). Ventrally, in the posterior wall of the orbit, the septum orbitotemporale, the postorbital contacts the palatine medially and the jugal laterally. The jugal contact is the same thickness as the postorbital but the palatine is replaced by the pterygoid posteriorly. Thus, the posterior surface of this wall, which forms the anterior wall of the fossa temporalis, shows the postorbital contacting the jugal ventrolaterally and the pterygoid ventromedially.

Structures of medial process: The ventral process of the postorbital in *Euraxemys* forms part of the septum orbitotemporale. Medially the process forms the lateral margin for the sulcus palatinopterygoideus.

PREMAXILLA (figs. 39–42)

Preservation: Both right and left premaxillae are preserved in FR 4922. The internal and external surfaces of both are visible.

Contacts: Laterally the premaxilla contacts the maxilla in a suture that is parasagittal anteriorly but curves posteromedially behind the premaxilla, preventing exposure of the premaxilla on the edge of the apertura narium interna. Posteromedially the single vomer contacts both premaxillae and slightly separates them on the midline.

Structures on dorsal surface: The dorsal surface of the premaxilla in *Euraxemys* has a low median ridge comparable to that in *Podocnemis* and lower than in *Kurmademys*. The ridge rises posteriorly to meet the vomer and completely separates the two choanal passages. The foramen praepalatinum is clearly visible on each premaxilla with a shallow, anterior trough leading into it. The foramen is completely formed within the premaxilla on both ventral and dorsal surfaces, although it is placed posteriorly near the vomer suture, as in most *Podocnemis* and other Pelomedusoides.

Structures on ventral surface: The ventral surface of the premaxilla in *Euraxemys* has narrow labial ridge continuous with the maxilla. The ridge is unusually thin and sharp, much thinner than in any of the living Pelomedusoides. There is a shallow median notch, narrower than in *Kurmademys* and other members of the Pelomedusoides. The anterior margin of the apertura narium externa does not protrude anteriorly past the labial ridge in *Euraxemys* as it does in *Podocnemis* and *Pelusios*. The part of the premaxilla that forms the continuation of the triturating surface is relatively flat and forms only a very broad and shallow median concavity, in contrast to the more clearly demarcated concavities seen in *Podocnemis* and *Kurmademys*.

MAXILLA (figs. 39–43)

Preservation: Both right and left maxillae are complete in FR 4922, but matrix obscures the internal areas on the left one while the right maxilla is completely visible everywhere.

Contacts of vertical plate: The maxilla in *Euraxemys* contacts the premaxilla anteromedially, the jugal posterodorsally, and the prefrontal anterodorsally.

Structures of vertical plate: The vertical or alveolar plate of the maxilla is deep and narrow in *Euraxemys*, as deep as in *Podocnemis* but much thinner. The labial ridge is slightly broken along its ventral edge but it seems to have had only a slight curve to it in lateral view. The dorsal process of the maxilla is damaged dorsally on both sides but seems to fit into the prefrontal, as in other Pelomedusoides. The process lies between the apertura narium externa and the fossa orbitalis, forming the lateral wall of the fossa nasalis. On the internal side of the fossa nasalis the prefrontal-maxilla suture is lower than on the external side where the prefrontal extends more dorsally. Posteriorly the alveolar plate of the maxilla in *Euraxemys* forms the lower border of the cheek emargination, contacting the jugal between the orbital margin and the cheek emargination.

Contacts of horizontal plate: The horizontal plate of the maxilla in *Euraxemys* contacts the premaxilla anteromedially, the vomer medially, the palatine posteromedially, and the jugal posterolaterally. There is no midline contact of the maxillae.

Structures of horizontal plate: The horizontal plate of the maxilla bears the triturating surface on its ventral side. In *Euraxemys* the maxilla in ventral view is expanded anteriorly and tapers posteriorly. Anteriorly there is a curved suture with the premaxilla that borders a medial process of the maxilla. This process contacts the vomer and is just separated from meeting the other maxilla by a midline contact between premaxillae and vomer. Posterior to the vomer the maxilla forms the margin of the apertura narium interna, and then tapers to contact the palatine. The combined premaxillae, vomer, and maxillae form a triturating surface that is relatively large anteriorly, much larger than in *Pelusios*, *Pelomedusa*, and

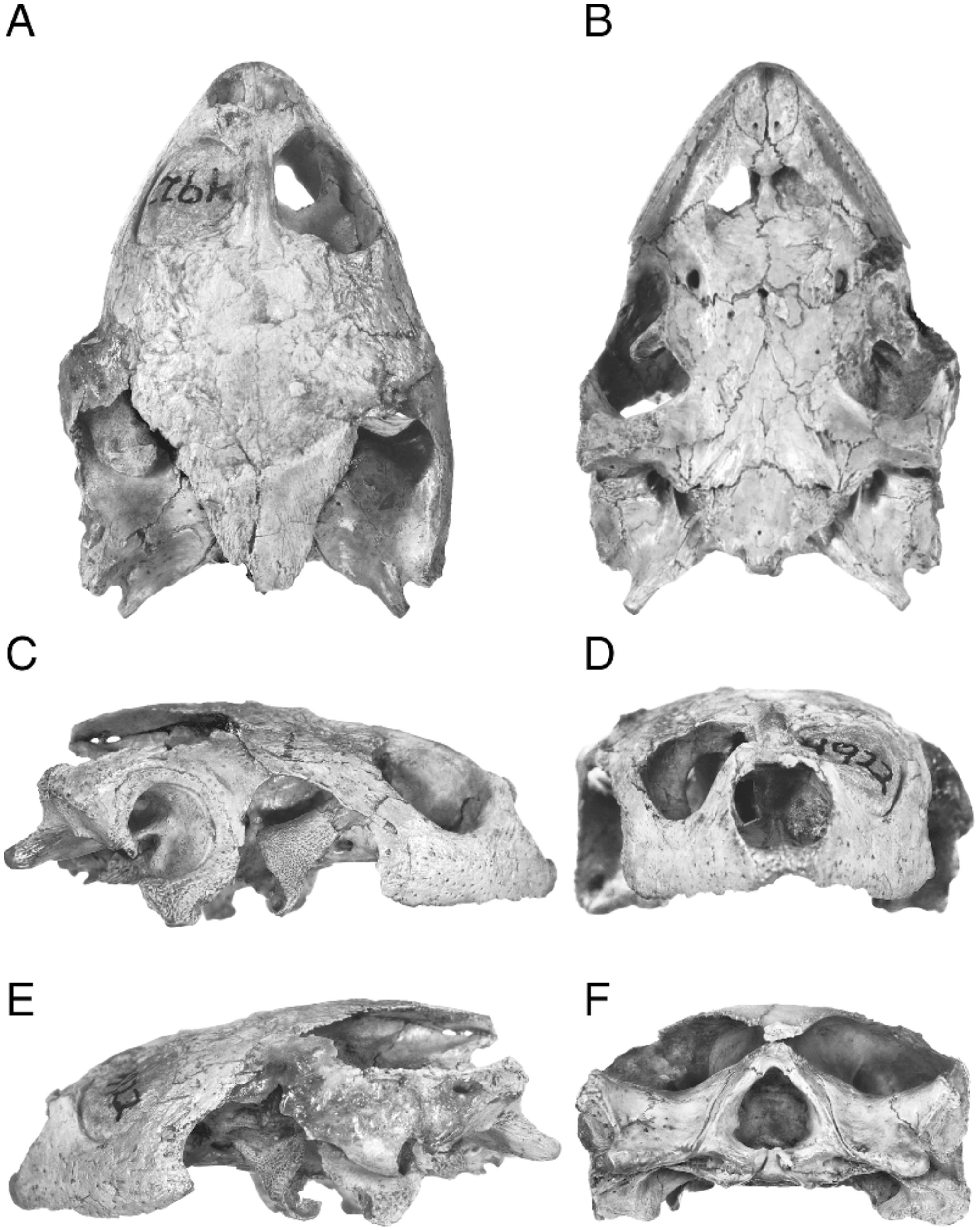

Fig. 41. *Euraxemys essweini*, n. gen. et sp., FR 4922 holotype. **A**, dorsal; **B**, ventral; **C**, right lateral; **D**, anterior; **E**, left lateral; **F**, posterior. [E. Heck, del.]

Kurmademys, and slightly larger than in *Podocnemis*. *Euraxemys* is unique in having the triturating surfaces expanded anteriorly and narrowed posteriorly. In *Podocnemis* the medial maxillary processes meet on the midline to form the expanded area, while in *Erymnochelys* and *Peltocephalus* the maxillae usually do not meet on the midline.

The triturating surface of *Euraxemys* (fig. 40) is relatively flat in the region of the

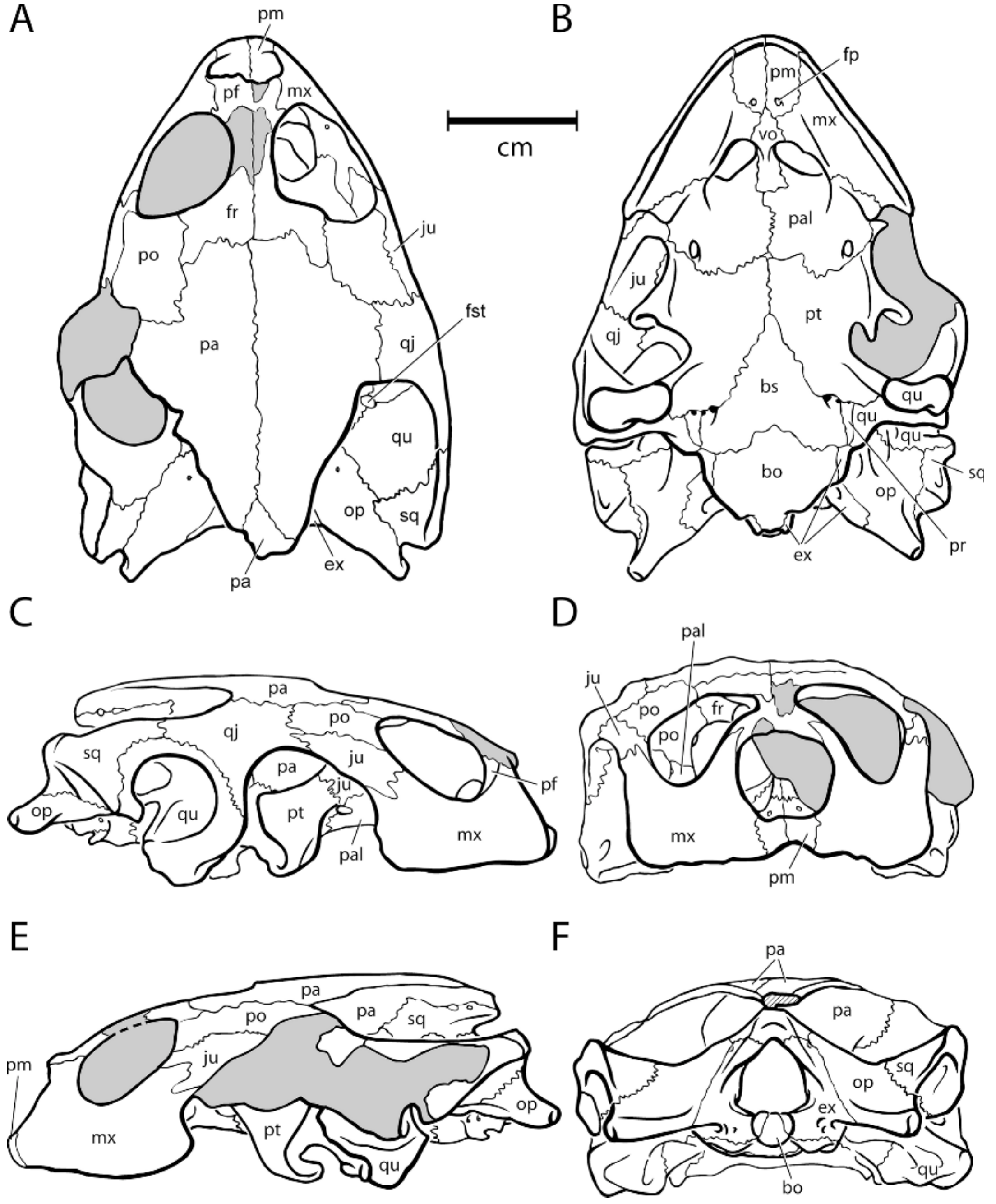

Fig. 42. *Euraxemys essweini*, n. gen. et sp., FR 4922 holotype. **A**, dorsal; **B**, ventral; **C**, right lateral; **D**, anterior; **E**, left lateral; **F**, posterior. [L. Redniss, del.]

premaxilla; there is no midline concavity as seen in *Pelusios*. Just at the premaxilla-maxilla suture the maxillary portion of the triturating surface begins the low accessory ridge that runs between the labial ridge and the margin of the apertura narium interna. This ridge roughly parallels the labial ridge but bends anteriorly so that it is closer to the labial ridge. In *Dirqadim* the accessory ridge is higher and parallels the labial ridge for its entire length. The triturating surface continues medial to the accessory ridge in the anterior part of the triturating surface to the edge of the apertura narium interna. There is no distinct lingual ridge in either *Euraxemys* or *Dirqadim*. The accessory ridge in *Euraxemys* is broader and blunter than the small accessory ridges of *Podocnemis* and is not exactly duplicated in any other Pelomedusoides.

The maxilla forms most of the lateral wall of the fossa nasalis and the choanal chambers leading to the apertura narium interna. This region varies among Pelomedusoides. *Euraxemys* is more similar to *Podocnemis* in having a broad floor for the fossa and a posterior position for the apertura narium interna.

VOMER (figs. 39–42)

Preservation: The vomer in FR 4922 is present and complete. The dorsal surface is not visible due to matrix and I'm too chicken to throw it back into the acid. Anteriorly the vomer slightly separates the premaxillae and contacts the maxillae anterolaterally. The posterior expansion of the vomer in *Euraxemys* contacts the palatines and separates them for the length of the vomer at least on the ventral surface.

Structures: The dumbbell-shaped, unpaired vomer of *Euraxemys* separates the apertura narium interna and is formed into a more ventral, anterior part, and a more dorsal posterior part.

PALATINE (figs. 39–43)

Preservation: Both palatines are preserved in FR 4922, but only the right one has its dorsal surface free of matrix. The anterior edge of both palatines is very thin, and some bone may be missing, particularly on the left palatine, which is less extensive than the right palatine. The right palatine is still in matrix dorsally; although its edge is fragmented, it is nearly complete.

Contacts: The palatine in *Euraxemys* contacts the maxilla anterolaterally, the vomer anteromedially, the other palatine medially, the pterygoid posteriorly, and the jugal laterally. On the dorsal surface the palatine also contacts the parietal medially and the postorbital laterally.

Structures on dorsal surface: On the dorsal surface of the palatine there is a small process rising to meet the postorbital (fig. 43A). This process is developed to about the same height seen in most *Pelusios*, *Pelomedusa*, and *Podocnemis*. It is higher than in chelids like *Emydura*, and much lower than in *Kurmademys*. Laterally the palatine contacts the jugal and participates in the foramen that runs between the orbital floor and the anterior wall of the adductor fossa (unlabeled foramen in fig. 43C).

Structures on ventral surface: On the ventral surface, the palatine contacts the vomer anteromedially, forms the posterior margin of the apertura narium interna anteriorly, and contacts the maxilla anterolaterally. The area of the palatine contacting the maxilla forms part of the triturating surface in general and the low lingual ridge close to the maxillary contact. The palatine does not form a large portion of the triturating surface, as in the Bothremydini and some podocnemidids, but it is greater than in *Pelomedusa* and most *Pelusios*. It is close to the presumed primitive condition seen in chelids such as *Emydura*. In *Araripemys* the triturating surface is very narrow and the palatine parallels the labial ridge, barely forming the posterior margin of the surface. The entire palatine in *Euraxemys* is larger than in *Araripemys*; however, the palatine contribution to the triturating surface is larger in *Araripemys* than in *Euraxemys*.

Laterally, near the contact with the jugal, a foramen penetrates from the floor of the fossa orbitalis ventrally into the fossa temporalis (fig. 43C). It is formed by the palatine medially and the jugal laterally. On the ventral surface the foramen is continuous with a groove that curves ventrolaterally along the jugal-palatine suture and ends at two foramina in the maxilla (partially formed by jugal and palatine also). Clearly, a vessel penetrated from the fossa orbitalis into the maxilla by means of this groove and foramina. In the living cryptodires, a characteristic set of foramina and canals, the foramen supramaxillare and associated structures (Gaffney, 1979a: 88–89), is found in the maxilla. In pleurodires these structures seem to be absent except in some podocnemidids. The foramen in *Euraxemys* may be for the arteria supramaxillaris of Albrecht (1976), but it lies in the jugal-palatine suture rather than directly in the maxilla, as described by Albrecht. In any case, the foramina and associated groove as described are unique to *Euraxemys*.

Posterolaterally the palatine contacts the pterygoid just anterior to the base of the processus trochlearis pterygoidei. The foramen palatinum posterius is formed completely by the palatine, although it is very close to the pterygoid suture. The relative degree of participation in the foramen by these two bones is variable in pleurodires, although among recent members of the Pelomedusoides most *Podocnemis* have the foramen well within the palatine and most pelomedusids have some pterygoid contribution. Medially the palatines in *Euraxemys* have a long contact exposed ventrally, but largely covered on the dorsal surface by the pterygoids, as in most pleurodires. Posteriorly there is a transverse contact with the pterygoid, as in most turtles.

The plane of the palatine is curved anterodorsally where it forms the posterior margin of the apertura narium interna. The posterior margin of the apertura is higher than the anterior margin, as in *Podocnemis* and primitive chelids, and it is not in the same plane as in *Pelomedusa* and *Araripemys*.

QUADRATE (figs. 39, 42, 281A)

Preservation: Both quadrates are preserved and complete in FR 4922, but only the right quadrate is completely free of matrix and visible on all sides. The left quadrate still has matrix in the cavum tympani.

Contacts on the lateral surface: In lateral view the quadrate of *Euraxemys* contacts the quadratojugal anterodorsally and the squamosal posterodorsally. The posterolateral corner of the quadrate is covered by the squamosal, as in most turtles. On the skull roof the squamosal sends a narrow process anteriorly to contact the quadratojugal, preventing the quadrate from being exposed on the edge of the temporal emargination, as is the case in most Pelomedusoides, but in contrast to *Kurmademys*. Anteriorly the quadrate contacts the quadratojugal in a contact that is slightly more extensive than in *Kurmademys* but less extensive than in *Pelusios*. The amount of quadrate exposed on the cheek emargination in *Euraxemys* is greater than in *Pelusios* but less than in *Kurmademys*.

Structures on the lateral surface: As in all turtles, most of the quadrate in *Euraxemys* is involved in the formation of the cavum tympani and its two spaces, the antrum postoticum and fossa precollumellaris (fig. 281A). The antrum postoticum of *Euraxemys* is moderate in size, smaller than that of *Kurmademys* and chelids like *Emydura*, and larger than *Podocnemis*. The antrum postoticum of *Euraxemys* is nearly the same size as in most *Pelusios*. The fossa precolumellaris in *Euraxemys* is present but shallow, shallower than in *Emydura*, *Pelusios*, *Kurmademys*, and *Araripemys*. The fossa precolumellaris in *Euraxemys* is similar in size to that in *Podocnemis*.

The incisura columellae auris of *Euraxemys* (fig. 281A) is open, but it is elongated and has the form of the incisura that encloses both stapes and eustachian tube, in contrast to the bothremydids with an open incisura, like *Cearachelys* and *Foxemys*, which have a much more constricted incisura (fig. 281B). *Notoemys* also has an open incisura columellae auris and a moderate antrum postoticum. In *Euraxemys* the open incisura columellae auris, moderate antrum postoticum, and fossa precolumellaris are all consistent with what would be expected in the primitive condition for Pelomedusoides.

Contacts on the dorsal and anterior surface: On the dorsal surface of the otic chamber, the quadrate in *Euraxemys* (figs. 43A, 45A) contacts the prootic anteriorly, where both bones form the foramen stapedio-temporale, as in other turtles. Posterior to the prootic contact in *Euraxemys* the quadrate has a long contact with the opisthotic. In the living pleurodires, the opisthotic and quadrate have a broad contact preventing quadrate-supraoccipital contact. In *Euraxemys* the prootic and opisthotic are almost completely separated by a close approximation of the supraoccipital and quadrate. Essentially all four bones meet at a single

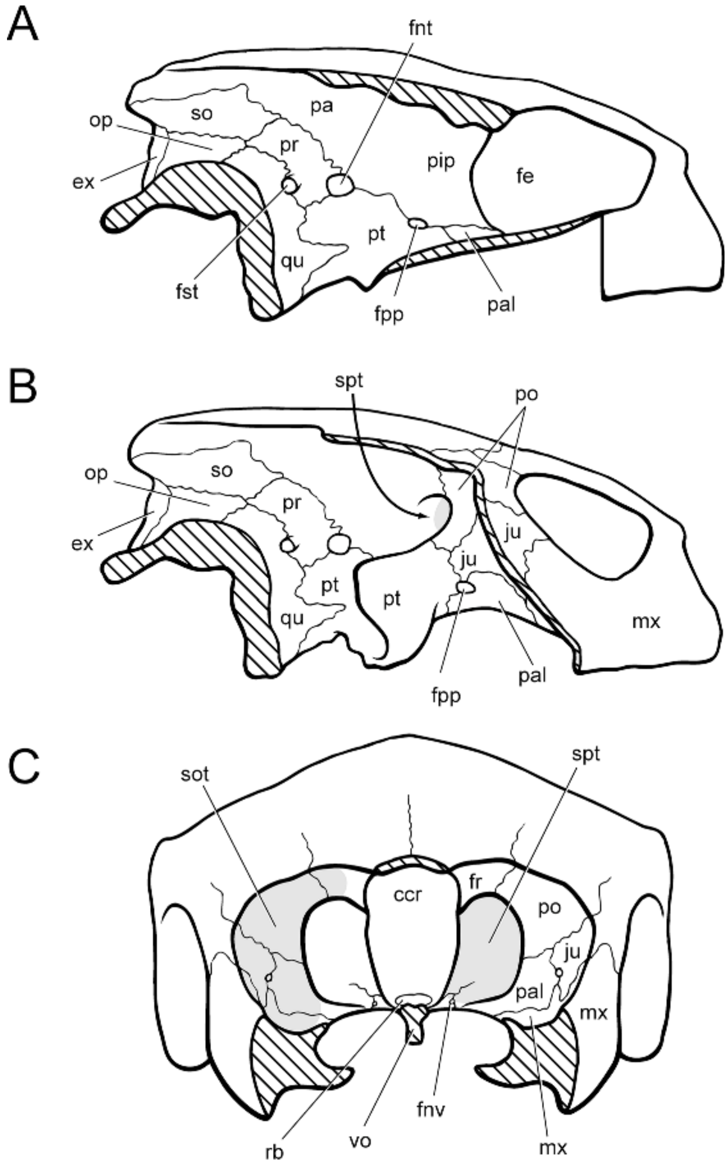

Fig. 43. *Euraxemys essweini*, n. gen. et sp., FR 4922 holotype. **A**, parasagittal section of right side, medial to processus trochlearis pterygoidei; **B**, parasagittal section of right side, lateral to processus trochlearis pterygoidei; **C**, anterior view of section through middle of fossa orbitalis, septum orbitotemporale (sot) shown in gray in right fossa orbitalis, sulcus palatinopterygoideus (spt) shown in gray on left side. All sections are hypothetical and are based on the intact skull. [E. Heck, del.]

point (fig. 45A). On the right otic chamber none of the four meets precisely at the apices but the small fragments of bone present suggest that the supraoccipital and quadrate met on the surface. On the left side, more of the surface bone is missing and the underlying prootic-opisthotic contact is visible. Even if a clear supraoccipital-quadrate contact is absent in *Euraxemys*, the close approach of both bones is markedly different from all the living pleurodires. In the Kurmademydini, the Cearachelyini, and the Bothremydini there is an extensive contact of the supraoccipital and quadrate. This quadrate-supraoccipital contact is only on the surface; internally the prootic and opisthotic plus supraoccipital meet at a triple junction to form the ossifications of the inner ear labyrinth, as in all vertebrates.

Structures on the dorsal and anterior surfaces: The foramen stapedio-temporale is placed anteriorly on the otic chamber in *Euraxemys* (figs. 43A, 45A), and it opens dorsally, as in *Kurmademys*, pelomedusids, and *Araripemys*. In all other bothremydids, the foramen stapedio-temporale is placed more anteriorly and medially, close to the foramen nervi trigemini. The *Euraxemys* condition is probably primitive for Pelomedusoides because it is also seen in *Emydura*.

Contacts on ventral surface: In ventral view the quadrate of *Euraxemys* contacts the pterygoid anteromedially, the prootic medially, and the exoccipital posteromedially (figs. 44A, 46). The processus interfenestralis of the opisthotic lies above the exoccipital contact. The quadrate contacts the opisthotic posteriorly above the incisura columellae auris.

There is some variation in the contacts of the medial process of the quadrate on both sides of FR 4922. There is a slightly different degree of ossification in the area where quadrate, prootic, exoccipital, and basisphenoid come close to each other. On both sides the quadrate comes very close to the exoccipital but the contact area is limited to a few projections of bone actually making contact. On the left side the prootic is slightly longer than on the right and nearly comes in contact with the exoccipital. On the right side the shorter prootic allows a near contact of the quadrate and basisphenoid, but there is open space between them as preserved. The quadrate does not come so close to the basisphenoid on the left side.

The prootic-quadrate contact in *Euraxemys* is very similar to that contact in pelomedusids and chelids. It is roughly parasagittal and runs the length of the prootic. However, in pelomedusids the basisphenoid intervenes so that there is a basisphenoid-quadrate contact, absent in euraxemydids and chelids. In pelomedusids there is no pterygoid-prootic contact, present in euraxemydids and chelids and presumed to be primitive for the hyperfamily Pelomedusoides.

In *Euraxemys* the pterygoid curves ventrally in a sheet along the anterolateral margin of the processus articularis of the quadrate to the condylus mandibularis. The degree of contact on this surface is similar in all pleurodires. The posterior extent of the pterygoid varies, however, and in *Euraxemys* the pterygoid extends posteriorly slightly more than in chelids and pelomedusids, but not to the extent seen in most bothremydids.

Structures on ventral surface: *Euraxemys* has no fossa pterygoidea, and the quadrate does not participate in the foramen posterius canalis carotici interni. The condylus mandibularis of *Euraxemys* is well anterior to the condylus occipitalis, as in pelomedusids, chelids, and *Araripemys*.

Contacts on posterior surface: In *Euraxemys* the quadrate as seen on the occipital surface contacts the squamosal dorsolaterally, the opisthotic dorsomedially, and the exoccipital in a very narrow contact posteromedially.

Structures on posterior surface: The fenestra postotica (fig. 46) is formed laterally and ventrally by the quadrate, although much of the cavum acustico-jugulare is relatively open in *Euraxemys* compared with podocnemidids and bothremydids.

The posterior margin of the quadrate is a free edge that forms part of the fenestra postotica margin, as in *Emydura*, pelomedusids, and *Podocnemis*. Dorsolaterally this margin slopes into the groove supporting the stapes that is a medial continuation of the incisura columellae auris. Medially the ventral limits of the processus interfenestralis of the opisthotic contacts the quadrate medial process in a very short suture. On the right side of FR 4922 the stapedial foot plate and a portion of the stem are preserved and lie on top of the medial process of the quadrate (fig. 46).

The foramen chorda tympani inferius is preserved clearly in both quadrates of FR 4922. The foramen is at the end of a cleft-shaped opening just ventral to the groove containing the stapes (fig. 46). The foramen in *Euraxemys* is much more dorsal than in *Podocnemis*, where it is farther down on the processus articularis.

PTERYGOID (figs. 39–44, 46)

Preservation: Both pterygoids are preserved in FR 4922, but only the right one is visible on its dorsal surface.

Contacts on ventral surface: The pterygoid in *Euraxemys* begins anteriorly in a transverse suture with the palatine. On the ventral surface the suture trends anterolaterally just behind the foramen palatinum posterius, which the pterygoid does not enter. The pterygoid margin then bends dorsally to contact the jugal and, above it, the postorbital.

Medially the pterygoid contacts the other pterygoid anteriorly and the basisphenoid posteriorly. The amount of separation of the pterygoids by the basisphenoid is greater in *Euraxemys* than in most other pleurodires. It is comparable to that in *Pelusios* and *Pelomedusa* but not as much as in *Araripemys*, which has the pterygoids almost completely separated (but not completely separated as figured by Meylan, 1996).

Structures on ventral surface: The processus trochlearis pterygoidei of *Euraxemys* is relatively well preserved on both sides. Portions of the thin ventral flanges are missing, but more of the flanges are present than is usually the case in fossil pleurodires. The shape and depth of the processus trochlearis pterygoidei in *Euraxemys* is very similar to that in *Emydura*. In *Euraxemys* and *Emydura* the dorsoventral depth of the processus is greater than in the living pelomedusids or in *Araripemys*. In *Araripemys* and pelomedusids the processus trochlearis pterygoidei is not as divergent from the midline of the skull as it is in *Euraxemys* and chelids. In these latter taxa and many other Pelomedusoides, the processus trochlearis pterygoidei diverges at about a 45° angle from the midline. It is not as close to a right angle as seen in many podocnemidids.

The lateral surface of the processus trochlearis pterygoidei in all pleurodires is a roughened surface, bearing in life a covering of tissue forming the sliding articulation with the main adductor tendon. This roughened surface in *Euraxemys* ends ventrally on a ridge separating the lateral surface from the more medial and ventral surface. This feature is also found in *Pelomedusa* and is variably developed in other Pelomedusoides.

The ventral surface of the pterygoid in Pelomedusoides in the region between the processus trochlearis pterygoidei and the posterior end of the pterygoid is often the site of depressions and markings reflecting attachments of the pterygoideus musculature (Schumacher, 1973). In *Euraxemys* this surface is smooth, with only a faint ridge marking an area extending from the base of the processus trochlearis pterygoidei posteriorly to the foramen posterior canalis carotici interni. The posterior edge of the pterygoid, particularly the ventral process lying along the quadrate, along with the adjoining basisphenoid, prootic, and quadrate form a shallow, ill-defined, posteroventrally facing concavity that is presumably the more posterior region of the pterygoideus muscle attachment. *Araripemys* lacks this concavity and differs from *Euraxemys* in having a small but distinct concavity in the anterior region of the attachment area, near the base of the processus trochlearis pterygoidei. This concavity and a low ridge forming its anterior and medial margin are very similar to the condition seen in *Emydura*. Pelomedusids are smooth in the entire area and usually lack muscle attachment markings.

The foramen posterius canalis carotici interni in *Euraxemys* lies at the posterior margin of the pterygoid, in the suture between the basisphenoid and pterygoid (fig. 44A). Most of the foramen, the dorsal, lateral, and medial walls, is formed by the basisphenoid. The pterygoid forms the ventral margin of the foramen and sends a narrow process posteromedially along the ventral edge of the basisphenoid. On both sides the part of the pterygoid that forms the ventral margin of the foramen posterius canalis carotici interni is missing. The left side is more complete and it appears to be missing a small triangular section of pterygoid that would extend the floor of the foramen laterally. It is possible that more pterygoid is missing and that there was a separate foramen contained entirely within the pterygoid for the foramen nervi vidiani. It seems more likely that there was a common opening for the foramen posterius

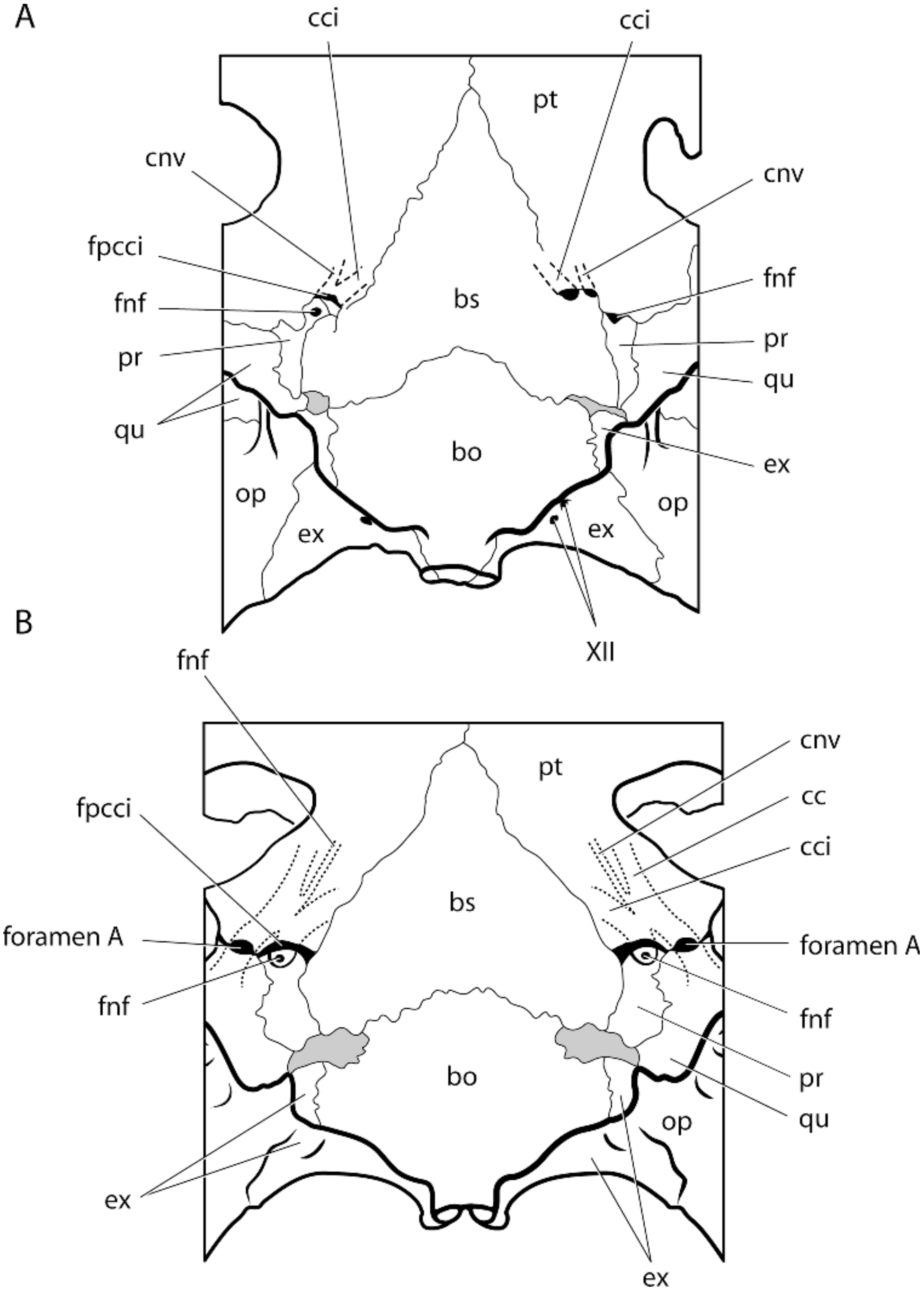

Fig. 44. Comparison of the basicranium in ventral view in the Euraxemydidae, showing the foramen posterius canalis carotici interni and its associated canals. **A**, *Euraxemys essweini*, n. gen. et sp., FR 4922 holotype; **B**, *Dirqadim schaefferi*, n. gen. et sp., MDEt 41 holotype, AMNH 30038. See text for discussion of foramen A in *Dirqadim*. [A. Venjara, del.]

canalis carotici interni and the foramen nervi vidiani.

The foramen nervi vidiani in FR 4922 can be seen on both sides, but the right side has had some crushing and breakage, reducing the apparent size of the canal. On the left side the canal can be probed for some distance into the pterygoid but not to its end. The canal for the vidian nerve is roughly one-third to one-fourth the diameter of the canalis caroticus internus.

A small part of the posterior edge of the pterygoid contacts the prootic between the contacts of the basisphenoid and quadrate. There is a very small foramen on the left side that is formed mostly by the prootic but with the pterygoid entering into the margin slightly. This foramen may be for the facial nerve, palatine branch, but it seems to be too small for that nerve. Also, it is absent on the well-preserved right side.

Lateral to the prootic, the pterygoid contacts the quadrate. This posterolateral part of the pterygoid is twisted from the flat, horizontal main body, to form a short flange that extends along the processus articularis of the quadrate. This process is quite similar to that in chelids and *Pelusios* and appears to be primitive for pleurodires.

Contacts on dorsal surface: Anteriorly, the pterygoid has a strong contact at the base of the processus trochlearis pterygoidei, with the jugal ventrally and the postorbital dorsally, where all three bones combine to form the lateral wall of the sulcus palatinopterygoideus (fig. 43B).

The posterior contact of the pterygoid on the dorsal surface is with the quadrate, which has a short, anteriorly pointed process ending in a small concavity, presumably for the remnant of the palatoquadrate cartilage (fig. 43A). This process is absent in most pelomedusids but seems to be present in *Araripemys* and is clearly present in *Emydura*. It is also absent in *Hamadachelys* and *Kurmademys*.

Structures on dorsal surface: The dorsal surface of the pterygoid in *Euraxemys* is best seen on the right side of FR 4922. The dorsal surface of the pterygoid bears various structures but the most prominent is the parasagittal crista pterygoidea, which extends for most of the length of the pterygoid (fig. 43A). The crista separates the medial cavum cranii (only slightly visible in *Euraxemys*) from the lateral sulcus palatinopterygoideus. The crista pterygoidea of *Euraxemys* contacts the processus inferior parietalis of the parietal anteriorly. The crista is low anteriorly and rises posteriorly where it forms the ventral margin of the foramen nervi trigemini. Although the available material of *Araripemys* is poorly preserved in this area, the crista seems to be similar in *Araripemys* and *Euraxemys*.

The right side of the cavum cranii in FR 4922 is largely free of matrix. By using a small mirror, the length of the rostrum basisphenoidale and sulcus cavernosus can be seen, but not the sella turcica, which is covered by matrix. The floor of the sulcus cavernosus and the pterygoid-basisphenoid suture is visible posterior to the anterior foramen nervi abducentis, which is formed entirely by the basisphenoid. There is no sign of a foramen caroticum laterale along the length of the pterygoid-basisphenoid suture. However, this foramen is quite small in members of the Pelomedusoides and it would be easy to miss. In the absence of confirmation from another specimen or even the left side of FR 4922, the presence or absence of the foramen caroticum laterale is unknown.

The foramen nervi trigemini in *Euraxemys* is formed by the pterygoid ventrally, the parietal anterodorsally, and the prootic posterodorsally, as in *Araripemys* and pelomedusids. In *Emydura* there is a parietal-pterygoid contact dorsal to the foramen, preventing prootic exposure.

SUPRAOCCIPITAL (figs. 39, 42, 43)

Preservation: The supraoccipital in *Euraxemys* is almost completely preserved. The ventral portion containing the semicircular canals and forming the roof of the foramen magnum is complete and well preserved.

Contacts: The crista supraoccipitalis, normally a prominent feature of turtle skulls, is relatively small in *Euraxemys*, and there is clearly a separation between the dorsalmost portion of the supraoccipital and the parietal on the skull roof. This separation looks very much like a suture and lies beneath the right parietal. The two parietals are unequally developed here; the left parietal stops short of the right and has a finished posterior margin. The midline parietal suture swings left slightly as it extends posteriorly so that the most posterior part of the skull roof is formed only by the right parietal. However, at the posterior edge of the right parietal margin is a half-formed suture trending anteromedially. There is no indication on the ventral surface that this bone is a continuation of the supraoccipital; rather, there is a distinct separation between the supraoccipital and the parietal on the skull roof. Nonetheless, although it is best interpreted as parietal, it is possible that the supraoccipital has a horizontal skull roof portion that is separated by a break from the main body of the supraoccipital. As interpreted here, however, the supraoccipital of *Euraxemys* has no dorsal exposure. In any case, at most there would be a small horizontal plate of supraoccipital on the skull roof.

Structures: The very small crista supraoccipitalis in *Euraxemys* is unusual, and one this small does not occur in other pleurodires. Both chelids and pelomedusids have well-developed cristae. *Araripemys* is not well preserved in this area, but much of a crista supraoccipitalis is preserved in THUg 1357. In this specimen the crista is low and short but larger than in *Euraxemys*. Although the posterior margin may be a broken edge, the crista could not have been very much extended because the articulated specimens, THUg 1907 and AMNH 24454, show that the atlas-axis would contact a long crista. Although *Euraxemys* and *Araripemys* are similar in having a small crista supraoccipitalis, the crista in *Araripemys* is not uniquely small; it is comparable in length and depth to that in small specimens of *Pelomedusa*. Additionally, THUg 1357 shows what seems to be a horizontal lateral shelf on each side of the crista, similar to that seen in some cryptodires (e.g., Gaffney, 1979a: fig. 184). Chelids typically have a very short crista supraoccipitalis, often not extending posterior to the foramen magnum. However, the crista is usually deep enough to form a vertical plate on the midline. In *Euraxemys* there is almost no vertical plate formed by the supraoccipital.

The supraoccipital main body is divided into two paired blocks, each containing the recessus labyrinthicus supraoccipitalis. The contacts of the block are primarily with the prootic anterolaterally and with the opisthotic posterolaterally. In *Euraxemys* the prootic and opisthotic are nearly prevented from meeting by a close approximation of the quadrate and supraoccipital. In *Araripemys* and chelids there is a broad prootic-opisthotic contact. Posterolaterally there is a contact with the exoccipital in *Euraxemys*, just as in *Araripemys* and nearly all turtles.

EXOCCIPITAL (figs. 39, 42, 46)

Preservation: The exoccipital is a paired element preserved almost completely on both sides of FR 4922. The internal portions are visible on the right side.

Contacts: The exoccipital in *Euraxemys* contacts the supraoccipital dorsally, the opisthotic laterally, the basioccipital ventrally, the prootic anteriorly (on the left side but not on the right), and the basisphenoid anteromedially. There is a narrow contact with the quadrate on the ventral surface.

Structures: The exoccipital forms most of the margins of the foramen magnum, except for the intervening portion formed by the supraoccipital dorsally and the narrow exposure of the basioccipital ventrally. The exoccipitals do not meet on the midline.

The dorsal portion of the exoccipital in *Euraxemys* is a dorsomedially–ventrolaterally expanded plate, as in all turtles. Anterodorsally, it contacts the supraoccipital; anteroventrally, it contacts the opisthotic. On the internal surface, the dorsal portion forms the posterior margin of the foramen jugulare anterius. These features are the same as in all turtles. Ventrolaterally, the exoccipital curves under the opisthotic and so forms a portion of the posterolateral process of the occiput characteristic of pelomedusids. In *Araripemys* the posterolateral process of the exoccipital is developed to about the same extent as in *Euraxemys*, extending halfway along the length of the opisthotic. This is similar to its extent in *Pelusios* and *Pelomedusa*, but it is much longer than in *Emydura*. The process consisting of the exoccipital and opisthotic forms a carina or ridge along the posterior margin of the skull. This ridge is small in chelids but large in *Euraxemys*,

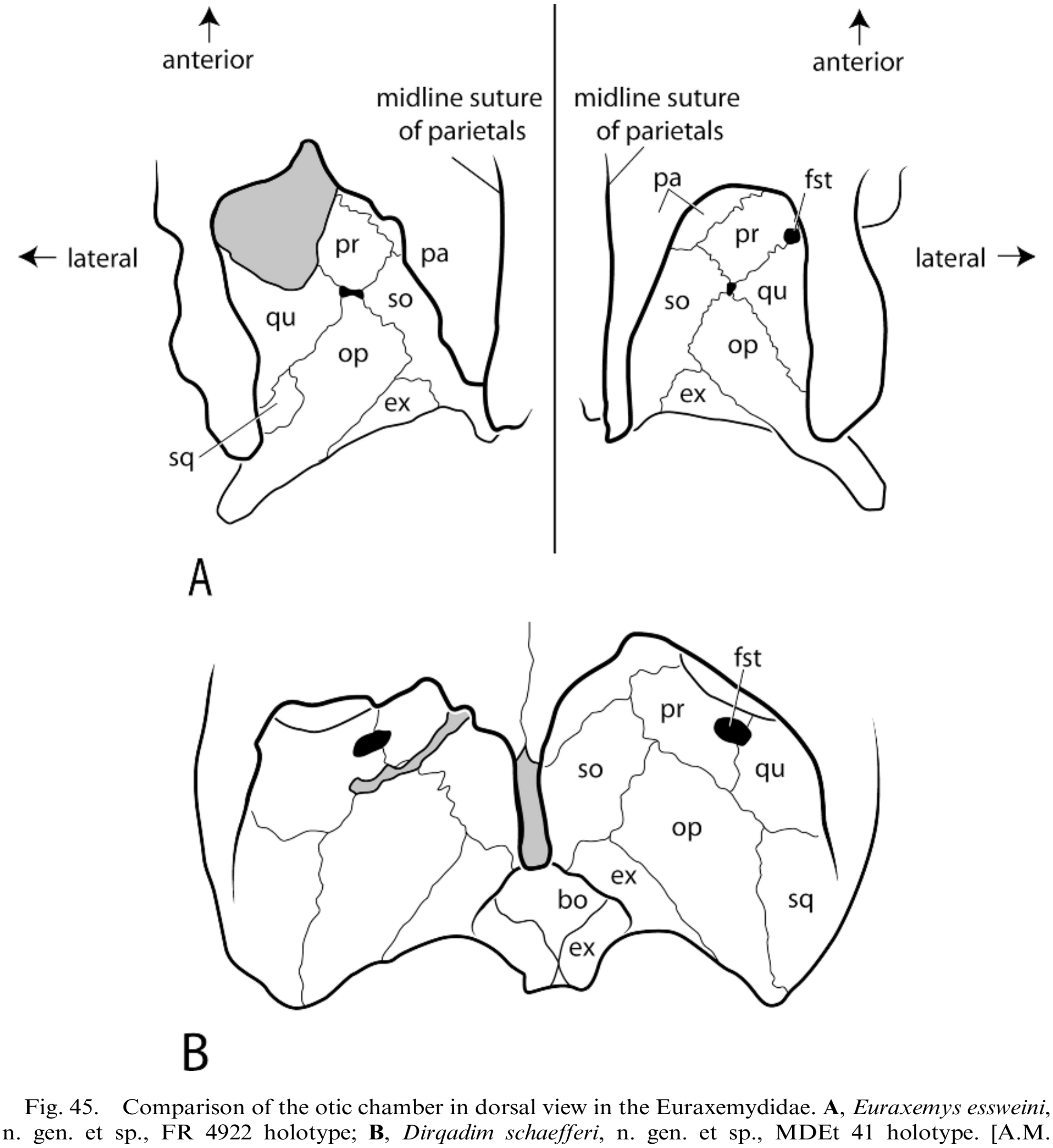

Fig. 45. Comparison of the otic chamber in dorsal view in the Euraxemydidae. **A**, *Euraxemys essweini*, n. gen. et sp., FR 4922 holotype; **B**, *Dirqadim schaefferi*, n. gen. et sp., MDEt 41 holotype. [A.M. Phillips, del.]

Araripemys, and pelomedusids. It is large but curved ventrally in podocnemidids.

The exoccipital narrows between the dorsal plate and the ventral, footlike enlargement. This narrowing forms the posterior part of the pathway for the vena cerebralis posterior, the tenth cranial nerve, and the jugular vein with its openings, the foramen jugulare anterius and the foramen jugulare posterius. This region is similar in all turtles and within all Pelomedusoides. However, the formation and shape of the foramen jugulare posterius vary. In chelids the foramen is closed by being mostly encircled by the exoccipital (completely in some *Emydura*, AMNH 110487), with a ventral to ventrolateral contribution by the basioccipital. In *Euraxemys* the foramen is open (on both sides) laterally, although there is a short dorsolateral spur and a low ventral ridge that form a partial margin. One of the four *Araripemys* specimens has a completely closed foramen jugulare posterius with a thick process of the opisthotic laterally and no contribution by the basioccipital. The foramen jugulare posterius, closed by roughly equal amounts of the exoccipital and opisthotic, is also the condition in pelomedusids and podocnemidids.

The orientation of the foramen jugulare posterius also varies within the hyperfamily Pelomedusoides. In chelids the foramen faces posteriorly and lies in the same plane as the foramina hypoglossi (Gaffney, 1979a: fig. 150). This is also the condition in podocnemidids and most bothremydids. In euraxemydids, *Araripemys*, and pelomedusids, the plane of the bony surface that these foramina penetrate is orientated more posterolaterally, so that the foramen jugulare posterius exits anterior to the foramina nervi hypoglossi, and it faces more posterolaterally. In *Euraxemys* itself the foramen is a little more ambiguous because it lacks a lateral margin, but it is clearly more similar in position to the *Araripemys*-pelomedusid condition than to the chelid condition.

Most pleurodires have two foramina nervi hypoglossi penetrating the narrow section of the exoccipital. There is individual variation. For example, AMNH 10062, a *Pelusios* sp. skull, has three on each side. There is often a much smaller foramen, possibly for another hypoglossal branch or the variable accessory (XI) nerve. In *Euraxemys* there are two foramina nervi hypoglossi and one much smaller foramen lateral to them on both sides. *Araripemys* also has this condition, which can be seen in most pelomedusids.

In *Euraxemys* the exoccipital has a ventral process exposed on the ventral surface of the skull just lateral to the basioccipital. *Araripemys* also has this process but it is much larger and more extensive than in *Euraxemys* because the basioccipital is unusually narrow in *Araripemys*. This modification of the ventral "foot" or expansion of the exoccipital is unusual. In chelids and podocnemidids the exoccipital meets the flat, horizontal plate of the basioccipital, as in nearly all other turtles.

The ventral portion of the exoccipital expands to form the condylus occipitalis. The exoccipital in *Euraxemys* forms the dorsolateral part of the condyle, each forming less than the usual one-third of the condyle. In *Euraxemys* the exoccipitals do not meet on the dorsal surface of the condyle; instead, the basioccipital completely separates them. In *Araripemys* the exoccipitals meet on the midline of the condyle dorsally, as in most turtles, forming two-thirds of the condyle.

BASIOCCIPITAL (figs. 39, 42, 44, 46)

Preservation: The basioccipital of *Euraxemys* is completely preserved. Matrix covers the anterior part of its dorsal surface.

Contacts: The anterior contact with the basisphenoid is bluntly projecting anteriorly on the midline, in contrast to the straight contact in *Araripemys*. Laterally the basioccipital contacts the small exoccipital process. In *Araripemys* the exoccipital contact is more extensive, continuing posteromedially to constrict the degree of basioccipital exposure posteriorly. The condylus occipitalis of *Euraxemys* is mostly made up of basioccipital, with the typical exoccipital contributions smaller than in *Araripemys*, so that the basioccipital is exposed on the dorsal surface and neck of the condylus occipitalis. The basioccipital contacts the exoccipitals dorsally. The contact in *Euraxemys* is relatively straight, just below the foramina nervi hypoglossi.

Structures: The basioccipital in *Euraxemys* in ventral view is wider than long and bilaterally symmetrical but irregular, similar to pelomedusids rather than the clearly triangular basioccipital of *Araripemys*. Below the exoccipital contact, the paired tubercula basioccipitale form the posterior margin of the basioccipital on either side of the condylus occipitalis. Each tuberculum is relatively well developed, extending posteriorly so that the contact with the exoccipital and the foramina nervi hypoglossi is not visible in ventral view. The size of the tubercula in *Euraxemys* is comparable to that seen in chelids and pelomedusids, but much larger than in *Araripemys*, in which the tubercula are very small and close to the neck of the condylus occipitalis.

The visible part of the dorsal surface of the basioccipital in *Euraxemys* differs from other pelomedusids in having no midline contact of the exoccipitals over the basioccipital.

PROOTIC (figs. 39, 42, 43, 44A, 45A)

Preservation: The prootic of *Euraxemys* is preserved completely on both sides, although some of the dorsal and anterior surface is covered by matrix on the left side.

Contacts: In order to understand the morphology of *Euraxemys*, it is worth reviewing the prootic morphology in other pleurodires, beginning with chelids. In primitive chelids (*Emydura*, *Pseudemydura*, fide Gaffney, 1977b) the prootic is exposed ventrally, contacting the pterygoid anteriorly, and lying between and separating the quadrate and basisphenoid. Posteriorly, the prootic may be separated from the processus interfenestralis of the opisthotic by cartilage or it may visibly contact the opisthotic. In any case, there is no basisphenoid-quadrate contact. The foramen posterius canalis carotici interni is formed by the prootic with a varying small contribution by the basisphenoid. Close examination shows that the foramen also includes the exit of the facial (VII) nerve, which is consistently contained within the prootic in all turtles.

In pelomedusids the prootic and its contacts in ventral view are basically the same as in chelids except that the quadrate and basisphenoid have a narrow band of contact anterior to the prootic, preventing a prootic-pterygoid contact. This quadrate-basisphenoid contact is present throughout the Podocnemididae and Bothremydidae. *Araripemys* also has a chelidlike prootic. It is not rectangular, as in *Emydura*, but is L-shaped with a small lateral projection of the basisphenoid fitting into the anteromedial corner of the prootic. Contrary to the figure of the damaged prootic in Meylan (1996: fig. 4), new specimens show that the foramen posterius canalis carotici interni of *Araripemys* lies at the posterior margin of the prootic, and there is no second foramen. As in chelids, there is no quadrate-basisphenoid contact in *Euraxemys*, and the prootic barely contacts the exposed processus interfenestralis of the opisthotic posteriorly.

In ventral view the prootic in *Euraxemys* is wider anteriorly where it contacts the pterygoid. Its long sides separate the basisphenoid medially and the quadrate laterally. Posteriorly, the prootic narrows to a point. On the left side the prootic nearly reaches the exoccipital, but on the right side a small hooklike process of the quadrate curves around the posterior end of the prootic to nearly contact the basisphenoid, completely preventing prootic-exoccipital contact. The foramen posterius canalis carotici interni is not formed by the prootic in *Euraxemys*, in contrast to the condition in *Araripemys* and chelids. Rather, *Euraxemys* has the foramen formed by the basisphenoid and pterygoid (fig. 44A).

Structures: The prootic in FR 4922 contains the foramen for the hyomandibular branch of the facial (VII) nerve. Differential breakage on either side has exposed different parts of the foramen and the prootic (fig. 44A). The more complete is the left side, which shows the foramen formed by the prootic anteriorly, very close to the pterygoid contact. The pterygoid here is a thin sheet covering the prootic. On the right side the pterygoid is broken away, revealing more of the prootic and the more anterior part of the canal for the hyomandibular branch. At this point the pterygoid and basisphenoid would completely cover the prootic.

The prootic of *Euraxemys* can be interpreted as having a morphology that is intermediate between the more primitive condition of chelids, pelomedusids, and *Araripemys* on the one hand, versus the more advanced condition of bothremydids and podocnemidids (figs. 276, 277). In the primitive condition the prootic bears the foramen posterius canalis carotici interni, but in the more advanced condition the foramen is excluded from the prootic in ventral view by thin sheets of other bones. In bothremydids the prootic is completely or almost completely covered ventrally to varying degrees by thin processes of basisphenoid, quadrate, and pterygoid. In *Euraxemys* the foramen is excluded from the prootic, but a portion of the prootic is still exposed ventrally despite the presence of a lateral process of the

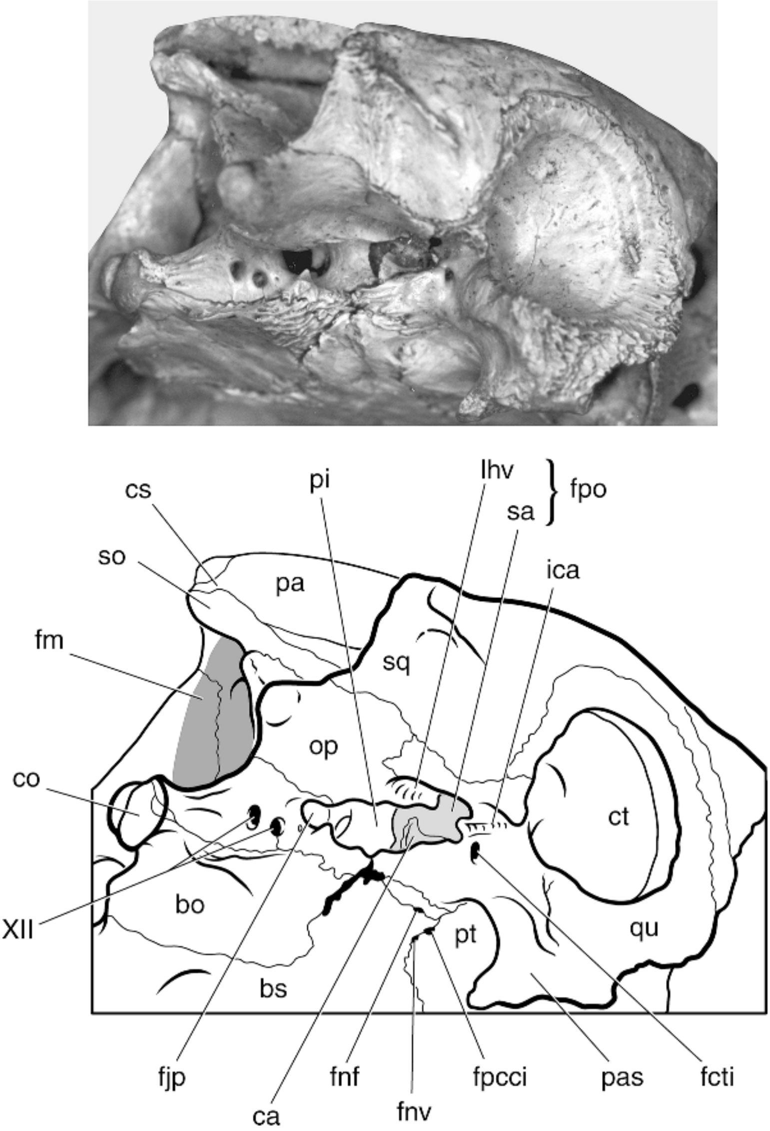

Fig. 46. *Euraxemys essweini*, n. gen. et sp., FR 4922 holotype. Posterior oblique view of skull. [E. Heck and E.S. Gaffney, del.]

basisphenoid. In podocnemidids, the prootic remains exposed ventrally, but the foramen posterius canalis carotici interni is not in it. In both podocnemidids and bothremydids there is a wide contact of quadrate and basisphenoid, either posterior to the prootic (podocnemidids) or posterior and ventral to the prootic (bothremydids). It is likely that the posterior contact is homologous in these two groups. In *Euraxemys* there is no broad quadrate-basisphenoid contact posterior to the prootic, but both bones are only separated by a narrow band of prootic, distinctly advanced over the chelid-pelomedusid-*Araripemys* condition in which quadrate and basisphenoid are widely separated.

Opisthotic (figs. 39, 42, 45, 46)

Preservation: Both opisthotics are preserved completely in FR 4922, with more matrix removed on the right side, revealing the internal morphology.

Contacts: The opisthotic in *Euraxemys* is similar to that bone in most other turtles in that it consists of a large posterior plate forming much of the external occipital region and a small, anterior complex of processes forming parts of the inner ear and braincase. The large, external plate forming the dorsal part of the otic chamber in *Euraxemys* contacts the supraoccipital anteromedially and the quadrate anterolaterally, much as in chelids, *Araripemys*, and pelomedusids. However, in contrast to these forms, *Euraxemys* (fig. 45A) has a very slight (left) or no (right) contact of the opisthotic with the prootic, bringing the supraoccipital and quadrate close together. Chelids, *Araripemys*, and pelomedusids have a well-developed prootic contact. A strong supraoccipital-quadrate contact is present in the Kurmademydini, Cerachelyini, and Bothremydini. Posteromedially the opisthotic in *Euraxemys* contacts the exoccipital, and posterolaterally it contacts the squamosal, all similar to *Araripemys* and pelomedusids.

The ventral surface of the opisthotic contacts the quadrate anterolaterally, the squamosal laterally, and the exoccipital posteromedially, as in *Araripemys*, chelids, and pelomedusids. The basisphenoid contact in *Araripemys* mentioned in Meylan (1996: 27) does not occur in that taxon or in chelids, pelomedusids, or *Euraxemys*.

Structures: In chelids the opisthotic is strongly curved, so that its posterior surface is nearly vertical. However, in *Araripemys* and pelomedusids the opisthotic is much flatter and nearly horizontal. In *Euraxemys* the surface is curved but not to the degree seen in chelids. The combined opisthotic-exoccipital process is weak in chelids but strong in *Euraxemys*, *Araripemys*, and pelomedusids. The posterior end of the opisthotic becomes rodlike and has a roughened posterior surface as if it were finished in cartilage. Some *Pelusios* also have this feature.

The anterior margin of the foramen jugulare anterius and the adjacent chamber, the recessus scalae tympani, are formed by the opisthotic in *Euraxemys* and all other turtles. In *Euraxemys* this region is relatively open ventrally, exposing the curved groove for the perilymphatic sac in the recessus scalae tympani. This is quite similar to chelids and pelomedusids. The posterior surface of the processus interfenestralis of the opisthotic in *Euraxemys* contains the fenestra perilymphatica and the foramen externum nervi glossopharyngei, again as in nearly all turtles. In *Araripemys*, however, the expansion of the exoccipital has covered the ventral exposure of the recessus scalae tympani and groove for the perilymphatic sac. This condition is unique for *Araripemys*. In *Euraxemys* and three of four *Araripemys* specimens the foramen jugulare posterius (formed by the exoccipital) is incomplete laterally, but in one *Araripemys* the opisthotic completes the lateral margin of the foramen with an extensive exoccipital-opisthotic contact absent in *Euraxemys*. In chelids the lateral margin of the foramen may be completed by the opisthotic, but the exoccipital also extends around the foramen in some specimens. In pelomedusids the opisthotic completes the foramen. The open foramen jugulare posterius of *Euraxemys* may be primitive for Pelomedusoides or it may be an autapomorphy for that taxon.

The processus interfenestralis of the opisthotic forms the posterior half of the fenestra ovalis and the posterior wall of the cavum labyrinthicum (fig. 46). It is a very stable feature in turtles and can serve as a landmark to compare features (fig. 276). In primitive chelids the processus interfenestralis in the dried bony skull is nearly isolated in ventral view, being completely exposed. This is the same condition in pelomedusids (except for *Pelusios niger*) and is interpreted as primitive for Pelomedusoides. *Araripemys* also has a ventrally exposed processus interfenestralis. In *Euraxemys*, however, the processus is covered ventrally by a lateral process of the basisphenoid, a medial process of the quadrate, and a slight anterior extension of the exoccipital. In bothremydids and podocnemidids, the processus interfenestralis is extensively covered ventrally, but by the quadrate plus basioccipital and basisphenoid in a pattern distinct from *Euraxemys*.

On the ventral surface of the opisthotic are the ridges that partially divide the perilymphatic system (periotic sac) and the cranioquadrate space. The periotic sac lies lateral to and behind the processus interfenestralis of the opisthotic. The floor of this space, the recessus scalae tympani, is often open in turtles, as it is in *Euraxemys*, but its posterodorsal and dorsolateral margin is a curved ridge on the opisthotic. This C-shaped ridge is preserved in *Euraxemys* on both sides and is visible in ventral view. The area of the recessus scalae tympani is nearly closed in *Araripemys* and pelomedusids by the ridge extending ventrally. In *Euraxemys* there is no ventral process and the area of the recessus is largely open laterally and ventrally, more so than in pelomedusids and chelids. Bothremydids and podocnemidids are extensively covered in this region.

The cranioquadrate space is represented on the occiput by the fenestra postotica (fig. 46). In *Euraxemys* the fenestra postotica is formed by the opisthotic and the quadrate. Although the fenestra in *Euraxemys* is not completely closed, as in bothremydids and podocnemidids, only a small part of the ventral margin is unossified. The opisthotic sends a process ventrolaterally, and the quadrate has a ventromedial process to largely define the fenestra. Within the fenestra postotica near the opisthotic-quadrate suture, there is a low ridge dividing the fenestra into a more lateral, oval-shaped opening for the stapedial artery and a more medial opening for the lateral head vein.

BASISPHENOID (figs. 39, 42, 44A, 46)

Preservation: The basisphenoid is complete in FR 4922 and completely visible in ventral view. Its dorsal surface, however, is visible in only one area at the anterior margin of the cavum cranii.

Contacts on ventral surface: Laterally the basisphenoid in *Euraxemys* contacts the prootic, and posteriorly there is a long transverse contact with the basioccipital. The posterolateral corner of the basisphenoid has a free edge and forms a margin for a small, irregular, unossified space just anterior to the exoccipital. It is likely that a better ossified (or possibly, better preserved) specimen would show a small contact of the posterolateral corner of the basisphenoid and the exoccipital, as shown in the reconstruction in figure 39.

Structures on ventral surface: The foramen posterius canalis carotici interni in *Euraxemys* is formed in the suture between the pterygoid and the basisphenoid (fig. 44A). Most of the foramen (the dorsal, lateral, and medial walls) are formed by the basisphenoid. This is in strong contrast to the primitive position of the foramen, seen in chelids, pelomedusids, and *Araripemys*, where it is formed by the prootic (fig. 276). In some chelids and in some species of *Pelusios*, the basisphenoid overlaps the prootic so that it forms a part of the margin of the foramen posterius canalis carotici interni, although this is interpreted as independently acquired variation. In most bothremydids and podocnemidids the foramen posterius canalis carotici interni is formed by the basisphenoid, the basisphenoid plus pterygoid, or the pterygoid plus quadrate. It seems likely, however, that the primitive condition for podocnemidids is seen in *Hamadachelys*, where the foramen is contained within the basisphenoid but very close to the pterygoid suture. Similarly, the primitive condition for bothremydids is probably seen in *Kurmademys*, which has the foramen contained within the basisphenoid but close to the pterygoid suture. As in *Euraxemys*, *Kurmademys* has a smaller-foramen formed by the pterygoid just lateral to the foramen posterius canalis carotici interni. In *Cearachelys*, another presumed primitive bothremydid, the foramen lies in the suture between basisphenoid and pterygoid.

The posterior portion of the canalis caroticus internus is visible on both sides due to breakage of the ventral (pterygoid) edge of the foramina posterius canalis carotici interni (fig. 44A). On the left side the opening into the canalis caroticus internus is clearly seen. The basisphenoid curves around dorsally and ventrally and meets to pinch out the pterygoid laterally in the formation of the canal. This can also be seen on the right side, although there is more damage laterally. The basisphenoid forms a wall separating the canalis caroticus internus laterally from a smaller canal, the vidian nerve canal. Most of this canal is formed by the pterygoid. Because the amount of pterygoid that is missing is unknown, it is possible that the vidian foramen was completely separated from the foramen posterius canalis carotici interni.

The condition in *Notoemys*, in which the foramen posterius canalis carotici interni seems to be formed by the basisphenoid but close to the pterygoid suture, should be interpreted as advanced over chelids and pelomedusids, as in podocnemidids and bothremydids, rather than as primitive for all pleurodires (Fernandez and Fuente, 1994).

The foramen posterius canalis carotici interni in *Euraxemys* is at the posterolateral margin of the basisphenoid. However, its position relative to all of the ventral features of the skull is not very different from the position of that foramen in pelomedusids and chelids. Rather, it seems as if the basisphenoid has a lateral extension that covers part of the prootic, and the foramen is still in that position even though covered by basisphenoid.

Contacts on dorsal surface: The pterygoid contact can be seen laterally, but the prootic and other sutures are not discernable.

Structures on dorsal surface: The anterior end of the rostrum basisphenoidale of *Euraxemys* is visible through the right foramen interorbitale. It is a long, thin rostrum, similar to that seen in the living *Podocnemis*. No foramina are visible on either side of the rostrum that could be a foramen caroticum laterale. Foramina could be present more posteriorly, however. The processus clinoideus of FR 4922 is visible on the right side through the foramen nervi trigemini and along the right side of the cavum cranii. The processus extends dorsolaterally to contact a short ventral process of the prootic and to produce an enclosed, more medial trigeminal ganglion foramen (see Gaffney, 1976: fig. 40).

Dirqadim schaefferi

There are two skulls available for *Dirqadim*, a nearly complete one (MDEt 41) and one lacking the anterior half (AMNH 30038). The preservation of both is good with little crushing. *Dirqadim* is the sister taxon to *Euraxemys*. Together they make up the family Euraxemydidae.

PREFRONTAL (figs. 47, 50)

Preservation: Both prefrontals are present and complete in MDEt 41; both are missing in AMNH 30038.

Contacts: The prefrontal in *Dirqadim* contacts the frontal posteriorly, the maxilla anteroventrolaterally, and the other prefrontal medially. The contacts are the same as in the Pelomedusidae and *Euraxemys*, and in nearly all Pelomedusoides.

Structures: The prefrontal in *Dirqadim* has the usual shape, as seen in the Pelomedusidae and *Euraxemys*. The bar between the apertura narium externa and the orbital margin is slightly thicker in *Euraxemys* than in *Dirqadim*, which is nearly identical to the thickness of the bar in the Pelomedusidae. As in *Euraxemys*, the descending process of the prefrontal in *Dirqadim* forms the anterior edge of the foramen orbitonasale and is widely separated from the palatine by the maxilla. The interorbital distance is narrow in *Dirqadim* and *Euraxemys*, as in pelomedusids but in contrast to most bothremydids.

FRONTAL (figs. 47, 50)

Preservation: Both frontals are present and complete in MDEt 41. The left frontal is present in AMNH 30038, but it is damaged anteriorly.

Contacts: The frontal in *Dirqadim* contacts the prefrontal anteriorly, the parietal posteriorly, the postorbital posterolaterally, and the other frontal medially. There is no anteromedial process separating the prefrontals, as in some chelids.

Structures: The shape of the frontal in *Dirqadim* is very similar to that in the Pelomedusidae. *Euraxemys* has a slightly greater degree of orbital exposure; otherwise, it is also very similar to *Dirqadim*. The ventral surface has a sulcus olfactorius that is about the same size and shape as in *Euraxemys* and is narrower than in most Pelomedusidae.

PARIETAL (figs. 47, 50, 52)

Preservation: Both parietals are present in MDEt 41, but the temporal margin has some breakage. Both parietals are also present in AMNH 30038. The temporal margin of the left one is complete, but the right one is broken.

Contacts of dorsal plate: The contacts in *Dirqadim* are with the frontal anteriorly, the postorbital anterolaterally, the quadratojugal laterally, and the other parietal medially. These contacts are as in *Euraxemys*, but *Dirqadim* also has a posterolateral contact between the parietal and squamosal that is absent in *Euraxemys*. This absence of this contact in *Euraxemys* is related to the more extensive temporal emargination seen in *Euraxemys*. *Araripemys* and Pelomedusidae lack the quadratojugal-parietal contact as well as the squamosal contact, and they have an even greater temporal emargination.

Structures of the dorsal plate: The temporal emargination of *Dirqadim* (fig. 50A; in fig. 45B the skull is tilted anteriorly to show the foramen) does not expose the foramen stapedio-temporale, as in *Euraxemys*, Pelomedusidae, and *Araripemys*. The lateral part of the parietal dorsal plate is relatively more extensive posteriorly than in these forms. However, on the medial side of the plate, it is thinner in *Dirqadim* than in *Euraxemys*, resulting in a shallow temporal margin in *Dirqadim*, in contrast to the narrower and deeper emargination of *Euraxemys* (fig. 6).

Contacts of processus inferior parietalis: The processus in *Dirqadim* contacts the palatine anteroventrally, the pterygoid ventrally, the prootic posteroventrally, and the supraoccipital posteriorly, as in *Euraxemys* and the Pelomedusidae.

Structures of processus inferior parietalis: The processus in *Dirqadim* is very similar to that structure in *Euraxemys*. It meets the crista pterygoidea ventrally and forms the medial wall and a small part of the roof of the relatively short sulcus palatinopterygoideus, as in *Euraxemys* and the Pelomedusidae. It forms the anterodorsal margin of the foramen nervi trigemini, with the prootic and pterygoid forming the remaining part of the foramen.

JUGAL (figs. 47, 50)

Preservation: The right jugal is complete and the left is slightly broken in MDEt 41. In AMNH 30038 both jugals are missing.

Contacts of lateral plate: The jugal contacts the maxilla anteroventrally, the postorbital dorsally, and the quadratojugal posteriorly, as in *Euraxemys* and the Pelomedusidae.

Structures of lateral plate: The jugal in *Dirqadim* is nearly identical to that in *Euraxemys*. It is relatively narrow, enters the orbital margin anterodorsally, and forms part of the cheek emargination posteroventrally. The Euraxemydidae agree with the Pelomedusidae, *Araripemys*, and chelids in this, which is presumed to be primitive for Pleurodira.

Contacts of the medial process: The medial process in *Dirqadim* is visible in the floor of the orbit and the postorbital wall. In the floor of the orbit the jugal contacts the maxilla anteriorly, the palatine medially, and the postorbital dorsally. As in *Euraxemys*, the jugal sends a narrow finger of bone anteriorly into the maxilla, producing a V-shaped suture. In the postorbital wall the jugal contacts the postorbital dorsomedially, the pterygoid medially, the palatine ventromedially, and the maxilla ventrally. All these contacts are as in *Euraxemys* and the Pelomedusidae.

Structures of medial process: The medial process in *Dirqadim* agrees closely with that in *Euraxemys*.

QUADRATOJUGAL (figs. 47, 50)

Preservation: Both quadratojugals are present in MDEt 41; the right one is complete, but the left is slightly damaged. In AMNH 30038 only the posterodorsal part is present on both sides.

Contacts: The quadratojugal in *Dirqadim* contacts the postorbital anterodorsally, the jugal anteroventrally, the quadrate posteroventrally, the parietal medially, and the squamosal posteriorly, all as in *Euraxemys*. The parietal contact is absent in the Pelomedusidae and *Araripemys*. Chelids lack the quadratojugal.

Structures: The quadratojugal of *Dirqadim* differs from *Euraxemys* in having no exposure on the temporal margin. There is a broad parietal-squamosal contact preventing quadratojugal exposure in *Dirqadim*. This is a consequence of the shallower temporal emargination in *Dirqadim*. The cheek emargination in *Dirqadim* is slightly less excavated in the quadratojugal area than in *Euraxemys*, so that the highest part of the emargination is more anterodorsal in *Dirqadim*, while it is

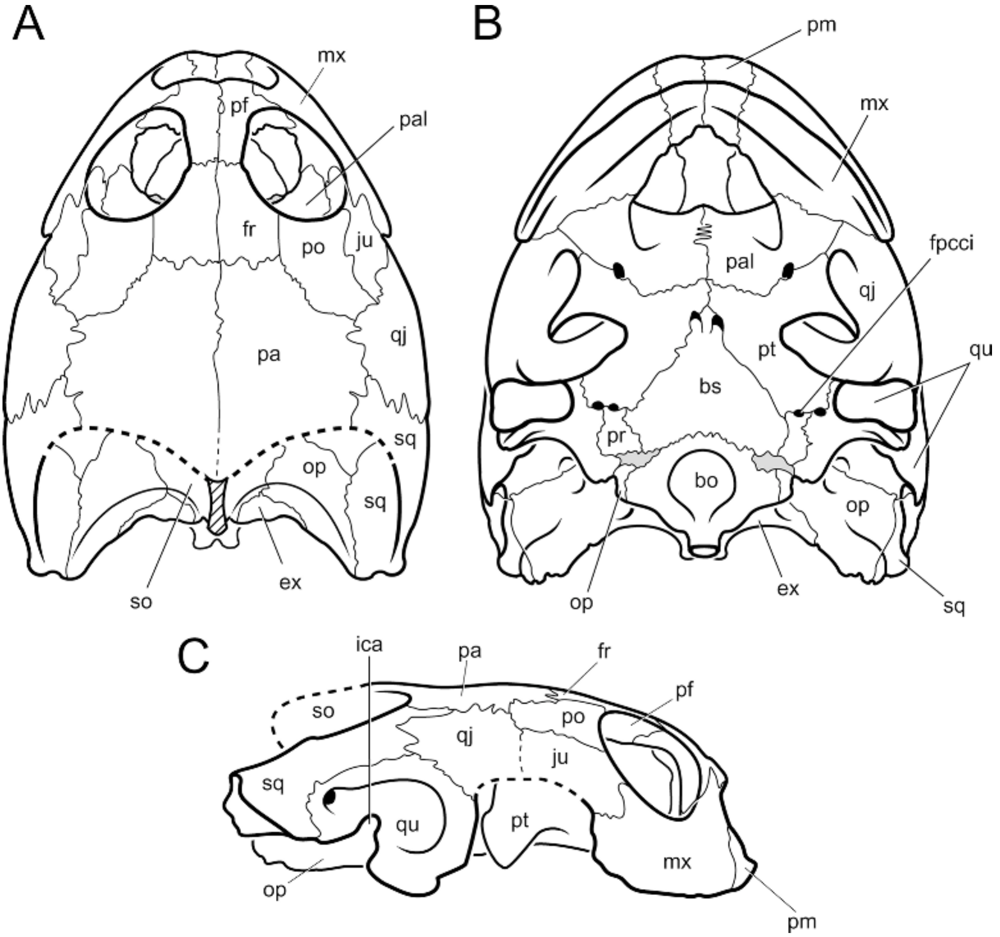

Fig. 47. *Dirqadim schaefferi*, n. gen. et sp. Partially restored skull based on MDEt 41 holotype and AMNH 30038. **A**, dorsal; **B**, ventral; **C**, lateral. See figure 44 for more detailed view of basicranial foramina and canals. [F. Ippolito, del.]

more posterodorsal in *Euraxemys*. The amount of emargination is slightly less in *Dirqadim* than in *Euraxemys*. The size of the quadratojugal is similar in both euraxemydids and similar to living pelomedusids, but *Araripemys* and *Kurmademys* have a narrower quadratojugal.

SQUAMOSAL (figs. 47, 50, 52)

Preservation: Both squamosals are present and nearly complete in MDEt 41 and AMNH 30038.

Contacts: The cone-shaped squamosal in *Dirqadim* meets the quadratojugal anterodorsolaterally in a contact that is wider than in *Euraxemys*. The squamosal contacts the quadrate anteriorly and anteromedially and the opisthotic medially, as in *Euraxemys*. Anteromedially, the squamosal in *Dirqadim* meets the parietal. This squamosal-parietal contact is rare in the hyperfamily Pelomedusoides, occurring only in *Dacquemys* and an undescribed African podocnemidid (UCMP 42008), but it is present in chelids, *Proganochelys*, and *Kayentachelys*.

Structures: The squamosal of *Dirqadim* agrees closely with that in *Euraxemys*, except that the antrum postoticum is slightly smaller in *Dirqadim* than in *Euraxemys* (see Quadrate).

POSTORBITAL (figs. 47, 50)

Preservation: Both postorbitals are present and complete in MDEt 41. Most of the

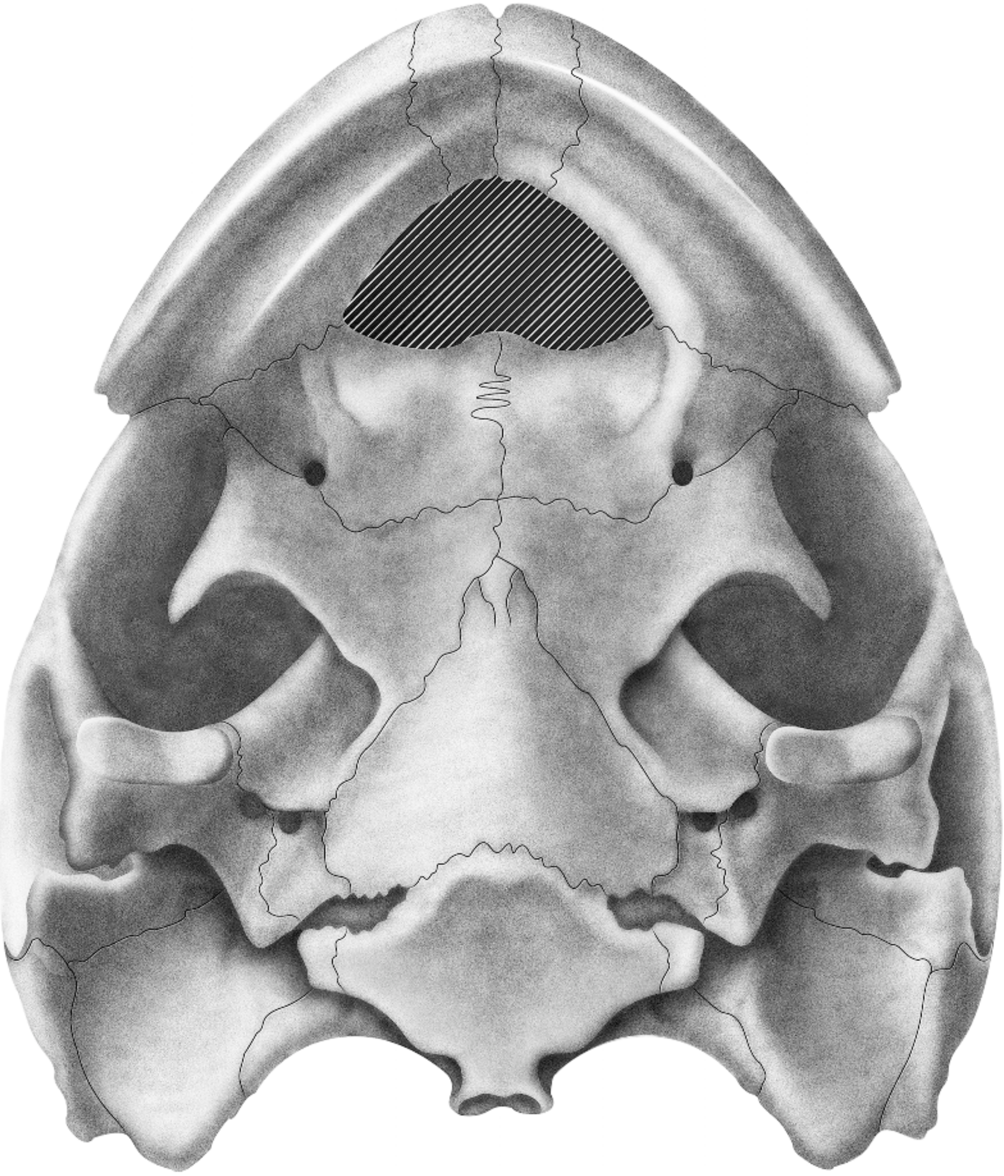

Fig. 48. *Dirqadim schaefferi*, n. gen. et sp. Partially restored ventral view based primarily on MDEt 41 holotype with additions from AMNH 30038. [J. Kane, del.]

left one is present in AMNH 30038, but only a small part of the posterior end remains.

Contacts of lateral plate: The postorbital in *Dirqadim* contacts the frontal anteromedially, the jugal laterally, the parietal posteromedially, and the quadratojugal posteriorly, all as in *Euraxemys*.

Structures of lateral plate: The postorbital in *Dirqadim* is very similar to that bone in *Euraxemys*.

Contacts of medial process: In the anterior view of the septum orbitotemporale in *Dirqadim*, the postorbital contacts the frontal dorsomedially, the palatine ventrally, and the jugal ventrolaterally, as in *Euraxemys*. In posterior view, the postorbital contacts the pterygoid ventrally and the jugal laterally, also as in *Euraxemys*.

Structures of medial process: This process of the postorbital in *Dirqadim* agrees with that in *Euraxemys*.

PREMAXILLA (figs. 47, 48, 50)

Preservation: Both right and left premaxillae are present in MDEt 41 and are nearly complete, but their posterior margins are broken edges. Both premaxillae are missing in AMNH 30038.

Contacts: The premaxilla contacts the maxilla posterolaterally and the other premaxilla medially. The possible vomer contact posteriorly is not determinable, because the vomer is missing and the posterior margin of the premaxilla is a broken edge.

Structures on dorsal surface: The premaxilla in *Dirqadim* has a low median ridge, as in *Euraxemys*. The apertura narium externa in *Dirqadim* is wider and relatively larger than in *Euraxemys*. The ventral margin of the apertura in *Dirqadim* is formed into a thin ridge that extends slightly anterodorsally, so that the anterior surface of the premaxilla faces anteroventrally. This is in contrast to *Euraxemys*, which has only a low, blunt ridge with the anterior surface facing directly anteriorly. The foramen praepalatinum is in the more posterior part of the floor of the fossa nasalis in both euraxemydid genera.

Structures on ventral surface: As in *Euraxemys*, the ventral surface of the premaxilla has a narrow labial ridge continuous with that on the maxilla. The ridge is more acute and thinner in *Euraxemys* than in *Dirqadim*, which has an acute edge but broadens dorsally. Posterior to the labial ridge is a low, blunt accessory ridge that continues laterally onto the maxilla. In *Dirqadim* the accessory ridge is well developed on the premaxilla; in *Euraxemys* there is no accessory ridge on the premaxilla, but a low one is on the maxilla. In the terminology as used here, there is no distinct lingual ridge. The triturating surface slopes off into the apertura narium interna. One could use the term lingual ridge for what I am calling the accessory ridge.

Posterior to the accessory ridge in *Dirqadim*, the premaxilla forms a midline concavity, as seen in bothremydids. *Euraxemys* has a slightly concave premaxillary surface, but no midline concavity. The ventral margin of the labial ridge in *Dirqadim* has a slight curve, concave ventrally, similar to that in *Euraxemys*.

MAXILLA (figs. 47, 48, 50)

Preservation: Both maxillae are present and nearly complete in MDEt 41, and both are completely lacking in AMNH 30038.

Contacts of vertical plate: The maxilla in *Dirqadim* contacts the premaxilla anteromedially, the jugal posterodorsally, and the prefrontal anterodorsally, all as in *Euraxemys*, Pelomedusidae, and *Araripemys*.

Structures of vertical plate: The orbital margin in *Dirqadim* has its lower portion formed by the maxilla, as in *Euraxemys*. The dorsal process of the maxilla is relatively thin in *Dirqadim* and *Euraxemys*. It is variable in Pelomedusidae and Chelidae, but it would seem that the thin condition is primitive for both. Bothremydids generally have a thicker bar between the apertura narium externa and the orbital margin. The labial ridge in *Dirqadim* is curved, much as in *Pelomedusa* and *Emydura*, not relatively straight, as in *Euraxemys*. Both *Euraxemys* and *Dirqadim* have relatively large orbits with a distinct rim forming the lower margin and a low, lateral wall for the floor of the fossa orbitalis. The choanal passages are separated from the fossa orbitalis by a thin flange of bone, as seen in chelids, pelomedusids, and most other pleurodires. The foramen orbitonasale, which communicates between these two spaces, is slightly larger in *Dirqadim* than in *Euraxemys*.

The cheek emargination in *Dirqadim* (see Jugal and Quadratojugal) is slightly different from that in *Euraxemys*. The maxilla in *Dirqadim* has a short posterior process, absent in *Euraxemys*. This process extends into the emargination. A similar process can be seen in some *Pelomedusa* and *Pelusios*.

Contacts of horizontal plate: The horizontal plate of the maxilla in *Dirqadim* contacts the premaxilla anteromedially, the palatine posteromedially, and the jugal posterolaterally. The medial extension of the maxilla ends in a broken edge and the vomer is missing, but it is likely that the maxillae did not meet on the midline and may not have extended as far medially, as in *Euraxemys*. Otherwise, the contacts agree closely with those in *Euraxemys*.

Structures of horizontal plate: The triturating surface of the maxilla in *Dirqadim* is similar to that in *Euraxemys*, but the labial ridge is thicker, slightly more curved anteromedially, and has a more distinct accessory ridge. The accessory ridge in *Dirqadim* is curved, convex ventrally, separating a shallow trough laterally from a dorsoventrally inclined surface medially, rather than the flatter surface in *Euraxemys*. Given the absence of the vomer, the position of the apertura narium interna is not definitely determinable, but it seems to be slightly wider and more anterior than in *Euraxemys*.

VOMER

Preservation: The vomer is missing in both MDEt 41 and AMNH 30038, presumably due to breakage.

PALATINE (figs. 47, 48, 50)

Preservation: Both palatines are present in MDEt 41, but both are missing a small part along their anterior edges. Both palatines are missing in AMNH 30038.

Contacts: The palatine in *Dirqadim* contacts the maxilla anterolaterally, the pterygoid posteriorly, the other palatine medially, and the jugal anterolaterally. On the dorsal surface, the processus inferior parietalis reaches the pterygoid but not the palatine, as it does in *Euraxemys*, because the pterygoid intervenes. As in *Euraxemys*, the palatine sends a short process dorsally to reach the postorbital and the jugal in the septum orbitotemporale.

Structures on the dorsal surface: The palatine forms part of the floor of the fossa orbitalis, as well as the anterior part of the floor of the sulcus palatinopterygoideus, as in *Euraxemys* and the Pelomedusidae.

Structures on ventral surface: The palatine forms only a very small, posteromedial part of the triturating surface in *Dirqadim*, only slightly less than in *Euraxemys*. The choanal groove is very similar in size and position to that in *Euraxemys*. As in *Euraxemys*, the foramen palatinum posterius is formed almost entirely by the palatine with some contribution from the pterygoid.

QUADRATE (figs. 47, 50, 53)

Preservation: Both quadrates are preserved in MDEt 41, but matrix still fills the right cavum tympani. In AMNH 30038 both quadrates are preserved; the right one is missing a small part of the cavum tympani margin, exposing the interior of the antrum postoticum.

Contacts on lateral surface: The quadrate in *Dirqadim* contacts the quadratojugal anterodorsally and the squamosal posterodorsally, as in *Euraxemys* and pelomedusids. The quadrate is widely separated from the temporal margin by a broad contact of the squamosal and quadratojugal.

Structures on lateral surface: The cavum tympani in *Dirqadim* is slightly lower, more oval than circular, than in *Euraxemys*, but this may be due to slight compression in both specimens of *Dirqadim*. AMNH 30038 has the right antrum postoticum broken open, showing its full extent. The antrum postoticum in *Dirqadim* (fig. 52C) is smaller than that in *Euraxemys* (fig. 281A), but not as small as in *Galianemys* (fig. 284). Both *Dirqadim* and *Euraxemys* would be regarded as “moderate” in size and smaller than in *Kurmademys* and chelids. The antrum varies a great deal in size in pleurodires, and it is too subjective to identify multiple sizes intermediate between the large size of *Kurmademys* and the small size of *Bothremys* and *Chedighaii*, although distinguishing any two species is usually easy.

The fossa precolumellaris is present in *Dirqadim*, and it is relatively shallow, as in *Euraxemys*, not deep, as in pelomedusids, chelids, *Araripemys*, and *Kurmademys*.

The incisura columellae auris in *Dirqadim* is open, as in *Euraxemys*, and very similar in shape to that genus. The incisura is wide enough to contain the eustachian tube, not narrow, as in *Foxemys* and *Polysternon*.

Contacts on dorsal and anterior surfaces: The quadrate in *Dirqadim* contacts the prootic anteromedially, the opisthotic posteromedially, and the squamosal posteriorly and posterolaterally. In contrast to *Euraxemys*, where the quadrate nearly contacts the supraoccipital, in *Dirqadim* there is

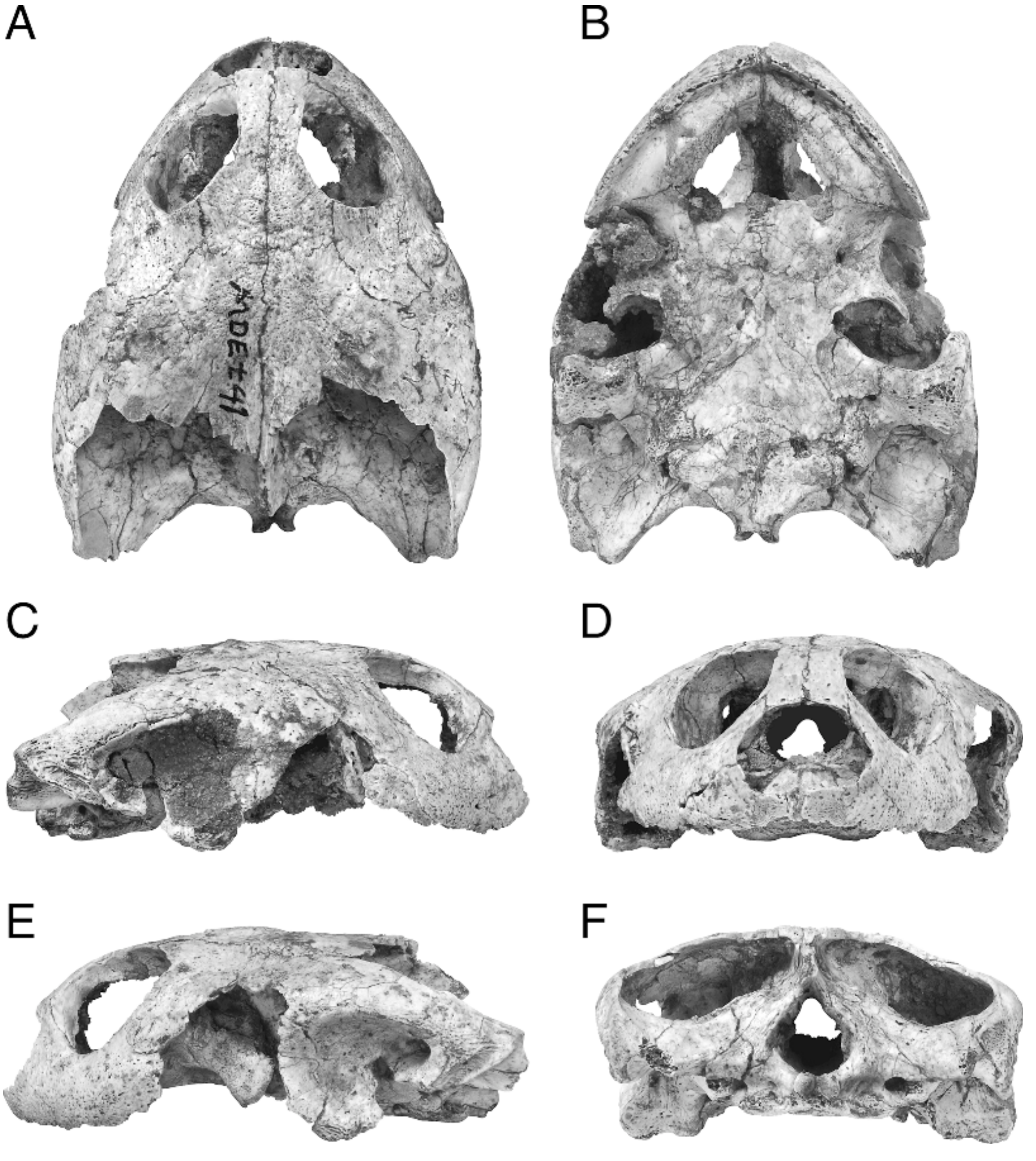

Fig. 49. *Dirqadim schaefferi*, n. gen. et sp., MDEt 41 holotype. **A**, dorsal; **B**, ventral; **C**, right lateral; **D**, anterior; **E**, left lateral; **F**, posterior. [J. Kane, del.]

a broad prootic-opisthotic contact preventing this (fig. 45B).

Structures on dorsal and anterior surfaces: The foramen stapedio-temporale is formed in the quadrate-prootic suture, as in *Euraxemys* (and nearly all turtles except bothremydids). The canalis stapedio-temporalis in *Dirqadim* communicates with the canalis cavernosus by means of an unusual opening described below.

Contacts on ventral surface: In *Dirqadim* the quadrate contacts the pterygoid anteromedially and the prootic medially, as in *Euraxemys*. In MDEt 41, the quadrate also contacts the exoccipital posteromedially, also as in *Euraxemys*. As preserved, the quadrate and exoccipital are separated in AMNH 30038 by an unossified space exposing the more dorsal opisthotic. In *Euraxemys* there is also some variation in the nature of this

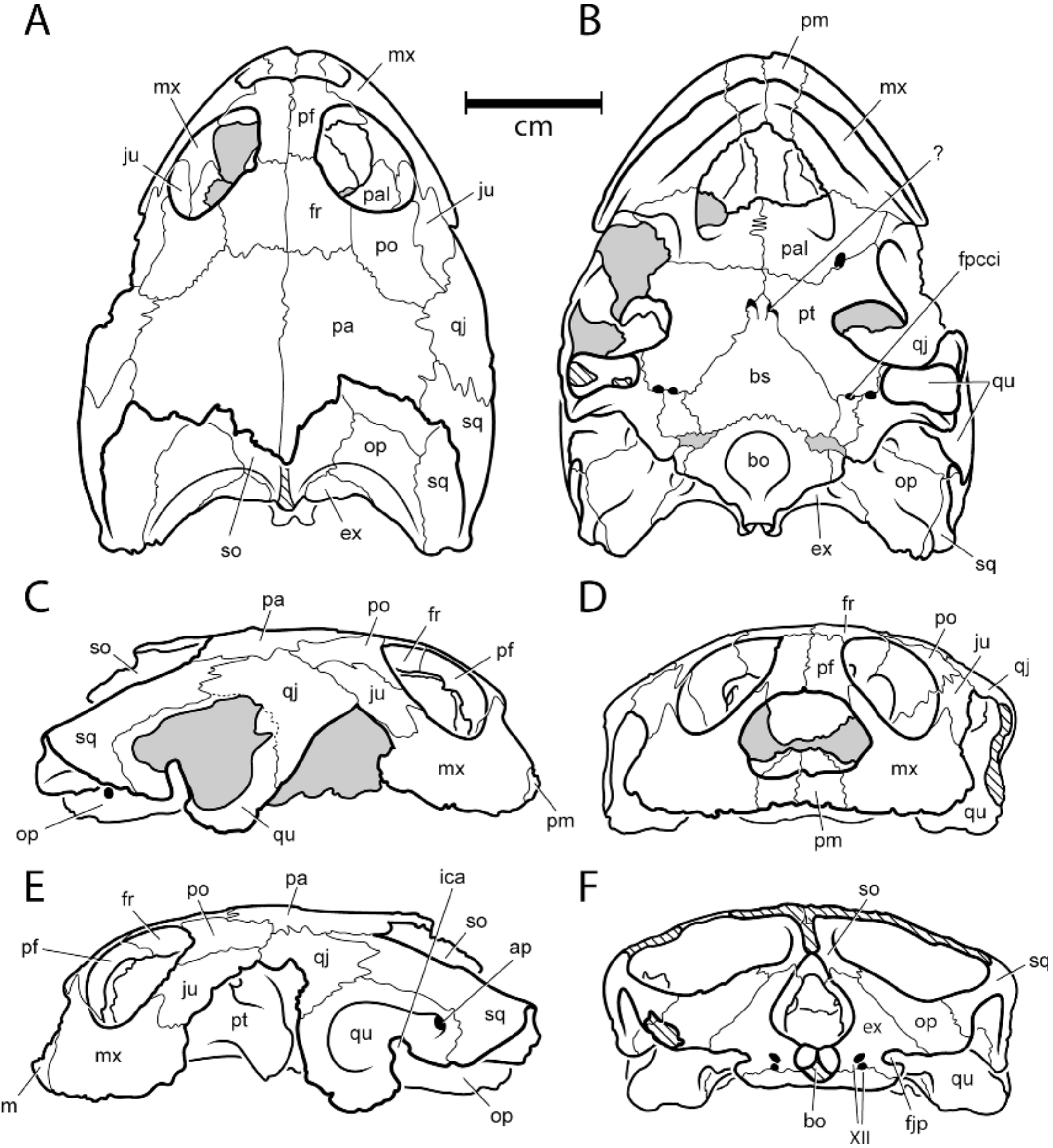

Fig. 50. *Dirqadim schaefferi*, n. gen. et sp., MDEt 41 holotype. **A**, dorsal; **B**, ventral; **C**, right lateral; **D**, anterior; **E**, left lateral; **F**, posterior. In panel **B**, see text for discussion of unknown foramen ("?"). [J. Kane, del.]

contact due to a presumably cartilaginous space, and MDEt 41 also has an unossified space in this area, although it is smaller than in AMNH 30038. AMNH 30038 is a bit chewed on in this area, with some loss of bone due to postmortem damage. The exoccipital and quadrate are thin here in any case, and are more liable to damage. It is likely that AMNH 30038 had an exoccipital-quadrate contact in life and that its absence is due to postmortem damage.

Structures on ventral surface: AMNH 30038 and *Euraxemys* have no fossa pterygoidea, and the condylus mandibularis is well anterior to the condylus occipitalis in both. The quadrate of *Dirqadim*, as in *Euraxemys*, does not participate in the foramen posterius canalis carotici interni. However, *Dirqadim* does differ from *Euraxemys* in having a foramen just lateral to the foramen posterius canalis carotici interni. This foramen is, as far as I can tell, unique to *Dirqadim*.

In all pleurodires (and all turtles), the cavum acustico-jugulare extends anteriorly into the aditus canalis stapedio-temporalis dorsally and the canalis cavernosus ventrally (Gaffney, 1979a: fig. 10). These represent the openings for the more dorsal stapedial artery and the more ventral lateral head vein (vena capitis lateralis). In *Dirqadim* the canalis stapedio-temporalis is formed by prootic and quadrate and curves dorsally to open on the dorsal surface of those bones. The canalis cavernosus curves ventrally, as in nearly all other turtles. However, in *Dirqadim* there is a foramen (foramen "A" in fig. 44B) and short canal on the ventral surface of the skull, just lateral to the foramen posterius canalis carotici interni and formed by pterygoid and quadrate, that leads into the canalis cavernosus. This canal and foramen are visible in AMNH 30038, which has been prepared on the left side showing the canal for most of its length. CT scans of this specimen confirm its presence on both sides. The canalis cavernosus in *Dirqadim* is not the relatively straight canal seen in most turtles, which curves slightly as it extends anteriorly from the cavum acustico-jugulare. In *Dirqadim* the canal drops almost straight down from the cavum acustico-jugulare to this unnamed foramen A, then turns anteriorly at a nearly right angle to enter the more anterior cavum acustico-jugulare, then enters the sulcus cavernosus. The reason for this peculiarity is not known. The foramen A seems too small to actually contain the lateral head vein. Its contents could have been an artery, vein, or nerve, or it could simply be a sinus. Most of the lateral part of the canalis cavernosus is formed by quadrate, with the prootic, then pterygoid, forming the more medial and anterior parts.

The ventrally opening foramen A described above is formed anteriorly by a nearly horizontal plate of the pterygoid, with the quadrate forming its dorsal margin. The foramen on both sides of both specimens faces posteriorly. It is directly lateral and partially confluent with the foramen posterius canalis carotici interni. This latter foramen is formed by the pterygoid anteriorly and ventrally, and by the prootic posteriorly and dorsally. The two foramina are barely separable in ventral view (fig. 44B), but a close posteroventral examination shows that they are separated by a thin wall of prootic and quadrate. Anteriorly, the canalis caroticus internus and canalis cavernosus are not separated by even the thin wall based on the CT scans of both sides in AMNH 30038. However, the wall, if present, would have been thin in this area and it is possible that its absence is an artifact of preservation.

Contacts on posterior surface: In *Dirqadim*, as in *Euraxemys*, the quadrate as seen in occipital view contacts the squamosal dorsolaterally, the opisthotic dorsomedially, and the exoccipital in a narrow contact posteromedially (except in AMNH 30038, but see discussion above).

Structures on posterior surface: The fenestra postotica is formed laterally and ventrally by the quadrate, with a largely open cavum acustico-jugulare, as in *Euraxemys* and in contrast to the more closed cavum of bothremydids.

The foramen chorda tympani inferius is present on the posterior surface of the processus mandibularis, below the incisura columellae auris. In *Dirqadim* the foramen is more ventrally located than in *Euraxemys*.

PTERYGOID (figs. 44B, 47, 50)

Preservation: In MDEt 41 both pterygoids are nearly complete, only lacking some of the thin, posterolateral flange. In AMNH 30038 the anterior edges are broken off and only a partial left processus trochlearis pterygoidei remains, dislocated by a break.

Contacts on ventral surface: The pterygoid in *Dirqadim* contacts the palatine anteriorly, the other pterygoid medially, the basisphenoid posteromedially, the prootic posteriorly, and the quadrate posterolaterally, all as in *Euraxemys*. *Dirqadim* differs from *Euraxemys* in having a much shorter midline contact of the pterygoids. The basisphenoid in *Dirqadim* seems to be slightly larger relatively, and the skull shape in *Dirqadim* is shorter and wider, all possibly related to the length of the median pterygoid contact. This short midline pterygoid contact is unusual in Pelomedusoides, but is found also in *Araripemys* and sporadically in the Bothremydidae.

Structures on ventral surface: The processus trochlearis pterygoidei in *Dirqadim* is very similar in shape and orientation to that in *Euraxemys*. There is a parasagittal ventral ridge in *Euraxemys* that is absent in *Dirqadim*. This ridge supports a thin flange that is more vertical and probably larger in *Euraxemys* than in *Dirqadim*. *Dirqadim* is closer to the chelid and pelomedusid condition of this flange than is *Euraxemys*.

Dirqadim has a distinct ridge marking the pterygoideus muscle attachment site. The enclosed area is only slightly depressed; there is no clearly defined fossa pterygoidea. This ridge delimits a curved, somewhat triangular area, medial to the quadrate ramus of the pterygoid.

The foramen posterius canalis carotici interni in *Dirqadim* is formed by the pterygoid, basisphenoid, and prootic (fig. 44B). The pterygoid forms the anterior and ventral margin, the prootic forms the dorsal and posterior margin, and the basisphenoid forms the medial margin. In *Euraxemys* the basisphenoid forms the medial and posterior margin, and the prootic is excluded. This is not a particularly great difference between *Euraxemys* and *Dirqadim*; on the right side of *Euraxemys*, a thin flange of basisphenoid is broken off, revealing the overlying prootic and resulting in a condition very similar to that in *Dirqadim*.

The canalis caroticus internus in *Dirqadim* can be seen in AMNH 30038 both visually and in CT scans. The canal is about the size of the canalis stapedio-temporalis, suggesting that the arteria stapedialis and arteria carotidis (Albrecht, 1967, 1976) are roughly the same size also. The canalis caroticus internus is formed by both basisphenoid and pterygoid, much as in pelomedusids, although it seems that the anterior part is formed more by the basisphenoid and the posterior part is formed more by the pterygoid. The canalis caroticus internus extends anteromedially from the foramen posterius canalis carotici interni in a slightly S-shaped canal to open in the foramen anterius canalis carotici interni.

The vidian nerve (Gaffney, 1979a; Soliman, 1964) branches off the facial nerve anterior to the canalis nervi facialis and travels directly anteriorly to exit the pterygoid in the vicinity of the foramen palatinum posterius. This seems to be relatively consistent in all turtles. In *Pelusios*, presumably the primitive condition for turtles, this can be seen reflected in the bony canal, the canalis nervi vidiani, branching anteriorly off the canalis nervi facialis in the prootic and extending anteriorly through the pterygoid to the foramen palatinum posterius. In *Dirqadim*, the canalis nervi facialis opens ventrally in the roof of the foramen posterius canalis carotici interni, which is a fairly large space that also communicates with the canalis cavernosus in this species. In the CT scans of AMNH 30038 the canalis nervi vidiani has its posterior opening in the floor of the canalis cavernosus. The canalis cavernosus and canalis caroticus internus communicate at this point (fig. 44B). It is likely that the vidian nerve traveled anteriorly from the ventral opening of the foramen nervi facialis, crossing both the canalis caroticus internus and the canalis cavernosus to enter the canalis nervi vidiani, which runs anteriorly beneath the canalis cavernosus to the region of the foramen palatinum posterius. Although the bony structures in *Dirqadim* housing the internal carotid, lateral head vein, facial nerve, and vidian nerve are different from the condition in pelomedusids, it is primarily due to ossification differences and differences in the relative positions of these soft structures, rather than to a more fundamental morphological distinction.

The foramen palatinum posterius in *Dirqadim* is formed by pterygoid and palatine; it is similar in size and position to that in *Euraxemys*. The flange posterior to the processus pterygoideus trochlearis in *Dirqadim* is the typical thin web of pleurodires extending along the quadrate ramus of the pterygoid.

Contacts on dorsal surface: Anteriorly, the pterygoid has a strong contact with the jugal ventrally and the postorbital dorsally, where all three bones form the lateral wall of the sulcus palatinopterygoideus, as in *Eur-*

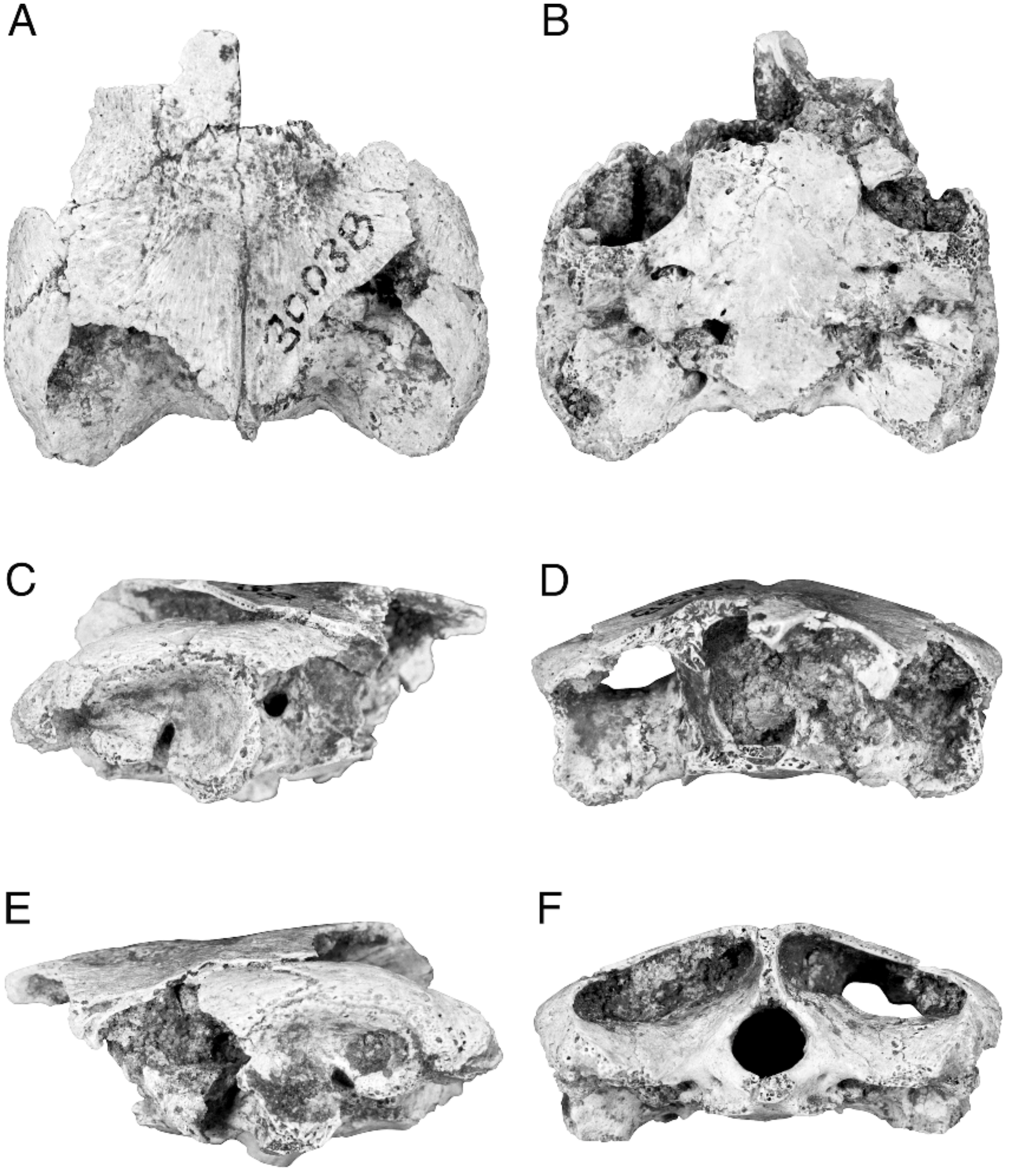

Fig. 51. *Dirqadim schaefferi*, n. gen. et sp., AMNH 30038. **A**, dorsal; **B**, ventral; **C**, right lateral; **D**, anterior; **E**, left lateral; **F**, posterior. [G. Giardina, del.]

axemys. The palatine in *Dirqadim* extends dorsally anterior to the foramen palatinum posterius to a greater extent than in *Euraxemys*.

The crista pterygoidea of *Dirqadim* is visible in both specimens and in CT scans of AMNH 30038, but both specimens are variably crushed along the braincase wall. The best preserved wall is the right side of AMNH 30038. As in other Pelomedusoides, the crista pterygoidea meets the processus inferior parietalis dorsally, with the pterygoid

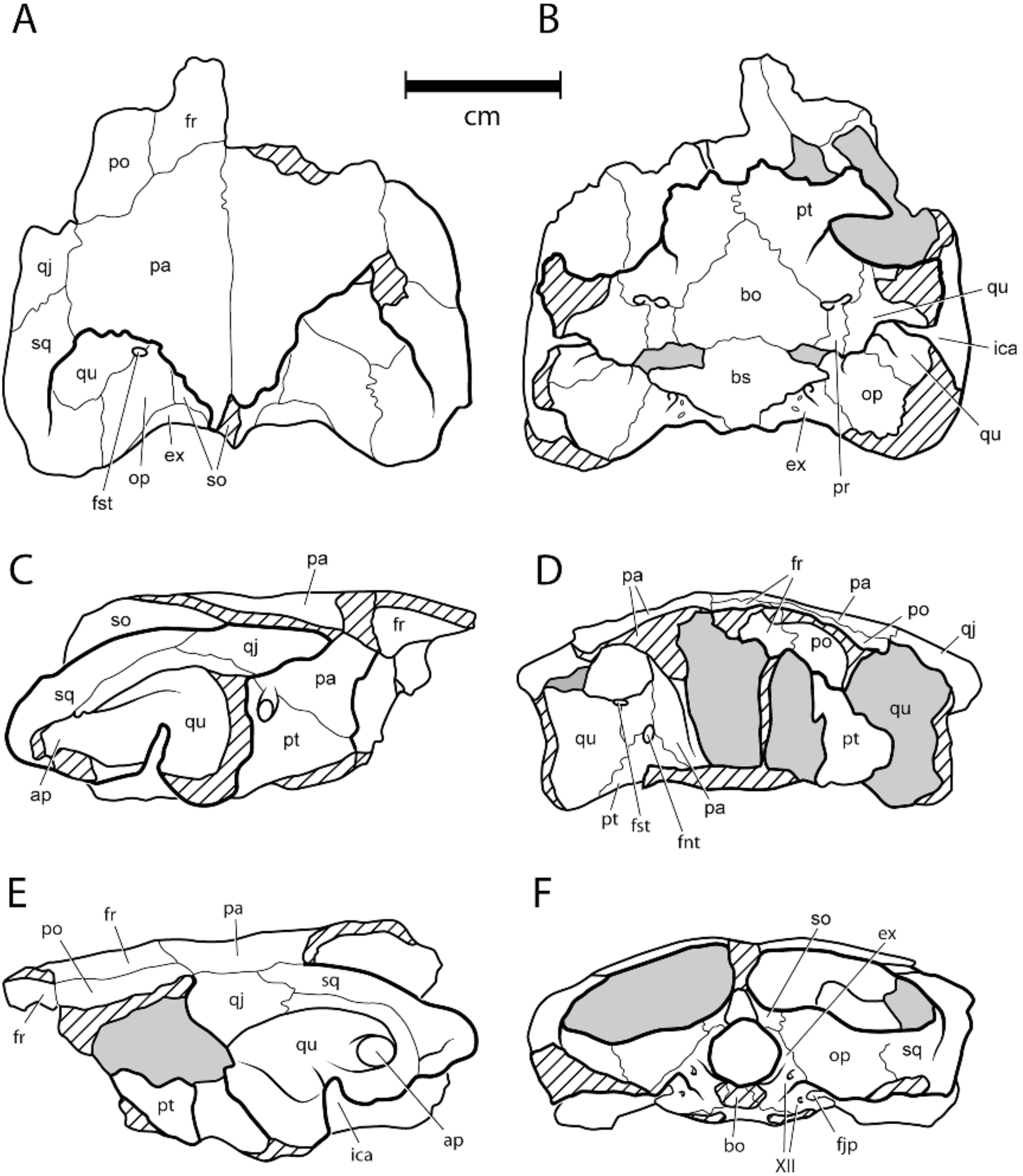

Fig. 52. *Dirqadim schaefferi*, n. gen. et sp., AMNH 30038. **A**, dorsal; **B**, ventral; **C**, right lateral; **D**, anterior; **E**, left lateral; **F**, posterior. [D. Marques, del.]

being higher posteriorly and lower anteriorly. The pterygoid forms the ventral margin of the foramen nervi trigemini, with the parietal and prootic forming the rest of the margin.

Anteriorly, the pterygoid in *Dirqadim* has a space between it and the more dorsal basisphenoid, rather than a tight contact. This space is clearly seen in both specimens, but in MDEt 41 it has been exaggerated into a paired foramen by overpreparation. Both visual and CT scans show that this space between pterygoid and basisphenoid is not a foramen or canal. A similar space is seen in recent pelomedusids and chelids, although this separation is subject to a wide degree of variation.

Structures on dorsal surface: The crista pterygoidea in *Dirqadim* is very similar to that in *Euraxemys*. The sulcus palatinopterygoideus in *Dirqadim* is also very similar to that in *Euraxemys*, being formed by the palatine and pterygoid ventrally and the parietal and postorbital dorsally. The sulcus palatinopterygoideus in *Euraxemys* and *Dirqadim* is also comparable in size and extent to that in the more generalized bothremydids, like *Galianemys*.

SUPRAOCCIPITAL (figs. 47, 50, 53)

Preservation: The supraoccipital is present in both AMNH 30038 and MDEt 41, but the posterior part of the crista pterygoidea is missing in both.

Contacts: The supraoccipital in *Dirqadim* contacts the parietals anteriorly and dorsally. There may be some exposure of the supraoccipital on the skull roof in contrast to *Euraxemys*, but this area is broken in both skulls. The supraoccipital contacts the prootic anterolaterally, the opisthotic posterolaterally, and the exoccipital posteroventrally. There is no quadrate contact and the supraoccipital does not approach the quadrate, as in *Euraxemys* (see Quadrate).

Structures: The crista supraoccipitalis is broken off at its base in both skulls, so its extent is unknown. It could have been short, as in *Euraxemys*.

EXOCCIPITAL (figs. 47, 50, 53)

Preservation: Both exoccipitals are present in both specimens. They are complete in MDEt 41, but the condylus occipitalis portion is broken in AMNH 30038.

Contacts: The exoccipital in *Dirqadim* contacts the supraoccipital dorsally, the opisthotic laterally, the basioccipital ventrally, and the quadrate ventrolaterally, all as in *Euraxemys*. The exoccipital is separated from the prootic and basisphenoid by a space that may have had thin bone or cartilage. In *Euraxemys*, the exoccipital contacts these elements, but there is a narrow prootic contact only on one side.

Structures: The foramen magnum in *Dirqadim* is very similar in size and shape to that in *Euraxemys*. In contrast to *Euraxemys*, the exoccipitals do meet narrowly on the midline in the floor of the foramen magnum. The condylus occipitalis in *Dirqadim* is formed equally by the two exoccipitals and the basioccipital. In *Euraxemys* there is a slightly greater contribution by the basioccipital. The foramen nervi hypoglossi penetrate the ventral part of the exoccipital, as in *Euraxemys*.

The foramen jugulare posterius (fig. 53) is widely open on both sides of MDEt 41 and on the left side of AMNH 30038. However, on the right side of AMNH 30038, the foramen is partially closed by a ventral process of the opisthotic nearly reaching the exoccipital. There is some damage on the right side of MDEt 41 and on the left side of AMNH 30038, but the right side of MDEt 41 clearly shows no ventral process of the opisthotic, and it is likely that the other two foramina also lacked the process. It seems, then, that the partially closed foramen is only on the right side of AMNH 30038, and that this difference is individual variation within the species.

Euraxemys and *Dirqadim* are almost unique among pleurodires in having a ventral process of the exoccipital (fig. 44) that forms a distinct process or ventral "foot" just lateral to the basioccipital and ventral to the exoccipital main body (see Exoccipital: *Euraxemys*). This does occur in some *Phrynops* (*Mesoclemys*) (Gaffney, 1979a: fig. 147), but it does not seem to occur in *Emydura* or other chelids. However, the ventral extension of the exoccipital in *Emydura* would be very similar to that in euraxemydids if it were expanded ventrally.

BASIOCCIPITAL (figs. 44, 47, 53)

Preservation: Both specimens of *Dirqadim* have the basioccipital, but it is nearly complete in MDEt 41. In AMNH 30038 the tuberculum basioccipitale is eroded on both sides and the condylus occipitalis contribution is broken.

Contacts: As in *Euraxemys*, the basioccipital in *Dirqadim* contacts the basisphenoid anteriorly and the exoccipital posterodorsally. As in *Euraxemys*, there is no quadrate contact due to the contact (or near contact) of exoccipital and prootic.

Structures: The basioccipital in *Dirqadim* is similar to that in *Euraxemys*, but

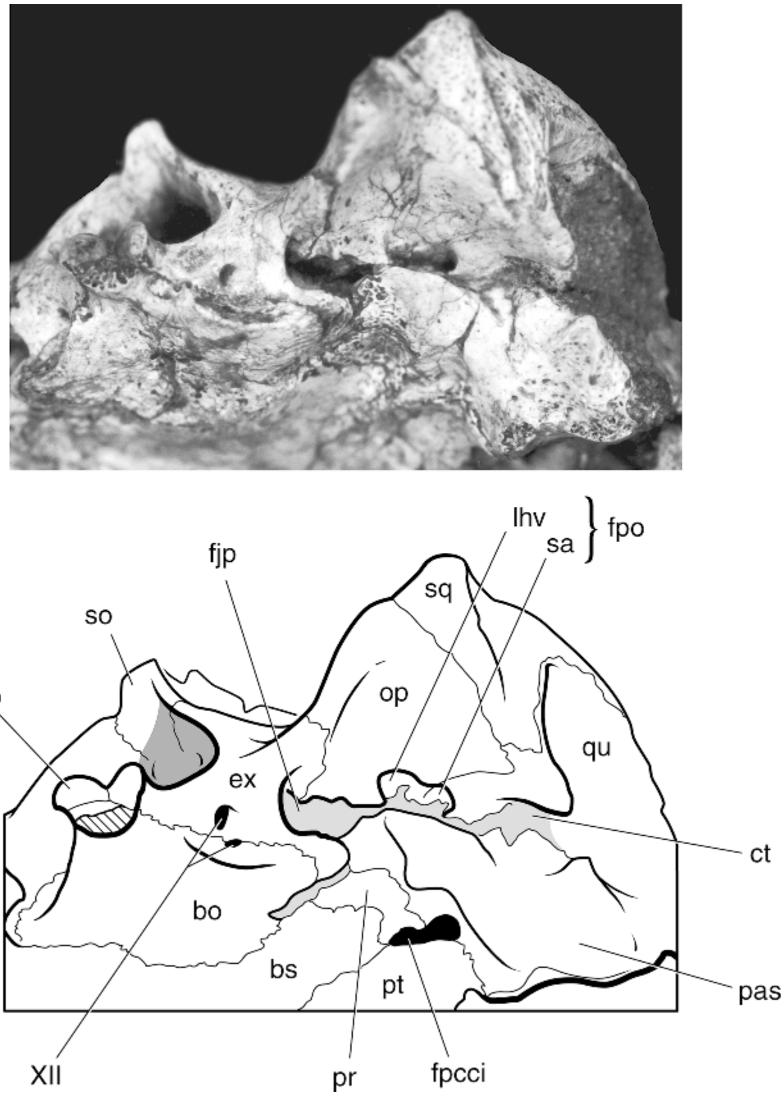

Fig. 53. *Dirqadim schaefferi*, n. gen. et sp., MDEt 41 holotype. Posterior oblique view of skull. [A. Venjara and E.S. Gaffney, del.]

slightly wider. The contribution of the basioccipital to the condylus occipitalis is equal to that of each exoccipital in *Dirqadim*, rather than greater, as in *Euraxemys*. The tuberculum basioccipitale in *Dirqadim* is similar in position and shape to that in *Euraxemys*, but it is slightly shorter and does not extend posteriorly in a thin flange as much as in *Euraxemys*.

PROOTIC (figs. 44B, 45B, 47, 50)

Preservation: Both AMNH 30038 and MDEt 41 have both prootics preserved. Although the right one in AMNH 30038 is nearly perfectly preserved, the others have some crushing and surface breakage as well as obscuring matrix.

Contacts: The prootic in *Dirqadim* contacts the parietal dorsomedially, the quadrate laterally, the supraoccipital posterodorsally, the pterygoid ventrally, and the opisthotic posteriorly. In contrast to *Euraxemys*, the prootic in *Dirqadim* has a wide contact with the opisthotic (fig. 45). On the ventral surface (fig. 44) the prootic in *Dirqadim* is exposed in a narrow strip between the basisphenoid medially and the quadrate laterally, with the pterygoid contacting anteriorly, all as in *Euraxemys*. In contrast to the complete exposure of the prootic in chelids, pelomedusids, and *Araripemys* (also primitive cryptodires and *Proganochelys*), the euraxemydids have a partially covered prootic, seen in both CT scans and as a result of specimen breakage, where the basisphenoid partially covers the prootic ventrally. In podocnemidids and bothremydids the prootic is completely or almost completely covered ventrally, producing a broad, quadrate-basisphenoid contact absent in euraxemydids, *Araripemys*, and chelids. Pelomedusids have only a narrow basisphenoid-quadrate contact with little ventral covering of the prootic (see Prootic: *Euraxemys* for further discussion).

Structures: The foramen nervi trigemini in *Dirqadim* has its posterodorsal margin formed by the prootic. The foramen is similar in position and shape to that in *Euraxemys*. The foramen stapedio-temporale, formed by both quadrate and prootic, faces dorsally and slightly anteriorly, as in chelids, pelomedusids, *Araripemys*, and *Euraxemys*. The foramen stapedio-temporale and foramen nervi trigemini are not closely opposed, as in Bothremydini and Taphrosphyini.

The foramen nervi facialis penetrates the prootic from its ventral surface dorsomedially to the fossa acustico-facialis. The ventral opening (see Pterygoid) is in the anterior part of the prootic in *Dirqadim*, as it is in *Euraxemys* (fig. 44). In both, it is partly covered in ventral view by the thin, posterior flange of the pterygoid. The foramen nervi facialis lies in the roof of the foramen posterius canalis carotici interni in *Dirqadim*, but not in *Euraxemys* where these two structures are separated (see Pterygoid). The CT scans of AMNH 30038 show the canal for the chorda tympani branching off the canalis nervi facialis and curving posteriorly to exit the skull in the anterior wall of the incisura columellae auris. The vidian nerve branch leaves the facial nerve ventral to the foramen nervi facialis, crosses the canalis caroticus internus, and enters the pterygoid near the canalis cavernosus (see Pterygoid).

OPISTHOTIC (figs. 45B, 47, 50, 53)

Preservation: In both skulls, both opisthotics are preserved, with the right one in MDEt 41 being nearly perfect and the other three with slight breakage along the posterior edge.

Contacts: The opisthotic in *Dirqadim* contacts the supraoccipital anteromedially, the prootic anteriorly, the quadrate anterolaterally, the squamosal posterolaterally, and the exoccipital posteromedially. The prootic contact is broad, in contrast to the narrow to absent contact in *Euraxemys*. In *Dirqadim* the processus interfenestralis of the opisthotic is visible as unfinished bone above the level of the ventral skull surface. In both skulls, the adjoining basioccipital, exoccipital, basisphenoid, and quadrate have irregular, unfinished edges, suggesting that thin bone, cartilage, or a combination of both had filled the space below the processus interfenestralis, producing the condition seen in *Euraxemys*.

Structures: The foramen jugulare posterius is roofed by the opisthotic in *Dirqadim* and is open laterally except on the right side of AMNH 30038, where a ventral process of the opisthotic nearly closes it (see Exoccipital). The fenestra postotica is open in both euraxemydids laterally so that it communicates with the incisura columellae auris. The roof of the fenestra postotica is divided by a variably developed ridge into a more lateral channel leading into the aditus canalis stapedio-temporalis and a more medial channel for the lateral head vein leading into the canalis cavernosus.

The fenestra ovalis and recessus scalae tympani can be seen visually and in the CT scans. The processus interfenestralis is relatively open, clearly dividing the two areas. This region is very similar to that in *Euraxemys* (see Opisthotic: *Euraxemys*).

The processus paroccipitalis of the opisthotic extends close to the posterior margin of the squamosal in *Dirqadim*, in contrast to the longer, more rodlike processus seen in *Euraxemys*, which extends much farther posteriorly.

BASISPHENOID (figs. 44B, 47, 48, 50)

Preservation: The basisphenoid is present and nearly complete in both specimens, although there is some breakage along the sutural margins.

Contacts on ventral surface: The basisphenoid in *Dirqadim* contacts the pterygoid anterolaterally, the basioccipital posteriorly, and the prootic posterolaterally. As in *Euraxemys*, there may have been a small contact with the exoccipital.

Structures on ventral surface: The foramen posterius canalis carotici interni in *Dirqadim* is formed medially by the basisphenoid, as in *Euraxemys*; in contrast to *Euraxemys*, the basisphenoid of *Dirqadim* forms less of the foramen, with the pterygoid and the prootic forming more (fig. 44B). In *Euraxemys* the basisphenoid has a thin, lateral sheet of bone covering some of the exoccipital ventrally and preventing its exposure as a significant part of the margin of the foramen posterius canalis carotici interni (see Pterygoid). In both genera the dorsally opening foramen nervi facialis is within or adjacent to the margin of the foramen posterius canalis carotici interni. Also, based on the position of the foramen/canalis nervi vidiani, that nerve traversed the foramen posterius canalis carotici interni from the foramen nervi facialis anteriorly to reach the foramen nervi vidiani in both genera.

The foramen posterius canalis carotici interni in *Dirqadim* is formed by the basisphenoid medially, the pterygoid anteroventrally, and the prootic posterodorsally. Much of the canalis caroticus internus is formed by the basisphenoid, based on the CT scans. The canalis caroticus internus extends medially and slightly anteriorly from the foramen to reach the foramen anterius canalis carotici interni in the sella turcica, much as in pelomedusids and other pleurodires. From the CT scans it appears that the basisphenoid-pterygoid suture parallels and lies just ahead of the canalis caroticus internus.

Contacts on dorsal surface: From the CT scans, it is possible to see that *Dirqadim* has the usual pleurodire basisphenoid contacts: pterygoid anterolaterally, prootic laterally, and basioccipital posteriorly.

Structures on dorsal surface: The basisphenoid of *Dirqadim* has a dorsum sellae that slightly overhangs the sella turcica, much as in pelomedusids. The sella turcica is oval, with the foramen anterius canalis carotici interni being posterolaterally placed. The foramen nervi abducentis penetrates the processus clinoideus, also as in pelomedusids. The rostrum basisphenoidale is fused anteriorly, but forms a flat plate, not a distinct rod, as in most pelomedusids and podocnemidids. There is no sign of a foramen caroticum laterale or a canalis caroticus lateralis.

FAMILY BOTHREMYDIDAE
TRIBE KURMADEMYDINI
Kurmademys kallamedensis

Kurmademys is represented by one well-preserved skull and four partial skulls that combine to provide a complete reconstruction. The nearly complete skull shows very little crushing and most of its internal area is matrix-free, but the other four partial skulls are crushed. The nearly complete skull, ISI R152, was described by Gaffney, Chatterjee, and Rudra (2001), and that description is modified and incorporated here. *Kurmademys* is the sister taxon to *Sankuchemys* together making up the tribe Kurmademydini which is the sister group to all other bothremydids.

PREFRONTAL (figs. 54, 59, 61)

Preservation: The type skull, ISI R152, lacks the prefrontals, but both prefrontals are present in ISI R158, and the right prefrontal is preserved in ISI R159. In ISI R158 the dorsal and ventral surfaces are visible.

Contacts: The prefrontal in *Kurmademys* contacts the maxilla anteroventrolaterally, the frontal posteriorly, and the other prefrontal medially, as in most pleurodires.

Structures: There is a slight anterior projection on the midline of the prefrontal, narrower and shallower than in *Galianemys*. A narrow, ventral process of the prefrontal lies on the inner edge of the maxilla along the foramen orbitonasale, as in many other pleurodires.

FRONTAL (figs. 54, 57)

Preservation: Both frontals are nearly complete in ISI R152, but their anteriormost margins are breaks rather than sutures, so the contact with the prefrontals is not determinable. More complete frontals are preserved in ISI R158 and show this contact. Some frontal portions are also present in ISI R159, ISI R155A, and ISI R155B.

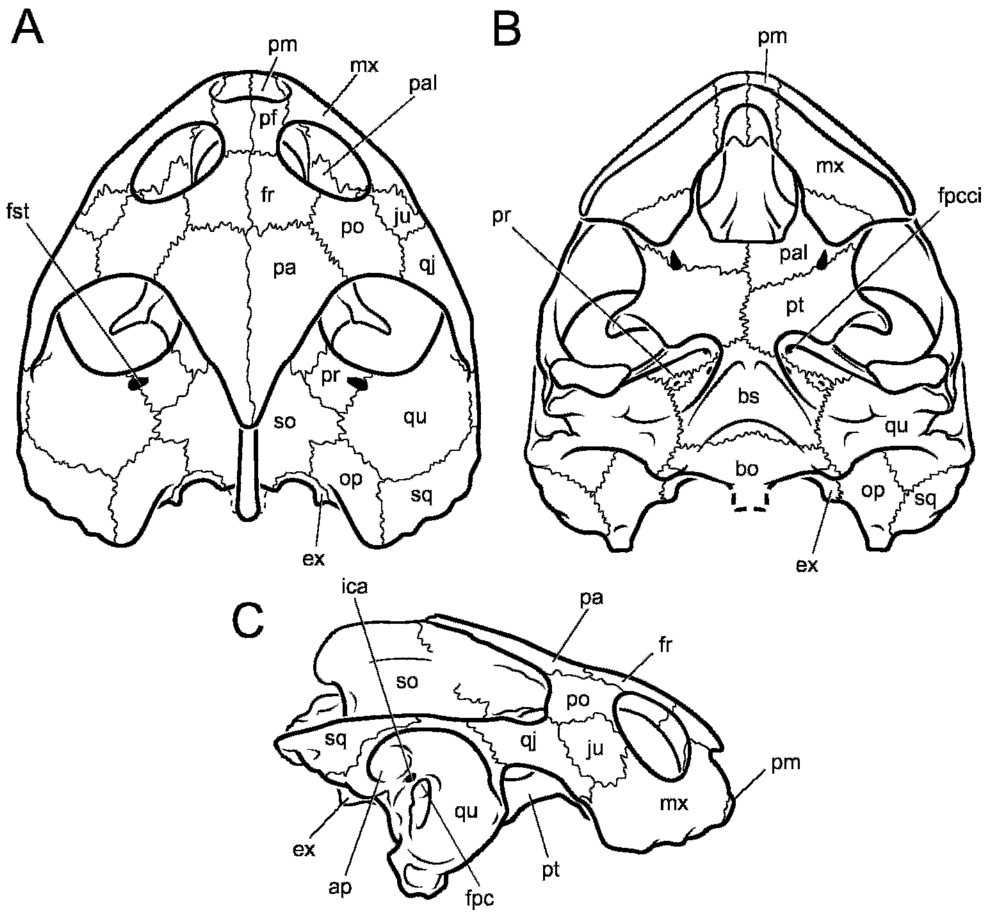

Fig. 54. *Kurmademys kallamedensis* Gaffney, Chatterjee, and Rudra, 2001. Partially restored views of skull based primarily on ISI R152 holotype with additions from ISI R158. **A**, dorsal; **B**, ventral; **C**, lateral. See figure 63 for detailed view of basicranium and figure 282 for detailed view of quadrate. [R. Rogge, del.]

Contacts: The frontal in *Kurmademys* contacts the prefrontal anteriorly, the postorbital posterolaterally, the parietal posteriorly, and the other frontal medially.

Structures: The frontal in *Kurmademys* forms the interorbital area along with the prefrontal. The interorbital distance is narrower in *Kurmademys, Cearachelys*, and probably *Sankuchemys* than it is in *Galianemys*, but it is wider than in *Araripemys* and *Euraxemys*.

On the ventral surface, the frontal of *Kurmademys* has a parasagittal ridge separating the fossa orbitalis from the sulcus olfactorius. The sulcus is slightly narrower anteriorly than in *Pelusios*, but it widens posteriorly, as in *Pelusios* and most Pelomedusoides. The processus inferior parietalis meets the posterior edge of the frontal ridge dorsally, as in *Euraxemys*, without a ventral process, as in *Pelusios*.

In other Pelomedusoides, such as *Euraxemys*, and *Pelusios*, the frontal is thickened lateral to the sulcus olfactorius ridge and forms part of the septum orbitotemporale anteriorly and a dorsal margin of the sulcus palatinopterygoideus posteriorly. In *Kurmademys* the frontal is relatively thin here, and there is no ridge connecting the sulcus olfactorius ridge and the septum orbitotemporale. The sulcus palatinopterygoideus is relatively open dorsally, at its anterior end, in contrast to most other Pelomedusoides and particularly other bothremydids, which have a more restricted ridge of bone here.

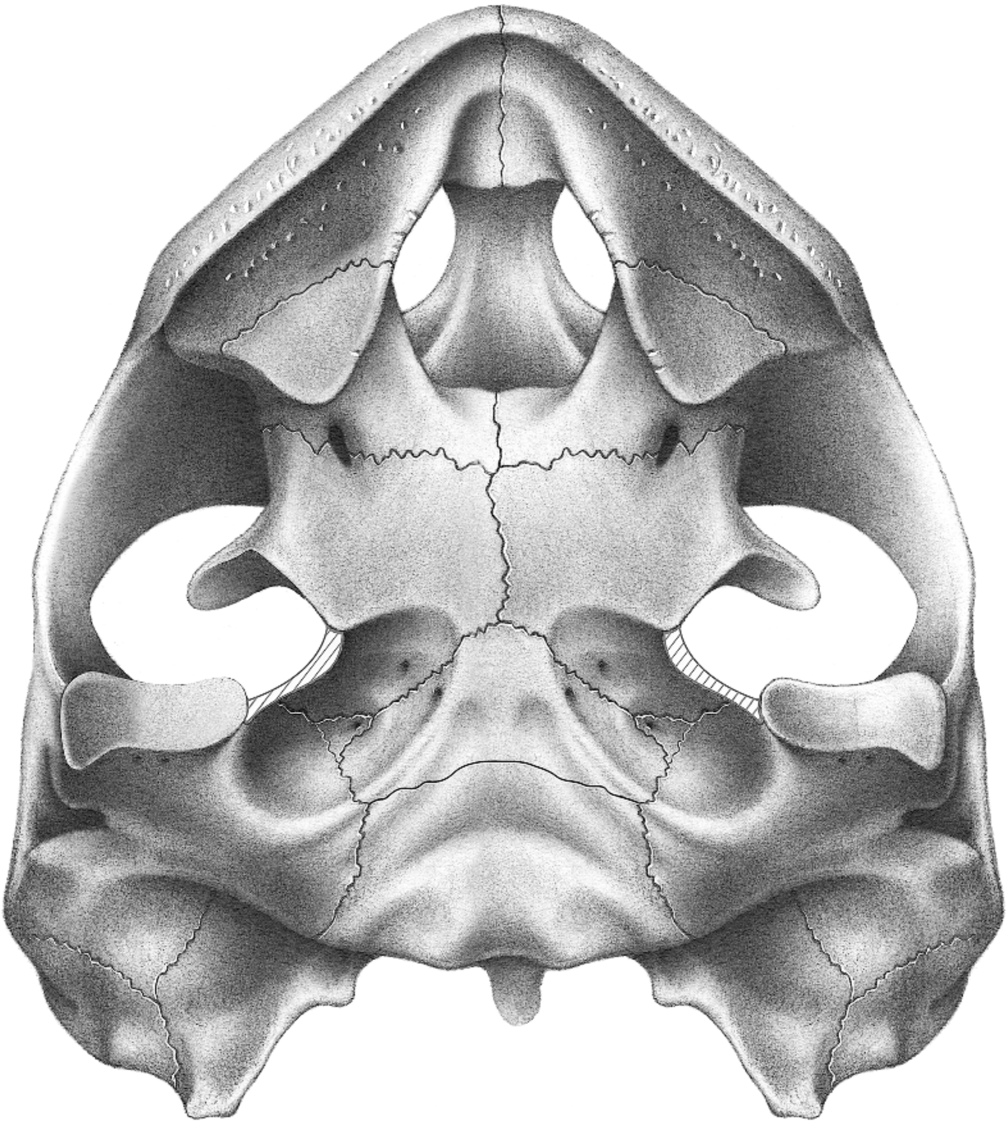

Fig. 55. *Kurmademys kallamedensis* Gaffney, Chatterjee, and Rudra, 2001. Partially restored ventral view based on ISI R152 holotype. [E. Heck and F. Ippolito, del.]

PARIETAL (figs. 54, 57, 62)

Preservation: Both right and left parietals are complete in ISI R152, except for small cracks and breaks. Parts of the parietal also are found in ISI R159, ISI R158, ISI 155A, and ISI R155B.

Contacts of the dorsal plate: The dorsal plate of the parietal is not extensive in *Kurmademys*. Anteriorly there is a transverse contact with the frontal, and laterally there is a contact with the postorbital. There is no contact between the parietal and quadratojugal; the postorbital is widely exposed along the edge of the temporal emargination, as in *Araripemys*.

Structures of dorsal plate: The temporal part of the parietal is about as extensive as in the living *Pelomedusa*, which is slightly more emarginate than in most *Pelusios*.

Contacts of processus inferior parietalis: The ventral wall of the parietal, the processus inferior parietalis, can be seen in both sides of ISI R152. The wall is similar to that in other Pelomedusoides. The anterior margin of the wall is formed completely by the parietal and curves ventrally without the posterior indentation seen in some *Pelusios*. Ventrally the parietal contacts the pterygoid, which is low until it reaches the area anterior to the foramen nervi trigemini where the pterygoid-parietal contact is more dorsal. The foramen nervi trigemini in *Kurmademys* is formed by the parietal, pterygoid, and prootic, as in most other Pelomedusoides. Posteriorly the parietal contacts the supraoccipital and prootic, as in other pleurodires.

Structures of processus inferior parietalis: The parietal of *Kurmademys* has a short ventral process below its lateral margin that contacts the dorsal process of the palatine in the lateral wall of the sulcus palatinopterygoideus. This contact is absent in *Galianemys*.

JUGAL (figs. 54, 57, 62)

Preservation: The jugal in ISI R152 is preserved on both sides, but surrounding contacts are seen only on the right side. Some of the medial and lateral parts of both jugals are preserved in ISI R158, although damaged. Fragments of the jugal are in ISI R159, ISI R155A, and ISI R155B.

Contacts of the lateral plate: The jugal in *Kurmademys* contacts the maxilla anteroventrally, the postorbital dorsally, and the quadratojugal posteriorly.

Structures of the lateral plate: The jugal is relatively small in *Kurmademys*, similar to that in *Pelusios* and *Pelomedusa*, and much smaller than in podocnemidids. The jugal is exposed in the posterior margin of the orbit, but its exposure is reduced by a posterodorsal process of the maxilla. The jugal is not exposed on the dorsal edge of the cheek emargination due to a contact of the quadratojugal and maxilla. This is unusual because *Kurmademys* has a cheek emargination at least as extensive as in *Pelomedusa* and *Pelusios*, and they have a large exposure of the jugal along this emargination.

Contacts of medial process: The medial process of the jugal in ISI R152 is preserved and visible on both sides. It is basically similar to that area described by Gaffney (1979a: figs. 53, 130) for *Pelusios*. The medial process of the jugal in *Kurmademys* contacts the palatine medially and the maxilla on the anterior surface of the septum orbitotemporale, as in most Pelomedusoides. The jugal contacts the postorbital medially and the pterygoid ventromedially on the posterior surface of the septum orbitotemporale. Ventrally the jugal contacts the maxilla.

Structures of medial process: The jugal in *Kurmademys* and *Sankuchemys* do not extend onto the triturating surface as they do in *Cearachelys* and *Galianemys whitei* and many Bothremydini.

QUADRATOJUGAL (figs. 54, 57)

Preservation: The quadratojugal in ISI R152 is nearly complete on the right side. Some small parts of the dorsal and ventral margin are probably missing, but based on the tapering of the bone and on surrounding bones, very little of the quadratojugal is missing. On the left side, however, only the anterior part and a small fragment of the posterodorsal contact with the quadrate are preserved. The quadratojugal is absent in the other specimens.

Contacts: The quadratojugal contacts the quadrate posteriorly, the postorbital anterodorsally, the jugal anteriorly, and the maxilla anteroventrally.

Structures: The quadratojugal of *Kurmademys* is unusually small for Pelomedusoides, because the temporal and cheek emarginations are both extensive. *Kurmademys* is unique among bothremydids in having such a small quadratojugal and narrow temporal arch. The dorsal margin of the quadratojugal forms the lateral edge of the temporal emargination, and the ventral margin forms the dorsal edge of the cheek emargination.

SQUAMOSAL (figs. 54, 57, 282B)

Preservation: Both right and left squamosals are present in ISI R152 and both have some damage to their posterolateral margins, but they are otherwise complete. Fragments of the squamosal are preserved in ISI R158, ISI R159, and ISI R155B.

Contacts: As in most turtles, the squamosal of *Kurmademys* is cone-shaped, forming the posterolateral portion of the antrum postoticum. As in other turtles, the squamosal of *Kurmademys* fits onto the circular posterior end of the quadrate and contacts the opisthotic medially. *Kurmademys* has extensive temporal emargination, and the squamosal has no contact with parietal, postorbital, or quadratojugal. The right side of ISI R152 also shows that although the squamosal has a narrow anterior process lying on the quadrate, the process does not reach the quadratojugal. In *Pelusios* and *Pelomedusa* there is usually a contact between the quadratojugal and squamosal, although there is some individual variation, with some specimens having a very slight contact or no contact. However, none of the specimens of *Pelusios* or *Pelomedusa* available to us shows the degree of reduction of quadratojugal and squamosal or the extent of dorsal exposure of the quadrate seen in *Kurmademys*. This feature is unique to *Kurmademys*.

Structures: The dorsolateral surface of the squamosal in *Kurmademys* is rounded, with no parasagittal ridge or wall seen in other Pelomedusoides. This ridge is a function of the degree of temporal emargination and is present to a varying extent in all other Pelomedusoides.

The antrum postoticum is preserved on both sides of ISI R152, and its internal extent is visible. The antrum is larger in *Kurmademys* than in any other Pelomedusoides. The Pelomedusidae and Euraxemydidae have a large antrum postoticum, but the antrum of *Kurmademys* is even larger. The size of the antrum postoticum in the Pelomedusidae and Euraxemydidae is interpreted as the primitive condition for Pelomedusoides, because this is the condition in chelids. The antrum postoticum is unknown in *Sankuchemys*.

POSTORBITAL (figs. 54, 57, 62)

Preservation: The postorbital is preserved on both sides of ISI R152. The posterior edge of the left postorbital is missing bone when compared with the more complete right postorbital. Small parts of the postorbital are present in ISI R158, ISI R159, and ISI R155A.

Contacts of lateral plate: The size and relations of the postorbital in *Kurmademys* are very similar to the postorbital in the Pelomedusidae and *Sankuchemys*. The postorbital of *Kurmademys* lies between the orbit anteriorly and the temporal margin posteriorly and forms part of the margins of those openings. Medially the postorbital contacts the frontal anteriorly and the parietal posteriorly. Laterally the postorbital contacts the jugal anteriorly and the quadratojugal posteriorly. All of these contacts are as in *Pelusios* and *Pelomedusa*. *Euraxemys*, representing the primitive condition, differs in having a broad contact of the parietal and quadratojugal posterior to the postorbital.

Structures of lateral plate: The postorbital forms the posterior margin of the orbit and the anterior margin of the temporal emargination.

Contacts of medial process: The medial or ventral process of the postorbital is similar to that in Pelomedusidae. As exposed on the posterior surface of the septum orbitotemporale in ISI R152 (fig. 62), the postorbital contacts the parietal medially, the pterygoid ventrally, and the jugal laterally. On the right side, which is better preserved than the left side, there is a small contact between the parietal and pterygoid, preventing exposure of the postorbital in the sulcus palatinopterygoideus at this point. On the anterior surface of the septum orbitotemporale, the ventral process of the postorbital contacts the dorsal process of the palatine medially in a sloping suture. Laterally the postorbital contacts the jugal.

Structures of medial process: The medial surface of the ventral process of the postorbital forms the lateral wall and the lateral part of the roof of a relatively short sulcus palatinopterygoideus.

PREMAXILLA (figs. 54, 55)

Preservation: Both premaxillae are present in ISI R152 and are nearly complete. The anterior parts of both premaxillae are preserved in ISI R158.

Contacts: Laterally the premaxilla contacts the maxilla in a parasagittal suture, and it contacts the other premaxilla medially. The posterior margin of the premaxilla forms at least part of the apertura narium interna, but it has a broken edge medially. The broken edge does not show a sutural surface anywhere, and there is no fragment of a vomer, but it is possible that one was present.

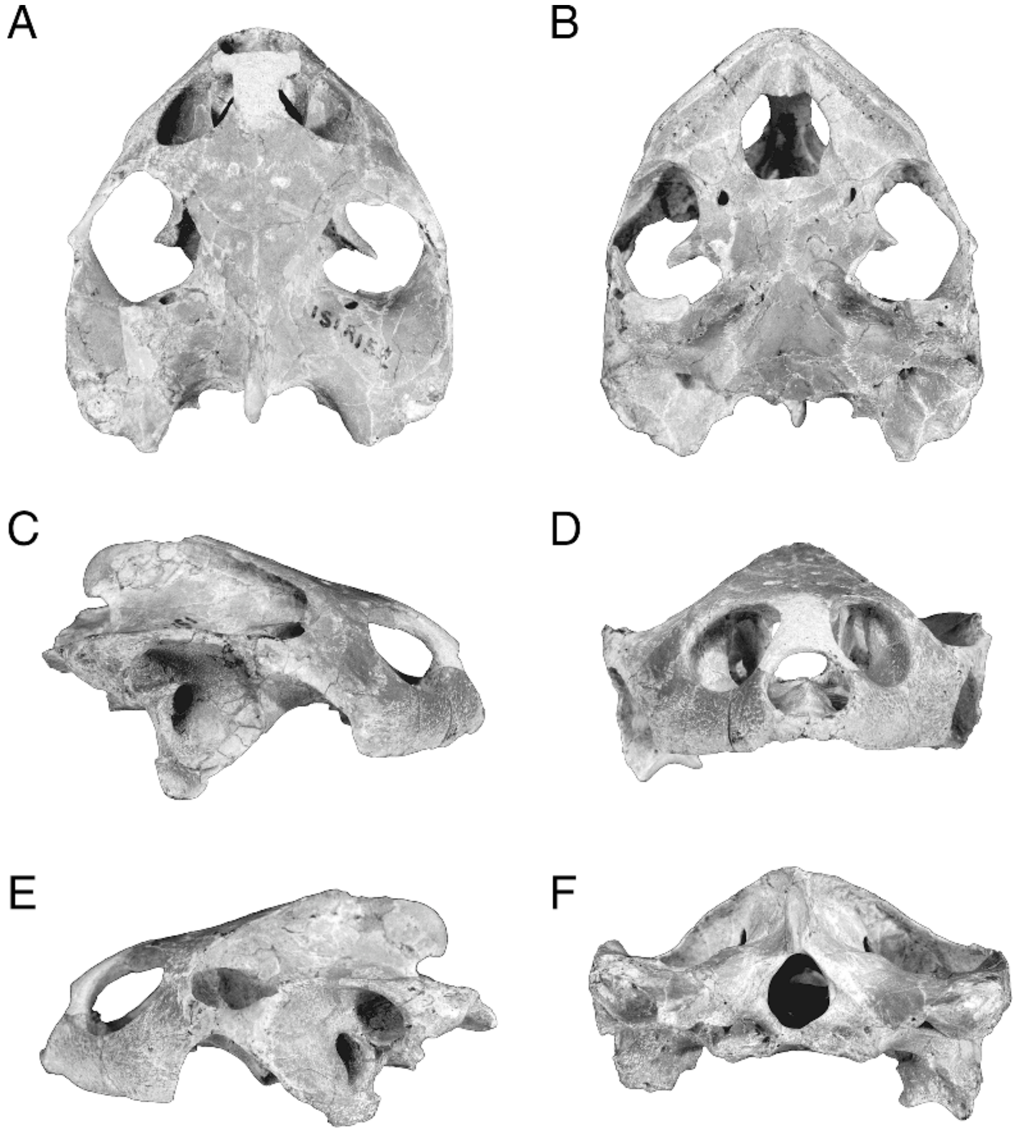

Fig. 56. *Kurmademys kallamedensis* Gaffney, Chatterjee, and Rudra, 2001. ISI R152 holotype. **A**, dorsal; **B**, ventral; **C**, right lateral; **D**, anterior; **E**, left lateral; **F**, posterior (from Gaffney, Chatterjee, and Rudra, 2001). [E. Heck, del.]

Structures on dorsal surface: The dorsal surface of the premaxilla forms part of the floor of the fossa nasalis. In *Kurmademys* the premaxillae curve dorsally to form a sharply rising median ridge in the fossa. This median ridge is present in other Pelomedusoides, but it is lower and smaller than in *Kurmademys*.

Structures on ventral surface: The ventral surface of the premaxilla bears the continuation of the labial ridge. The labial ridge of *Kurmademys* is narrower than in *Pelusios* and lacks the anterior projection of the margin of the apertura narium externa in that form. This area between the apertura narium externa and labial ridge is very thin in *Kurmademys*, similar to *Euraxemys*. *Kurmademys* has a shallow median notch similar to *Pelusios* and wider than in *Euraxemys*. In contrast to *Pelusios* and *Pelomedusa*, *Kurmademys* has a posterior extension to the

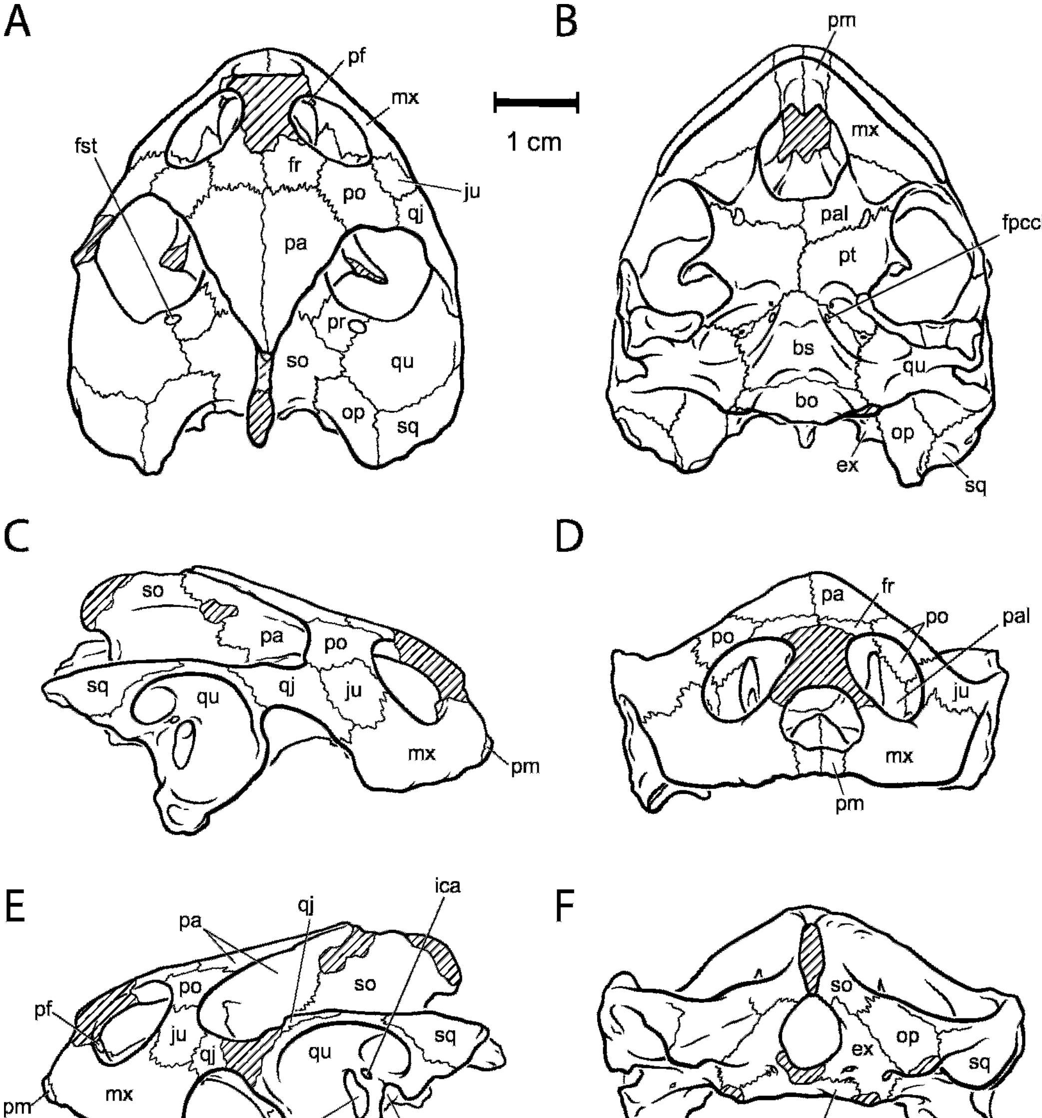

Fig. 57. *Kurmademys kallamedensis* Gaffney, Chatterjee, and Rudra, 2001. ISI R152 holotype. **A**, dorsal; **B**, ventral; **C**, right lateral; **D**, anterior; **E**, left lateral; **F**, posterior (from Gaffney, Chatterjee, and Rudra, 2001). [E. Heck, del.]

premaxilla that bears a distinct, ventrally facing concavity on the midline that is the ventral surface of the dorsal ridge in the fossa nasalis. Lower jaws of *Kurmademys* (fig. 233) show a marked symphyseal hook that presumably fitted into the concavity. The flat part of the triturating surface (fig. 55) narrows considerably to form a narrow shelf between the concavity and the labial ridge. This morphology is also seen in *Bothremys* and *Rosasia* as well as in *Neochelys* and some cryptodires like baenids. There is no sign of a foramen praepalatinum.

MAXILLA (figs. 54, 55, 57)

Preservation: Both maxillae of ISI R152 are complete except for the distal ends of the dorsal processes, which are missing. ISI R158 has most of both maxillae, but they are missing their medial edges. ISI R159 has most of the right maxilla. ISI R155A and ISI R155B have the vertical plate of the right maxilla.

Contacts of vertical plate: The maxilla in *Kurmademys* contacts the premaxilla anteromedially, the jugal posterodorsally, the prefrontal anterodorsally, and the quadratojugal posteriorly.

Structures of vertical plate: The vertical or alveolar plate of the maxilla is deep and fairly massive, not narrow, as in *Euraxemys*, but similar to *Podocnemis*. The maxilla forms the apertura narium externa anteriorly, and it is wider at its base than in *Euraxemys*, similar to most other Pelomedusoides. The apertura is not extended anteriorly, as in *Pelusios* and *Podocnemis*. The dorsal process of the maxilla in *Kurmademys* is thinner than in *Pelusios* and *Pelomedusa* and is similar to *Euraxemys*. The ventral margin of the orbit, which is formed by the maxilla, has a dorsal process along the posterior margin of the orbit reducing or preventing the contribution made by the jugal to the orbit. Forms such as *Euraxemys* and *Podocnemis* have a posterodorsal process, but it is separated from the orbit by the jugal. *Pelusios* and *Pelomedusa* do not have this process, but its expression is variable in Pelomedusoides. The posterior edge of the maxilla forms the anterior margin of the cheek emargination. Between the cheek emargination and the jugal, the maxilla contacts the quadratojugal.

Contacts of horizontal plate: The maxilla in *Kurmademys* contacts the premaxilla anteromedially, the palatine posteromedially, and the jugal posterolaterally. The horizontal plate of the maxilla is exposed in the orbital floor where the maxilla contacts the palatine medially and forms a small part of the border of the large foramen orbitonasale.

Structures of horizontal plate: The triturating surfaces of *Kurmademys* are narrow anteriorly and widely expanded posteriorly, as in the Cearachelyini and Bothremydini. The maxilla itself, however, tapers posteriorly so that the palatine forms the posterior and the medial portions of the triturating surface. The triturating morphology is similar to that in *Galianemys* and Bothremydini like *Foxemys*, which is also narrow anteriorly and expanded posteriorly, with a significant contribution from the palatine. In all these taxa the narrow, anterior part has a raised medial edge along the lingual ridge. *Foxemys* has a slight pinching of the snout anteriorly, as in *Rosasia*, which is absent in *Kurmademys*, where the margin of the snout is straight. *Foxemys* has two accessory ridges, absent in *Kurmademys*. The triturating surface in *Kurmademys* is raised anteriorly along the margin of the apertura narium interna. The posterior expanded area is slightly concave. There are no accessory ridges on the triturating surface, which ends posteriorly in a V-shaped margin completely formed by the palatine.

Sankuchemys differs from *Kurmademys* in having a less expanded triturating surface and a distinct accessory ridge on the maxilla paralleling the labial ridge.

VOMER

There is no vomer present nor are there sutural surfaces remaining for a vomer in any of the skulls, but the bone edges in this area are not complete. The morphology surrounding the apertura narium interna in the *Kurmademys* skulls, as they are preserved, is very close to that in other bothremydids that have a well-developed vomer. Thus, it is quite possible that one was present in *Kurmademys*.

PALATINE (figs. 54, 55, 57)

Preservation: Both palatines are present in ISI R152, but both are missing some of the anterior edges that form the margin of the apertura narium interna and the possible vomerine contact. The posterior part of the palatine is present in ISI R158 and ISI R155A, and a small fragment is present in ISI R159.

Contacts: The palatine in *Kurmademys* in ventral view contacts the maxilla anterolaterally, the other palatine medially, and the pterygoid posteriorly. On the dorsal surface the palatine contacts the jugal laterally, the postorbital dorsolaterally, and the parietal dorsomedially.

Structures on dorsal surface: On the dorsal surface both right and left palatines of ISI R152 are visible and free of matrix. The palatine forms the medial part of the orbital floor and the lateral margin of the large foramen orbitonasale.

Posteriorly the palatine of *Kurmademys* has a large dorsal process forming the lateral wall of the sulcus palatinopterygoideus. This process contacts the jugal laterally, the postorbital dorsolaterally, and the parietal dorsomedially. The process tapers dorsally such that its medial edge is higher than its lateral edge. The medial edge forms the lateral margin of the sulcus palatinopterygoideus. This dorsal process of the palatine reaches the parietal in the postorbital wall, which is quite unusual and has not been found so far in other Pelomedusoides. The septum orbitotemporale is complex in Pelomedusoides and particularly so in *Kurmademys*. Behind the dorsal process of the palatine are the ventromedial process of the postorbital and a short ventral process of the parietal, all visible on the posterior surface of the septum orbitotemporale.

Structures on ventral surface: The anterolateral part of the palatine in *Kurmademys* contacts the maxilla and forms the posteromedial part of the triturating surface. The triturating surface is a low platform that ends in a V-shaped margin completely formed by the palatine. The palatine forms the posterior margin of the apertura narium interna, but most of this margin is missing in ISI R152. The choanal grooves are barely discernible in *Kurmademys*. The foramen palatinum posterius is formed in the palatine-pterygoid suture by both bones, as in many bothremydids and in contrast to *Euraxemys*, *Pelusios*, *Pelomedusa*, and *Podocnemis*, in which most of the foramen is in the palatine. As in other pleurodires, there is a median contact with the other palatine and a transverse, posterior contact with the pterygoid.

QUADRATE (figs. 54, 57, 64, 282B)

Preservation: Most of both quadrates of ISI R152 are complete and free of matrix. Part of the medial area of the left quadrate is broken and partially restored with something awful. The right quadrate of ISI R159 is nearly complete and well preserved. In ISI R158 the quadrate parts are poorly preserved. In ISI R155A fragments of the quadrate are present, and in ISI R155B the dorsal and medial quadrate areas are present.

Contacts on lateral surface: In *Kurmademys* the quadrate contacts the quadratojugal anterodorsally and the squamosal posterodorsally. The squamosal lies at the posterolateral corner of the quadrate, and its relations and contacts with the quadrate in *Kurmademys* are similar to those in *Pelusios* and *Pelomedusa*. The quadrate exposure along the lateral edge of the temporal emargination prevents contact of squamosal and postorbital. Anteriorly the quadrate contacts the quadratojugal, but the contact is relatively small because of the extensive temporal and cheek emargination. The quadratojugal contact is smaller in *Kurmademys* than in *Pelusios*, *Pelomedusa*, or *Euraxemys*

Structures on lateral surface: Most of the quadrate is involved in the formation of the cavum tympani and its two spaces, the antrum postoticum and the fossa precolumellaris (fig. 282B). The antrum postoticum of *Kurmademys* is unusually large for Pelomedusoides; it is as large as the antrum in *Emydura*, the presumed primitive condition for Pelomedusoides. The antrum of *Kurmademys* is swollen to completely fill the area formed by squamosal and quadrate, in contrast to all euraxemydids and other bothremydids. The fossa precolumellaris is also deep and very large in *Kurmademys*, and it is also comparable in size to primitive chelids. Other Pelomedusoides, such as *Pelusios* and *Pelomedusa*, have a large fossa precolumellaris, but the fossa is absent in all other bothremydids. In these features, the cavum tympani of *Kurmademys* is more primitive than in other bothremydids.

The other feature of interest in the cavum tympani is the incisura columellae auris, which still has the stapes present in the right quadrate of ISI R152. The incisura is reduced to a completely closed, small foramen containing only the stapes in *Kurmademys*, as in all bothremydids except *Foxemys* and *Polysternon*. In Pelomedusidae, Euraxemydidae, *Araripemys*, and chelids, the incisura columellae auris is open. The combination of a completely closed incisura columellae auris with a gigantic antrum postoticum is a com-

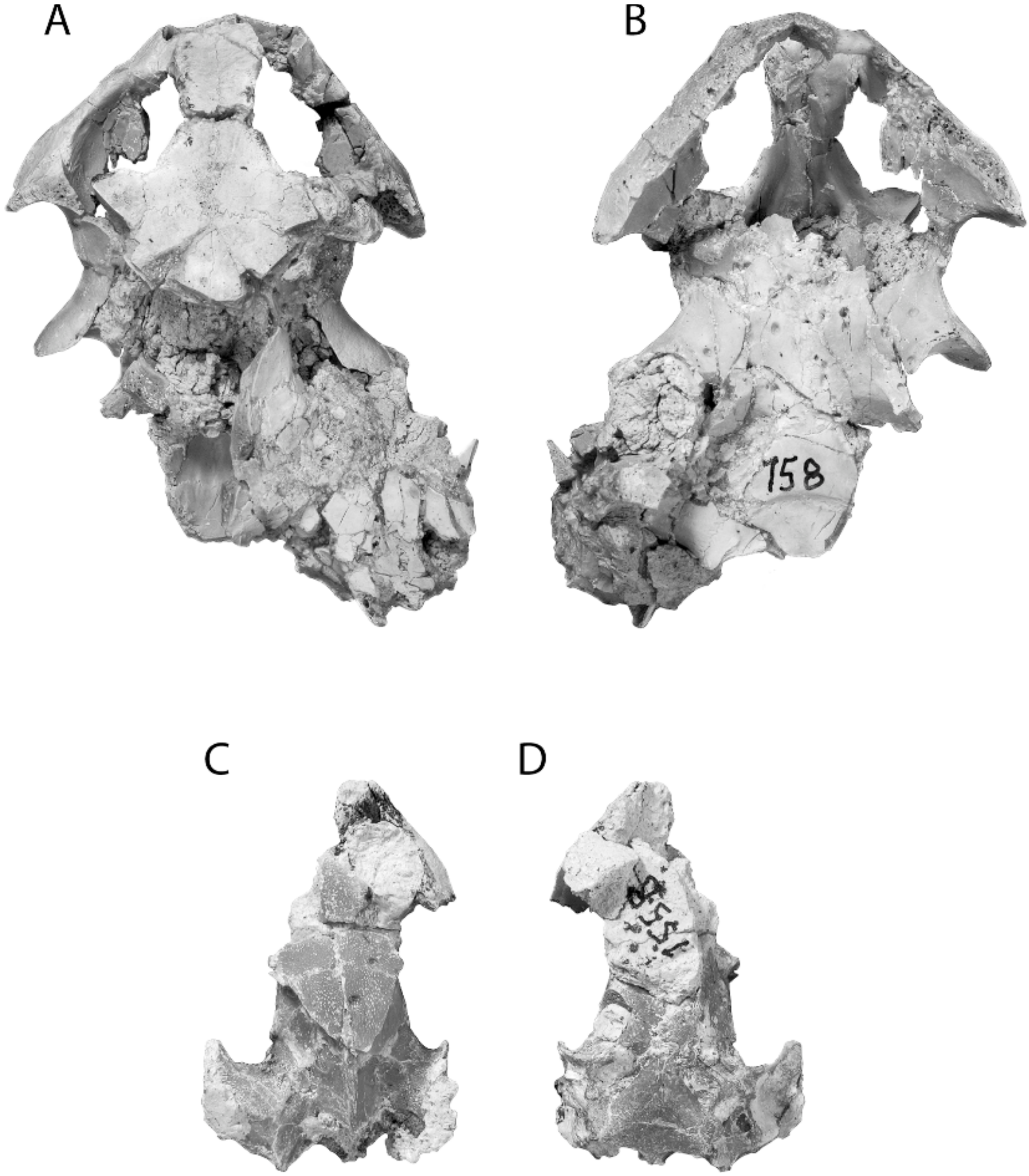

Fig. 58. *Kurmademys kallamedensis* Gaffney, Chatterjee, and Rudra, 2001. **A**, ISI R158, dorsal view; **B**, ISI 158, ventral view; **C**, ISI R155B, dorsal view; **D**, ISI R155B, ventral view. [K. Luckenbill, del.]

bination known in no other pleurodire. The quadrate of *Kurmademys* has a kidney-shaped cavum tympani, as in most other bothremydids. Although the incisura columellae auris is completely closed by bone, a groove for the eustachian tube is present behind it in the quadrate (fig. 64). Dorsally the groove slopes up to a horizontal, straight-edged ridge that separates the eustachian tube surface from the opening for the stapedial artery in the fenestra postotica.

Contacts on dorsal and anterior surfaces: In *Kurmademys* the quadrate contacts the prootic anteromedially, the opisthotic posteromedially, the supraoccipital medially, and the squamosal posterolaterally.

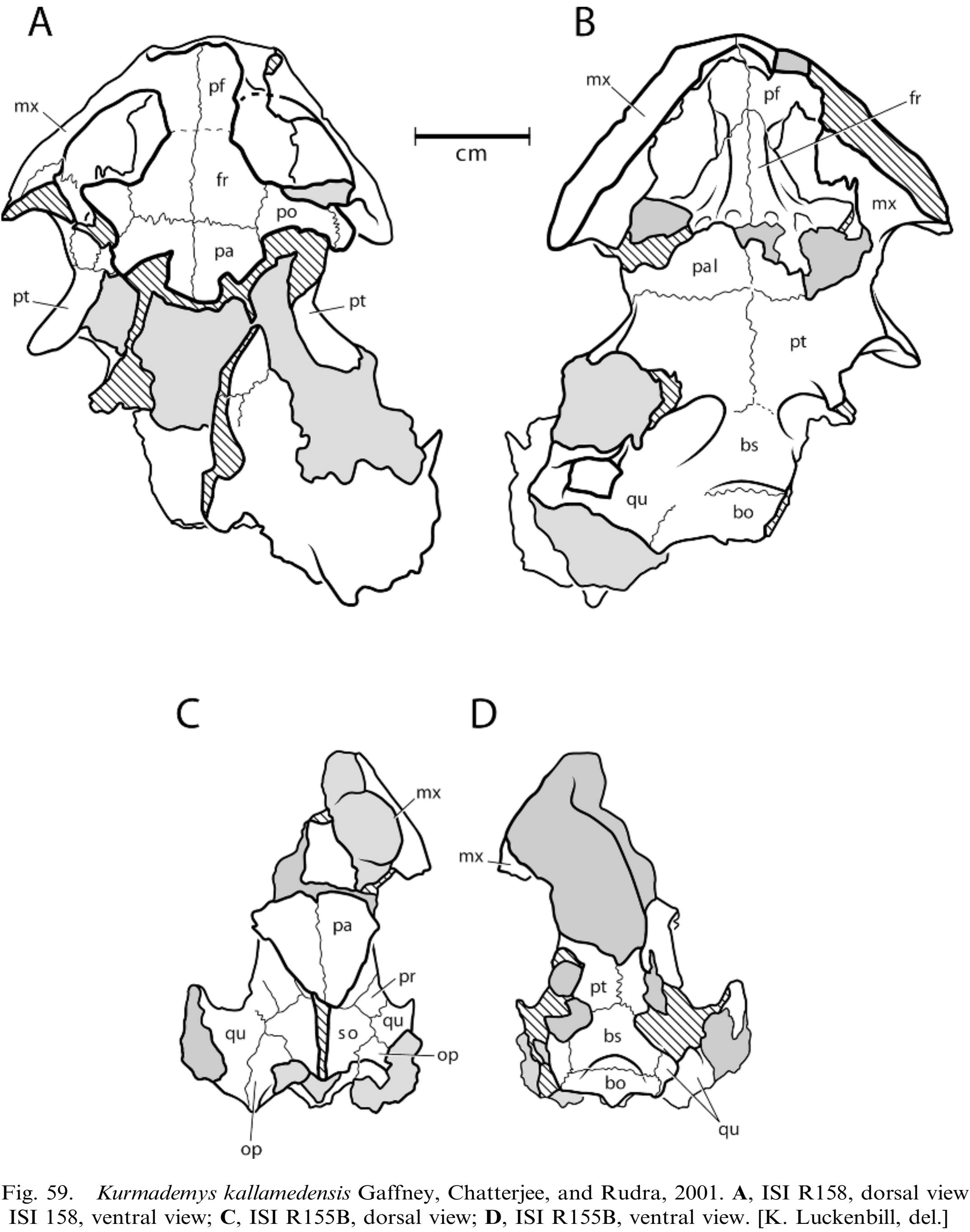

Fig. 59. *Kurmademys kallamedensis* Gaffney, Chatterjee, and Rudra, 2001. **A**, ISI R158, dorsal view; **B**, ISI 158, ventral view; **C**, ISI R155B, dorsal view; **D**, ISI R155B, ventral view. [K. Luckenbill, del.]

Structures on dorsal and anterior surfaces: The foramen stapedio-temporale in *Kurmademys* is placed more anteriorly than in chelids, but not more so than in pelomedusids or euraxemydids. *Sankuchemys* is not well preserved, but as preserved, it does not have the foramen stapedio-temporale visible in dorsal view. All other bothremydids also have the foramen farther anterior than in *Kurmademys*.

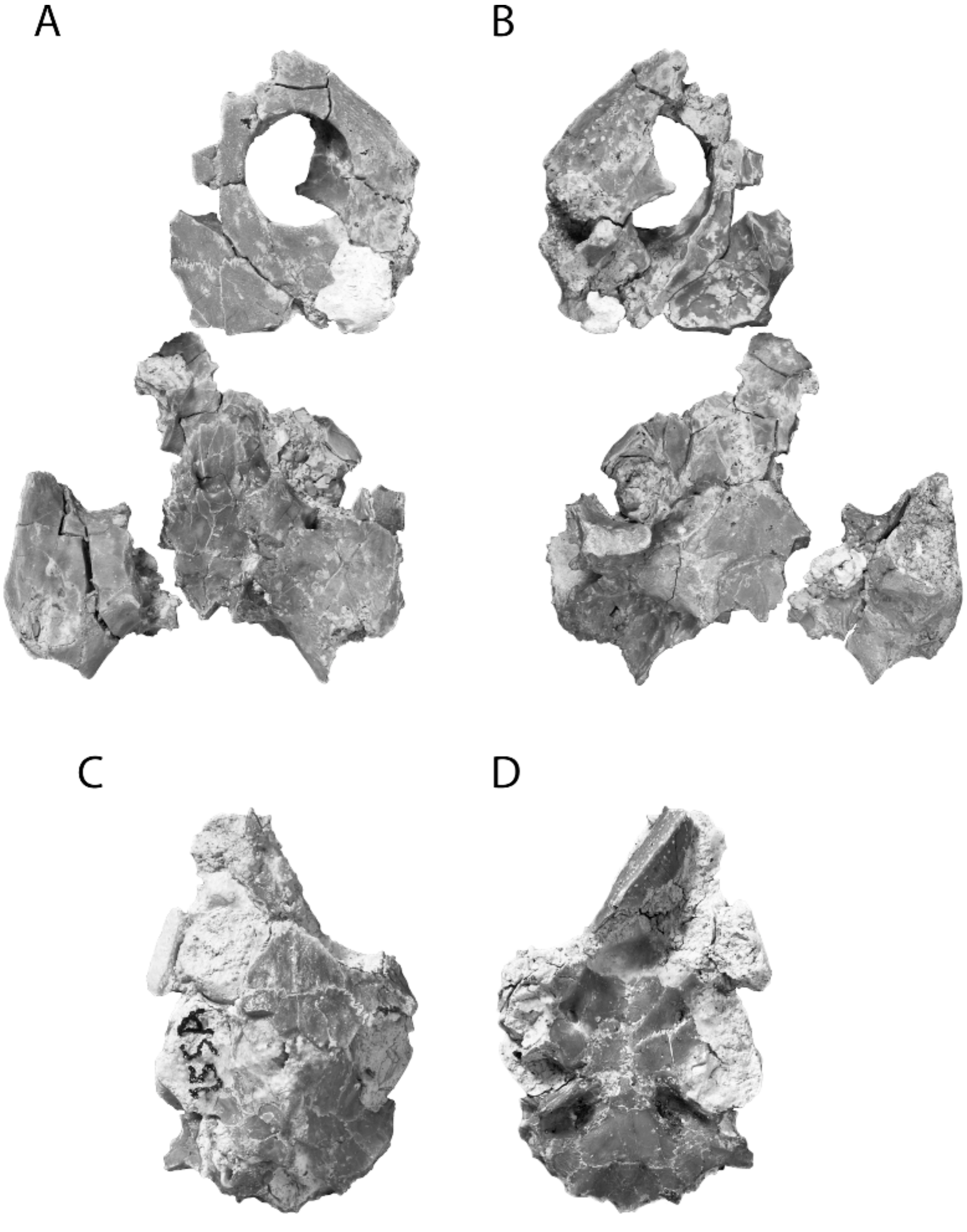

Fig. 60. *Kurmademys kallamedensis* Gaffney, Chatterjee, and Rudra, 2001. **A**, ISI R159, dorsal view; **B**, ISI R159, ventral view; **C**, ISI R155A, dorsal view; **D**, ISI R155A, ventral view. [K. Luckenbill, del.]

Contacts on ventral surface: The quadrate in *Kurmademys* contacts the pterygoid anteromedially, the prootic anteromedially (behind the pterygoid), the basisphenoid medially, and the basioccipital posteromedially. *Kurmademys* along with *Sankuchemys*, *Cearachelys* (in part), *Galianemys emringeri*, and *Foxemys* have a medial process of the quadrate that contacts a narrowly exposed prootic (fig. 63). Behind the basisphenoid, the quadrate has a broad contact with the basioccipital. The basioccipital contact of the

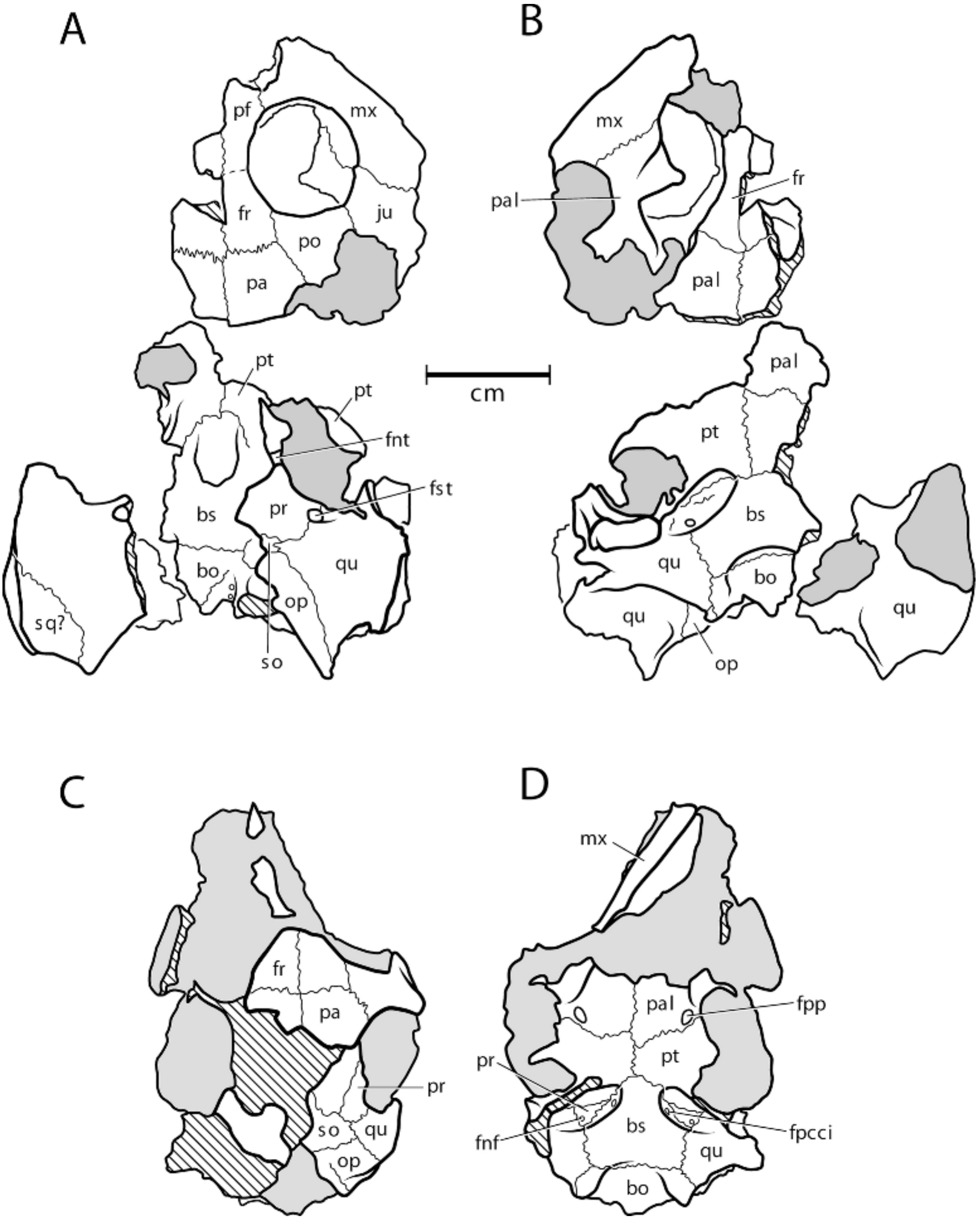

Fig. 61. *Kurmademys kallamedensis* Gaffney, Chatterjee, and Rudra, 2001. **A**, ISI R159, dorsal view; **B**, ISI R159, ventral view; **C**, ISI R155A, dorsal view; **D**, ISI R155A, ventral view. [K. Luckenbill, del.]

quadrate characterizes the superfamily Podocnemidoidea (Bothremydidae and Podocnemididae), but the quadrate-exoccipital contact is more restricted, found so far only in the Bothremydidae.

Structures on ventral surface: The fossa pterygoidea (see Pterygoid) is formed posterolaterally by the quadrate.

The condylus mandibularis in *Kurmademys* is well anterior to the condylus occipitalis and is close to the anterior margin of the basisphenoid, as in *Sankuchemys*, *Polysternon*, and some of the tribe Taphrosphyini. In all other bothremydids, however, the condylus mandibularis is relatively more posterior than in *Kurmademys*.

Contacts on posterior surface: The quadrate of *Kurmademys* contacts the squamosal dorsolaterally, the opisthotic dorsomedially, the exoccipital medially, and the basioccipital ventromedially. The medial contacts of the quadrate include the opisthotic and prootic, as in other turtles (fig. 62).

Structures on posterior surface: The roof of the fenestra postotica (aditus canalis stapedio-temporalis) has a low parasagittal ridge presumably separating the passage of the more lateral stapedial artery from the more medial (and ventral) lateral head vein. This ridge is largely formed by the quadrate, with the opisthotic contributing medially. The opisthotic forms this wall dorsally, and the quadrate forms it ventrally. On both sides of ISI R152 the contact of these two bones is broken, and some compression is visible. The fenestra postotica is broken in most specimens, but the restored condition (see Opisthotic) is a closed fenestra postotica (fig. 64).

There is a well-developed quadrate-exoccipital contact medially, as in most bothremydids; this is considerably more extensive than the small contact in Euraxemydidae.

The presumed foramen chorda tympani inferius is present on the posterior surface of the processus articularis, roughly similar in position to *Podocnemis*. Because of glue and crud on the right quadrate, this is only visible on the left.

Pterygoid (figs. 54, 55, 57, 62, 63)

Preservation: Both pterygoids are preserved in ISI R152 and both are nearly complete. Most of the thin pterygoid flange extending ventrally from the quadrate process is missing from both pterygoids; the right one has more of it preserved than does the left. Some of the processus trochlearis pterygoidei is missing; more of the right one is preserved than the left. A complete processus is in ISI R158, on both sides, but the more posterior parts of the pterygoid are damaged in this specimen. Partial pterygoids are preserved in ISI R159, ISI R155A, and ISI R155B.

Contacts on ventral surface: On the ventral surface the pterygoid contacts the palatine in a roughly transverse suture that trends slightly anterolaterally. The foramen palatinum posterius is formed in the palatine-pterygoid suture, as in nearly all bothremydids. Medially the pterygoids meet on the midline for a bit less than half their length. They are separated posteriorly by the triangular basisphenoid. The pterygoid has a short contact with the prootic posteriorly and contacts the quadrate posterolaterally.

Structures on ventral surface: As in all pleurodires, there is a laterally projecting processus trochlearis pterygoidei. In *Kurmademys* the processus does not extend at a sharp right angle, as in the *Galianemys*, but is only slightly less than a right angle, much as in *Foxemys*. It is not at an acute angle, as in chelids and *Araripemys*. The flange or web that extends ventrally from the base of the processus trochlearis pterygoidei along the quadrate process in all pleurodires is mostly missing in *Kurmademys*. The portion preserved is consistent with that seen in other bothremydids.

The posterolaterally extended quadrate processus in *Kurmademys* is narrower and longer than in Euraxemydidae, *Araripemys*, pelomedusids, and chelids. In these groups the process is relatively flat and more horizontal, while in *Kurmademys* and other bothremydids with a deep fossa pterygoidea, such as *Foxemys*, it is narrower and more vertical. This condition seems to be related to the presence of a deep fossa pterygoidea. In *Kurmademys* the fossa is shallower than in *Nigeremys* and *Foxemys*, but it covers a larger area. Its margins are not as well defined in *Kurmademys* as they are in those taxa. There is no development of an overhang of this depression by the pterygoid, as in the cavum pterygoidei of the Podocnemididae.

The foramen posterius canalis carotici interni in *Kurmademys* lies entirely within the basisphenoid; the pterygoid does not participate in its formation, as it does in many other bothremydids (fig. 63). The *Kurmademys* condition is unique within Pelomedusoides. The posterior margin of the pterygoid contacts the narrowly exposed prootic between the basisphenoid and quadrate contacts.

Contacts on dorsal surface: The anterior contacts of the pterygoid at the base of the processus trochlearis pterygoidei are visible on both sides of ISI R152. The pterygoid plus the palatine and jugal form the postorbital wall, as exposed posteriorly in the adductor muscle chamber. The pterygoid has a very narrow contact with the parietal medially, and broader contacts with the postorbital and with the jugal laterally (fig. 62).

The contacts of the crista pterygoidea are with the parietal dorsally, the prootic posterodorsally, and the quadrate posterolaterally.

Structures on dorsal surface: Most of the dorsal surface of the pterygoid is visible in *Kurmademys* ISI R152, although the region inside the cavum cranii is variably obscured by pieces of matrix. The crista pterygoidea is relatively low. The pterygoid forms the ventral margin of the foramen nervi trigemini, as in other bothremydids, but the foramen is not placed very close to the foramen stapedio-temporale as it is in many other bothremydids, such as *Bothremys* and *Foxemys*. The pterygoid forms the floor of the sulcus palatinopterygoideus, which lies between the side wall of the cavum cranii and the septum orbitotemporale.

SUPRAOCCIPITAL (figs. 54, 57, 62)

Preservation: The supraoccipital in ISI R152 is complete ventrally and anteriorly but is missing the posterior part of the crista supraoccipitalis. The other specimens of *Kurmademys* have the anterior part of the supraoccipital but none of the crista supraoccipitalis.

Contacts: In nearly all turtles the supraoccipital has a tripartite suture, with the prootic and opisthotic visible on the dorsal surface of the otic chamber. It is unusual to find that in most bothremydids the supraoccipital contacts the quadrate and separates the prootic from the opisthotic. In *Kurmademys* this unusual condition is present. The supraoccipital on the right side has a broad contact with the quadrate laterally and separates the prootic from the opisthotic. On the left side the supraoccipital is complete and separates the prootic and opisthotic, but the quadrate is damaged. *Sankuchemys* is not clear in this area, but the tribes Cearachelyini and Bothremydini (except *Zolhafah*) have the contact between the quadrate and supraoccipital.

Structures: The crista supraoccipitalis is usually relatively short in bothremydids. In *Kurmademys* it is broken posteriorly and its length is indeterminate.

EXOCCIPITAL (figs. 54, 57, 64)

Preservation: In ISI R152 both exoccipitals are preserved but both lack the condylus occipitalis. There is also some breakage around the foramen jugulare posterius. In ISI R158, ISI R155A, and ISI R159 the condylus occipitalis is also broken off, but in ISI R155B (fig. 59C, D) the condylus occipitalis is preserved.

Contacts: The exoccipital contacts the supraoccipital dorsally, the opisthotic dorsolaterally, the quadrate ventrolaterally, and the basioccipital ventrally. The quadrate-exoccipital contact occurs in all Bothremydidae and is absent in other pleurodires.

Structures: Dorsomedially the exoccipital forms the lateral and ventral margins of the foramen magnum. The condylus occipitalis is formed by the exoccipitals and the basioccipital in *Kurmademys*, as seen in ISI R155B. *Kurmademys* is the only bothremydid to have this condition, although the basioccipital enters the neck of the condylus in *Cearachelys* and *Galianemys*. Close examination of ISI R155B (fig. 59C, D) shows that it is a small individual, compared to ISI R152, and that it may be a juvenile. As preserved, the condyle itself is slightly disarticulated along the sutures and the articular surface is not completely finished, suggesting that it may have had some cartilage as a component. The adult condyle may have had less or no basisphenoid contribution to the condyle in *Kurmademys*. Nonetheless, it is scored in the dataset as having a basioccipital contribution to the condyle, because that is the way it is preserved in the only specimen in which it can be seen.

The foramen jugulare posterius in *Kurmademys* is formed entirely by the exoccipital. The bone surrounds most of the foramen, but on each side of ISI R152 the foramen is open laterally due to the presence of a narrow fissure. This fissure is different in shape on

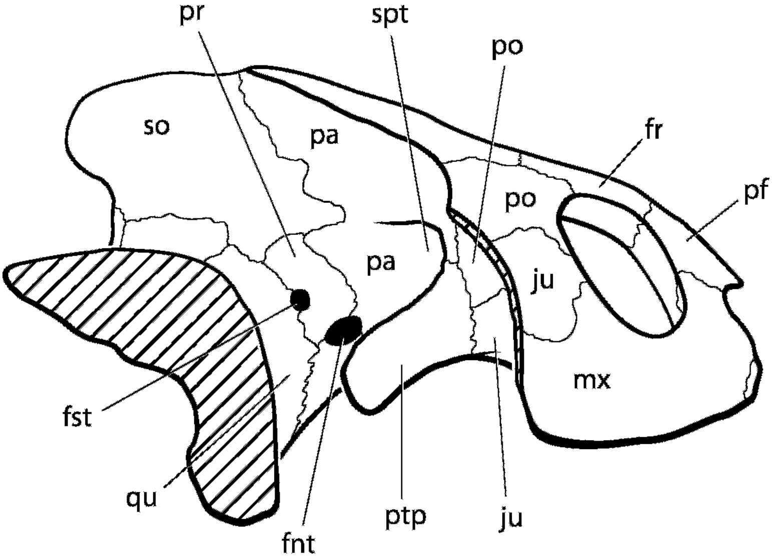

Fig. 62. *Kurmademys kallamedensis* Gaffney, Chatterjee, and Rudra, 2001. Partially restored parasagittal section based on the intact skull of ISI R152 holotype. [A. Venjara, del.]

the two sides due to breakage. The foramen is enclosed by the exoccipital in ISI R155B, ISI R155A, and ISI R159. *Kurmademys* has two foramina nervi hypoglossi, as in all other Pelomedusoides. They lie near the base of the condylus occipitalis, ventrolateral to the foramen magnum. The more dorsal foramen is formed entirely within the exoccipital, but the more ventral one is formed in the exoccipital-basioccipital suture.

Basioccipital (figs. 54, 57, 64)

Preservation: The basioccipital in ISI R152 is nearly complete except for the condylus occipitalis. A small amount of breakage is visible on each tuberculum

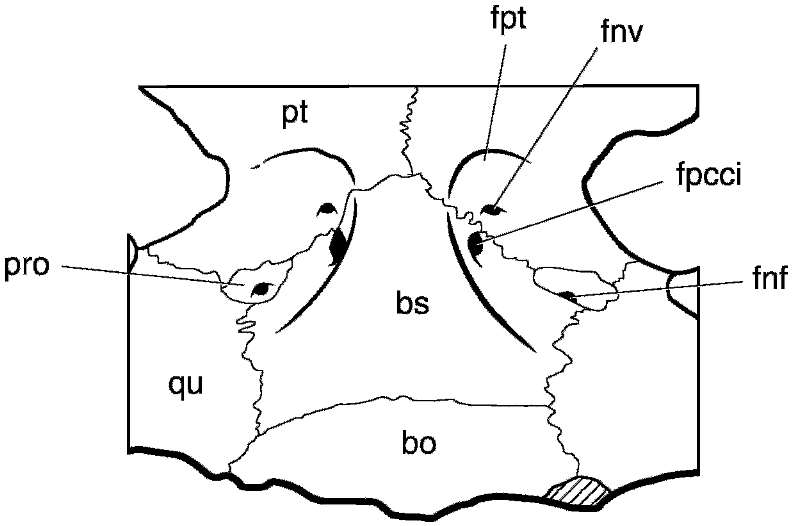

Fig. 63. *Kurmademys kallamedensis* Gaffney, Chatterjee, and Rudra, 2001. ISI R152 holotype. Ventral view of basicranium showing foramen posterius canalis carotici interni and associated structures. [A. Venjara, del.]

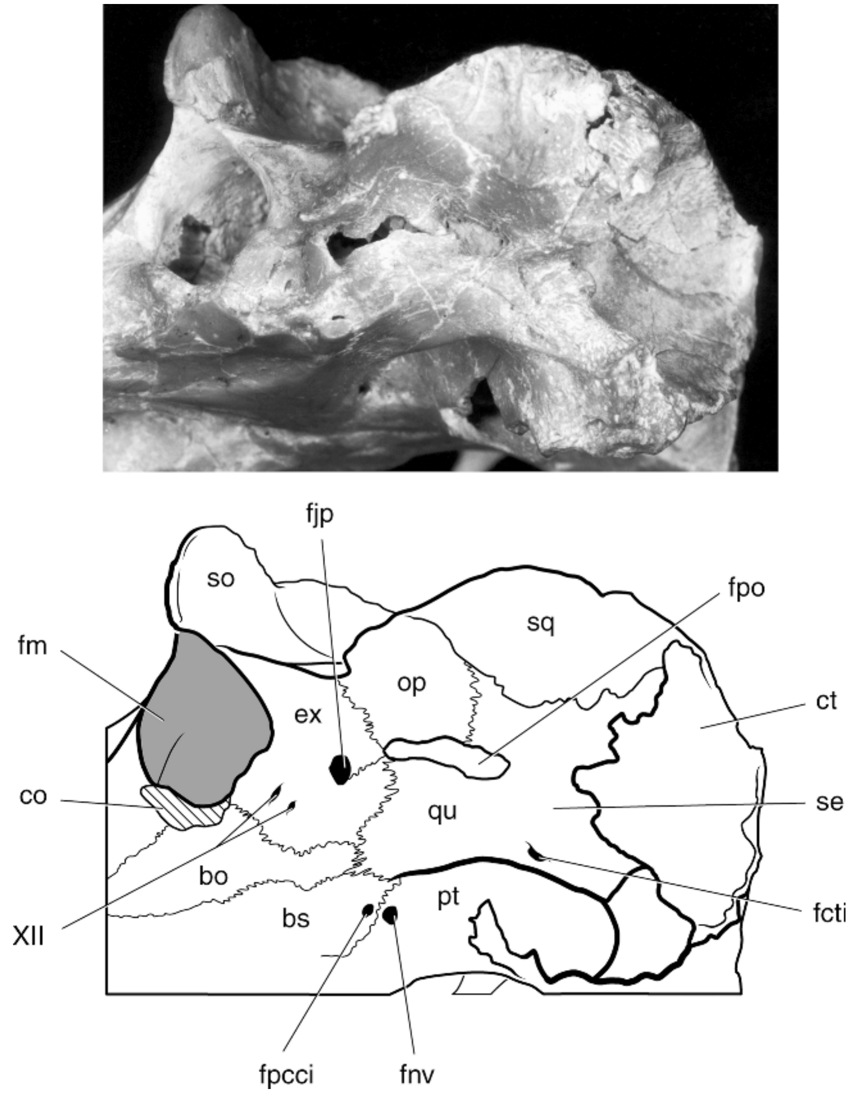

Fig. 64. *Kurmademys kallamedensis* Gaffney, Chatterjee, and Rudra, 2001. ISI R152 holotype. Posterior oblique view reversed from left side. Drawing restores breakage seen in ISI R152 from ISI R155A, ISI R155B, and ISI R159. [E.S. Gaffney and A. Venjara, del.]

basioccipitale, and the broken condylus occipitalis does not clearly show basioccipital sutures. The basioccipital of ISI R155B is complete. In ISI R159 the basioccipital seems to have the condylus occipitalis component, but the exoccipitals are missing so the presence of the basioccipital in the condyle articular surface is not determinable. ISI R158 has only a small part of the basioccipital, while ISI R155A is missing only the condyle.

Contacts: The basioccipital of *Kurmademys* has a broad, transverse contact with the basisphenoid anteriorly. Laterally the basioccipital contacts the quadrate, and posterodorsally there is a broad contact with the exoccipitals.

Structures: The tuberculum basioccipitale is formed about equally by the quadrate and exoccipital. A shallow, median concavity lies between the paired tuberculae and is formed almost entirely by the basioccipital.

(See Exoccipital above for condylus occipitalis discussion.)

PROOTIC (figs. 54, 57, 62–64)

Preservation: Both prootics in ISI R152 are preserved; the right one is nearly complete and the left one has a partially eroded dorsal surface. The prootics are present in ISI R155A, ISI R155B, and ISI R159, but only fragments of them are preserved in ISI R158.

Contacts: The prootic is exposed on the dorsal and anterior surface of the otic chamber with the following contacts: the parietal medially, the quadrate laterally, the supraoccipital posteriorly, and the pterygoid ventrally. There is no prootic-opisthotic contact in *Kurmademys*.

Structures: The foramen stapedio-temporale in *Kurmademys* is formed in the prootic-quadrate suture. In contrast to all other bothremydids, the foramen opens anterodorsally rather than anteriorly. It is visible in dorsal view in *Kurmademys*, but in other bothremydids it is barely or not visible in dorsal view. The position of the foramen stapedio-temporale in *Kurmademys* is very similar to that in pelomedusids and chelids.

The foramen nervi trigemini is formed by the prootic dorsolaterally, the parietal dorsomedially, and the pterygoid ventrally. The foramen is best preserved on the right side of ISI R152; the left foramen nervi trigemini is larger due to broken edges.

On the ventral surface, the prootic is exposed where the pterygoid, basisphenoid, and quadrate meet (fig. 63). This is particularly visible in ISI R159, ISI R155A, and ISI R152. This is in the deepest part of the fossa pterygoidea, presumed to be for the pterygoideus muscle attachment. The prootic has a distinct foramen, the foramen nervi facialis (VII), for the facial nerve, usually associated with the prootic ossification in tetrapods. The primitive condition of the ventral prootic exposure occurs in chelids, pelomedusids, and *Araripemys*, all of which have a large prootic exposure with the foramen posterius canalis carotici interni in the prootic. In all bothremydids, podocnemidids, and euraxemydids, the prootic does not form the entry into the skull of the internal carotid artery (i.e., the foramen posterius canalis carotici interni) as it does in chelids and pelomedusids. In euraxemydids the prootic is partially exposed in a narrow space between the basisphenoid and quadrate, similar to the primitive position found in chelids and pelomedusids, but it is distinctly posterior to the position of the prootic as exposed in *Kurmademys*, *Galianemys emringeri*, *Sankuchemys*, and *Foxemys*. It is likely that the prootic exposure in these taxa is not a retention of a primitive state, but is related to the formation of the deep fossa pterygoidea that penetrates the covering elements. This is supported by the distribution of this character (see discussion in character 68 and fig. 305).

OPISTHOTIC (figs. 54, 57, 64)

Preservation: Both opisthotics are preserved in ISI R152; the right one is nearly complete and the left one is missing a small part anteriorly. Opisthotics are represented only by fragments and damaged areas in ISI R155B and ISI R158. In ISI R155A and ISI R159 the opisthotics are damaged and incomplete, but both provide useful information about the fenestra postotica.

Contacts: In dorsal view, the opisthotic of *Kurmademys* has these contacts: supraoccipital anteromedially, squamosal laterally, quadrate anterolaterally, and exoccipital posteromedially. There is no prootic-opisthotic contact. In ventral view the opisthotic contacts the quadrate laterally and ventrally.

Structures: Further preparation of ISI R155A and ISI R159 shows that the original description of ISI R152 in Gaffney, Chatterjee, and Rudra (2001: 14) was in error in describing subdivisions of the fenestra postotica. These are now interpreted as the result of postmortem crushing and loss of bone. The fenestra postotica is not subdivided (fig. 64, line drawing restored) but is closed. This is in contrast to the Cearachelyini and in agreement with the Bothremydini and Taphrosphyini. The *Sankuchemys* condition is not known.

BASISPHENOID (figs. 54, 57, 63)

Preservation: The basisphenoid is complete and well preserved in ISI R152. The cavum cranii is largely free of matrix, and some of the dorsal surface of the basisphenoid is visible. The basisphenoid is also present in ISI R155A, ISI R155B, ISI R158, and ISI R159.

Contacts on ventral surface: The basisphenoid in *Kurmademys* is not strongly triangular, as in other bothremydids, but is more pentagonal. It is a relatively large element, wider than long. The anterior contact with the pterygoids trends posterolaterally and anteromedially, and the angle that this suture makes with the midline is similar to that in *Foxemys* and *Zolhafah*. A short contact with the prootic is at the anterolateral corner of the basisphenoid, between the pterygoid and quadrate contacts. In most bothremydids, except *Galianemys emringeri*, *Foxemys*, and *Sankuchemys*, the prootic is covered, so this contact is unusual (see Prootic). The lateral margin of the basisphenoid is a long, parasagittal contact with the quadrate. This contact in *Kurmademys* is longer than in any other bothremydid; *Foxemys* and *Polysternon* most closely approach it. Posteriorly the basisphenoid has a transverse contact with the basioccipital.

Structures on ventral surface: In contrast to all other bothremydids, in *Kurmademys* the foramen posterius canalis carotici interni is completely formed by the basisphenoid, without participation of the pterygoid (fig. 63). However, the foramen is very close to the pterygoid suture, particularly on the right side. The foramen posterius canalis carotici interni in *Kurmademys* is also placed farther anteromedially than in any other bothremydid. This could be explained morphologically by a reduced ossification of the canalis caroticus internus posteriorly due to a deep fossa pterygoidea. The canalis in all bothremydids travels anteromedially and slightly dorsally to enter the sella turcica. If the canalis in a form like *Bothremys* (which has the foramen posterius canalis carotici interni placed far posterolaterally) were to be exposed by the removal of bone ventrally, the foramen would appear to migrate anteromedially along the path of the canalis caroticus internus. It is possible that this condition could result from the development of a deep pterygoideus muscle concavity, the fossa pterygoidea, which is formed directly ventral to the canalis caroticus internus. Contrary to this explanation is the fact that while *Kurmademys* has a distinct fossa pterygoidea, it is relatively shallow compared to such forms as *Foxemys* and *Galianemys emringeri*, and these taxa do not have the foramen posterius canalis carotici interni placed anteromedially in the basisphenoid.

Contacts on dorsal surface: In *Kurmademys* the basisphenoid contacts the pterygoid anterolaterally, the prootic laterally, the palatines anteriorly, and the basioccipital posteriorly, as in all turtles.

Structures on dorsal surface: The dorsal surface of the basisphenoid in *Kurmademys* is visible in ISI R152 and ISI R159, showing the dorsum sellae and sella turcica. The dorsum sellae overhangs the sella turcica so that the foramen anterius canalis carotici interni is also hidden in dorsal view at the posterolateral corner of the sella turcica. There is a small processus clinoideus. The shape and general proportions of the dorsum sellae and sella turcica are similar to those in *Pelusios*. The degree of overhang of the dorsum sellae, however, is greater in *Kurmademys* than it is in *Pelusios*. The rostrum basisphenoidale is fused into a single structure, but its anterior end shows two ossified trabeculae rather than the single rostrum seen in *Pelusios*. There is no sign of a foramen nervi vidiani in the left sulcus cavernosus.

Sankuchemys sethnai

The single skull of *Sankuchemys* is badly crushed dorsoventrally obscuring the cavum tympani and occipital features but showing the skull roof and palate. Although cracked, sutures are generally clear. Nonetheless, this is the most poorly known skull taxon in the core dataset. The skull was described by Gaffney et al. (2003) and that description is modified and incorporated here. *Sankuchemys* is the sister taxon to *Kurmademys*, and they make up the tribe Kurmademydini.

PREFRONTAL (figs. 65, 67)

Preservation: Both prefrontals are present but dorsoventrally crushed, disarticulated, and overlain laterally by the maxillae. The anterior margin is a broken edge so that no anterior projection is preserved.

Contacts: As preserved, the midline prefrontal contact and the posterior frontal

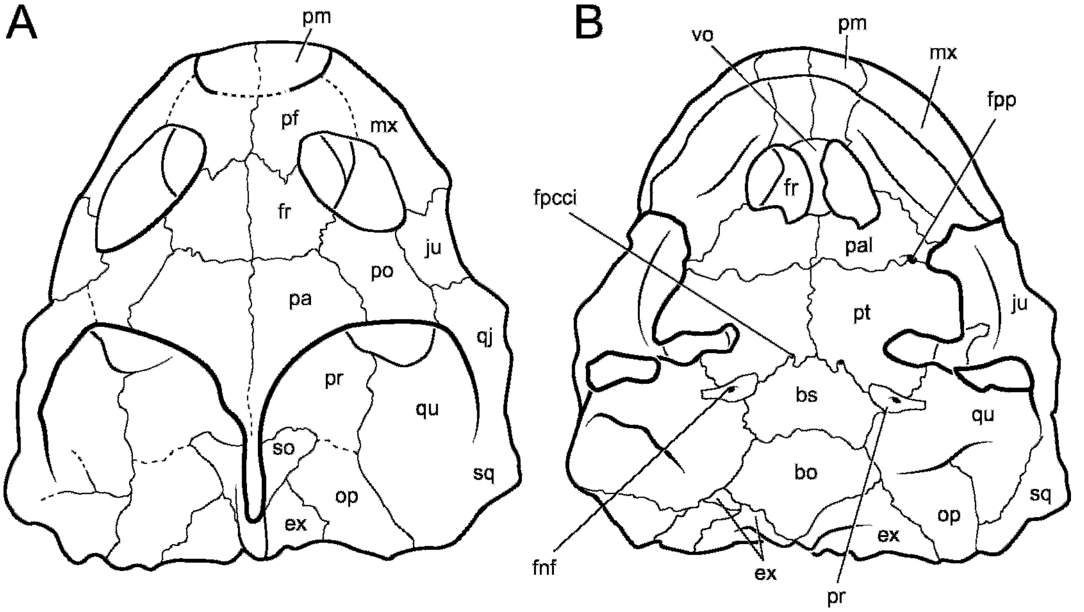

Fig. 65. *Sankuchemys sethnai* Gaffney, Sahni, Schleich, Singh, and Srivastava, 2003. Partially restored skull based on SDS/VPL 1125 holotype. **A**, dorsal; **B**, ventral. [A.M. Phillips, del.]

contacts are intact. The ventrolateral contact with the maxilla is displaced but was clearly present.

Structures: The dorsal margin of the apertura narium externa and anterodorsal margin of the orbit are formed by the prefrontal, as in other Bothremydidae. The foramen orbitonasale contribution is not visible.

FRONTAL (figs. 65, 67)

Preservation: Both frontals are present and fractured but complete. Part of the ventral surface is visible.

Contacts: As in other bothremydids, the frontal of *Sankuchemys* contacts the other frontal medially, the prefrontal anteriorly, the postorbital posterolaterally, and the parietal posteriorly.

Structures: The degree of frontal exposure in the orbit is about the same as in *Kurmademys* and *Galianemys*. The sulcus olfactorius is visible on the ventral surface.

PARIETAL (figs. 65, 67)

Preservation: Both parietals are present, but they are cracked and crushed ventrally, completely disintegrating the processus parietalis inferior.

Contacts of dorsal plate: As in *Kurmademys* and *Galianemys*, the parietal of *Sankuchemys* contacts the other parietal medially, the frontal anteriorly, and the postorbital laterally. Although damaged, it is clear that there is no parietal-quadratojugal contact.

Structures of the dorsal plate: The extreme degree of temporal emargination with little overhang onto the otic chamber and fossa temporalis is found only in *Sankuchemys* and *Kurmademys*, within the Bothremydidae. The dorsal plate of the parietal is very similar in these genera, but the parietal seems to be slightly more emarginate in *Sankuchemys*.

Contacts and structures of processus inferior parietalis: This structure is crushed and not visible in *Sankuchemys*.

JUGAL (figs. 65, 67)

Preservation: Both jugals are present in *Sankuchemys*, but they are cracked and displaced from their original articulations, so that the relations of the medial process are ambiguous.

Contacts of lateral plate: The jugal of *Sankuchemys* contacts the maxilla anteriorly, the postorbital dorsomedially, and the quadratojugal posteriorly.

Structures of the lateral plate: The jugal enters the posteroventral margin of the orbit as in *Kurmademys*. As preserved, the jugal in SDS/VPL 1125 is exposed on the skull margin, preventing the maxilla-quadratojugal contact seen in *Kurmademys*. However, the jugal margin is a broken edge, and originally there may have been a quadratojugal-maxilla contact.

Structures and contacts of medial process: Although part of the jugal is identifiable on the ventral surface, the relations and limits of the jugal are unclear. Enough of the triturating surface is preserved to show that the jugal does not form a significant part of it as in the tribe Bothremydini.

QUADRATOJUGAL (figs. 65, 67)

Preservation: At least portions of both quadratojugals are present in SDS/VPL 1125, although they are badly broken due to crushing and their limits are unclear laterally and posteriorly.

Contacts: The quadratojugal in *Sankuchemys* contacts the jugal anteriorly and the postorbital anteromedially. As preserved the quadratojugal does not contact the maxilla (see Jugal), but this may be due to breakage. Quadrate and squamosal contacts, although almost certainly present, are obscured by breakage.

Structures: The quadratojugal forms the lateral margin of the temporal emargination. Its exposure on the cheek is too deformed to determine.

SQUAMOSAL (figs. 65, 67)

Preservation: At least part of both squamosals are present, but they are poorly preserved.

Contacts: The anteromedial contact with the quadrate and opisthotic is visible on the ventral surface. The quadratojugal contact is likely but is in a badly damaged area of the skull.

Structures: Due to the complete obliteration of the cavum tympani, the antrum postoticum is indeterminate. Any crest or process on the squamosal is also indeterminate.

POSTORBITAL (figs. 65, 67)

Preservation: The postorbitals are present on both sides but are badly fractured. Most of the dorsal surface contacts can be determined, but the medial process is completely obscured.

Contacts of lateral plate: The postorbital contacts the frontal anteromedially, the parietal posteromedially, the jugal anterolaterally, and the quadratojugal posterolaterally, as in *Kurmademys*.

Structures of lateral plate: The postorbital widely enters the orbit forming its posterior margin. It enters the temporal emargination posteriorly. The size and relations of the postorbital in *Sankuchemys* are very similar to those in *Kurmademys*. Among the Bothremydidae, the postorbital in *Sankuchemys* and *Kurmademys* is the shortest, close to the small size of the bone in the Pelomedusidae.

Contacts and structures of medial process: The presence of a medial postorbital process in *Sankuchemys* is not determinable, but the skull is thicker in this area, and there are bone fragments in the right place.

PREMAXILLA (figs. 65, 67)

Preservation: Both premaxillae are present and relatively well preserved.

Contacts: The contacts of the premaxilla in *Sankuchemys* in ventral view are with the maxilla laterally, the other premaxilla medially, and the vomer posteromedially, as in other Bothremydidae. Contacts on the dorsal surface are not visible.

Structures in dorsal view: The premaxilla in *Sankuchemys* forms the anterior margin of the apertura narium externa and the floor of the fossa nasalis, as in other Bothremydidae. The area is damaged and details are not visible. A prominent anterior premaxillary extension, however, can be ruled out.

Structures in ventral view: The labial ridge on the premaxilla in *Sankuchemys* is acute with a sharp ridge, as in *Kurmademys*, but it is thicker dorsally. The size of the premaxillary posterior shelf bearing the triturating surface is nearly the same in both genera, but *Kurmademys* has a deep median concavity absent in *Sankuchemys*.

MAXILLA (figs. 65, 67)

Preservation: Most of both maxillae are preserved in *Sankuchemys*, but there is

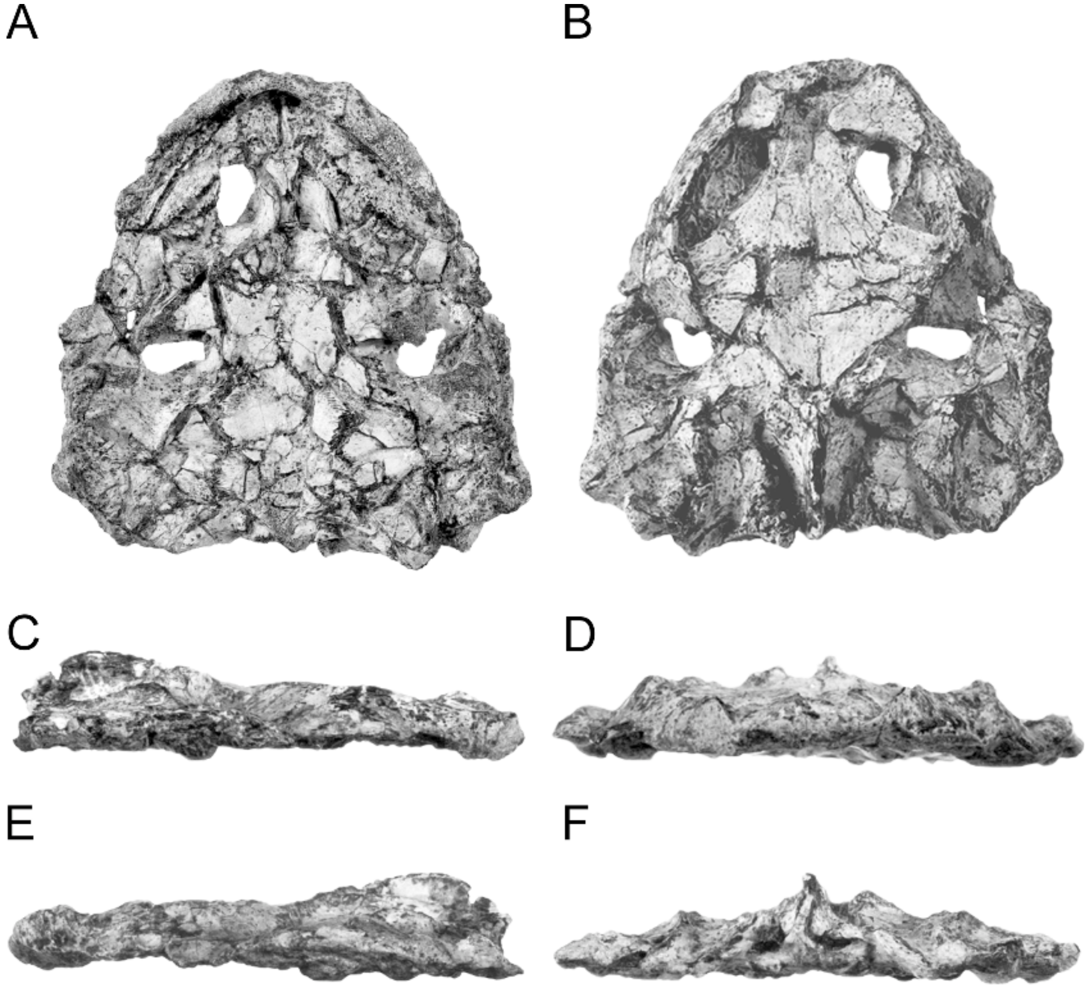

Fig. 66. *Sankuchemys sethnai* Gaffney, Sahni, Schleich, Singh, and Srivastava, 2003. SDS/VPL 1125 holotype. **A**, dorsal; **B**, ventral; **C**, right lateral; **D**, anterior; **E**, left lateral; **F**, posterior (from Gaffney, Sahni, Schleich, Singh, and Srivastava, 2003). [E. Heck, del.]

considerable damage due to crushing. The right lateral margin is a broken edge.

Contacts of vertical plate: Seen in dorsal view, the external surface of the maxilla in *Sankuchemys* contacts the premaxilla anteriorly, the prefrontal anterodorsally, and the jugal posteriorly, as in other Bothremydini. The posterior limits of the maxilla are damaged and a quadratojugal contact (see Jugal) may have been present.

Structures of vertical plate: The dorsal process of the maxilla seems complete on the right side and it forms the apertura narium externa margin anteriorly and the orbital margin posteriorly, as in all other bothremydids.

Contacts of horizontal plate: In ventral view the maxilla of *Sankuchemys* contacts the premaxilla anteromedially, the palatine posteromedially, and the jugal posteriorly, although the suture with the latter is unclear. As preserved, there is no vomer contact and the area seems well enough preserved for this to be original. The region of jugal contact with the palatine and pterygoid is a mush on both sides and undecipherable at least without something stronger to drink than cocoa.

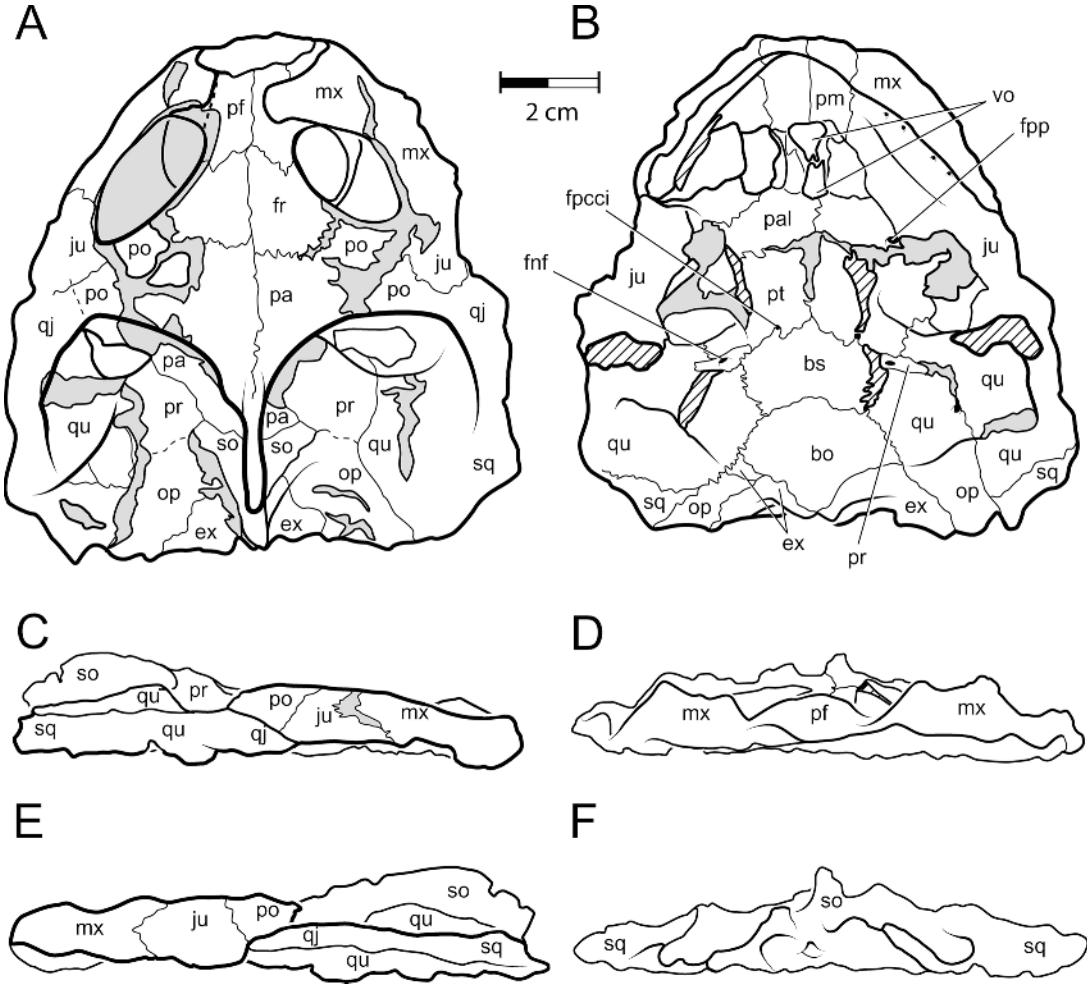

Fig. 67. *Sankuchemys sethnai* Gaffney, Sahni, Schleich, Singh, and Srivastava, 2003. SDS/VPL 1125 holotype. **A**, dorsal; **B**, ventral; **C**, right lateral; **D**, anterior; **E**, left lateral; **F**, posterior (from Gaffney, Sahni, Schleich, Singh, and Srivastava, 2003). [E. Heck, del.]

Structures of horizontal plate: The maxilla of *Sankuchemys* differs from *Kurmademys*, *Cearachelys*, and *Bothremys* in having a more parallel-sided triturating surface, rather than a triangular one, expanded posteriorly. The labial ridge is acute and sharp, as in *Kurmademys* and *Cearachelys*, but appears thicker dorsally, although this could be caused by crushing. The medial edge of the triturating surface is not particularly well preserved, but the posterior expansion seen in *Kurmademys* and *Cearachelys* seems to be absent. It is possible that this is a consequence of the poor preservation as the lingual ridge marking the triturating surface edge is very low. However, *Sankuchemys* does have a more expanded anterior part of the triturating surface than do other bothremydids and this is not preservational. The triturating surface of *Sankuchemys* has an accessory ridge paralleling the labial ridge and extending the complete length of the maxilla. This ridge is much lower than the labial ridge, and its height is constant along its length. It seems to begin on the premaxilla in a rugose area and runs to the maxilla-jugal suture. In addition to *Sankuchemys,* only some specimens of *Foxemys* among bothremydids have an accessory ridge on the triturating surface, although such a ridge does occur often in podocnemidids (i.e., *Podocnemis*, *Dacquemys*).

VOMER (figs. 65, 67)

Preservation: A well-preserved, although fractured, vomer is present in SDS/VPL 1125. It is visible only ventrally.

Contacts: The vomer in *Sankuchemys* contacts the premaxilla anteriorly and the palatines posteriorly. The vomer is not known in *Kurmademys*, but *Cearachelys* has the same contacts.

Structures: The vomer of *Sankuchemys* separates the paired, oval apertura narium interna, which are about the same size as in *Cearachelys*.

PALATINE (figs. 65, 67)

Preservation: At least some of both palatines are preserved in *Sankuchemys*, but these thin bones are badly fractured due to crushing.

Contacts: The palatine in *Sankuchemys* contacts the vomer anteromedially, the other palatine medially, the pterygoid posteriorly, and the maxilla anterolaterally, as in other Bothremydidae.

Structures on the dorsal surface: Only a small part of the dorsal palatine surface is visible in the orbital opening on the right side of SDS/VPL 1125. The complete crushing of this skull precludes information about the sulcus palatinopterygoideus and foramen orbitonasale.

Structures on the ventral surface: The palatine in *Sankuchemys* agrees with that of *Kurmademys* except for one feature. It does not extend anterolaterally to form part of the triturating surface, as it does in *Kurmademys* and *Cearachelys*. The area is well enough preserved to conclude that this is not due to damage or postmortem changes. A small part of the foramen palatinum posterius is present on the left palatine. It is consistent in size and position with that foramen in *Kurmademys*.

QUADRATE (figs. 65, 67)

Preservation: Both quadrates are present in SDS/VPL 1125, but they are so badly crushed dorsoventrally that the presence of a cavum tympani can only be inferred, not observed. The ventral surface of the quadrate is better preserved than the badly fractured dorsal surface.

Contacts and structures in lateral view: On the left side in lateral view there is a thin layer of matrix representing the crushed cavum tympani. As preserved, the quadrate lacks an anterior process contacting the maxilla, and the size of the jugal suggests this was originally the case as well.

Contacts in dorsal view: In dorsal view the contacts of the quadrate in *Sankuchemys* include the prootic anteromedially and the opisthotic posteromedially. Many of the sutures are obscured by breakage. The quadrate-supraoccipital contact is indeterminate.

Structures in dorsal view: The foramen stapedio-temporale is not identifiable in SDS/VPL 1125. Some of the quadrate-prootic suture is identifiable, but not enough to be sure of the position of the foramen.

Contacts in posterior and ventral view: The quadrate in *Sankuchemys* contacts the pterygoid anteromedially, the basisphenoid medially, and the basioccipital posteromedially, all contacts found in *Kurmademys* and *Cearachelys* as well. The quadrate also contacts the exoccipital as in all other bothremydids. The opisthotic contact is visible but badly obscured by crushing. Posterolaterally the squamosal contact is also visible but badly damaged. The prootic is exposed on the ventral surface (see Prootic) and the quadrate contacts it between the pterygoid and basisphenoid.

Structures in posterior and ventral view: The condylus mandibularis has been crushed, but it does not seem to have been moved significantly from its original position. The condylus mandibularis is located well anterior to the condylus occipitalis in *Sankuchemys*, as it is in *Kurmademys*, and not as far posterior as it is in *Cearachelys*. A fossa pterygoidea may have been present (see Pterygoid).

PTERYGOID (figs. 65, 67)

Preservation: Both pterygoids are present but badly fractured. Only their ventral surface is visible.

Contacts on ventral surface: The pterygoid in *Sankuchemys* contacts the palatine anteriorly, the quadrate posterolaterally, the other pterygoid medially, and the basisphenoid posteromedially, as in both *Kurmad-*

emys and *Cearachelys*. There is also a contact with the prootic posteriorly between the quadrate and basisphenoid (see Prootic), as in *Kurmademys*.

Structures on ventral surface: The processus trochlearis pterygoidei is partially preserved on both sides and appears to be directed laterally at nearly right angles to the midline, much as in *Kurmademys* and *Cearachelys*. The quadrate ramus is defined by sutures on both pterygoids but is badly fractured. The question of the presence of a deep fossa pterygoidea as found in *Kurmademys* cannot be answered definitely for *Sankuchemys* due to poor preservation. However, there is some evidence that one was present. The prootic surface on the right side (see Prootic) seems to be crushed, and the quadrate ramus of the pterygoid that is continuous with the prootic here forms a curved surface that, if restored, seems to be the lateral wall of a depression similar in depth to that in *Kurmademys*. Thus, even though in its present condition there is no concavity in *Sankuchemys*, it is likely that the fossa pterygoidea was present.

The position of the foramen posterius canalis carotici interni is also not definite in *Sankuchemys*, although the damaged remnants of the foramen margin can be seen on both sides. The foramen appears to be formed by pterygoid anteriorly and basisphenoid posteriorly. On the better preserved right side, the foramen posterius canalis carotici interni lies at the edge of a distinct dorsally curved surface of the pterygoid. This is further evidence of a fossa pterygoidea with the foramen in its anterior wall. On the right side the posterior or dorsal margin of the foramen seems to be formed by the basisphenoid, but the area is badly fractured and it could be prootic. However, on the left side, there seems to be a posterodorsal margin for the foramen that is formed in the basisphenoid. Due to crushing the left pterygoid has little evidence of a depression, and the pterygoid margin of the foramen posterius canalis carotici interni is damaged.

The area where the foramen palatinum posterius would be expected is badly broken on both sides. However, a margin of the foramen is present on the right palatine, and the pterygoid margin as preserved is consistent with this.

Contacts and structures on dorsal surface: The dorsal surface of the pterygoid in SDS/VPL 1125 is not visible.

Supraoccipital (figs. 65, 67)

Preservation: The supraoccipital is present in *Sankuchemys* and is relatively well preserved compared with the rest of the awful mess. The crista supraoccipitalis is partially preserved with its main surface still vertical. Its dorsal and posterior edges are broken.

Contacts: The laterally expanded base of the supraoccipital shows a clear anterior suture with the parietal on both sides. Posterolaterally the exoccipital suture can be made out on the left side. Laterally on both sides the more anterior prootic and more posterior opisthotic sutures are discernable but not definitive. There are a number of broken areas that could represent these sutures. The systematically important sutures that define the lateral lappet of the supraoccipital that contacts the quadrate seem to be absent, however, this is not certain.

Structures: The crista supraoccipitalis is present but badly broken, and its height and depth cannot be determined.

Exoccipital (figs. 65, 67)

Preservation: Both exoccipitals are present but crushed, although they retain enough three-dimensionality to allow some definition of the foramen magnum. On the dorsal surface the exoccipital has the usual contacts: supraoccipital dorsally, opisthotic laterally, quadrate ventrolaterally, and basioccipital ventromedially.

Structures: The foramen magnum margins are visible and, although broken, the base of the condylus occipitalis is present on both sides. The basioccipital is sufficiently preserved that it is possible to determine that the condylus is formed only by the exoccipitals. Parts of the medial margins of the foramen jugulare posterius are identifiable, but whether it was closed is not determinable. No foramen nervi hypoglossi is visible.

Basioccipital (figs. 65, 67)

Preservation: The basioccipital in SDS/VPL 1125 is broken but mostly intact with relatively clear sutures. The condylus occipitalis is eroded.

Contacts: The basioccipital in *Sankuchemys* contacts the basisphenoid anteriorly, the quadrate laterally, and the exoccipitals posterolaterally, all as in *Kurmademys* and other bothremydids.

Structures: The condylus occipitalis is not well preserved, but the posterior end of the basioccipital pinches out before entering what seems to be the articular surface of the condylus occipitalis. There is evidence of a low tuberculum basioccipitale, possibly developed to the extent seen in *Kurmademys*. There is no evidence of a median concavity, but one could have been present. As preserved, the basioccipital in *Sankuchemys* is slightly longer than in *Kurmademys*, relative to its width.

PROOTIC (figs. 65, 67)

Preservation: The dorsal surfaces of both prootics are broken but visible, with some sutures. Nonetheless, interpretation is difficult due to extensive cracking and smushing of bone. The ventral exposures are better preserved, but there is fracturing of both bones.

Contacts: As exposed in ventral view the prootic in *Sankuchemys* is a narrow, oval bone contacting the pterygoid anterolaterally, the basisphenoid medially, and the quadrate posterolaterally. On the dorsal surface the prootic contacts the supraoccipital posteromedially and the quadrate laterally. The question of a prootic-opisthotic contact, which cannot be determined confidently, is discussed under Supraoccipital.

Structures: The ventral exposure of the prootic in *Sankuchemys* is very similar to that in *Kurmademys* in its position, shape, and extent. In *Kurmademys* this exposure seems to be related to the development of a deep fossa pterygoidea. It is possible that the extensive crushing in *Sankuchemys* (see Pterygoid, Basisphenoid) has obscured this depression. In the center of the prootic in *Sankuchemys* is the foramen nervi facialis, for the facial nerve (VII). This foramen is also exposed in other taxa that have a deep fossa pterygoidea (see character 95).

On the dorsal surface both prootics are poorly preserved. Although there is no direct evidence for a dorsally exposed foramen stapedio-temporale, it is possible that one was present. An examination of the cracks and possible sutures in this area shows no clear margins of a possible foramen on either side. Due to the ambiguous preservation, this feature, character 92, is coded as missing in the dataset. The anterior surface of the prootic where this foramen and the foramen nervi trigemini might also be expected is not visible.

OPISTHOTIC (figs. 65, 67)

Preservation: Although both opisthotics are present in *Sankuchemys*, the transformation of a complex three-dimensional object into two dimensions has not been very kind to its morphology.

Contacts: On the ventral surface of both sides these contacts are visible: quadrate anterolaterally, squamosal posterolaterally, and exoccipital posteromedially. On the dorsal surface the supraoccipital contacts the opisthotic anteromedially and the quadrate laterally. The possible prootic contact is discussed under Supraoccipital.

Structures: Few of the occipital structures and foramina can be made out in *Sankuchemys*. On the left side there is an opening that could be interpreted as the sad remains of the fenestra postotica.

BASISPHENOID (figs. 65, 67)

Preservation: The basisphenoid is present in *Sankuchemys*, but it is fractured.

Contacts: The basisphenoid in *Sankuchemys* has the usual bothremydid contacts: pterygoid anterolaterally, quadrate posterolaterally, and basioccipital posteriorly. In addition there is the short, lateral contact with the prootic, also found in *Kurmademys* and *Galianemys emringeri*. The pterygoid contact includes a short anterolateral projection, presumed to be basisphenoid, forming the posterior margin of the foramen posterius canalis carotici interni (see Pterygoid).

TRIBE CEARACHELYINI

Cearachelys placidoi

Cearachelys placidoi is represented by three skulls. THUg 1798 is complete except for parts of the palate and right cheek. BSP 1976 I 160 has a good ventral surface and occiput, but the dorsal and lateral surfaces have been damaged and lack most of the original surface. The type skull, MPSC uncataloged, lacks the snout but is otherwise well preserved. There are two morphs among these skulls (see Discussion under *Cearachelys* in the Systematic section). MPSC and THUg 1798 are smaller, with narrower labial ridges and palates; BSP 1976 I 160 is larger and has wider triturating surfaces. The restored palate in figure 69 is based on the first two skulls, and the restored palate in figure 74 is based on BSP 1976 I 160. The three-view restoration in figure 68 is based on the first two skulls as well. Two of the skulls, MPSC and THUg 1798, were described by Gaffney, Campos, and Hirayama (2001), and that description is modified and incorporated here. *Cearachelys* is most closely related to *Galianemys*, and they make up the tribe Cearachelyini.

PREFRONTAL (figs. 68, 73)

Preservation: Both prefrontals are preserved completely in THUg 1798 with clear sutures. Both prefrontals are present in BSP 1976 I 160 but are badly eroded and damaged externally. The prefrontal is missing in MPSC.

Contacts: The prefrontal in *Cearachelys* has the usual pelomedusoid contacts: maxilla anterolaterally, frontal posteriorly, and the other prefrontal medially.

Structures: The prefrontal in *Cearachelys* is similar to that bone in living Pelomedusidae, but it differs from species such as *Pelomedusa subrufa* in projecting anteriorly to a greater extent, so that the dorsal margin of the apertura narium externa is more anterior than the ventral margin. The prefrontal in *Cearachelys* is dorsally convex, rather than flat, as in some Pelomedusidae. The resultant morphology gives *Cearachelys* a prominent and projecting preorbital aspect comparable to some of the Pelomedusidae, such as *Pelusios subniger*.

The prefrontal borders the orbit laterally and the apertura narium externa anteriorly. The ventral surface of the prefrontal in *Cearachelys* is smooth, concave ventrally in its anterior portion, but it bears the parasagittal ridge for the sulcus olfactorius more posteriorly. The prefrontal sends a process ventrally along the anterior margin of the fossa orbitalis comparable in size and extent to that in the recent Pelomedusidae. It contacts the maxilla for most of its length and does not reach other elements.

FRONTAL (figs. 68, 73)

Preservation: Both frontals are preserved completely in THUg 1798 and all sutures are clear. Both are present in BSP 1976 I 160 but are damaged on their dorsal surface; sutures are visible anteriorly. The frontal is missing in MPSC.

Contacts: The frontal in *Cearachelys* is similar in size, shape, and contacts to the living Pelomedusidae. The frontal contacts are with the prefrontal anteriorly, postorbital posterolaterally, parietal posteriorly, and the other frontal medially.

Structures: Anteriorly the frontal projects on the midline to a considerable extent on the ventral surface, but only slightly on the dorsal surface. The frontal forms the well-developed sulcus olfactorius on the ventral surface. In *Cearachelys* the sulcus is very similar to that in the Pelomedusidae. The frontal in *Cearachelys* does not have a ventral process along the edge of the processus inferior parietalis, although the frontal does reach the processus, as in the Pelomedusidae.

PARIETAL (figs. 68, 73, 78)

Preservation: The parietal is preserved on both sides in THUg 1798 and the MPSC specimen, although it is not entirely complete in either skull. The parietal of *Cearachelys* is nonetheless completely known through both specimens. In BSP 1976 I 160 both parietals are present but have their dorsal surfaces damaged, as do the prefrontals and frontals in this specimen. Some of the temporal margin edges are missing, but enough is present to show its original extent.

Contacts of dorsal plate: The dorsal plate of the parietal in *Cearachelys* contacts the frontal anteriorly and is excluded from the orbit, as in other Bothremydidae and the Pelomedusidae. Laterally the parietal contacts the postorbital, but not the quadratojugal, as occurs in *Euraxemys*.

Structures of dorsal plate: The temporal emargination in *Cearachelys* is more extensive than in living Podocnemididae and *Foxemys*, but not as extensive as in Pelome-

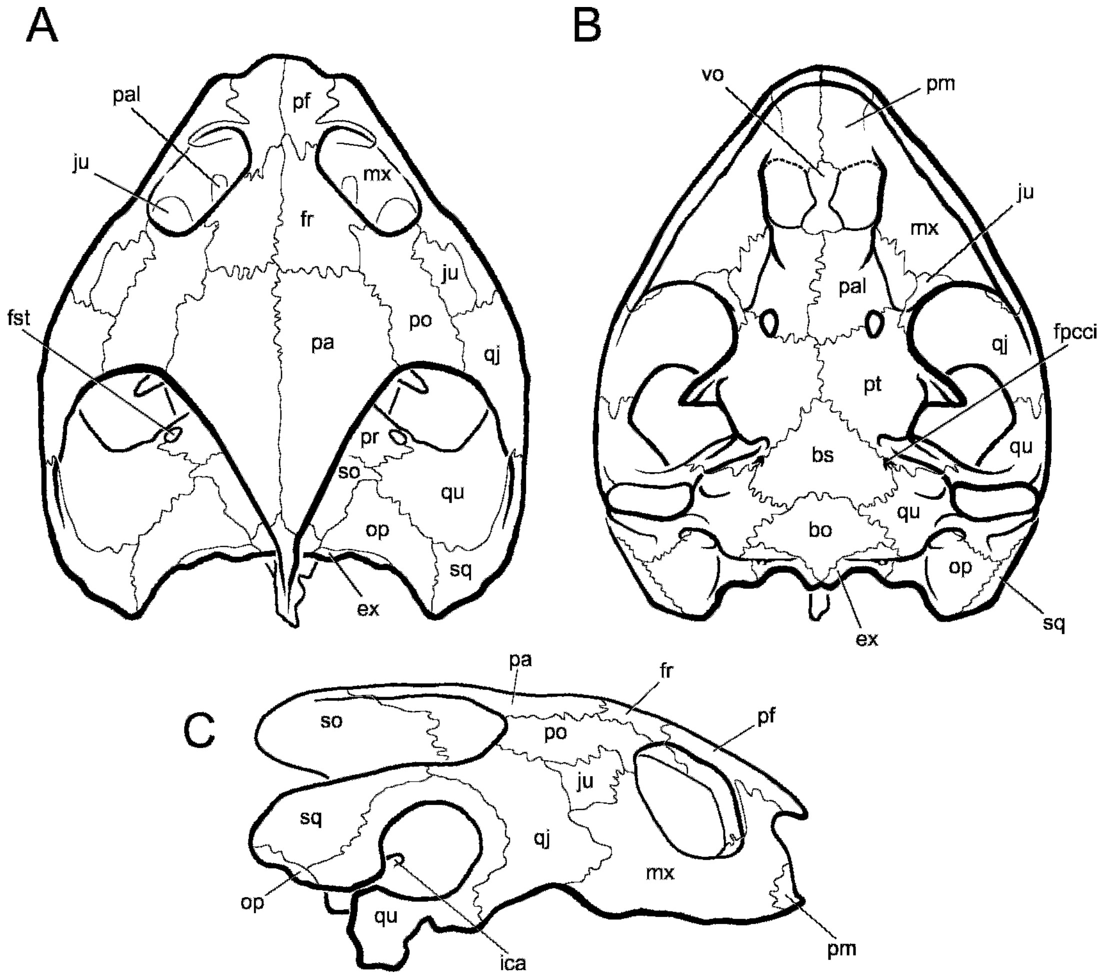

Fig. 68. *Cearachelys placidoi* Gaffney, Campos, and Hirayama, 2001. Partially restored skull based on THUg 1798 and MPSC holotype specimen. **A**, dorsal; **B**, ventral; **C**, lateral (from Gaffney, Campos, and Hirayama, 2001). See figures 276 and 277 for detailed views of basicranium and figure 283 for detailed views of quadrate. [F. Ippolito, del.]

dusidae. The otic chamber is completely uncovered, but there is a relatively long suture between the parietal and the postorbital relative to that seen in the Pelomedusidae.

Contacts of processus inferior parietalis: The ventral process of the parietal, the processus inferior parietalis, is well preserved in MPSC and THUg 1798. Anteriorly it contacts the palatine, and more posteriorly the pterygoid to form the side wall of the braincase (fig. 78). Posterior to the foramen nervi trigemini, the parietal contacts the prootic and then the supraoccipital in a suture that rises dorsally to the skull roof.

Structures of processus inferior parietalis: As in other bothremydids, the parietal of *Cearachelys* forms the anterodorsal margin of the foramen nervi trigemini, with the ventral margin formed by the pterygoid and the posterodorsal margin by the prootic.

JUGAL (figs. 68, 69, 71, 73, 77, 78)

Preservation: The jugal is preserved completely on the left side and in part on the right side of the MPSC specimen. In

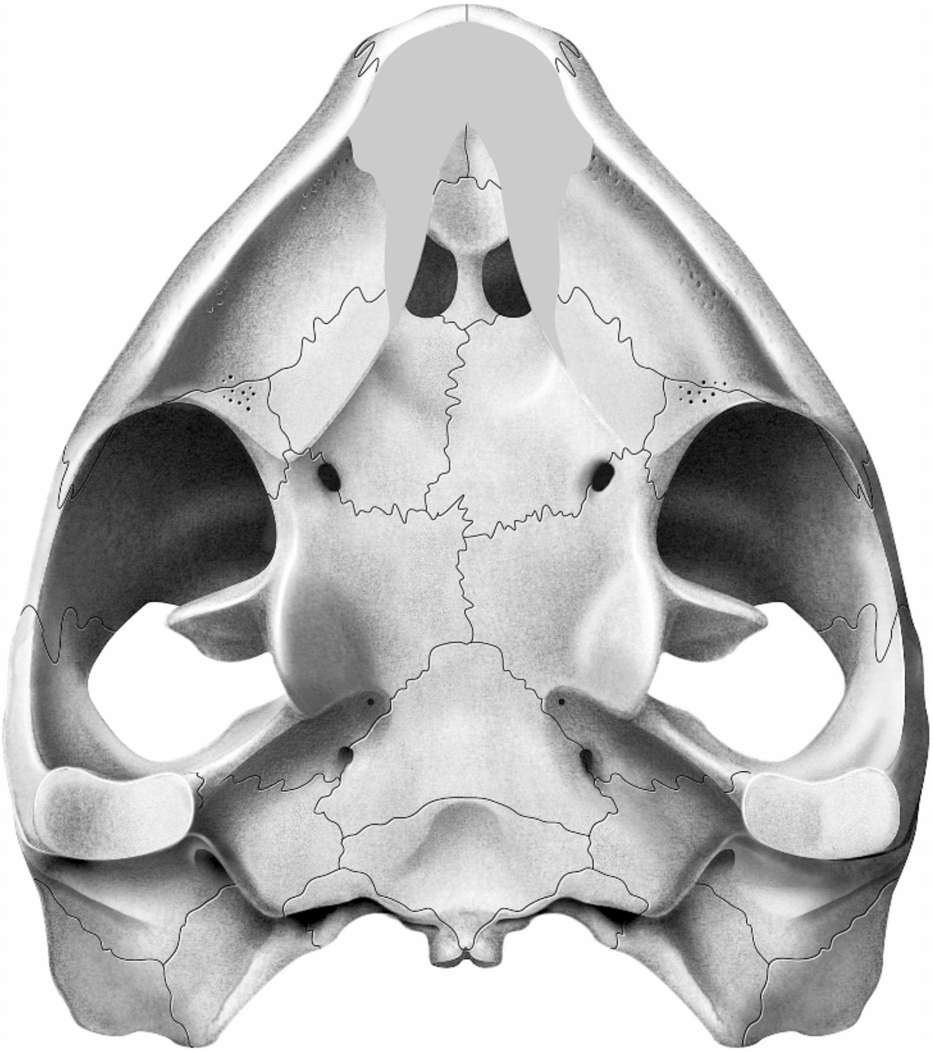

Fig. 69. *Cearachelys placidoi* Gaffney, Campos, and Hirayama, 2001. Partially restored ventral view based primarily on THUg 1798 with additions from MPSC holotype specimen. [F. Ippolito and E. Heck, del.]

THUg 1798 the left jugal is complete, but only part of the right jugal is preserved. The jugal is present on both sides of BSP 1976 I 160, but its external (lateral) surface is badly eroded. On the lateral surface of both sides the jugal-maxilla contact is visible, but the more dorsal areas are eroded. The right side is better preserved and shows the jugal entering the orbit, in contrast to the other two specimens of *Cearachelys*. However, the original orbital margin and most of the jugal, maxilla, and postorbital surfaces are broken away. The area presently exposed in BSP 1976 I 160 is actually within the fossa orbitalis, where the jugal is exposed in the other two skulls. It is not entirely clear whether the jugal was retracted from either orbital margin in BSP 1976 I 160, but the preserved morphology is nonetheless consistent with the other *Cearachelys* skulls.

Contacts of lateral plate: The jugal in *Cearachelys* contacts the maxilla anteroventrally, the postorbital dorsally, and the quadratojugal posteriorly.

Structures of lateral plate: The lateral exposure of the jugal in the tribe Cearachelyini is unusual among bothremydids in having at least some retraction of the jugal from the orbit. In *Cearachelys* the jugal lies just posterior to the orbital margin; however, in most bothremydids (except *Galianemys*) the jugal enters the orbital margin. In *Cearachelys* a very narrow process of the postorbital runs ventrally along the orbital margin to reach or nearly reach the maxilla and prevent jugal exposure (fig. 78). On the left side of the MPSC specimen there is some breakage along the orbital margin in this area, but it is clear that the postorbital contacts the maxilla in a narrow area of sutural interdigitation. In THUg 1798 both sides show the contact. *Galianemys* has a jugal that is completely retracted from the orbit with a strong postorbital-maxilla contact.

Contacts of medial process: The jugal is exposed in the floor and posterior wall of the orbit in *Cearachelys*, as in most of the Pelomedusoides. In the orbital floor the jugal contacts the postorbital dorsally and posteriorly, the maxilla laterally and anteriorly, and the palatine medially (fig. 78). The limited postorbital-maxilla contact barely separates the orbital floor exposure of the jugal from the cheek exposure of the jugal, a condition unique to *Cearachelys*. The postorbital wall of *Cearachelys* shows the jugal forming the more ventral portion, contacting the maxilla ventrolaterally, the quadratojugal laterally, the postorbital dorsally, and the pterygoid posteromedially.

Structures of medial process: Ventrally the jugal in all three *Cearachelys* is exposed to a limited extent on the triturating surface (fig. 77), similar to that seen in *Galianemys whitei* (but not *G. emringeri*).

The jugal in BSP 1976 I 160 is exposed on the triturating surface, posterior to the maxilla, lateral to the palatine, and contacting the pterygoid posteromedially. The amount of exposure in BSP 1976 I 160 is only slightly greater than in MPSC. The anterior-posterior dimension is greater in BSP 1976 I 160 than in MPSC, but the amount of jugal exposure along the margin of the temporal fossa is the same. In THUg 1798 there is about half the surface area of jugal exposed as in BSP 1976 I 160.

The jugal exposure on the triturating surface of BSP 1976 I 160 has a shallow concavity formed by the jugal and maxilla, with the jugal forming the apex of the concavity (fig. 74). It is very shallow compared with *Bothremys* or *Rosasia*, but it does have a slight ridge along the temporal fossa margin making it an enclosed concavity. Is this the ancestor of the infamous bothremydid pit? Is this animal trying to achieve exalted pitdom? I don't think so. In MPSC there is a shallower depression with a lower ridge, although the region is preserved only on the left side, and some of the maxilla is broken. In THUg 1798 the area is also only preserved on the left side and may be slightly eroded, but the depression and ridge are nearly absent.

In *Cearachelys* the jugal is widely exposed on the posterior surface of the postorbital wall, much as in *Kurmademys* and *Galianemys*.

QUADRATOJUGAL (figs. 68, 73)

Preservation: The quadratojugal is preserved on the left side of the MPSC specimen and on both sides of THUg 1798. The quadratojugal is present on both sides of BSP 1976 I 160 where it shows the anterior maxilla contact and the posterior quadrate contact as in the other *Cearachelys* skulls. The dorsal areas of both quadratojugals in BSP 1976 I 160 are broken and eroded, but the right one shows the quadratojugal reaching the squamosal and the temporal roof margin, as in the other two *Cearachelys* skulls.

Contacts: In *Cearachelys* the anterior contacts of the quadratojugal are with the maxilla anteroventrally, the jugal anterodorsally, and the postorbital dorsally. Posteriorly there is a long curved contact with the quadrate. Posterodorsally a very narrow process of the quadratojugal contacts the squamosal.

Structures: The quadratojugal of *Cearachelys* forms the posterior part of the cheek in *Cearachelys*. There is only a slight dorsal curve to the lower margin of the quadratojugal to suggest a cheek emargination; nothing like the emargination seen in the Pelomedusidae is present. The quadratojugal of *Cearachelys* extends from the anterior limit of the upper temporal emargination to the ventral margin of the cheek. In contrast to members of the Pelomedusidae, which have a well-developed cheek emargination and no quadratojugal-maxilla contact, *Cearachelys* has a broad maxilla-quadratojugal contact, as in *Galianemys*, *Kurmademys*, and the Bothremydini.

SQUAMOSAL (figs. 68, 73, 79, 283)

Preservation: Both squamosals are present and nearly complete in MPSC and THUg 1798. In BSP 1976 I 160 the right squamosal is complete, while the left one is damaged posterolaterally.

Contacts: The squamosal in *Cearachelys* contacts the quadrate anteriorly and anteromedially, the opisthotic medially, and the quadratojugal anterodorsolaterally.

Structures: The squamosal is a cone-shaped bone that sits on the posterodorsal corner of the quadrate and contains much of the antrum postoticum. The antrum of *Cearachelys* is moderately well developed relative to other Pelomedusoides (fig. 283). *Bothremys* and *Taphrosphys* have an antrum that is very small, merely an elongate canal, while the Pelomedusidae and *Kurmademys* have an antrum that is quite large. *Cearachelys* has an antrum postoticum intermediate in size between these, comparable to that in *Galianemys*.

POSTORBITAL (figs. 68, 73, 78)

Preservation: Both postorbitals are preserved in THUg 1798, but there is some damage and sutures are not entirely clear. However, by using information from both sides, the postorbital in this specimen can be fully restored. The MPSC specimen has only the left postorbital and that is missing part of its anterior edge. Most of both postorbitals in BSP 1976 I 160 are missing or only represented by internal bone surfaces attached to matrix. As preserved they agree with the two other skulls.

Contacts of lateral plate: The postorbital in *Cearachelys* contacts the frontal anteromedially, the parietal medially, the jugal ventrolaterally, and the quadratojugal posteroventrolaterally. A very narrow anteroventral process of the postorbital contacts the maxilla in the orbital margin, barely preventing jugal exposure in the orbital margin (fig. 78). Due to slight erosion the postorbital and maxilla are separated by less than a millimeter on the left side of MPSC and the left side of THUg 1798, although a contact is present on the better preserved right sides of both skulls. In BSP 1976 I 160 the orbital margin is badly damaged on both sides and the contact area is indeterminate. *Galianemys* agrees with *Cearachelys* in having a postorbital-maxilla contact, in contrast to all the other Bothremydidae, but in *Galianemys* the contact is much broader than in *Cearachelys*.

Structures of lateral plate: The postorbital in *Cearachelys* forms part of the edge of the temporal emargination, as in the Kurmademydini and Bothremydini but in contrast to *Euraxemys* and some Taphrosphyini in which the quadratojugal intervenes.

Contacts of medial process: The postorbital in *Cearachelys* forms part of the septum orbitotemporale (fig. 78). In anterior view the postorbital contacts the jugal ventrolaterally, the frontal dorsomedially, and the palatine ventromedially. In the posterior view of the postorbital wall, the postorbital contacts the pterygoid ventromedially, the parietal dorsomedially, the jugal ventrolaterally, and the quadratojugal dorsolaterally.

Structures of medial process: As in other bothremydids the postorbital forms the lateral margin and part of the roof of the sulcus palatinopterygoideus.

PREMAXILLA (figs. 68, 73)

Preservation: Both premaxillae are present, but damaged, in THUg 1798. They are absent in the MPSC specimen. Most of both premaxillae are present in BSP 1976 I 160 but they are eroded anteriorly, causing the anterior skull margin to appear more truncated than in THUg 1798. However, this difference in profile was probably not the case originally. The medial plate of the premaxilla is missing for both. The labial ridge is probably more complete on the left premaxilla in BSP 1976 I 160 and it is very similar to that ridge in THUg 1798.

Contacts: The premaxilla in *Cearachelys* contacts the maxilla posterolaterally, the vomer posteriorly, and the other premaxilla medially.

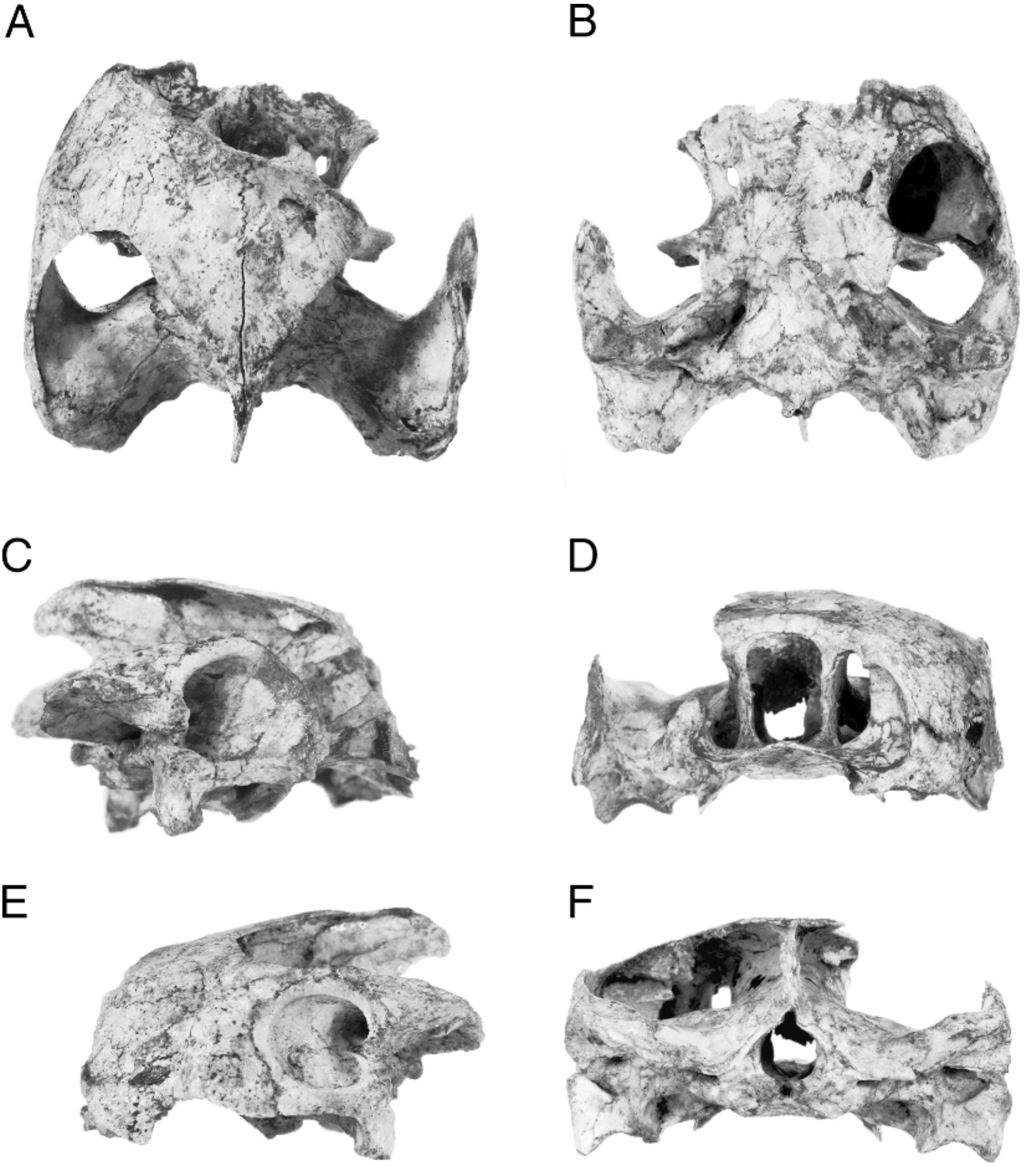

Fig. 70. *Cearachelys placidoi* Gaffney, Campos, and Hirayama, 2001. MPSC holotype specimen. **A**, dorsal; **B**, ventral; **C**, right lateral; **D**, anterior; **E**, left lateral; **F**, posterior (from Gaffney, Campos, and Hirayama, 2001). [E. Heck, del.]

Structures on dorsal surface: The dorsal surface of the premaxilla forms the anterior floor of the fossa nasalis and the margin of the apertura narium externa. As on the ventral surface, the dorsal surface slopes posterodorsally to meet the vomer. The apertura ventral margin is nearly straight in *Cearachelys*, with only a slight dorsal curve on the midline, similar to *Foxemys* but in contrast to the apertura narium externa margin in *Bothremys*, which has a sharp dorsal curve at the midline. Nuances of shape of the apertura narium externa, however, are variable even among species of living *Pelusios*.

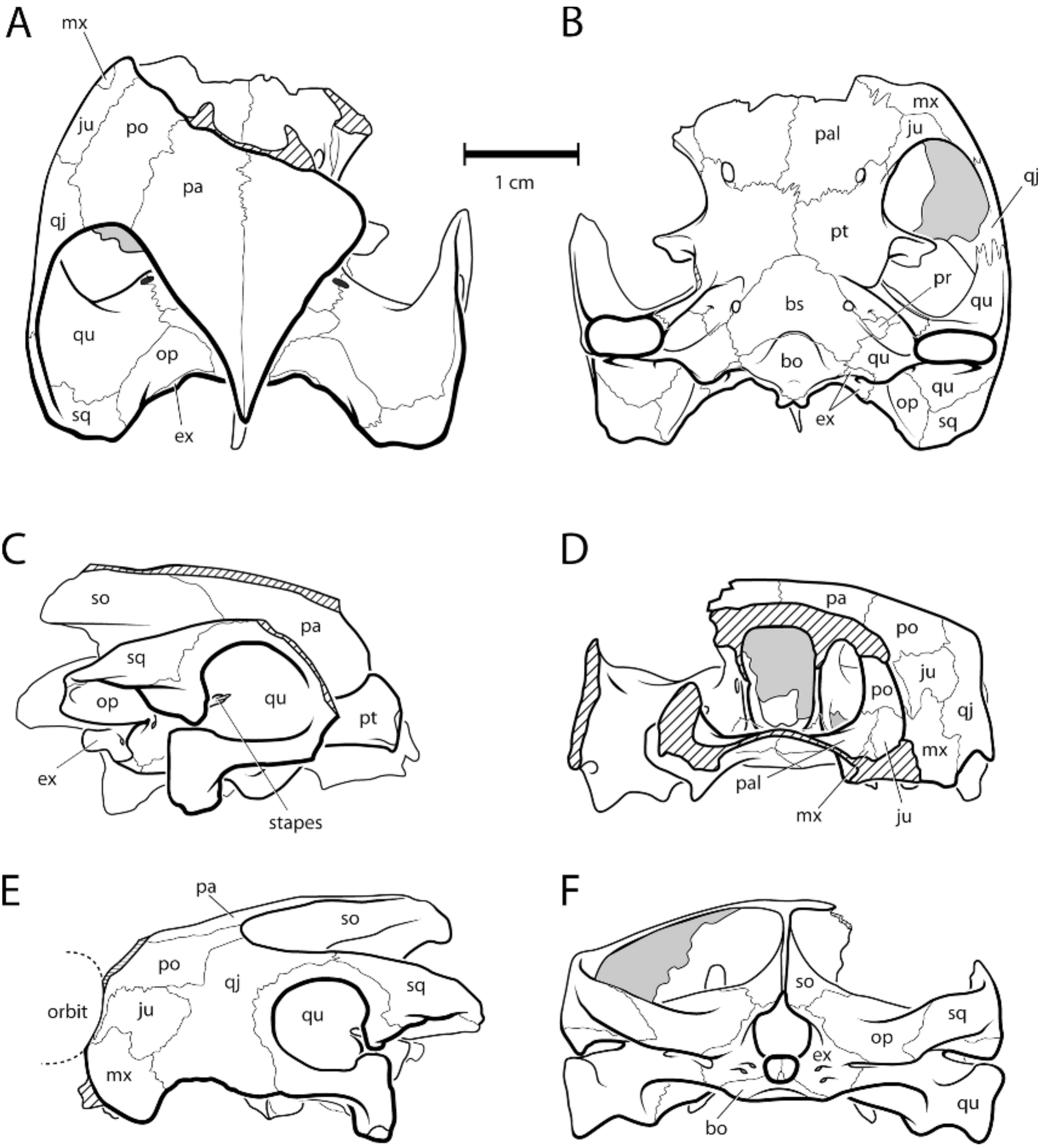

Fig. 71. *Cearachelys placidoi* Gaffney, Campos, and Hirayama, 2001. MPSC holotype specimen. **A**, dorsal; **B**, ventral; **C**, right lateral; **D**, anterior; **E**, left lateral; **F**, posterior (from Gaffney, Campos, and Hirayama, 2001). [F. Ippolito, del.]

Structures on ventral surface: The premaxilla of *Cearachelys* bears a distinct labial ridge anteriorly with a flat plate posteriorly. The labial ridge, however, is relatively thin in *Cearachelys* in anterior view, in contrast to the deeper ridge of *Foxemys*. Posterior to the labial ridge on the palatal surface, the premaxilla rises in a shallow, smooth arch to contact the vomer. In *Foxemys*, *Bothremys*, *Zolhafah*, and *Polysternon* there is a step on the triturating surface between the labial ridge and vomer. The premaxilla of *Cearachelys* is triangular, being broadest anteriorly and narrowing posteriorly. The lateral

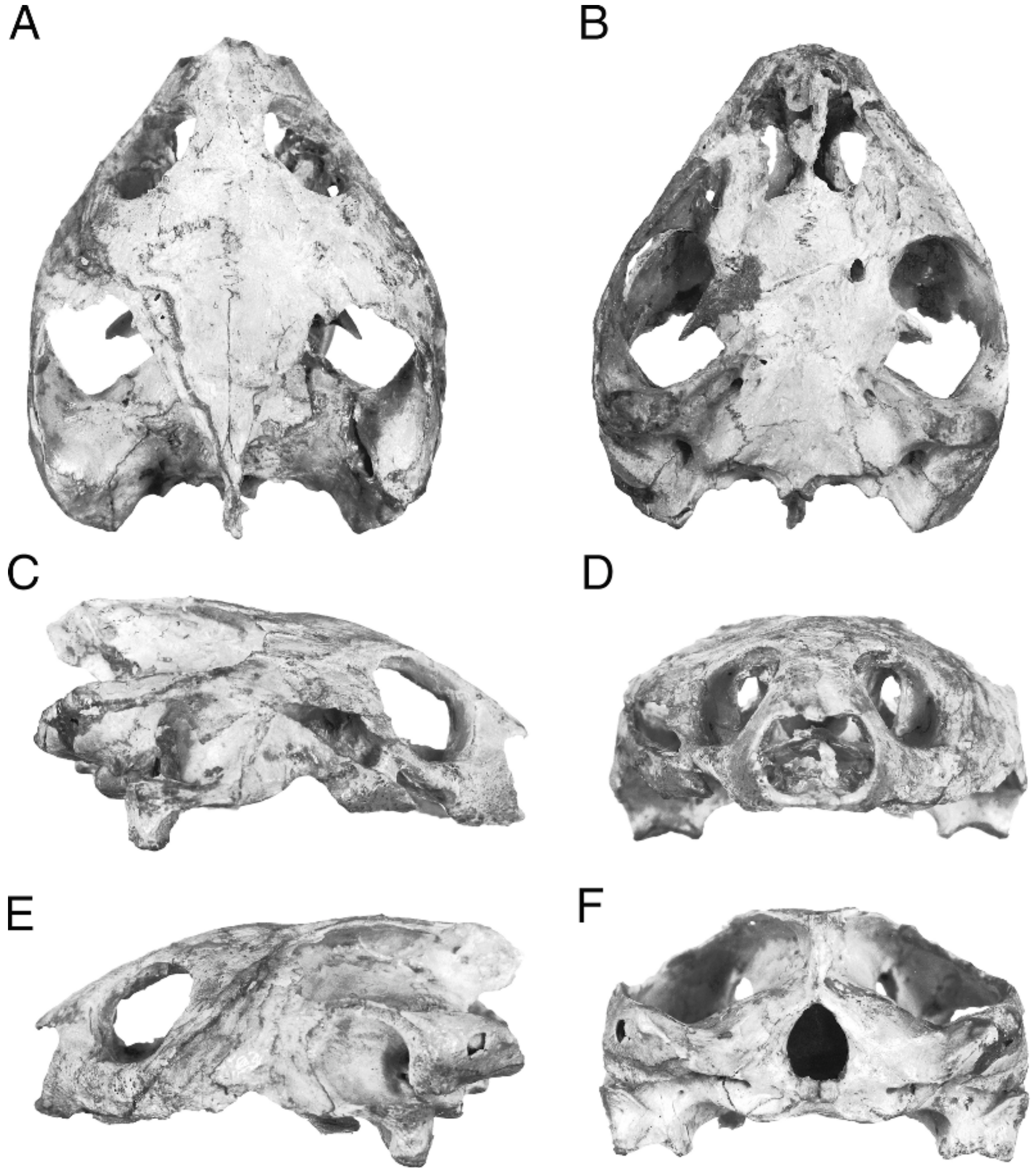

Fig. 72. *Cearachelys placidoi* Gaffney, Campos, and Hirayama, 2001. THUg 1798. **A**, dorsal; **B**, ventral; **C**, right lateral; **D**, anterior; **E**, left lateral; **F**, posterior (from Gaffney, Campos, and Hirayama, 2001). [E. Heck, del.]

limits, however, are represented by broken edges, and the precise position of sutures is not clear.

MAXILLA (figs. 68, 69, 73, 74, 76)

Preservation: The posterior portion of the left maxilla is preserved in the MPSC specimen. Most of both maxillae are present in THUg 1798, but both are damaged to the extent that the anteromedial edges and contacts are not known. Both maxillae are present in BSP 1976 I 160 and are nearly complete ventrally, but they are broken and missing portions more dorsally.

Contacts of vertical plate: The maxilla in *Cearachelys* contacts the premaxilla ante-

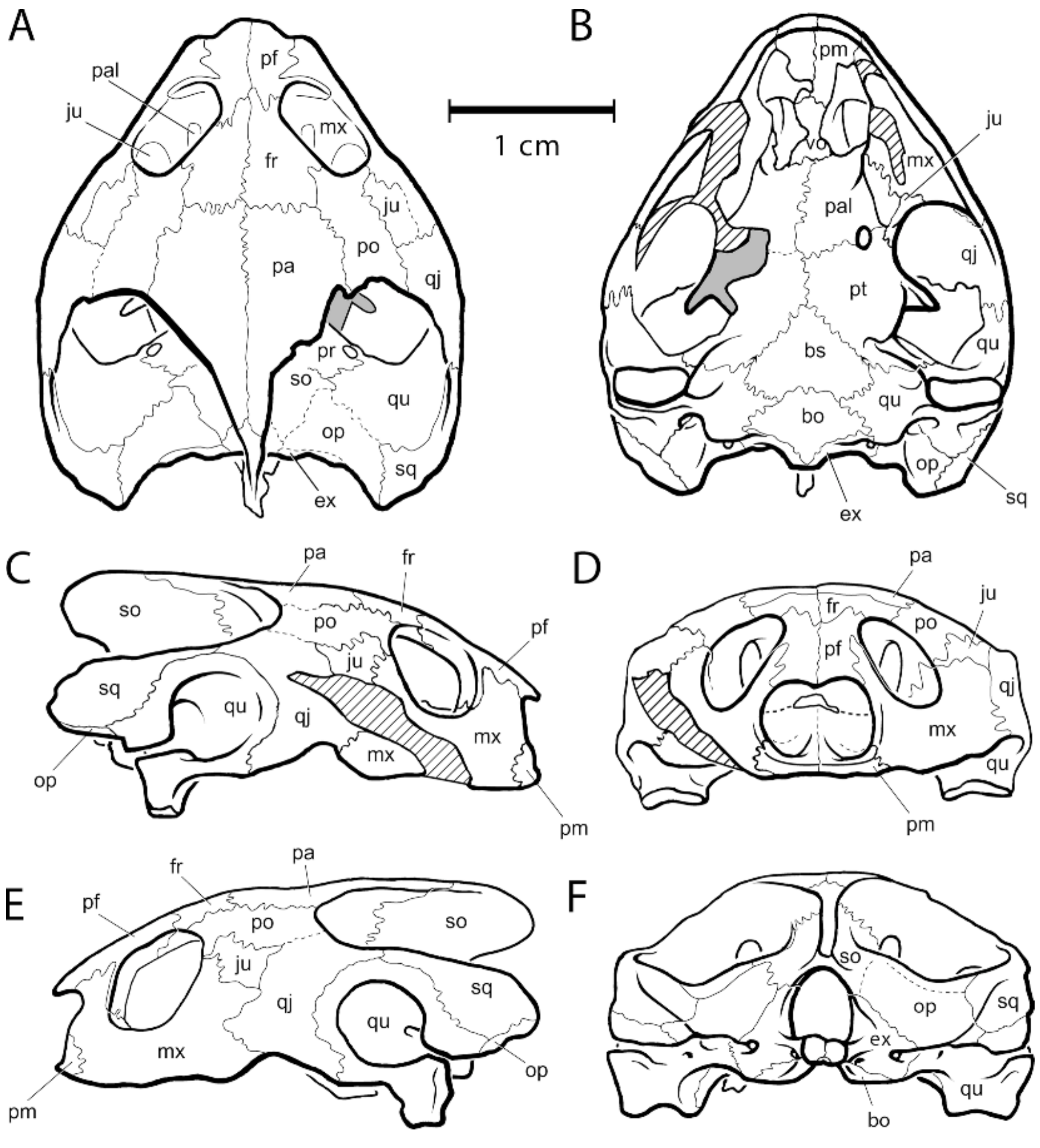

Fig. 73. *Cearachelys placidoi* Gaffney, Campos, and Hirayama, 2001. THUg 1798. **A**, dorsal; **B**, ventral; **C**, right lateral; **D**, anterior; **E**, left lateral; **F**, posterior (from Gaffney, Campos, and Hirayama, 2001). [F. Ippolito, del.]

romedially and the prefrontal anterodorsally. The posterior contacts of the maxilla are with the quadratojugal ventrally and the jugal dorsally. A very thin ventral process of the postorbital contacts the maxilla along the orbital margin (see Postorbital).

Structures of vertical plate: In lateral view the vertical plate of the maxilla in *Cearachelys* forms the posterior margin of the apertura narium externa, the ventral margin of the orbit, and the anterior portion of the cheek wall. The lateral margin of the apertura narium externa slopes posterodorsally, as in nearly all other bothremydids. The orbit is larger than in *Bothremys* and smaller than in *Pelomedusa*. There is a very slight cheek emargination, formed mostly by the quadratojugal, but the maxilla forms its anterior edge.

Contacts of horizontal plate: In dorsal view the exposure of the maxilla in the orbital floor is bordered by the jugal posteriorly and the palatine posteromedially. The palatine sends a narrow process anterolaterally into the maxilla, giving the sutural contact an interdigitating shape. In ventral view the maxilla in *Cearachelys* contacts the premaxilla anteriorly and the palatine posteromedially. Between the two contacts the maxilla limits are represented by broken edges, and the margin of the apertura narium interna is not definite. However, by using the bone edges as preserved on both sides, the limits of the apertura narium interna are determinable. Posteriorly the maxilla in *Cearachelys* contacts the jugal.

Structures of horizontal plate: The maxilla of *Cearachelys* forms most of the triturating surface. The labial ridge is relatively narrow, similar to *Kurmademys* and *Galianemys whitei*, in contrast to the thick labial ridge in *G. emringeri*, *Bothremys*, and *Rosasia*. The labial ridge in *Cearachelys*, however, is low, not deep as in *Taphrosphys*. The triturating surface of *Cearachelys* is smooth, without the deep pits seen in *Bothremys*, *Rosasia*, and *Zolhafah*. There is a shallow concavity (see Jugal) formed by the maxilla and jugal, but this is not the same as the pits seen in the tribe Bothremydini. The triturating surface, however, agrees with these taxa and *Polysternon* and *Foxemys* in being widened posteriorly to form a triangular area. On the left side of THUg 1798 the triangular triturating area is clearly visible. On the right side much of the surface is damaged and the medial limits are eroded.

The maxilla shape is the most obvious difference between BSP 1976 I 160 (fig. 74) and THUg 1798 (fig. 69) (the snout is absent in MPSC). In BSP 1976 I 160 the maxilla swells laterally so that the labial ridge is convex laterally; in THUg 1798 the labial ridge is nearly straight. The swelling also forms a pinched snout in BSP 1976 I 160, which is absent in THUg 1798.

VOMER (figs. 68, 69, 73)

Preservation: The vomer is preserved in THUg 1798, but its lateral margins are represented by broken edges. The posterior part of the vomer is preserved in BSP 1976 I 160, but not the center or anterior portion.

Contacts: The anterior end of the vomer in *Cearachelys* is swollen and contacts the paired premaxilla, a contact preserved only on the left side of THUg 1798. The posterior end, also swollen, contacts the palatine bones. A maxilla contact is possible but very unlikely.

Structures: The vomer of *Cearachelys* is roughly dumbbell-shaped, the presumed primitive condition for pleurodires and the hyperfamily Pelomedusoides. The anterior end of the vomer lies ventral to the posterior end, and between them is a narrow bar separating the paired apertura narium interna. The vomer of *Cearachelys* is quite similar in shape and proportions to that in *Galianemys* and it lacks the larger anterior end of *Bothremys* or the stout central bar of *Nigeremys*.

PALATINE (figs. 68, 73, 74, 77, 78)

Preservation: Palatines are preserved on both sides of all three specimens. In the MPSC specimen the left palatine is nearly complete, while the right one lacks part of its anterior edge. Preservation and sutures are clear. In THUg 1798 the right palatine is nearly complete, but the left one lacks its posterolateral portion and is poorly preserved, missing some of its ventral surface. Both palatines are present in BSP 1976 I 160, and they are more complete than in the other two *Cearachelys* skulls.

Contacts: On the ventral surface, the palatine in *Cearachelys* contacts the maxilla anterolaterally, the jugal laterally, the pterygoid posteriorly, the other palatine medially, and the vomer anteromedially. The contribution of the palatine to the triturating surface is about the same in *Cearachelys* as it is in *Galianemys* and *Kurmademys* (figs. 9, 10). This is more than the primitive condition seen in *Euraxemys* and the Pelomedusidae, contrary to the statement in Gaffney, Campos, and Hirayama (2001: 11). The palatine contribution in most of the tribe Bothremydini, however, is greater than in *Cearachelys*. On the dorsal surface of the palatine, there is a parietal contact.

Structures on dorsal surface: The dorsal surface of the palatine is well preserved and

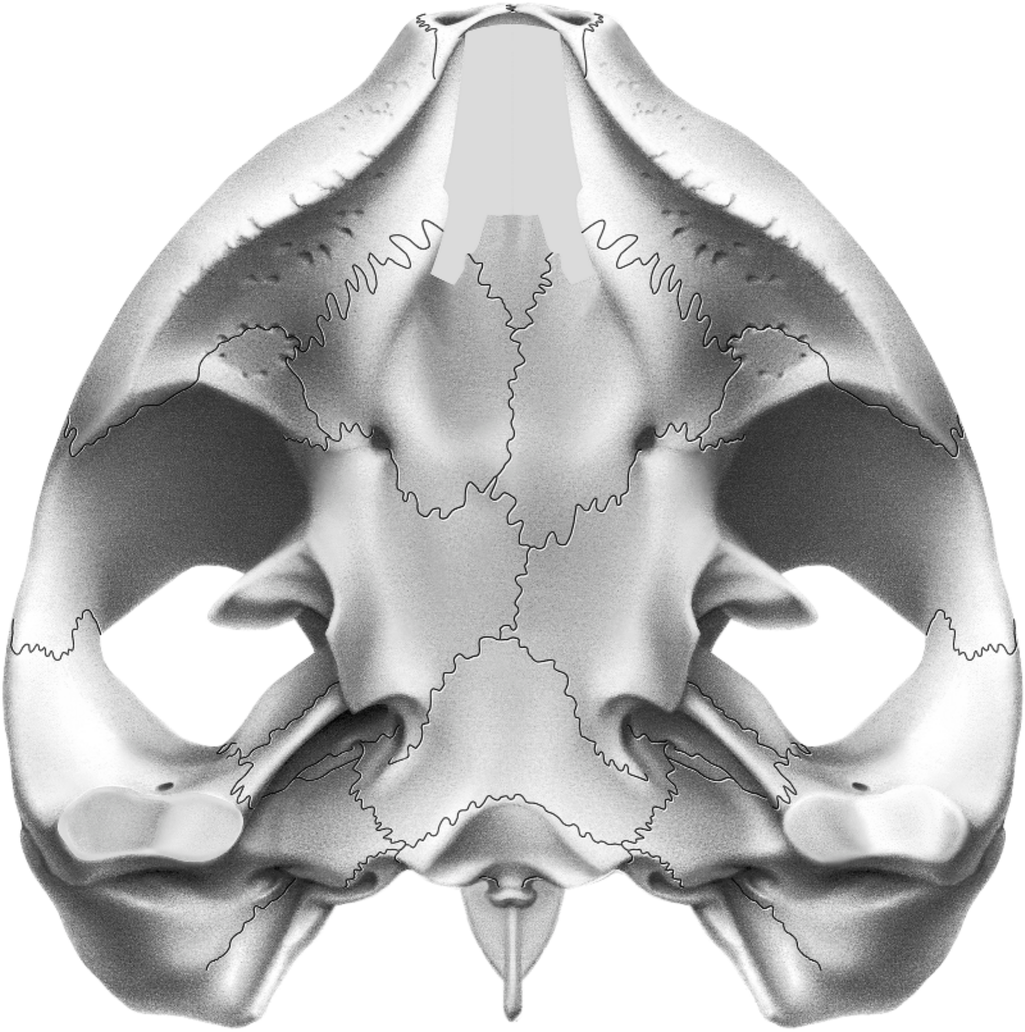

Fig. 74. *Cearachelys placidoi* Gaffney, Campos, and Hirayama, 2001. BSP 1976 I 160. Partially restored ventral view. For more detailed identification of structures in fossa pterygoidea, see figure 276F. [V. Storfer, del.]

easily seen in the MPSC specimen (fig. 78). There is a low dorsal ridge that contacts the processus inferior parietalis and forms the lower margin of the foramen interorbitale. This is in contrast to the condition in *Emydura* (and some *Pelusios*, e.g., USNM 42144), in which the palatine does not contact the parietal. However, in other *Pelusios* specimens (YPM 5429) there is a very similar condition to that in *Cearachelys*. In the posterior suture with the pterygoid both bones form the foramen palatinum posterius. The palatine has an anterolateral extension meeting the jugal, and the foramen lies in the suture along this extension.

Structures on ventral surface: *Cearachelys* has an apertura narium interna and choanal passage similar to those in *Galianemys* and *Kurmademys*. The high dorsal arching of some of the Taphrosphyini and the narrow apertura narium interna of some of the Bothremydini are absent.

QUADRATE (figs. 68, 71, 79, 80, 283)

Preservation: Both quadrates are present in all three specimens. They are nearly

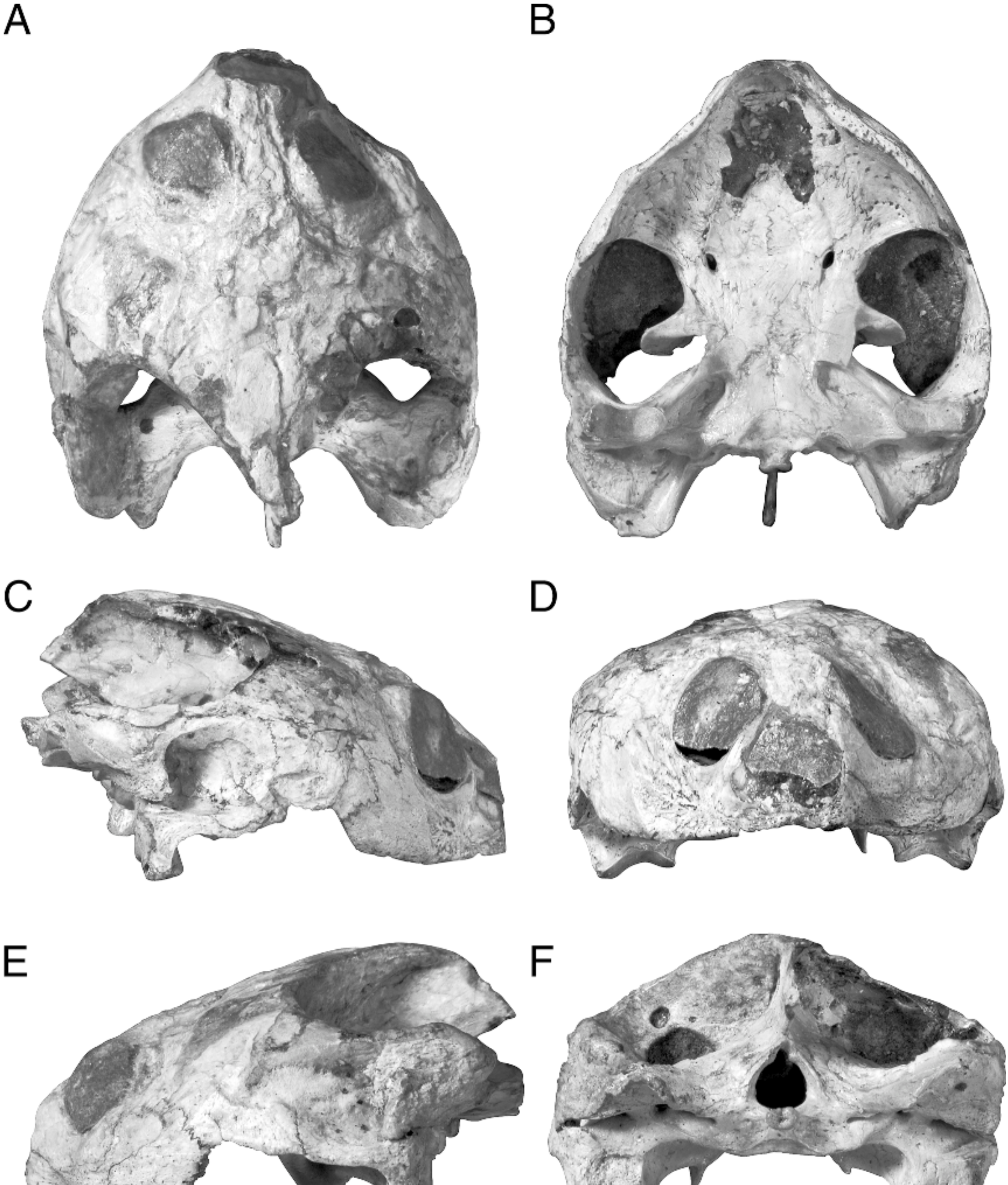

Fig. 75. *Cearachelys placidoi* Gaffney, Campos, and Hirayama, 2001. BSP 1976 I 160. **A**, dorsal; **B**, ventral; **C**, right lateral; **D**, anterior; **E**, left lateral; **F**, posterior. [G. Giardina, del.]

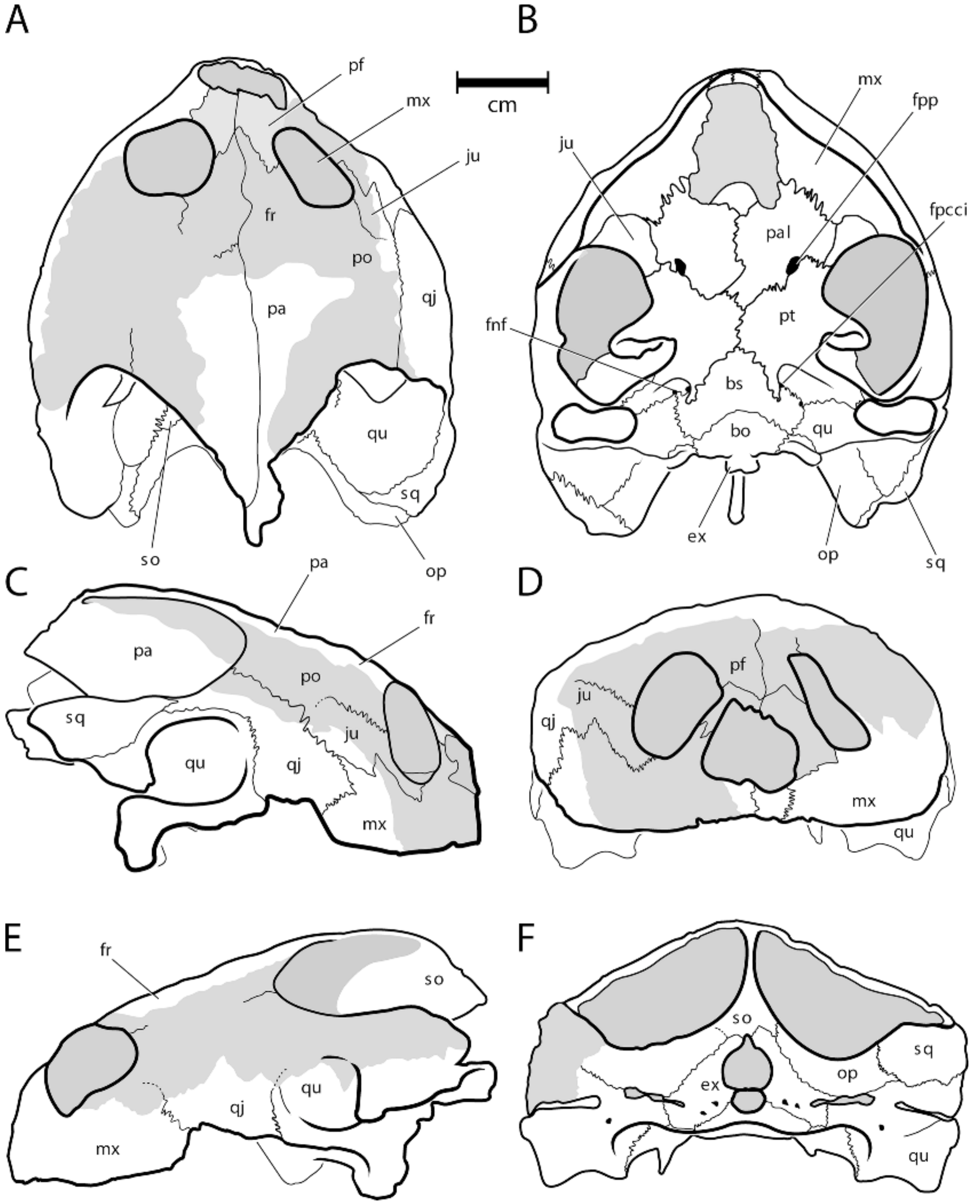

Fig. 76. *Cearachelys placidoi* Gaffney, Campos, and Hirayama, 2001. BSP 1976 I 160. **A**, dorsal; **B**, ventral; **C**, right lateral; **D**, anterior; **E**, left lateral; **F**, posterior. Gray tone indicates broken surfaces. [G. Giardina, del.]

complete in THUg 1798; the right quadrate of the MPSC specimen lacks its anterior edge along the cavum tympani. The left quadrate in BSP 1976 I 160 is damaged dorsally and posteriorly, but the right one is nearly complete and well preserved with all surfaces visible.

Lateral surface contacts: The quadrate of *Cearachelys* has a long, C-shaped anterior contact with the quadratojugal. Posteriorly the cone-shaped squamosal fits onto the posterodorsal corner of the quadrate. The narrow quadratojugal-squamosal contact prevents exposure of the quadrate along the temporal emargination.

Lateral surface structures: Most of the quadrate is involved in the formation of the cavum tympani (fig. 278). *Cearachelys* lacks any fossa precolumellaris, as is the case in nearly all bothremydids, but in contrast to most other Pelomedusoides and chelids. The antrum postoticum of *Cearachelys* is not extremely small, as in *Bothremys* and *Taphrosphys*, but it is significantly smaller than in *Kurmademys*, the Pelomedusidae, and *Euraxemys*.

The cavum tympani of most bothremydids is a hemispherical depression, with a canal in the center for the stapes, a small or absent antrum postoticum, and a shallow groove for the eustachian tube that is separated from the stapes by a wall of bone. This is the condition in nearly all Bothremydidae. However, *Cearachelys*, like *Foxemys* and *Polysternon*, has an open incisura columellae auris, so that there is no bony separation posteriorly between the eustachian tube and the stapes (figs. 79, 80). In the MPSC specimen there is a small bar of bone on the left side that closes the incisura at its most distal portion. On the right side the incisura is completely open, but a broken surface suggests that it was also probably closed originally. THUg 1798, however, is open on both sides and looks as if that was the original condition. The MPSC specimen is larger, and this difference in closure of the incisura columellae auris may be due to THUg 1798 being younger and generally less ossified.

Cearachelys and *Foxemys* differ in the shape of the incisura columellae auris, even though it is open in both. In *Cearachelys* the incisura is oval in shape, much as in pelomedusids, so that the eustachian tube was contained in it, and this is demonstrated by examination of Recent Pelomedusoides. In *Foxemys* the right incisura is complete in both available skulls, and it widens laterally only and is quite narrow for most of its length, in contrast to *Cearachelys*, showing that the eustachian tube was excluded from the incisura.

Dorsal and anterior surface contacts: The medial contacts of the quadrate in *Cearachelys* on the dorsal surface of the otic chamber are with the prootic anteromedially, the supraoccipital medially, and the opisthotic posteromedially. The prootic and opisthotic contacts are found in all pleurodires, but the quadrate and supraoccipital contact occurs only within the Bothremydidae (except Taphrosphyini and *Zolhafah*).

Dorsal and anterior surface structures: Medially the foramen stapedio-temporale is formed in the quadrate-prootic suture. As in nearly all other bothremydids, the foramen is on the anterior surface of the otic chamber in *Cearachelys*. The canalis stapedio-temporale is well preserved and open on the left side of THUg 1798. Although barely visible in dorsal view, the foramen in *Cearachelys* is not very close to the foramen nervi trigemini as it is in *Bothremys*. In *Galianemys* the foramen stapedio-temporale is completely on the anterior surface of the otic chamber, but in *Cearachelys* it is situated slightly more dorsally, although not to the degree seen in *Kurmademys*.

Contacts on ventral surface: On the ventral surface the quadrate contacts the pterygoid anteromedially, the basisphenoid medially, and the exoccipital posteromedially (figs. 276F, 277A). Between the basisphenoid and exoccipital contacts there is a narrow contact with the basioccipital. The basioccipital contact occurs in all bothremydids and podocnemidids. The basisphenoid-quadrate contact occurs in pelomedusids, podocnemidids, and all bothremydids. There is also a very narrow prootic contact anteromedially in BSP 1976 I 160 (fig. 276F) (see Prootic).

Structures on ventral surface: The fossa pterygoidea (see Pterygoid) is shallower in THUg 1798 and MPSC and deeper in BSP 1976 I 160 (figs. 276F, 277A). But even in BSP 1798 I 160 it is not as deep as it is in

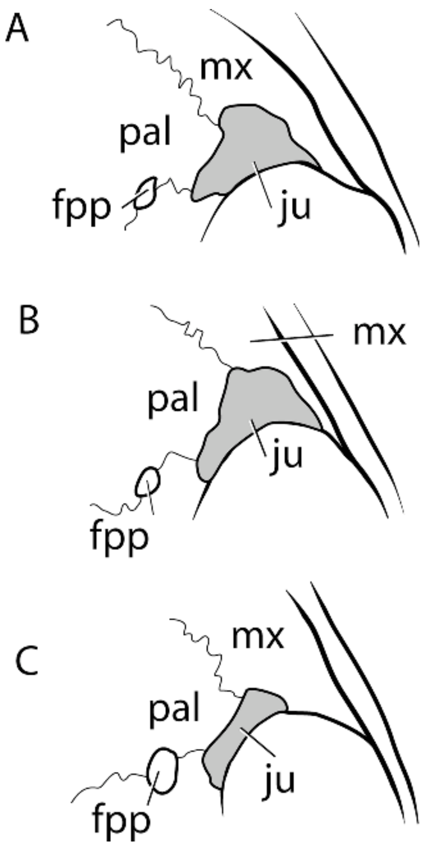

Fig. 77. *Cearachelys placidoi* Gaffney, Campos, and Hirayama, 2001. Comparative ventral views of lateral portion of palate showing variation in jugal exposure. **A**, BSP 1976 I 160; **B**, MPSC specimen; **C**, THUg 1798. [A.M. Phillips, del.]

Galianemys emringeri, *Polysternon*, or *Foxemys*. The condylus mandibularis in *Cearachelys* is similar in position, relative to the condylus occipitalis, to that seen in *Galianemys* and *Kurmademys*. It is anterior to the condylus occipitalis but not far anterior, as in *Polysternon* and *Taphrosphys*.

Contacts on posterior surface: The quadrate in *Cearachelys* contacts the squamosal dorsolaterally, the opisthotic dorsomedially, the exoccipital medially, and the basioccipital ventromedially, as in the other Bothremydidae.

Structures on posterior surface: The fenestra postotica in *Cearachelys* (see Opisthotic) is a short, slitlike structure, open medially, and communicating with the open foramen jugulare posterius (figs. 79, 80). This is also the condition in *Galianemys*, but does not occur in any other Bothremydidae. In BSP 1976 I 160 the right fenestra postotica is subdivided by a narrow process of bone that separates the more dorsal stapedial artery from the more ventral lateral head vein. The left fenestra postotica, however, lacks this process, making it identical to the fenestra postotica in the other skulls. This subdivision is interpreted as individual variation, similar to that seen in many other turtles (Gaffney, 1979a).

PTERYGOID (figs. 68, 69, 74, 76, 276F, 277A)

Preservation: In MPSC and BSP 1976 I 160, both pterygoids are complete and well preserved, except for the distal margins of the pterygoid flange. In THUg 1798, the left pterygoid is nearly complete, but the right one lacks a significant portion anteriorly and is damaged by erosion on its ventral surface. The dorsal structures of the pterygoid are visible and well preserved in the MPSC specimen.

Contacts on ventral surface: The pterygoid in *Cearachelys* contacts the palatine anteriorly, the other pterygoid anteromedially, the basisphenoid posteromedially, the quadrate posterolaterally, and the prootic posteriorly in BSP 1976 I 160 (figs. 276F, 277A). The pterygoid of *Cearachelys* has a roughly transverse suture with the palatine that trends anterolaterally to meet the jugal. The foramen palatinum posterius (fig. 77) is formed in the palatine-pterygoid suture, as in most pleurodires. Medially the pterygoids meet on the midline for about half their length. The basisphenoid separates them posteriorly.

Structures on ventral surface: As in all pleurodires, *Cearachelys* has a laterally projecting processus trochlearis pterygoidei. In *Cearachelys* the processus lies at a less acute angle to the midline in contrast to the more acute angle seen in pelomedusids, chelids, euraxemydids, and *Araripemys*. The flange of the pterygoid that extends ventrally from the base of the processus trochlearis pterygoidei along the quadrate process in all pleurodires is often broken in fossils, because it is so thin and fragile. It is partially preserved in all three *Cearachelys* specimens and seems to be

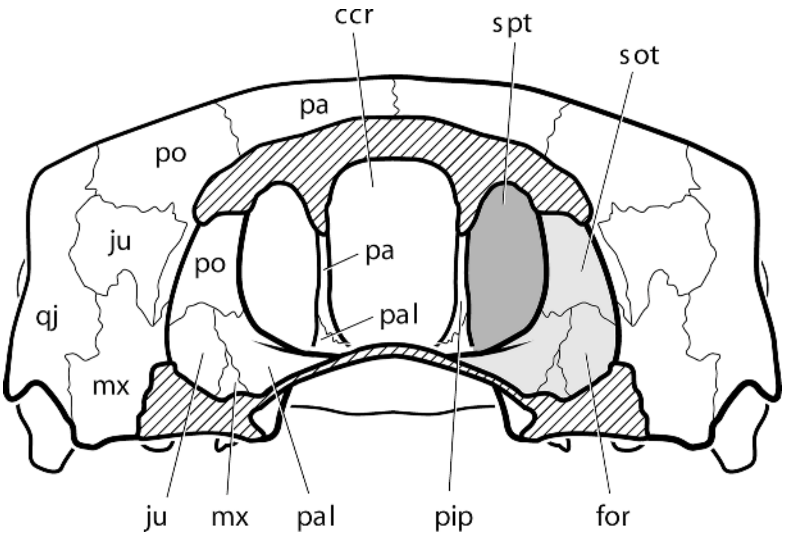

Fig. 78. *Cearachelys placidoi* Gaffney, Campos, and Hirayama, 2001. MPSC specimen. Partially restored anterior view of skull sectioned through posterior part of fossa orbitalis. Showing sulcus palatinopterygoideus and septum orbitotemporale. [A. Venjara, del.]

developed to about the extent seen in pelomedusids.

The posterolaterally extended quadrate process of the pterygoid in *Cearachelys* is distinctly narrower and longer than in *Euraxemys*, *Araripemys*, pelomedusids, or chelids. In the latter groups the processus is relatively flat and more horizontal, while in *Cearachelys* it is narrower and more vertical. This is related to the presence in *Cearachelys* of a shallow fossa pterygoidea in the posterolateral part of the pterygoid. This depression has a sharp anterolateral margin that extends posterolaterally along the processus articularis of the quadrate, and has a barely perceptible margin medially on the basisphenoid. In BSP 1976 I 160 the fossa pterygoidea is deeper but not as deep as in *Foxemys* or as the much deeper pterygoidea in *Nigeremys*.

The foramen posterius canalis carotici interni in *Cearachelys* lies in the basisphenoid-pterygoid suture, just anterior to the quadrate contact (figs. 276F, 277A). Its position is similar to that in *Rosasia* and *Foxemys*. It differs from the pterygoid-quadrate formation of the foramen seen in *Bothremys* and the pterygoid-quadrate-basisphenoid formation seen in *Taphrosphys*, *Zolhafah*, and *Arenila*. The lateral margin and most of the ventral margin of the foramen posterius canalis carotici interni in *Cearachelys* are formed by pterygoid. The medial edge is formed by the basisphenoid. The dorsal roof of the foramen is formed by both the basisphenoid and pterygoid. As in most of the other bothremydids, the foramen leads into the canalis carotici interni, lying in a nearly horizontal plane, so that the ventral margin of the foramen and canalis are quite thin. This is in contrast to the condition in pelomedusids, where the canalis is much more vertical.

There is some variability in the structures around the foramen posterius canalis carotici interni in *Cearachelys* (figs. 276F, 277A). The MPSC specimen shows very little damage of the thin bones in this region, but THUg 1798 is eroded to a varying extent on both sides. In the MPSC specimen the posterior flange of the pterygoid just posterolateral to the foramen posterius canalis carotici interni has a foramen opening out of a canal that parallels, just lateral to, the canalis carotici interni. This foramen and canal is the foramen nervi facialis and leads into the prootic, where this nerve goes dorsally. On the left side of the MPSC specimen a small hole in the floor of the canal allows determination of its size and location, but the opening into the prootic is not visible on either side of this specimen. In THUg 1798, however, the prootic and the foramen nervi facialis are visible. Due to either erosion or less ossification in life (perhaps related to the smaller size of THUg 1798), the pterygoid in THUg 1798 lacks the canal for the facial nerve seen in the MPSC specimen. On the right side of THUg 1798, the prootic is exposed in a narrow band leading out of the canalis carotici interni and forming part of the roof of the foramen posterius canalis carotici interni, between the pterygoid and basisphenoid. A dorsally extending foramen and canal, the foramen nervi facialis, is in the anterior part of the prootic exposure. On the left side of THUg 1798 more of the pterygoid is present, covering the foramen nervi facialis ventrally. The foramen can still be seen by looking along the length of the canalis carotici interni.

BSP 1976 I 160 agrees closely with the pterygoid in the other two *Cearachelys* skulls except in two areas: the position of the foramen posterius canalis carotici interni and the depth of the fossa pterygoidea (figs. 276F, 277A). It is likely that these features are related. The foramen posterius canalis carotici interni in BSP 1976 I 160 is formed in the suture between basisphenoid and pterygoid, as in the other *Cearachelys* skulls, but it opens almost laterally into the fossa pterygoidea;that is, it lies in the medial wall of the fossa pterygoidea. In the other two *Cearachelys* skulls the foramen is more posterolateral and is formed in a more horizontal plane, opening directly ventrally rather than laterally. This seems to be related to the deeper fossa pterygoidea in BSP 1976 I 160. Morphologically, the deeper fossa eroded the bone exposing the more anteromedial portion of the canalis caroticus internus, causing the foramen posterius canalis carotici interni to "migrate". The bone covering the canalis caroticus internus in THUg 1798 and in MPSC is very thin; only a small degree of deepening the fossa would expose the more medial portion of the canalis caroticus internus.

Contacts on dorsal surface: The contacts at the base of the processus trochlearis pterygoidei in *Cearachelys* are visible in THUg 1798 and are with the postorbital anterodorsally and the jugal anteroventrally. The crista pterygoidea contacts the processus inferior parietalis for all of its length posteriorly to the foramen nervi trigemini where it contacts the prootic.

Structures on the dorsal surface: The dorsal surface of the pterygoid is visible in the MPSC specimen. The crista pterygoidea is quite low, there is a low dorsal area on the outside of the crista anteriorly, and it rises again to form the ventral margin of the foramen nervi trigemini. The anterodorsal margin of this foramen is formed by the parietal, and the posterodorsal margin is formed by the prootic. The sulcus cavernosus is medial to the crista pterygoidea. It shows no sign of a foramen caroticum laterale.

Supraoccipital (figs. 68, 71)

Preservation: The supraoccipital is complete in all three skulls. In the MPSC specimen a small part of the ventral edge of the crista supraoccipitalis is missing, in THUg 1798 part of the crista on the right side is gone near its base, and in BSP 1976 I 160 the anterior part of the bone is covered by matrix.

Contacts: In cryptodires and most pleurodires the supraoccipital has a tripartite suture, with the prootic and opisthotic visible on the dorsal surface of the otic chamber. In *Cearachelys* the supraoccipital has a lateral projection that separates the prootic and opisthotic and contacts the quadrate. This contact is well preserved on both sides of the MPSC specimen, on the left side of THUg 1798, and on the left side of BSP 1976 I 160. On the right side of THUg 1798 and BSP 1976 I 160 the area is damaged and not determinable.

The supraoccipital-quadrate contact also occurs in all of the other Bothremydidae except *Zolhafah* and the Taphrosphyini. In *Cearachelys* the degree of contact is less than in the other bothremydids.

Structures: The crista supraoccipitalis is shorter in bothremydids than it is in most podocnemidids. In *Cearachelys* the crista extends posteriorly about as far as the posterior end of the squamosals, similar in length to other bothremydids. The crista in *Cearachelys* is slightly longer than in *Euraxemys*.

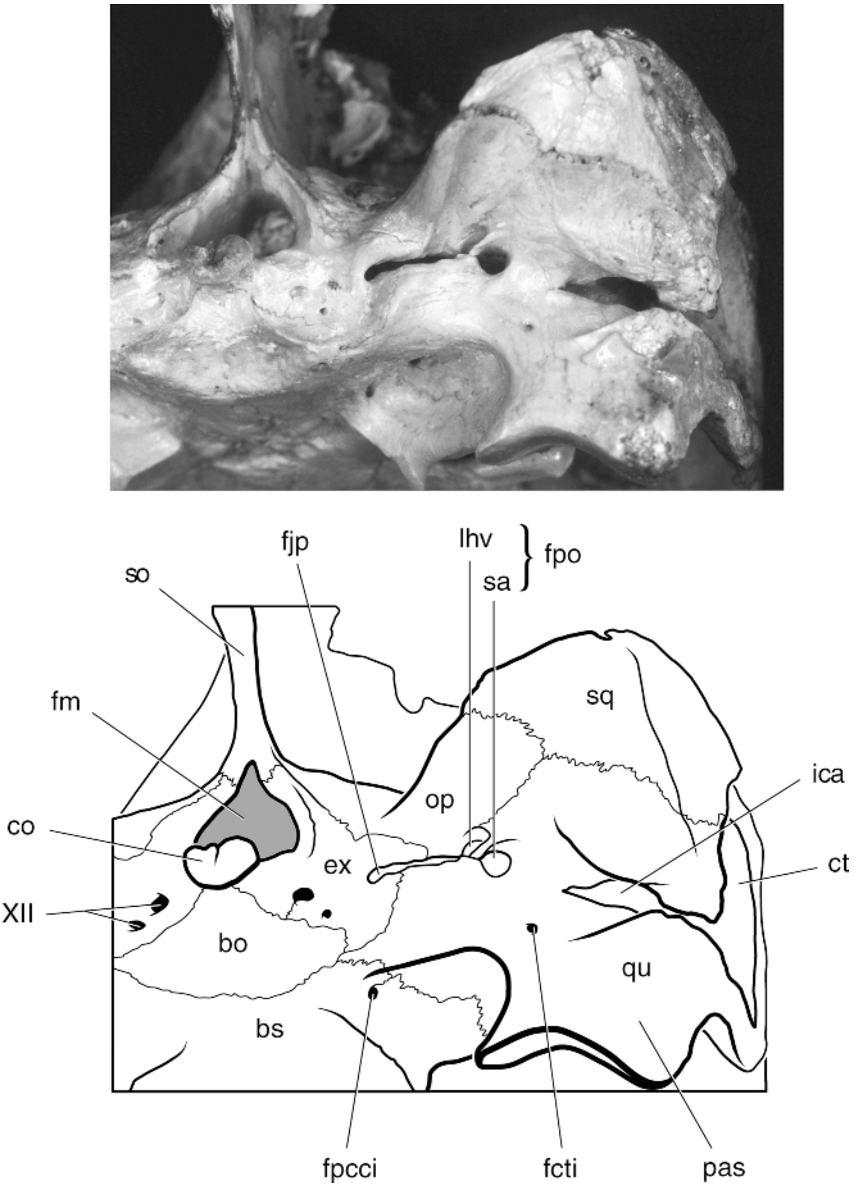

Fig. 79. *Cearachelys placidoi* Gaffney, Campos, and Hirayama, 2001. BSP 1976 I 160. Posterior oblique view. [A. Venjara and E.S. Gaffney, del.]

EXOCCIPITAL (figs. 68, 79, 80)

Preservation: The exoccipitals are complete and well preserved in all three skulls.

Contacts: The exoccipital in *Cearachelys* contacts the supraoccipital dorsally (the exoccipitals do not meet in the midline above the foramen magnum, as in some chelids) and the opisthotic laterally and anteriorly. Dorsomedially the exoccipital forms the lateral and ventral margin of the foramen magnum, a structure that varies little in Pelomedusoides. Ventromedially the two exoccipitals form the condylus occipitalis, with no contribution from the basioccipital on the surface of the condylus. Nonetheless, the basioccipital in *Cearachelys* does separate

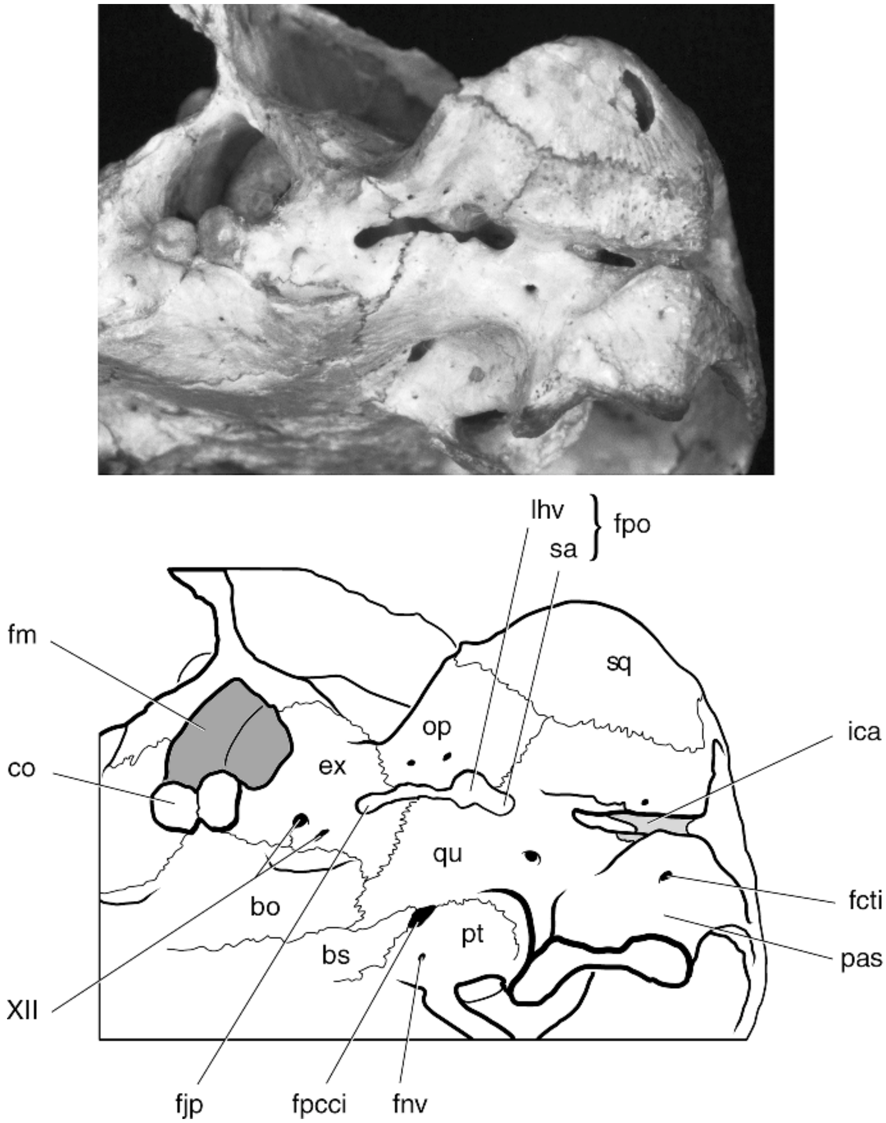

Fig. 80. *Cearachelys placidoi* Gaffney, Campos, and Hirayama, 2001. THUg 1798. Posterior oblique view reversed from left side. [A. Venjara and E.S. Gaffney, del.]

the exoccipitals in ventral view in the neck of the condylus occipitalis, as in *Galianemys*. In Bothremydini and Taphrosphyini the exoccipitals are in contact ventrally and make up the neck of the condylus occipitalis.

As in all other bothremydids, *Cearachelys* has an extensive quadrate-exoccipital contact below the fenestra postotica. This contact is absent in chelids, podocnemidids, pelomedusids, and *Euraxemys*.

Structures: Laterally the exoccipital in *Cearachelys* forms the medial portion of the foramen jugulare posterius, contacting the opisthotic dorsally and the quadrate ventrally (figs. 79, 80). In *Cearachelys* the foramen jugulare posterius is open laterally, as in *Foxemys*, not closed, as in *Bothremys*, *Taphrosphys*, pelomedusids, and chelids. In *Cearachelys*, however, the foramen jugulare posterius is partially closed or restricted laterally in comparison to the more open condition in *Araripemys* and euraxemydids. In *Cearachelys* there are two foramina nervi hypoglossi, as in all the other Pelomedusoides.

BASIOCCIPITAL (figs. 68, 69, 71, 79)

Preservation: The basioccipital is complete and well preserved in all three skulls. Its dorsal surface is visible in MPSC.

Contacts: The basioccipital in *Cearachelys* contacts the basisphenoid anteriorly, the quadrate laterally, and the exoccipitals dorsally and posteriorly.

Structures: The basioccipital in *Cearachelys* enters the short neck of the condylus occipitalis but does not completely separate the exoccipitals (see Exoccipitals). The basioccipital of *Cearachelys*, as in other bothremydids, is relatively shorter than in chelids and pelomedusids, but the width is about the same.

PROOTIC (figs. 68, 73, 276F)

Preservation: The prootic in MPSC is present and well preserved on both sides, but in THUg 1798 only the left prootic is well preserved, although both are present. Both prootics are present in BSP 1976 I 160 but are damaged on their dorsal surfaces. The sutures are clear, however.

Contacts: The prootic in *Cearachelys* contacts the parietal medially, the quadrate laterally, the supraoccipital posterodorsally, and the pterygoid ventrally. There is no opisthotic contact. There is variable exposure of the prootic on the ventral surface (figs. 276F, 277A), apparently because the covering bones are very thin and are affected by slight differences in the depth of the fossa pterygoidea and by damage. On the ventral surface of THUg 1798, the prootic is very narrowly exposed between the pterygoid anterolaterally, the basisphenoid medially, and the quadrate posteriorly. This exposure was probably completely covered ventrally by the pterygoid in life because remnants of the covering persist on both sides. The figures (figs. 68, 69, 277A) have been drawn showing it covered, but the exposure is so narrow it would not be wider than the line width in any case. In MPSC, the prootic is covered on the right side, but on the left a narrow exposure is visible, also between the pterygoid, basisphenoid, and quadrate. In BSP 1976 I 160, a small area is exposed on the left side, near the foramen nervi facialis, where interdigitating sutures make the actual identification of each bone projection difficult.

Structures: The foramen stapedio-temporale is formed in the prootic-quadrate suture, and the foramen nervi trigemini is formed between the parietal, pterygoid, and prootic. The foramen stapedio-temporale in *Cearachelys* is situated on the anterior face of the otic chamber, as in other bothremydids and in contrast to the primitive position in chelids and pelomedusids, where it is more posterior and faces dorsally. In *Cearachelys* and other bothremydids the foramen stapedio-temporale faces anteriorly and is barely visible in dorsal view. In chelids and pelomedusids the foramen lies on the dorsal surface of the otic chamber and opens more dorsally. Although *Cearachelys* has an anterior-facing foramen stapedio-temporalis, the foramen is not close to the foramen nervi trigemini, as in the tribes Taphrosphyini and Bothremydini.

As described under Supraoccipital, the prootic does not contact the opisthotic in *Cearachelys*, due to a supraoccipital-quadrate contact. This contact is found in most bothremydids. The prootic in *Cearachelys* forms the posterodorsal margin of the foramen nervi trigemini.

The foramen nervi facialis (the hyomandibular branch of the VII nerve) is formed in the prootic, but ventrally the pterygoid, quadrate, and basisphenoid variably cover the entry of the nerve into the prootic. In BSP 1976 I 160 the foramen nervi facialis is formed by the basisphenoid, pterygoid, and quadrate on the right side, and by pterygoid and quadrate on the left. In MPSC the foramen nervi facialis is formed by the pterygoid and prootic on the left side and completely by the pterygoid on the right. In THUg 1798, the foramen nervi facialis is formed by the prootic, basisphenoid, and pterygoid in the roof of the foramen posterius canalis carotici interni on both sides.

OPISTHOTIC (figs. 68, 71, 79, 80)

Preservation: Both opisthotics are present and complete in all three *Cearachelys* skulls. There is some damage to the dorsal surface in BSP 1976 I 160.

Contacts: The opisthotic in *Cearachelys* contacts the supraoccipital anteromedially, the quadrate anterolaterally, the squamosal posterolaterally, and the exoccipital posteromedially. There is no prootic contact.

Ventrally the opisthotic forms the roof and some subdivisions of the fenestra postotica. In *Cearachelys* the foramen jugulare posterius is open laterally and is continuous with the fenestra postotica. Laterally the fenestra postotica is bordered by the quadrate (see Quadrate), which also forms most of the floor. The exoccipital contacts the quadrate and forms the more medial part of the floor. In the tribes Bothremydini and Taphrosphyini the fenestra postotica is completely separated from the foramen jugulare posterius by a bar of bone formed by the opisthotic and quadrate. This bar is absent in *Cearachelys* and *Galianemys*. However, the fenestra postotica in *Cearachelys* is nonetheless smaller and more restricted than in chelids, pelomedusids, and *Araripemys*. The medial part of the fenestra postotica in *Cearachelys* is a narrow horizontal slit, as in *Galianemys* where the opisthotic and quadrate nearly meet. The more lateral part of the fenestra postotica is figure 8-shaped, because it is partially divided by low ridges into a more lateral portion for the lateral head vein and a more medial portion for the stapedial artery (see Quadrate).

The processus interfenestralis of the opisthotic is completely covered in *Cearachelys* as in all other bothremydids and podocnemidids. The fenestra postotica is so small that the fenestra ovalis is only barely visible in THUg 1798. The opisthotic in *Cearachelys* ends posteriorly at about the same level as the squamosal; it does not extend posterolaterally beyond the squamosal, as in pelomedusids, *Araripemys*, and *Euraxemys*.

BASISPHENOID (figs. 68, 71, 276F, 277A)

Preservation: The basisphenoid is present and complete in all three skulls, but in THUg 1798 it is slightly eroded. Most of the dorsal surface is visible in THUg 1798.

Contacts: In ventral view the contacts of the basisphenoid in *Cearachelys* are with the pterygoid anterolaterally, the quadrate posterolaterally, and the basioccipital posteriorly. There is a very narrow, variable contact with the prootic laterally in BSP 1976 I 160 and THUg 1798.

Structures on ventral surface: The basisphenoid is roughly triangular in shape, with its apex separating the pterygoids for about half their length. The basisphenoid forms the medial margin of the foramen posterius canalis carotici interni, but the foramen is close to the pterygoid-quadrate suture. The ventral surface of the basisphenoid in *Cearachelys* is broadly convex and does not participate in the pterygoideus muscle concavity.

Structures on dorsal surface: The dorsal surface of the basisphenoid in *Cearachelys* shows the oval sella turcica, low dorsum sellae, and fused rostrum basisphenoidale as seen in *Pelusios*, *Podocnemis*, and *Bothremys*. The long, narrow rostrum and only barely overhanging dorsum are more similar to *Bothremys*. The paired foramen anterius canalis carotici interni lie close together, as in *Podocnemis* and *Bothremys*. There is no foramen caroticum laterale. The foramen nervi abducentis is posterior to the base of the processus clinoideus, as in *Pelusios* and *Podocnemis*.

Galianemys emringeri and *Galianemys whitei*

In this section, both species of this genus are described together. The *Galianemys* species are quite similar to each other, and it makes sense to the senior author to combine the descriptions to avoid repetition. *Galianemys* is described and figured more extensively than some other taxa because it is a comparatively generalized bothremydid, known from a relatively large array of good material. The two species are represented by a total of 13 skulls, 6 of *G. emringeri* and 7 of *G. whitei* (table 9). Of these, *G. whitei* has six relatively complete skulls, and *G. emringeri* has three relatively complete skulls. Character variation in the genus is listed in table 9. In addition to the figures grouped with the descriptions (figs. 81–100), the reader should be aware of other *Galianemys* figures in the character descriptions section: figure 277 (foramen posterius canalis carotici interni), figure 278 (septum orbitotemporale), figure 280 (orbital floor), and figure 284 (quadrate). Much of this section is modified from

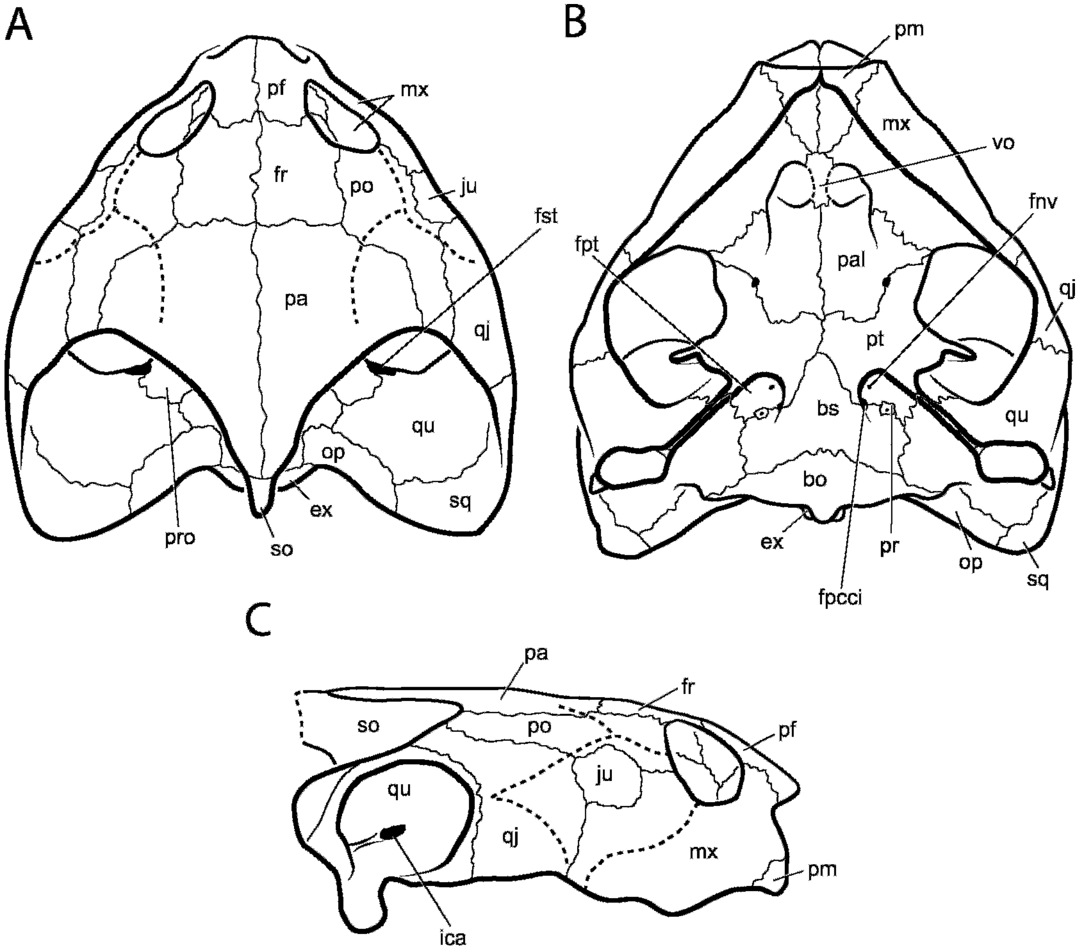

Fig. 81. *Galianemys emringeri* Gaffney, Tong, and Meylan, 2002. Partially restored skull based on AMNH 30035 with additions from AMNH 30037. Vomer restored from AMNH 30555 (*G. whitei*). **A**, dorsal; **B**, ventral; **C**, lateral. Dashed lines are scale impressions. [A.M. Phillips, del.]

Gaffney, Tong, and Meylan (2002) by the addition of new material and more comparisons. *Galianemys* is also shown in a series of CT scans on the DigiMorph University of Texas website: http://www.digimorph.org/specimens/Galianemys_emringeri/.

Galianemys is most closely related to *Cearachelys*. They make up the tribe Cearachelyini.

PREFRONTAL (figs. 81, 89, 97)

Preservation: The prefrontal is preserved in *Galianemys whitei* in AMNH 30036, 29987, 29986, 30028, 30027, 30555, and in MDEt 45. In *Galianemys emringeri* it is preserved in AMNH 30035, 30037, 29985, and 30040. It can be seen particularly well in AMNH 30027 and 29986 where the left prefrontal is lost, allowing the internal surfaces on the right side to be seen.

Contacts: As in *Pelusios* and all other Pelomedusoides, the prefrontal in both species of *Galianemys* contacts the maxilla anteroventrolaterally, the frontal posteriorly, and the other prefrontal medially. In *Galianemys emringeri* the prefrontal-frontal suture trends posteromedially for a short distance medial to the orbital margin, then trending anteromedially to form a midline projection of the frontal. In *G. whitei* the suture is nearly straight in AMNH 29986, 29987, 30036, 30027, 30555, and in MDEt 45. In AMNH

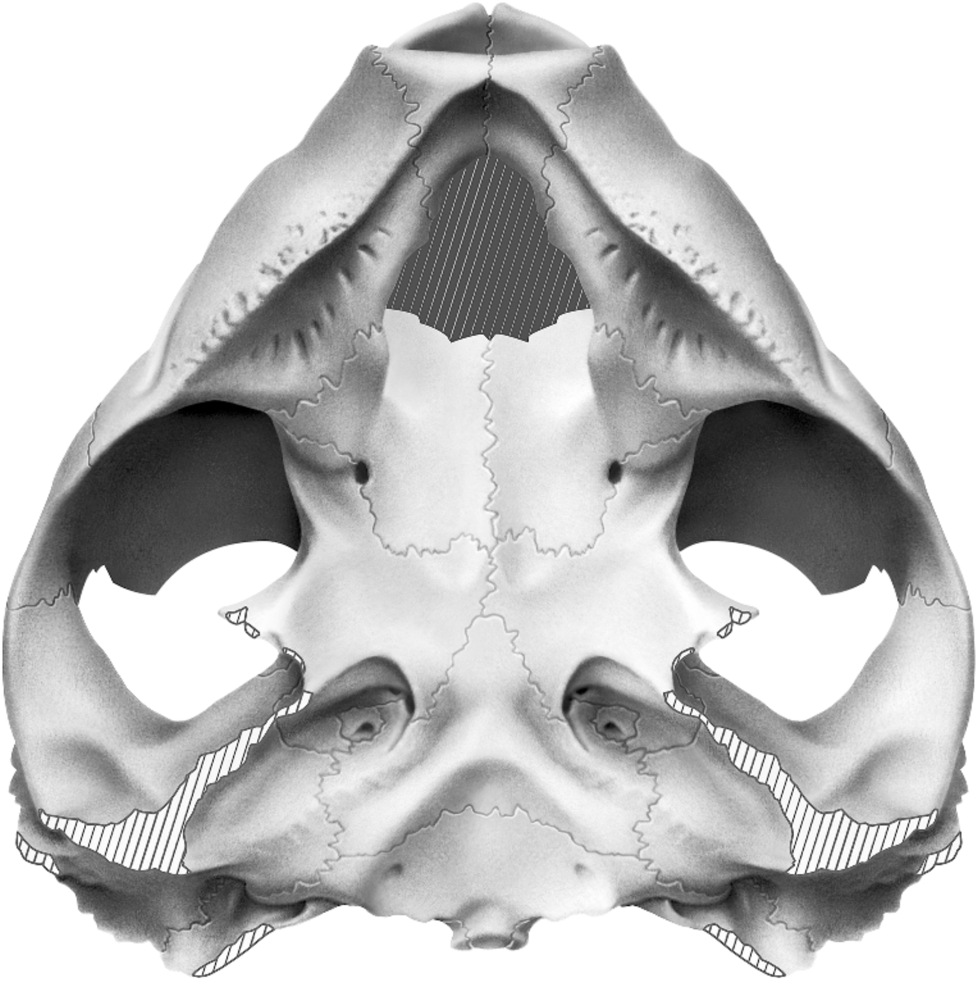

Fig. 82. *Galianemys emringeri* Gaffney, Tong, and Meylan, 2002. Partially restored ventral view based on AMNH 29985 holotype and AMNH 30035. For more detailed view of area around foramen posterius canalis carotici interni, see figure 277E. [V. Storfer, del.]

30028 the suture is asymmetric with the frontal projecting anteriorly on the right side but not on the left. *Cearachelys* and *Kurmademys* have an anteriorly convex suture, but it is nearly straight in *Bothremys* and *Rosasia* and slightly curved in other genera.

Structures: The prefrontal in *Galianemys* is similar to that in other Pelomedusoides. The dorsal plate forms the anterodorsal margin of the orbit and the dorsal margin of the apertura narium externa. The margin is slightly protruding over the apertura in *Galianemys*, as in most Pelomedusoides, but there is some variation within the available specimens. A specimen of *Galianemys whitei*, AMNH 29987, has a much thicker margin that forms a slightly concave profile in lateral view rather than convex, as in all the other skulls. The skulls of *G. emringeri* and *G. whitei* do not differ consistently in the prefrontal. The prefrontal in Galianemys is very similar to that bone in *Cearachelys* and *Kurmademys*.

FRONTAL (figs. 81, 89, 97)

Preservation: The frontal in *Galianemys whitei* is preserved in AMNH 29987, 29986, 30036, 30027, 30028, 30555, and in MDEt 45.

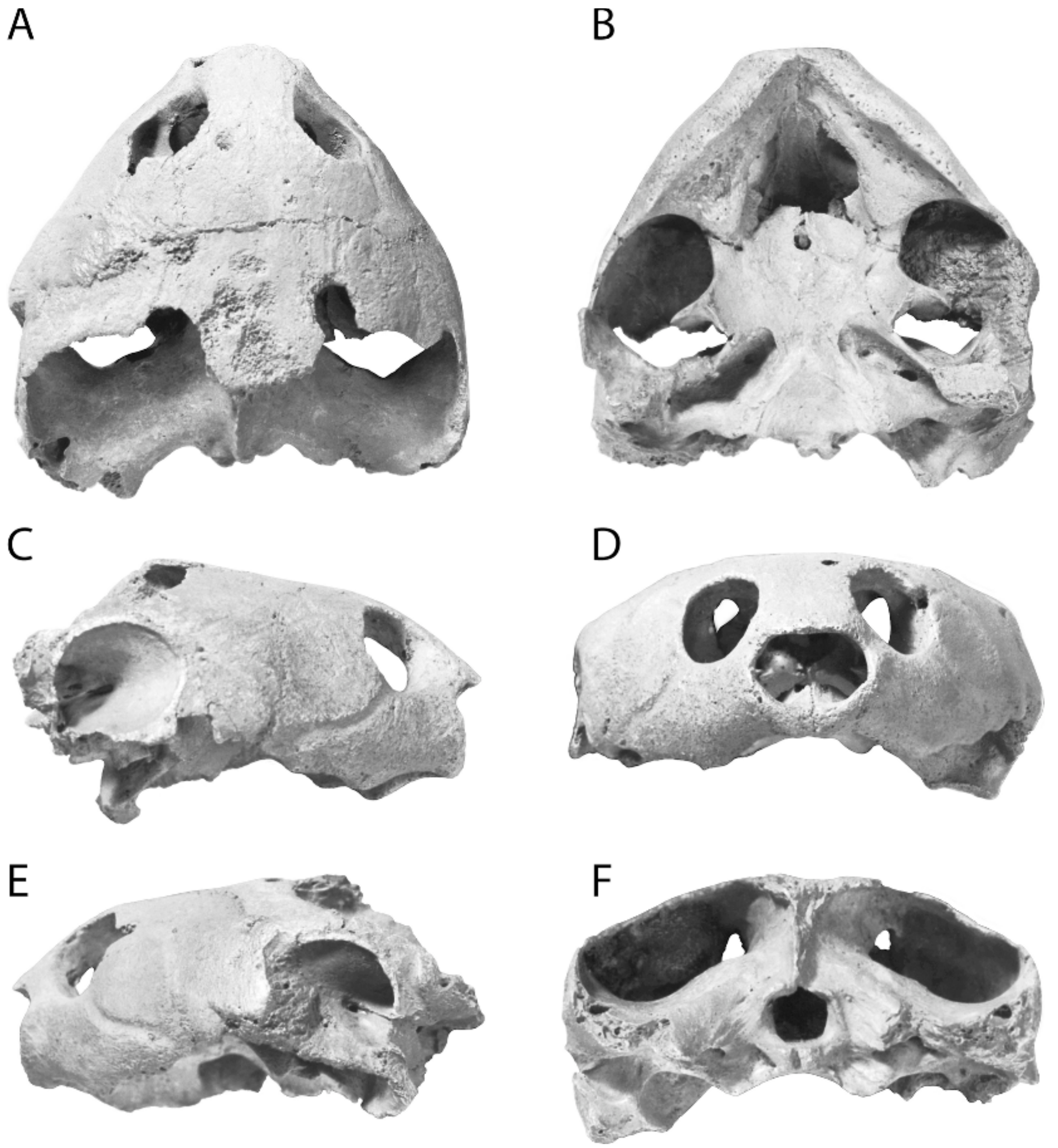

Fig. 83. *Galianemys emringeri* Gaffney, Tong, and Meylan, 2002. AMNH 30035. **A**, dorsal; **B**, ventral; **C**, right lateral; **D**, anterior; **E**, left lateral; **F**, posterior. [G. Giardina, del.]

In *Galianemys emringeri* it is preserved in AMNH 30037, 30040, 30035, and 29985. It is most visible in AMNH 30027, 29986, and 30037.

Contacts: The frontal contacts in *Galianemys* are with the prefrontal anteriorly, postorbital posterolaterally, parietal posteriorly, and the other frontal medially. These are the same in both *Galianemys* species and in *Cearachelys*.

Structures: The frontal is very similar in both *Galianemys* and *Cearachelys*. The ridge defining the sulcus olfactorius is deeper in *Galianemys* than in *Cearachelys*. There is some variation in this feature among the *Galianemys* specimens, but they are all deeper than in *Cearachelys*, *Kurmademys*, and the Pelomedusidae. The interorbital width is wider in *Galianemys* than in *Cearachelys*, *Kurmademys*, and the Pelomedusidae. This is

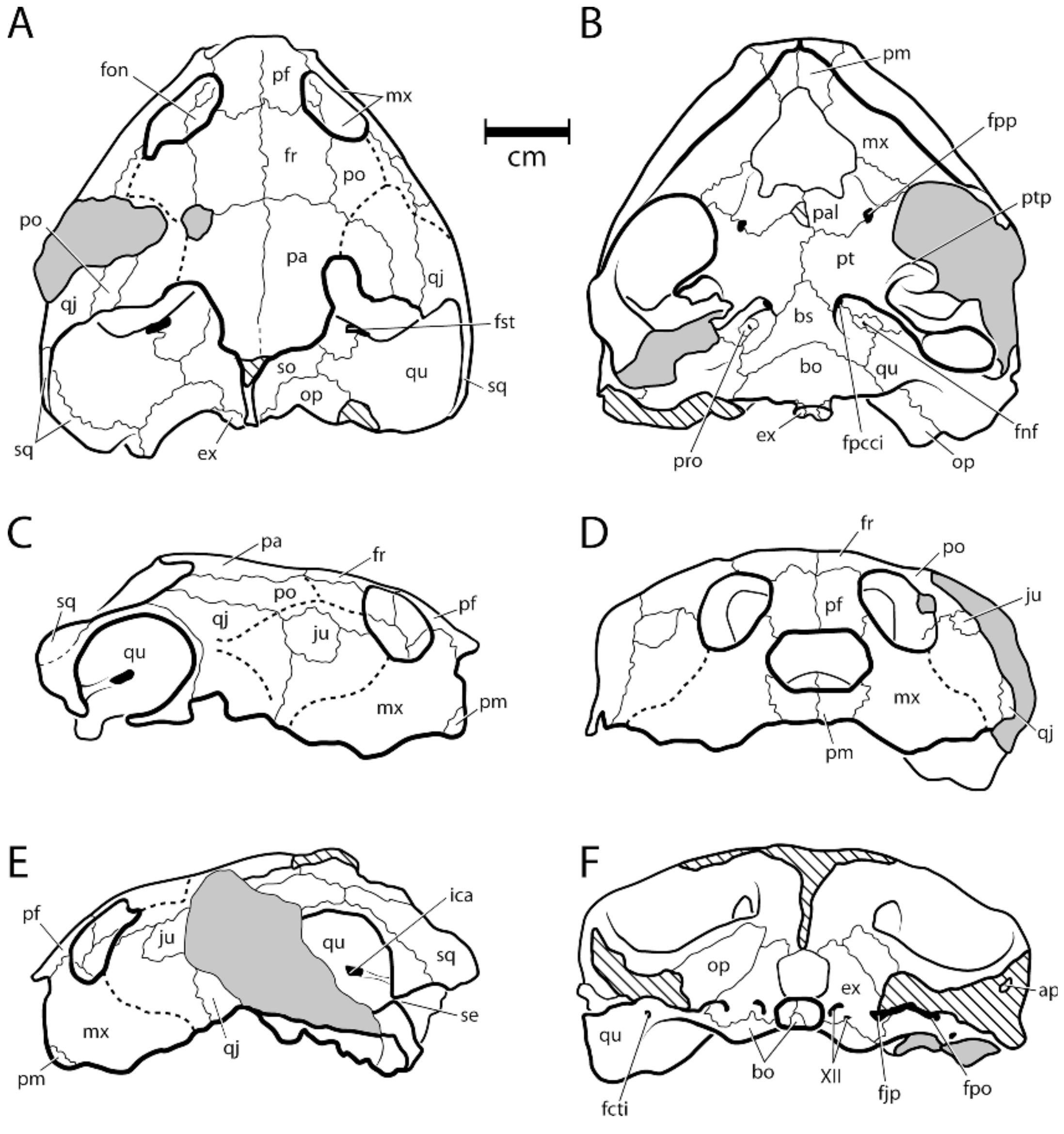

Fig. 84. *Galianemys emringeri* Gaffney, Tong, and Meylan, 2002. AMNH 30035. **A**, dorsal; **B**, ventral; **C**, right lateral; **D**, anterior; **E**, left lateral; **F**, posterior. [A.M. Phillips, del.]

the result of a greater overhang of the frontal over the fossa orbitalis lateral to the sulcus olfactorius.

PARIETAL (figs. 81, 89, 97)

Preservation: The parietal is preserved to some extent in all the *Galianemys* specimens. It is complete in AMNH 30028 and 30555 and is nearly complete in AMNH 29987 (all *Galianemys whitei*). In *Galianemys emringeri*, AMNH 30037 has the most complete parietals.

Contacts of dorsal plate: The parietal contacts in *Galianemys* are with the frontal anteriorly, the postorbital anterolaterally, and with the other parietal medially.

Structures of dorsal plate: The degree of emargination in *Galianemys* is similar to that seen in *Cearachelys* but is not as extensive. *Kurmademys* and the pelomedusids have the most extreme emargination, with *Cearachelys* being more covered and *Galianemys* more covered than *Cearachelys*. The temporal skull roof consists largely of parietal and postorbital. *Galianemys* is more emarginate than *Foxemys*. The other bothremydids do not have complete preservation of the roof for comparison.

In contrast to *Cearachelys*, *Kurmademys*, and pelomedusids, the parietal of *Galianemys* is wider posteriorly near the midline along the supraoccipital contact. Although the temporal emargination depth is not much less than in *Cearachelys*, the temporal opening in *Galianemys* is more covered due to the wider parietal roof along its posterior extension.

Contacts of processus inferior parietalis: The processus inferior parietalis (fig. 97) contacts the palatine anteroventrally, the pterygoid ventrally, the prootic posteroventrally, and the supraoccipital posteriorly, as in *Cearachelys*, the other Pelomedusoides, and most turtles.

Structures of processus inferior parietalis: The palatine has a dorsal extension, higher than the crista pterygoidea, so the processus inferior parietalis is deeper posteriorly than anteriorly. The processus is relatively long in contrast to most Taphrosphyini but like *Phosphatochelys*. The parietal forms the anterodorsal margin of the foramen nervi trigemini.

JUGAL (figs. 81, 89, 278, 280)

Preservation: The jugal is preserved in all specimens of both species of *Galianemys*. In AMNH 29985, the type of *Galianemys emringeri*, the jugal is incomplete posteriorly, but in AMNH 30037 and 30035 it is complete.

Contacts of lateral plate: The jugal in *Galianemys* contacts the postorbital dorsally, the maxilla anteroventrally, and the quadratojugal posteroventrally. These are as in *Cearachelys* except that the jugal of *Galianemys* is completely separated from the orbital margin by a wide postorbital-maxilla contact.

Structures of lateral plate: The jugal of *Galianemys* is excluded from the orbital margin by a postorbital-maxilla contact and is excluded from the cheek margin by a quadratojugal-maxilla contact.

Contacts of medial process: The medial jugal process is exposed in the orbital floor and the septum orbitotemporale (figs. 278, 280). In the orbital floor it contacts the maxilla anteriorly and anterolaterally, the palatine medially, and the postorbital posterodorsally. The postorbital and maxilla have a strong lateral contact widely separating the jugal exposure in the orbital floor from the cheek jugal exposure. In *Cearachelys* the postorbital and maxilla barely meet along the orbital margin barely separating the two parts of the jugal. The jugal is widely exposed on the orbital margin in *Kurmademys* and pelomedusids. The jugal is also exposed in the septum orbitotemporale. On its posterior surface, the jugal contacts the postorbital dorsomedially, the pterygoid posteromedially, and the maxilla anteroventrally. In *Galianemys whitei* the jugal also contacts the palatine ventromedially but in *Galianemys emringeri* this contact is smaller (AMNH 30037, 30035) or absent (AMNH 29985), and the maxilla and pterygoid are closer to each other.

Structures of medial process: The medial process of the jugal floors the orbit and forms part of the postorbital wall. In *Galianemys emringeri* the jugal is restricted to the vertical surface of the wall, but in *G. whitei* the jugal curves anteriorly and forms a small part of the triturating surface. This area of the triturating surface has a shallow but definitive depression in *G. whitei*, but it is flat in *G. emringeri*.

QUADRATOJUGAL (figs. 81, 89)

Preservation: The quadratojugal is present in *Galianemys whitei* specimens at least in part in AMNH 30036 and 29986, but it is most complete in AMNH 30028, 30555, and 29987. In *Galianemys emringeri* the quadratojugal is almost complete in AMNH 30035 and partial in AMNH 30037 and 30040.

Contacts: The quadratojugal contacts the maxilla anteroventrally, preventing exposure of the jugal on the ventral edge of the skull and producing the complete absence of a cheek emargination. Anteriorly the quadratojugal contacts the jugal and anterodorsally it contacts the postorbital. Posteriorly the quadratojugal has a long S-shaped contact with the quadrate; above this a narrow posterior process of the quadratojugal meets a narrow anterior process of the squamosal (preserved in AMNH 30040 and 30035 of *Galianemys emringeri*).

Structures: The quadratojugal is a large, flat plate that forms about half of the cheek in *Galianemys*. Cheek emargination as seen in *Kurmademys* is completely absent, and even the slight emargination seen in the cheek of *Cearachelys* is absent. Otherwise, the quadratojugal of *Galianemys* is very similar to that in *Cearachelys* in contacts, size, and shape.

SQUAMOSAL (figs. 81, 88, 89, 98, 284)

Preservation: The squamosal is present in AMNH 30037, 30040, and 30035 in *Galianemys emringeri*, and in AMNH 30028, 30027, 30036, 30555, 29987, and 29986 in *Galianemys whitei*.

Contacts: Squamosal contacts do not vary much in Pelomedusoides. The conical squamosal fits on the quadrate, contacts the opisthotic medially, and has a short anterior process reaching the quadratojugal anterodorsally.

Structures: The cone shape of the squamosal in *Galianemys* is very similar to that seen in *Cearachelys*. There is no vertical flange on its ventral surface, as in *Taphrosphys*.

POSTORBITAL (figs. 81, 89, 278)

Preservation: At least some of the postorbital is present in four *Galianemys emringeri* specimens and all seven *Galianemys whitei* skulls. Nearly complete postorbitals are in AMNH 30035, 30040, and 30037 for *G. emringeri* and AMNH 30028, 30555, and 29987 for *G. whitei*.

Contacts of lateral plate: The lateral plate of the postorbital forms part of the temporal roof and in *Galianemys* contacts the frontal anteromedially, the parietal posteromedially, the maxilla anteroventrally, the jugal ventrolaterally, and the quadratojugal posterolaterally.

Structures of lateral plate: The postorbital lateral plate forms most of the posterior orbital margin and extends posteriorly to reach the edge of the temporal margin.

Contacts of medial process: The medial process is exposed on both sides of the septum orbitotemporale with these contacts: palatine ventromedially, jugal ventrally, maxilla ventrolaterally, and frontal dorsomedially. In posterior view of the septum (fig. 278) the medial process of the postorbital has these contacts: parietal dorsomedially, jugal ventrolaterally, and pterygoid ventromedially. The strong postorbital-maxilla contact that broadly excludes the jugal from the orbital margin is unique among pleurodires.

Structures of the medial process: The medial process of the postorbital forms part of the roof and the lateral wall of the sulcus palatinopterygoideus and most of the septum orbitotemporale. All of these structures are very similar in *Galianemys* and *Cearachelys*.

PREMAXILLA (figs. 81, 82, 89, 96)

Preservation: The premaxilla is present in AMNH 30035 and 30037 in *Galianemys emringeri*, but in *Galianemys whitei* only the presumed juvenile, MDEt 45, and AMNH 30555, have the premaxilla preserved. This is unfortunate because, as preserved, this bone differs in the two species.

Contacts: The usual posterolateral contacts with the maxilla and with the other premaxilla on the midline occur in all four specimens. In AMNH 30037 and 30035 the vomer is not preserved and the premaxilla ends in a free margin on the apertura narium interna. But in MDEt 45 and AMNH 30555, the vomer is present and contacts the posteromedial margins of both premaxillae.

Structures on dorsal surface: In all four specimens the anterior margins of the premaxillae are broken, but they form the ventral margin of the apertura narium externa. In AMNH 30037 the premaxilla forms a high median ridge on the midline contact of the premaxillae, not seen in *Cearachelys* but similar to one in *Kurmademys*, partially dividing the fossa nasalis into paired choanal troughs. This ridge is not developed in MDEt 45, although whether this could be growth related is unknown. The ridge is not preserved in AMNH 30555.

Structures on ventral surface: The ventral surface of the premaxilla forms part of the labial ridge and the triturating surface. The premaxillary parts of these, as seen in the specimens available, are significantly different. In *Galianemys emringeri*, AMNH 30035 and 30037, the ridge is very thick, deep, and

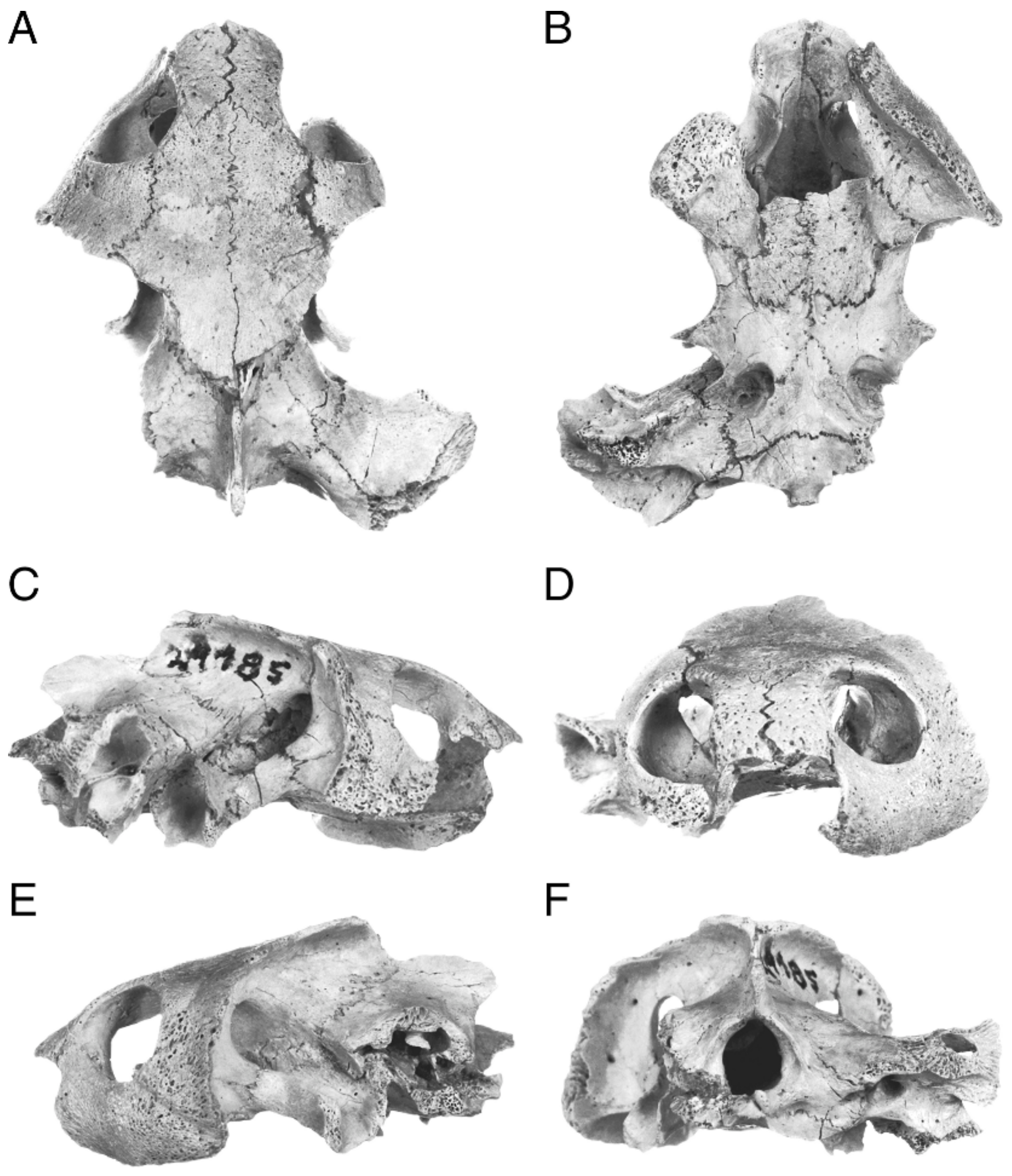

Fig. 85. *Galianemys emringeri* Gaffney, Tong, and Meylan, 2002. AMNH 29985 holotype. (From Gaffney, Tong, and Meylan, 2002) **A**, dorsal; **B**, ventral; **C**, right lateral; **D**, anterior; **E**, left lateral; **F**, posterior. [E. Heck, del.]

blunt. In *Galianemys whitei*, MDEt 45 and AMNH 30555, it is thin, shallow, and acute. Some degree of this variation is presumed to persist in the adult because *G. emringeri* has a thicker and blunter labial ridge than does *G. whitei*. In AMNH 30037 the premaxilla has the thick labial ridge anteriorly; posterior to that is an inclined triturating surface; and posterior to that is a more inclined surface forming a deep median concavity. Where the two surfaces meet, the foramen praepalatinum penetrates the bone. In MDEt 45 the

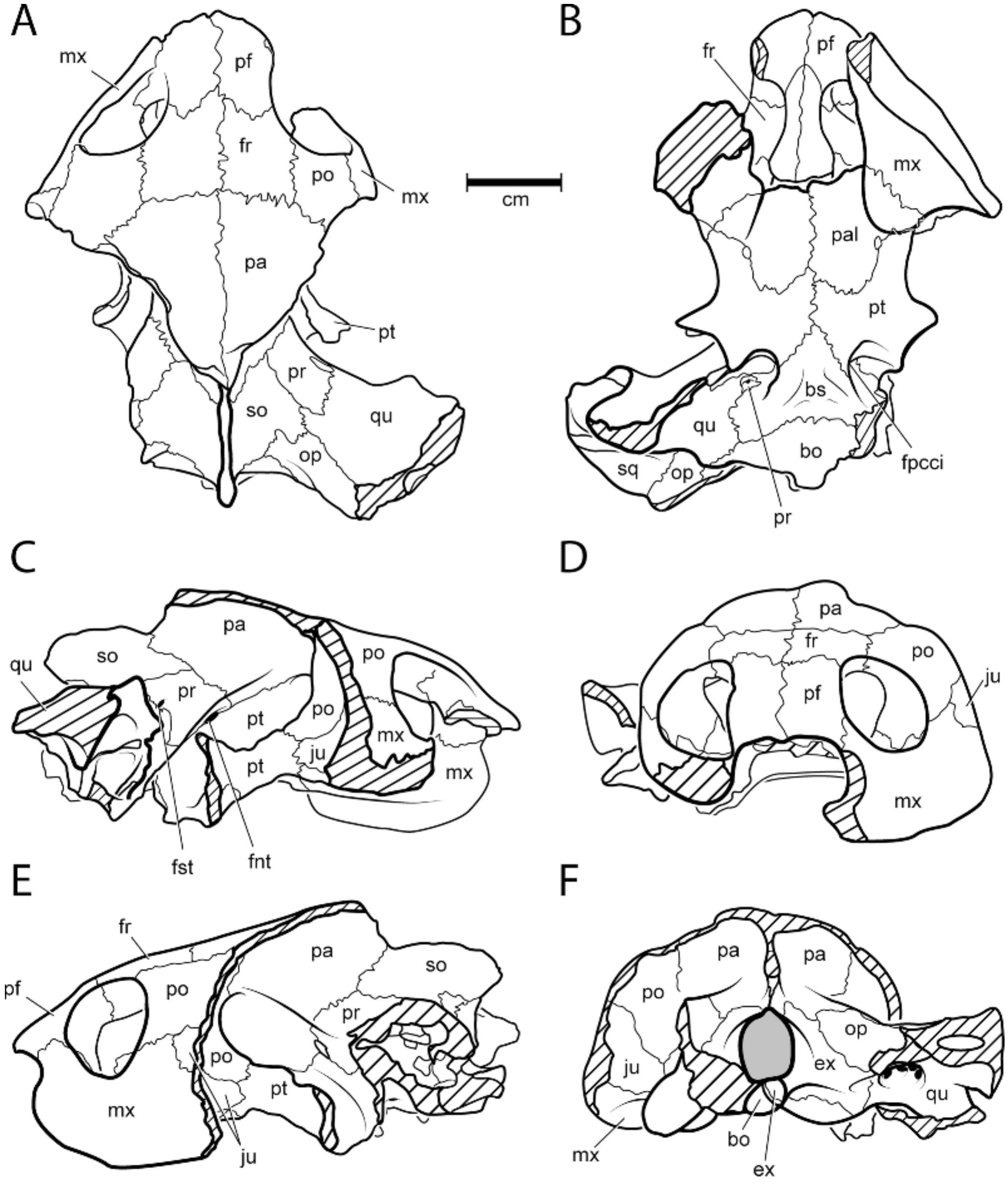

Fig. 86. *Galianemys emringeri* Gaffney, Tong, and Meylan, 2002. AMNH 29985 holotype. (From Gaffney, Tong, and Meylan, 2002) **A**, dorsal; **B**, ventral; **C**, right lateral; **D**, anterior; **E**, left lateral; **F**, posterior. [A.M. Phillips, del.]

foramen is visible on each side, but the entire surface posterior to the labial ridge is flat; there is no inclination and no median concavity. In MDEt 45, a medial process of the maxilla reaches the vomer to prevent the premaxilla from reaching the apertura narium interna. It is, of course, possible that MDEt 45 is yet a third species distinct from *G. emringeri* and *G. whitei*, but it does agree with *G. whitei* in other features.

MAXILLA (figs. 81, 82, 89, 90, 97, 280)

Preservation: The maxilla is present and nearly complete in all seven *Galianemys* *whitei* skulls and in four of the *Galianemys emringeri* skulls (AMNH 30037, 29985, 30035, and 30040); most show the sutures clearly.

Contacts of vertical plate: The vertical plate of the maxilla contacts the premaxilla anteromedially, the postorbital posterodorsally, the jugal posterodorsally (posterior to the postorbital), and the quadratojugal posteriorly.

Structures of vertical plate: The vertical plate of the maxilla forms the ventral orbital margin, the labial ridge of the triturating surface, and the anterior part of the cheek. The dorsal process of the maxilla lies between the apertura narium externa, and the orbit and is similar in size to that in *Cearachelys*, but thicker than in *Kurmademys*.

The snout just anterior to the orbit of some *Galianemys* specimens is more pinched, bent toward the midline, than others. In AMNH 29987 the pinching is most pronounced but other skulls of *Galianemys whitei*, AMNH 30036, 30028, 30555, and 29986, do not show this. This area of the maxilla in AMNH 29987 is rugose, and the pinching may be a pathology or just individual variation. The degree of pinching, however, is the same on both sides. In *Galianemys emringeri* there is a slight pinching of the snout in the same area, but not to the extent seen in AMNH 29987. At present we interpret this as an individual variation of AMNH 29987.

Contacts of horizontal plate: The horizontal plate (in ventral view) contacts the premaxilla anteromedially, the palatine posteromedially, and the jugal posteriorly. Among the 10 *Galianemys* skulls, the vomer is preserved in AMNH 30555 (fig. 96), *G. whitei*, and MDEt 45, a presumed juvenile of *G. whitei*. In both specimens the maxilla on both sides sends a process medially to meet the vomer and prevent the premaxilla from reaching the margin of the apertura narium interna. The condition is not determinable in either *Cearachelys* or *Kurmademys*.

Structures of horizontal plate: The horizontal plate of the maxilla forms the floor of the orbit in dorsal view (fig. 280). The maxilla forms the ill-defined lateral edge of the foramen orbito nasale, as in *Cearachelys* and other Pelomedusoides.

The horizontal plate in ventral view forms most of the triturating surface (figs. 82, 90). The triturating surface in *Galianemys* is very similar to that in *Cearachelys* in width and shape. It is slightly narrower than in *Kurmademys*. The labial ridge in *Galianemys* is distinctly thicker in both species than in *Cearachelys* and *Kurmademys*. The ridge is also thicker in *Galianemys emringeri* than in *Galianemys whitei*. In AMNH 30035 the ridge is thicker than in any other *Galianemys* specimen, but AMNH 29985 and 30037, the other two *G. emringeri* skulls, also have a thicker labial ridge than in any *G. whitei* skull. The type of *G. whitei*, AMNH 29987, has the thickest labial ridge in that species but it is still narrower than any of the *G. emringeri* skulls. Also, the labial ridge in *G. whitei* is relatively straight, but in *G. emringeri*, particularly AMNH 30035 and 30037, the ridge has a slight medial trend anteriorly, making it thicker there.

At this point we note that AMNH 30035 (figs. 81–84) differs from other *Galianemys emringeri* skulls in being much larger, wider, more robustly ossified, and in having thicker labial ridges. Because it has the other features of *G. emringeri*, we include it in this species. The maxilla of this skull is particularly distinct in its more massive form and ossification.

The triturating surface is flat in the skulls of *Galianemys emringeri*, but in *G. whitei* there is a very shallow concavity formed mostly by the jugal, which is exposed on the triturating surface in this species. The palatine forms a significant part of the triturating surface in *Galianemys*, as in *Cearachelys* and *Kurmademys*.

VOMER (figs. 89, 96)

Preservation: The vomer is present only in two specimens of *Galianemys*, MDEt 45 and AMNH 30555, both *Galianemys whitei*.

Contacts: The vomer contacts the premaxilla anteriorly, the maxilla anterolaterally, and the palatines posteriorly.

Structures: The vomer in *Galianemys* is slightly narrower than in *Cearachelys*, but it is expanded at both ends and separates the apertura narium interna. In contrast to most turtles that have the paired foramen praepalatinum on the vomer near the premaxilla

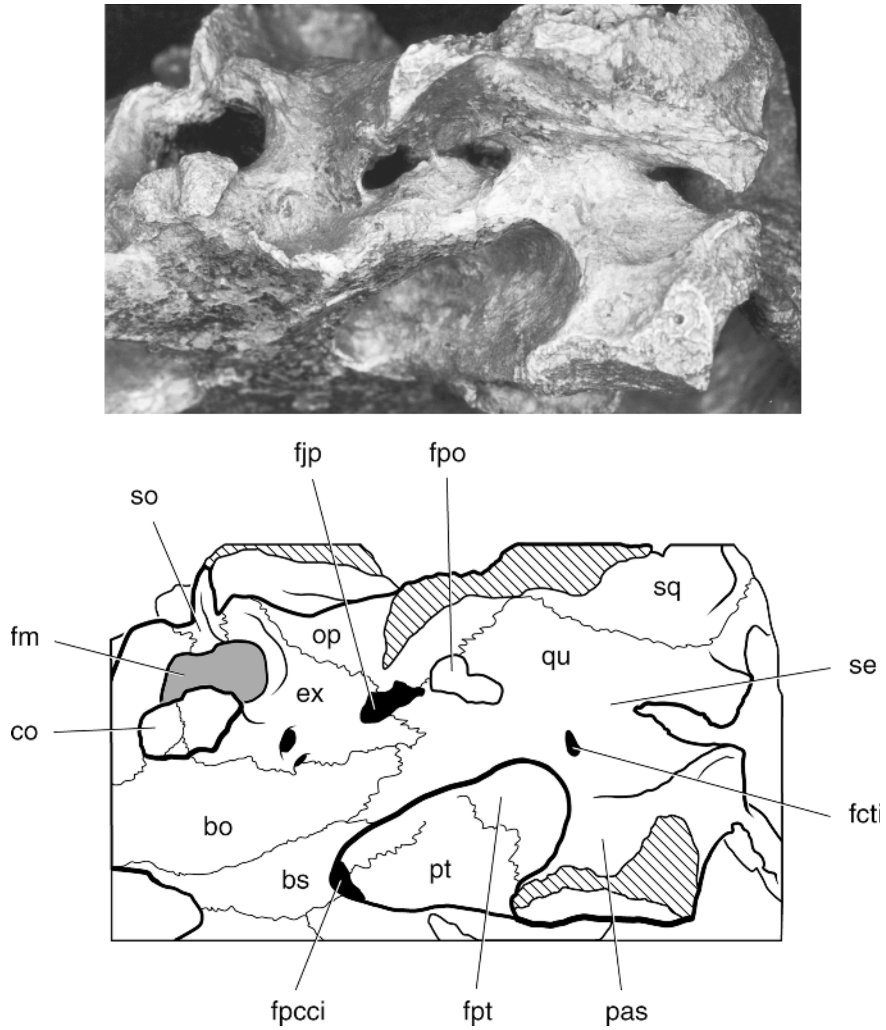

Fig. 87. *Galianemys emringeri* Gaffney, Tong, and Meylan, 2002. AMNH 30035. Posterior oblique view reversed from left side. [A. Venjara and E.S. Gaffney, del.]

suture, in *Galianemys* the foramina are in the middle of the premaxilla and not in the vomer.

PALATINE (figs. 81, 82, 89, 90, 97)

Preservation: The palatine is present in all seven *Galianemys whitei* skulls and in four of the *Galianemys emringeri* skulls. It is missing in MDEt 46 and AMNH 30026. Only MDEt 45 has the thin, original anterior margin completely preserved.

Contacts: The palatine contacts the vomer anteromedially (preserved only in AMNH 30555 and MDEt 45), the maxilla anterolaterally, the other palatine medially, the pterygoid posteriorly, and the jugal posterolaterally (except in AMNH 29985, see Jugal). On the dorsal surface the palatine contacts the parietal posteriorly, the jugal medially, the maxilla anteromedially, and the postorbital laterally (fig. 280).

Structures on dorsal surface: On the dorsal surface the palatine forms the posteromedial part of the orbital floor and the posterior margin of the foramen orbitonasale. There is a low dorsal process that meets

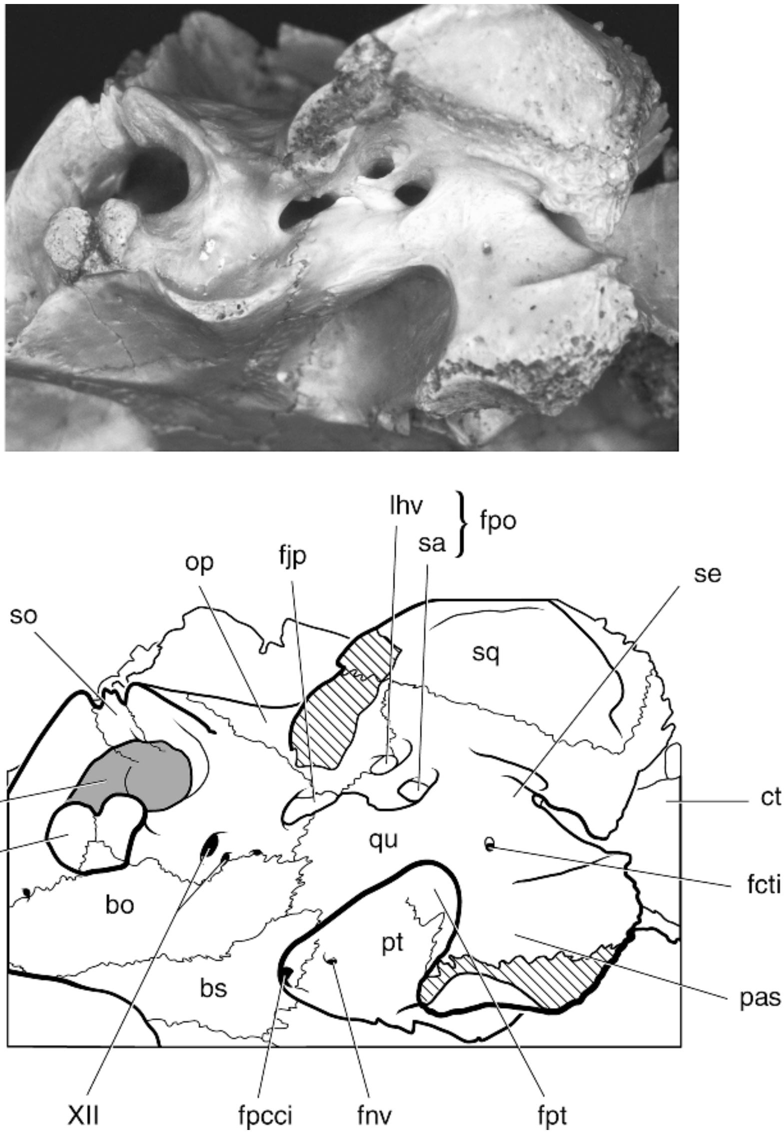

Fig. 88. *Galianemys emringeri* Gaffney, Tong, and Meylan, 2002. AMNH 30037. Posterior oblique view reversed from left side. [A. Venjara and E.S. Gaffney, del.]

the processus inferior parietalis (fig. 97). Lateral to this the palatine forms the anterior floor of the sulcus palatinopterygoideus.

Structures on ventral surface: Basically a flat bone, the palatine has different relations to surrounding bones on its ventral compared with its dorsal surfaces. On the ventral surface it forms the posteromedial part of the triturating surface and the posterior part of the choanal openings. These are all similar to *Cearachelys*. Posterolaterally the palatine forms the medial half of the foramen palatinum posterius. The foramen lies along a strong anterolateral process that is better developed in *Galianemys* than in *Cearachelys* and *Kurmademys*.

QUADRATE (figs. 81, 89, 284)

Preservation: The quadrate is present in all 13 *Galianemys* skulls, although it is detached in MDEt 45 and incomplete in AMNH 29985. All other specimens have at least one complete quadrate.

Contacts on lateral surface: In lateral view the quadrate contacts the quadratojugal anteriorly and the squamosal posterodorsally.

Structures on lateral surface: In lateral view the quadrate in *Galianemys* (fig. 284) does not form part of the temporal margin due to the quadratojugal-squamosal contact. The cavum tympani and its associated structures dominate the lateral view. The cavum itself is slightly deeper in *Galianemys* than in *Cearachelys*, but as in *Cearachelys*, there is no fossa precolumellaris, a structure seen in *Kurmademys*. The incisura columellae auris is completely closed by the quadrate and separated from the eustachian tube opening by bone in *Galianemys*. In *Cearachelys* the incisura is open, but it is closed in *Kurmademys* as in *Galianemys* (see also figs. 303 and 304 for distribution of these characters). The incisura in *Galianemys* is a teardrop-shaped foramen with the acute tip pointed posteriorly, in contrast to the symmetric oval of *Kurmademys* and most bothremydids. The apex of the teardrop shape in *Galianemys* is continued posteriorly as a trough that opens into the sulcus eustachii (the eustachian tube notch).

The antrum postoticum in *Galianemys* (fig. 284) is present and completely developed and is best seen in AMNH 30037, 29985 (internally, with the squamosal removed), and 30027. Its size varies slightly but perceptibly among the available skulls. It is smaller in AMNH 29987, 30028, and 29986, all *G. whitei*, and larger in AMNH 29985, 30037, and 30035, all *G. emringeri*. This is consistent with the recognition of two species, but AMNH 30036, a specimen of *G. whitei*, has a larger antrum, similar to that in *G. emringeri*. Among other genera, the antrum postoticum of *Galianemys* is smaller than that in *Cearachelys* and much smaller than that in *Kurmademys* and pelomedusids. It is larger, however, than in *Taphrosphys* and *Bothremys*.

The groove for the eustachian tube, the sulcus eustachii, in *Galianemys* is a nearly enclosed oval trending dorsomedially to ventrolaterally (fig. 284). It is open at its lateral end. It is narrow and extends for half of the distance between the incisura collumellae auris and the edge of the cavum tympani; there is no bone covering the other half. In *Kurmademys* the eustachian opening is wide open laterally, not constricted. In *Cearachelys* the sulcus eustachii and the incisura columellae auris are confluent. In other bothremydids, such as *Taphrosphys* and *Bothremys*, the sulcus eustachii is more widely open laterally and farther separated from the incisura columellae auris.

Contacts on dorsal and anterior surface: The quadrate contacts the prootic anteromedially, the supraoccipital medially, the squamosal posterolaterally, and the opisthotic posteromedially. The supraoccipital contact occurs in most bothremydids, except the Taphrosphyini and *Zolhafah*.

Structures on dorsal and anterior surface: The foramen stapedio-temporale in *Galianemys*, formed in the quadrate-prootic suture, is on the anterior surface of the otic chamber (fig. 97), as in nearly all other bothremydids, but it is not very close to the foramen nervi trigemini, as in *Bothremys* and other genera. In *Kurmademys* this foramen is slightly more posterior, just enough to make it more visible in dorsal view. It is only slightly more anterior in *Kurmademys* than in pelomedusids, and we judge the condition to be the same in both and primitive with respect to all other bothremydids.

Contacts on ventral surface: In ventral view the quadrate contacts the pterygoid anteromedially, the basisphenoid medially, the basioccipital posteromedially, and the squamosal posterolaterally. In *Galianemys emringeri* the quadrate forms the posterior part of the deep fossa pterygoidea that exposes the prootic, so in that species there is a small quadrate-prootic contact.

Structures on ventral surface: On the ventral surface, the quadrate forms the lateral margin of the foramen posterius canalis carotici interni in *Galianemys whitei*, but not in *G. emringeri* (see Pterygoid for discussion). In *G. emringeri* the quadrate and the prootic form a portion of the posterior wall of the large fossa pterygoidea (see Pterygoid for discussion). The condylus mandibularis in *Galianemys* is very similar in both species in position and shape. The condylus mandibularis is in about the same position with

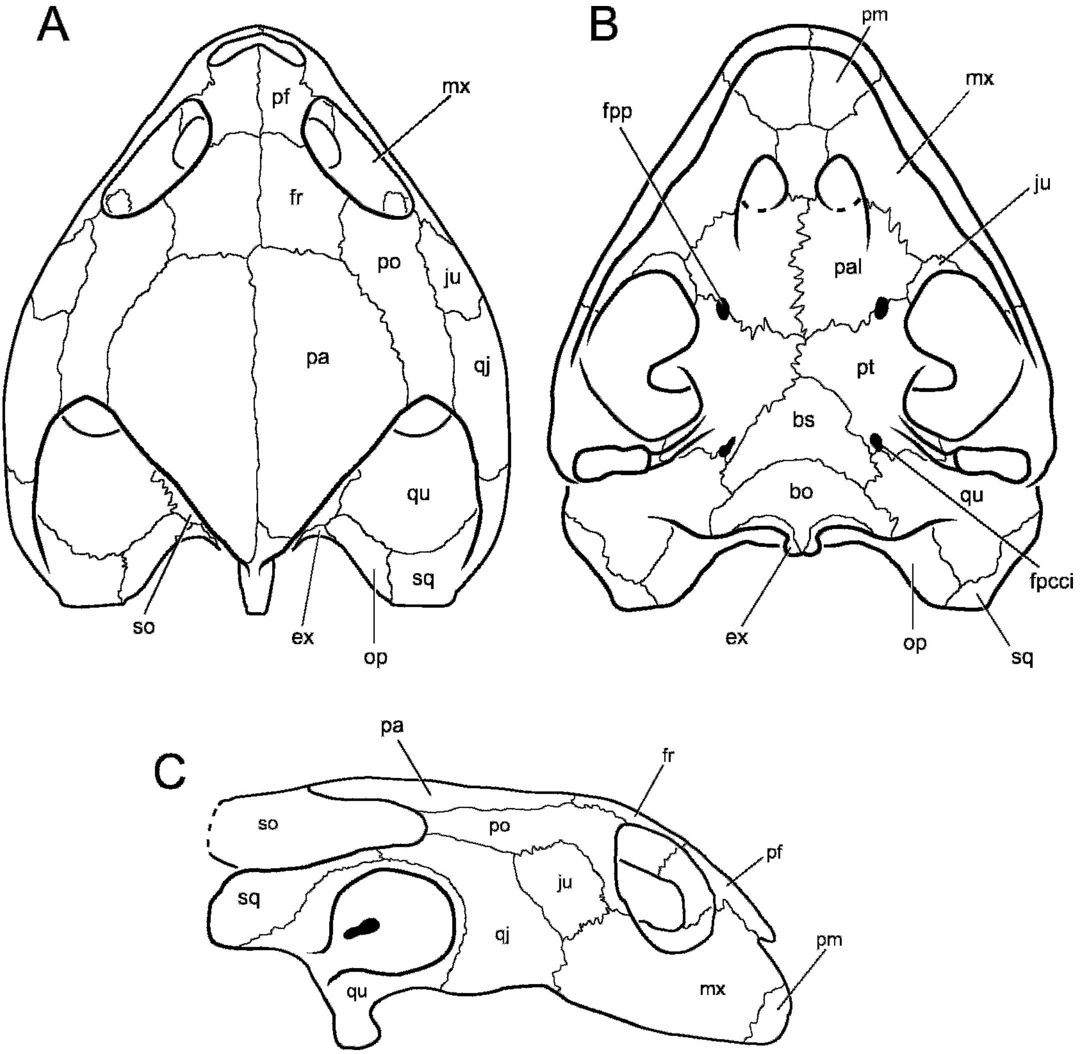

Fig. 89. *Galianemys whitei* Gaffney, Tong, and Meylan, 2002. Partially restored skull based on AMNH 30555. [E. Ullo, del.]

respect to the condylus occipitalis in *Cearachelys* and *Galianemys*, but in *Kurmademys* the condylus mandibularis is more anteriorly placed. The foramen for the chorda tympani is preserved in nearly all the *Galianemys* skulls and it is very close to its position in pelomedusids.

Contacts in posterior view: The quadrate in *Galianemys* contacts the squamosal dorsolaterally, the opisthotic dorsomedially, the exoccipital medially, and the basioccipital ventromedially.

Structures in posterior view: In posterior view the quadrate forms a number of structures in the occipital area (figs. 87, 88, 98–100). The quadrate forms the lateral margin of the fenestra postotica and its subdivisions. In *Galianemys* the fenestra postotica is preserved in nine skulls. In two of these the fenestra is subdivided into smaller foramina; in the rest there may be low ridges or spurs but these do not connect to completely subdivide the fenestra. The subdivided specimens are AMNH 30037, a skull of *Galianemys emringeri*, and AMNH 30027, a skull of *G. whitei*. Neither species shows more of a tendency toward subdivision than the other among the

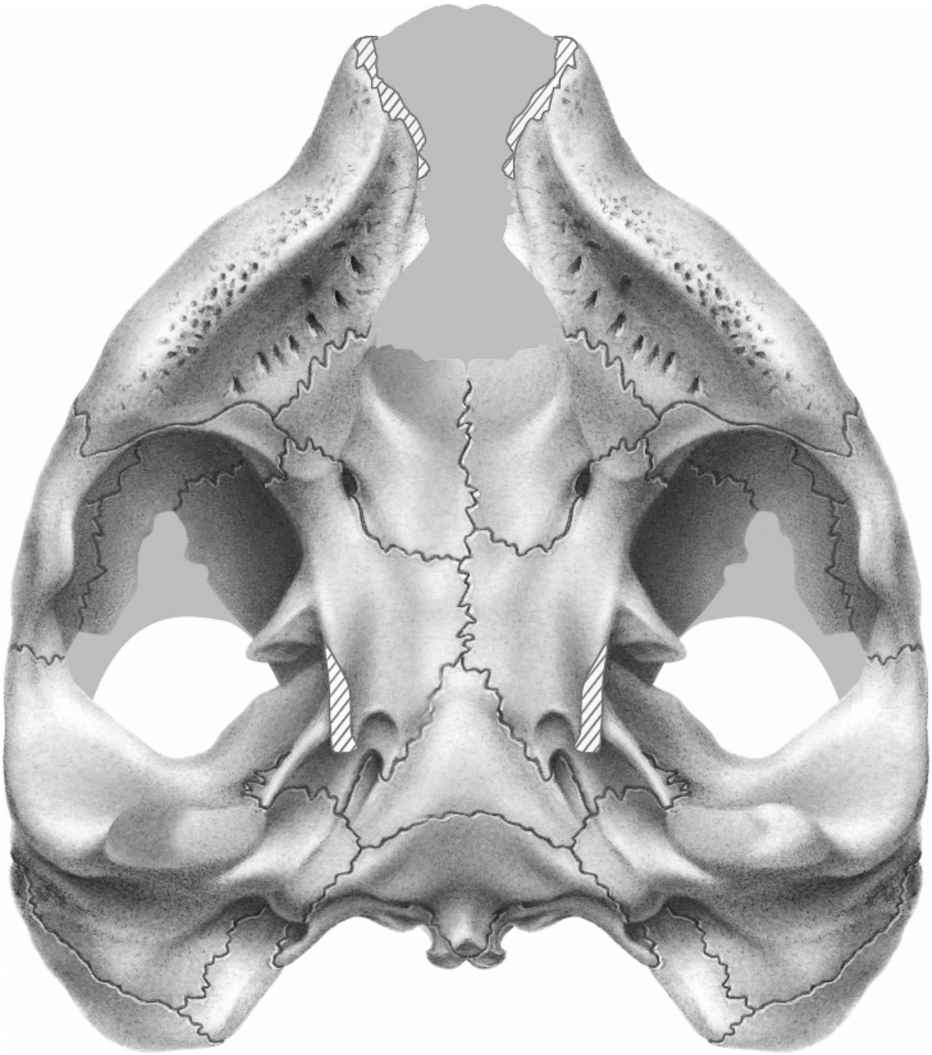

Fig. 90. *Galianemys whitei* Gaffney, Tong, and Meylan, 2002. Partially restored ventral view of skull based on AMNH 29987, holotype. For more detailed view of area around foramen posterius canalis carotici interni, see figure 277C. [V. Storfer, del.]

available material. In AMNH 30037 the fenestra postotica is subdivided into two foramina, an upper one, presumably for the stapedial artery, and a lower one, presumably for the lateral head vein. In AMNH 30027, however, there are three foramina as a result of the lower foramen being further subdivided into two. One of these must be the lateral head vein, but the other is a mystery. Wow. One foramen is ventral and the other ventrolateral. In AMNH 30027 this subdivision into three foramina was present on both sides, but was broken during preparation. The other skulls of both *Galianemys* species have variably developed grooves or spurs that are less ossified indications of these structures. In any case, the subdivision of the fenestra postotica in *Galianemys* is interpreted as an individual variation. In most individuals it is open as a narrow gap from the foramen jugulare posterius to the aditus canalis stapediotemporalis, a condition also seen in *Cearachelys*.

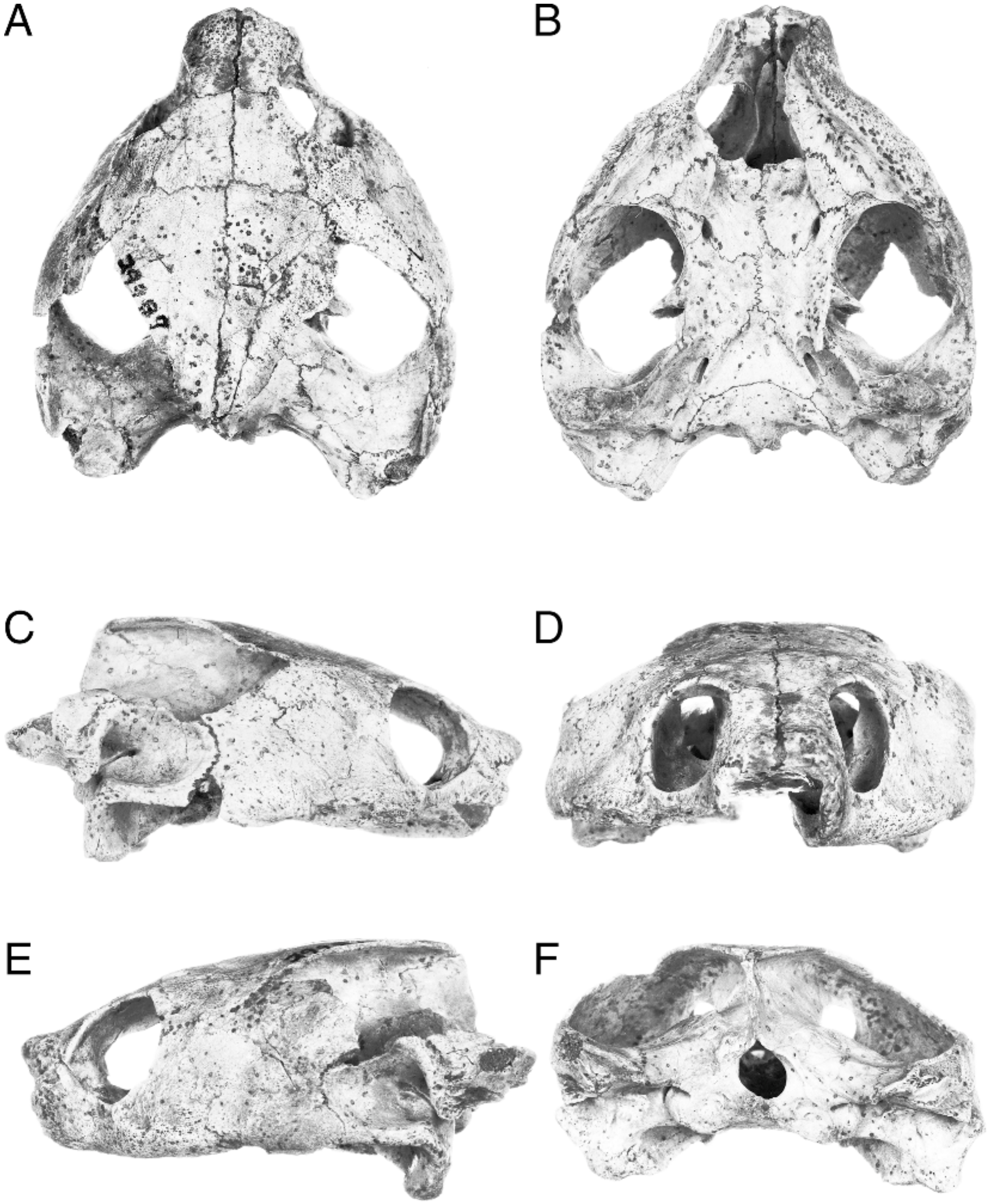

Fig. 91. *Galianemys whitei* Gaffney, Tong, and Meylan, 2002. AMNH 29987, holotype. (From Gaffney, Tong, and Meylan, 2002) **A**, dorsal; **B**, ventral; **C**, right lateral; **D**, anterior; **E**, left lateral; **F**, posterior. [E. Heck, del.]

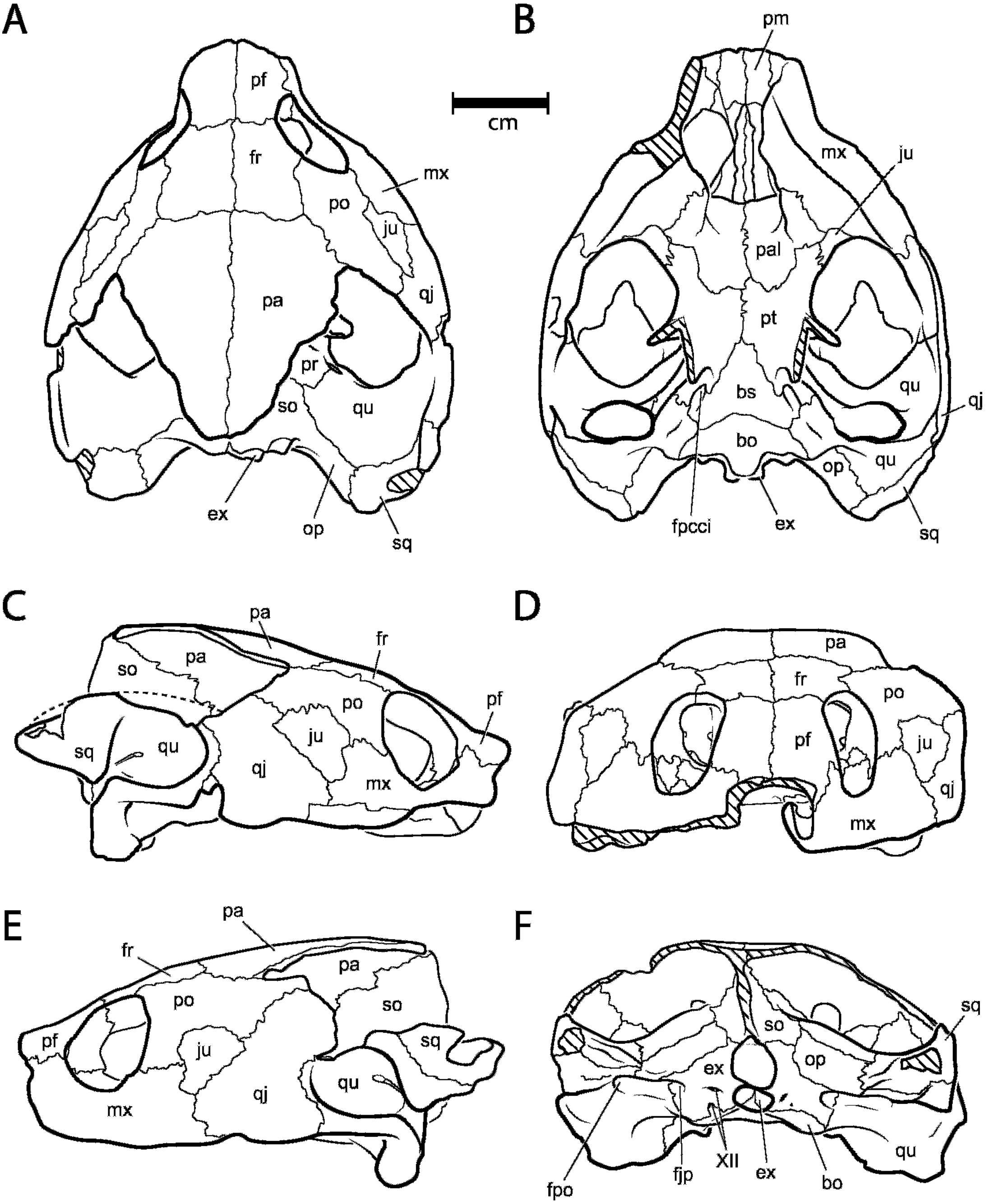

Fig. 92. *Galianemys whitei* Gaffney, Tong, and Meylan, 2002. AMNH 29987 holotype. (From Gaffney, Tong, and Meylan, 2002) **A**, dorsal; **B**, ventral; **C**, right lateral; **D**, anterior; **E**, left lateral; **F**, posterior. [A.M. Phillips, del.]

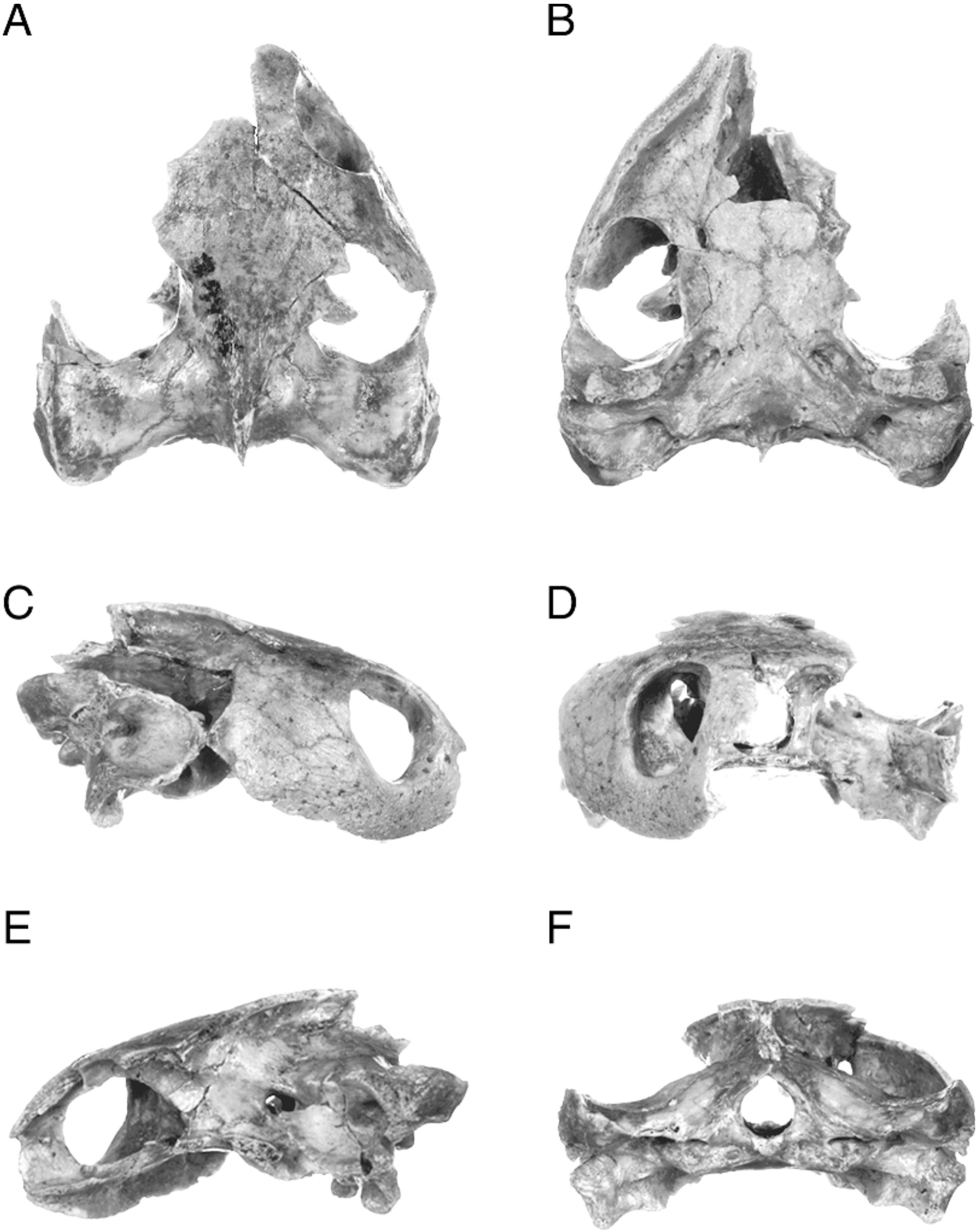

Fig. 93. *Galianemys whitei* Gaffney, Tong, and Meylan, 2002. AMNH 29986. **A**, dorsal; **B**, ventral; **C**, right lateral; **D**, anterior; **E**, left lateral; **F**, posterior. [K. Luckenbill, del.]

PTERYGOID (figs. 81, 82, 89, 90, 97, 277)

Preservation: The pterygoid is present in the three adult *Galianemys emringeri* skulls, AMNH 30035, 30037, and 29985, and in all six adult *G. whitei* skulls, AMNH 30036, AMNH 29987, 29986, 30028, 30555, and 30027. Among the supposed juveniles it is present on both sides in *Galianemys emrin-*

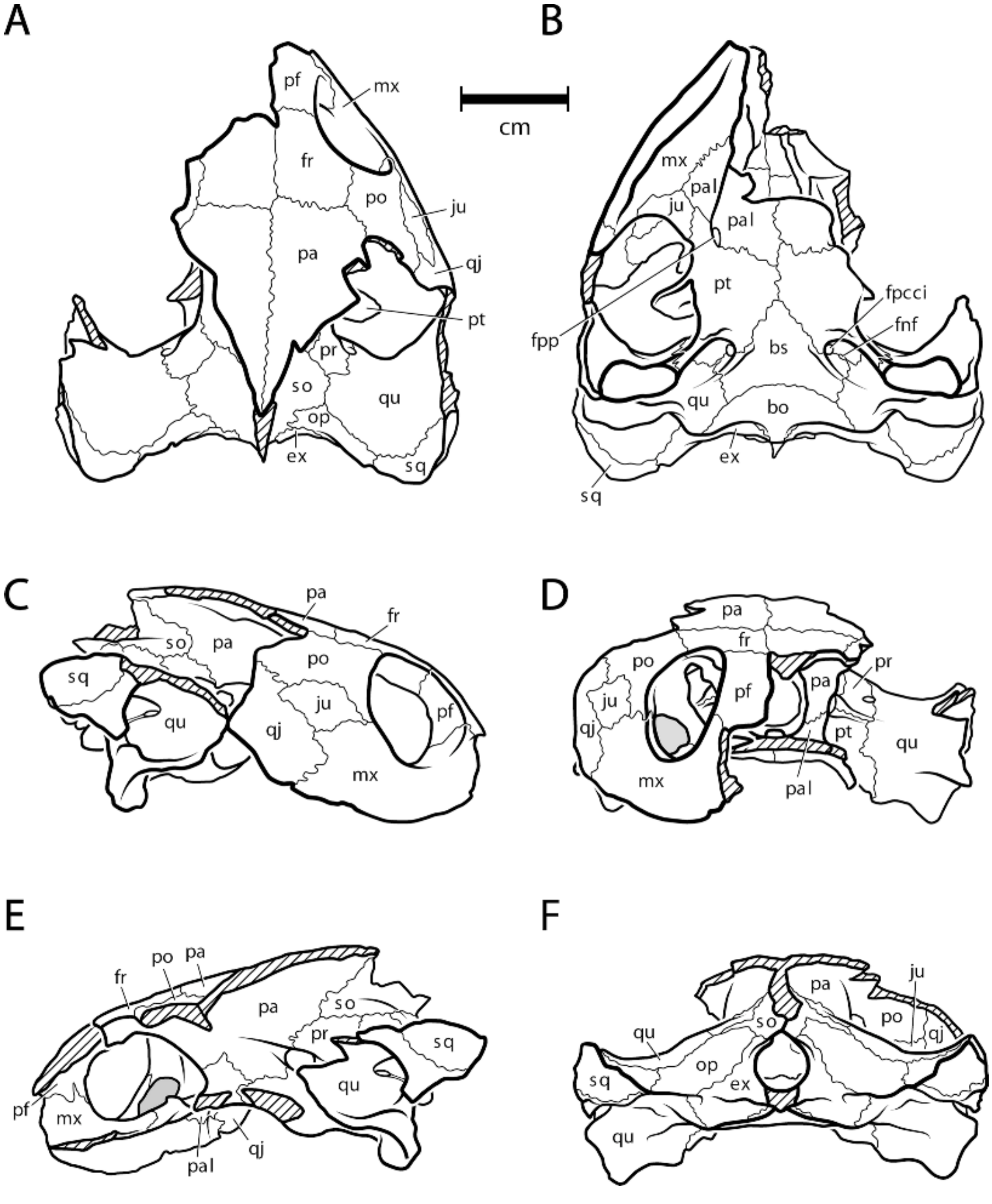

Fig. 94. *Galianemys whitei* Gaffney, Tong, and Meylan, 2002. AMNH 29986. **A**, dorsal; **B**, ventral; **C**, right lateral; **D**, anterior; **E**, left lateral; **F**, posterior. [K. Luckenbill, del.]

geri, AMNH 30040, but only partially in *Galianemys whitei*, MDEt 45.

Contacts on ventral surface: On the ventral surface, the pterygoid in *Galianemys* has the usual pelomedusoid contacts: palatine anteriorly, the other pterygoid anteromedially, basisphenoid posteromedially, and quadrate posterolaterally. In *Galianemys emringeri* there is also a posterior contact with the prootic that is present but not visible ventrally in *Galianemys whitei*.

Structures on ventral surface: On the ventral surface the pterygoid of both species shows variation in the structures around the

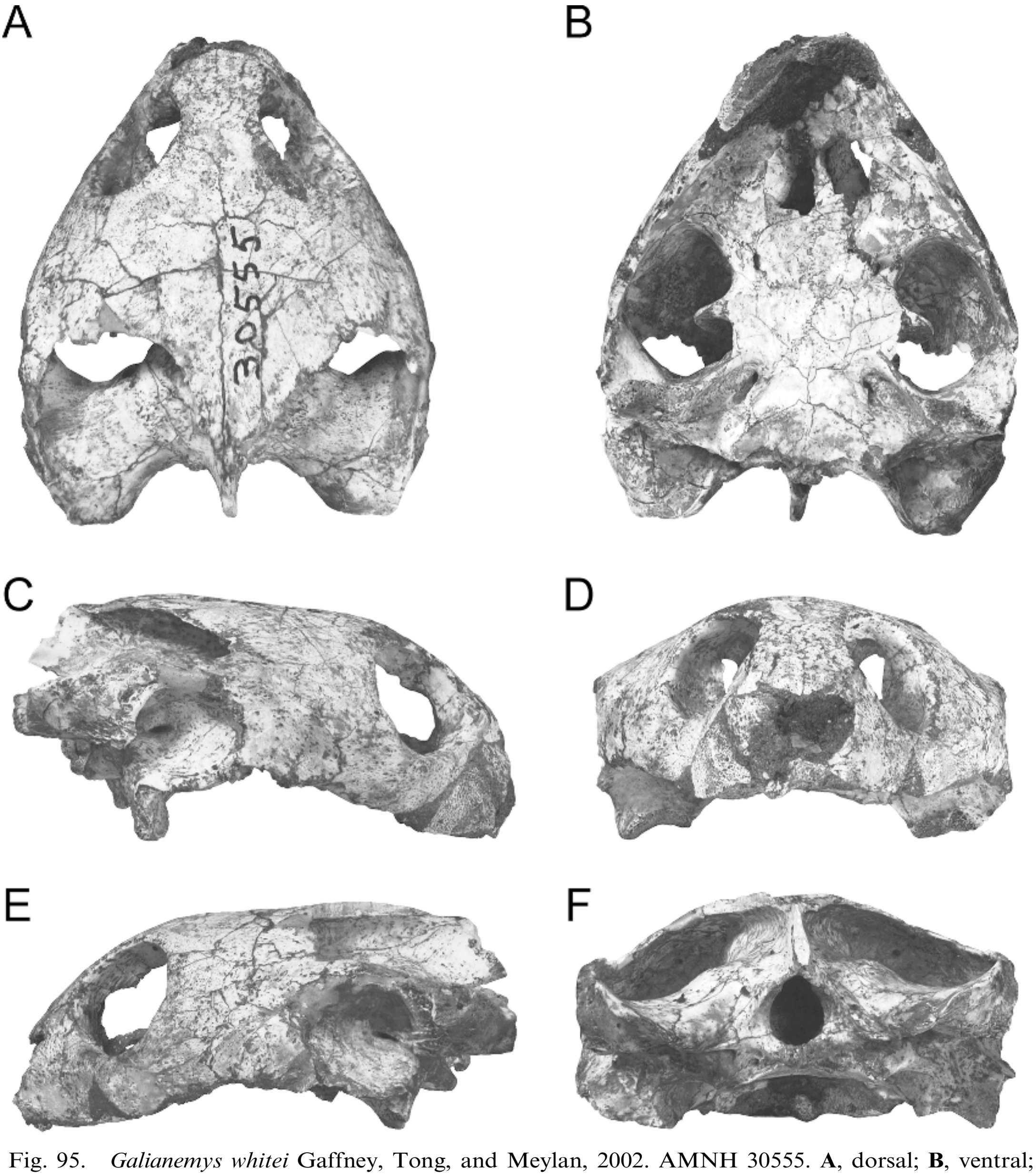

Fig. 95. *Galianemys whitei* Gaffney, Tong, and Meylan, 2002. AMNH 30555. **A**, dorsal; **B**, ventral; **C**, right lateral; **D**, anterior; **E**, left lateral; **F**, posterior. [K. Luckenbill, del.]

foramen posterius canalis carotici interni (fig. 277). In *Galianemys whitei* the foramen is formed anteriorly by the pterygoid and posteriorly by the basisphenoid. There is a slightly depressed area marking the attachment site of the M. pterygoideus, but the area medial to the quadrate ramus of the pterygoid in *G. whitei* is not a deep depression. In *G. emringeri*, however, the M. pterygoideus attachment area, the fossa pterygoidea, is a deep depression, as seen in some other bothremydids like *Foxemys*, *Polysternon*, *Nigeremys*, and *Arenila* (see also fig. 305 for distribution of this character).

This development of the fossa pterygoidea in *G. emringeri* "erodes" the quadrate, pterygoid, and basisphenoid as described in *Kurmademys* (above, *Kurmademys*, Ptery-

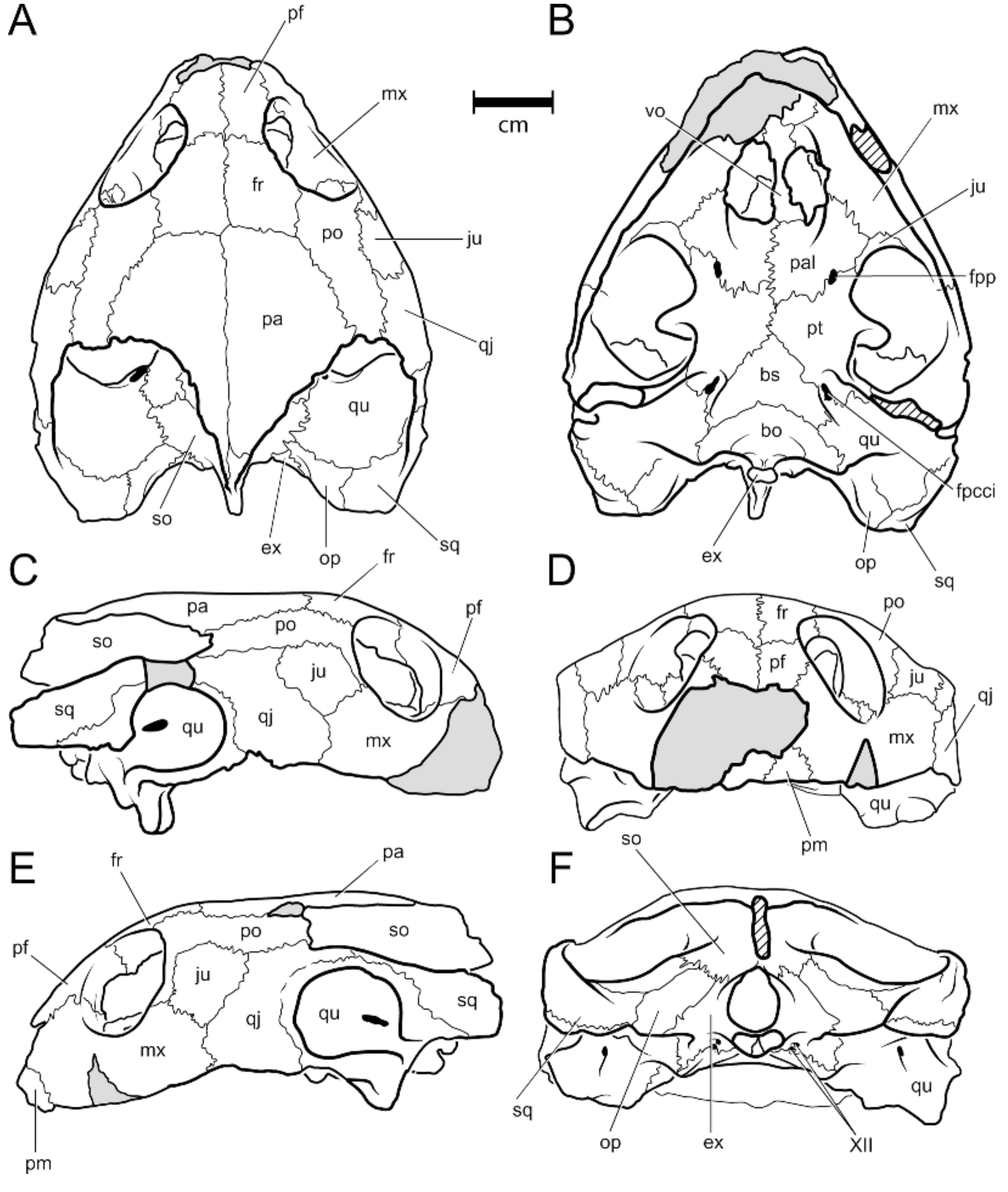

Fig. 96. *Galianemys whitei* Gaffney, Tong, and Meylan, 2002. AMNH 30555. **A**, dorsal; **B**, ventral; **C**, right lateral; **D**, anterior; **E**, left lateral; **F**, posterior. [K. Luckenbill, del.]

goid) and exposes structures present but not visible in the more ossified *G. whitei*. Thus, in *G. emringeri*, the foramen posterius canalis carotici interni is more anterior and formed mostly by the basisphenoid, with only a small pterygoid contribution to its margin. The deep fossa pterygoidea in *G. emringeri* exposes the prootic and the foramen nervi facialis within the prootic. In the anterior wall of the fossa pterygoidea the pterygoid has a small foramen exposed: the foramen nervi vidiani. In CT scans of AMNH 29987 and 30035 the entire canalis nervi vidiani can be followed.

The foramen palatinum posterius in *Galianemys* is formed by palatine and pterygoid, as in *Cearachelys* and *Kurmademys*. The processus trochlearis pterygoidei is very similar in both species of *Galianemys* and is similar in size and orientation to that process in *Kurmademys* and *Cearachelys*.

Contacts on dorsal surface: On the dorsal surface, the pterygoid of *Galianemys* also has the usual pelomedusoid contacts. The processus trochlearis pterygoidei contacts the postorbital dorsolaterally, the jugal anterolaterally, and the palatine anteroventrally. The crista pterygoidea contacts the palatine anteriorly, the parietal dorsally, the prootic posterodorsally, and the quadrate posteriorly.

Structures on dorsal surface: Structures on the dorsal surface of the pterygoid in *Galianemys* are visible and well preserved in a number of specimens (fig. 97). The sulcus palatinopterygoideus is floored by the pterygoid, as in all pleurodires, and in *Galianemys* its size is about the same as in *Cearachelys*, but longer than in *Kurmademys* and pelomedusids. The crista pterygoidea meets the palatine anteriorly and the processus inferior parietalis dorsally. It is lower than the palatine dorsal process. Posteriorly the crista pterygoidea forms the ventral margin of the foramen nervi trigemini. The anterodorsal margin of this foramen is formed by the parietal and its posterior margin by the prootic.

SUPRAOCCIPITAL (figs. 81, 86, 89)

Preservation: The supraoccipital is present in all the adult *Galianemys* specimens and in AMNH 30040, but the crista supraoccipitalis is broken, at least slightly, in all of them.

Contacts: As in other pleurodires, the supraoccipital of *Galianemys* contacts the parietals dorsally, the prootic anterolaterally, the opisthotic posterolaterally, and the exoccipitals posteroventrally. In both species of *Galianemys* there is also a supraoccipital-quadrate contact laterally that separates the prootic and opisthotic. This contact also occurs in *Kurmademys*, *Cearachelys*, *Bothremys*, *Rosasia*, *Foxemys*, and *Polysternon*, but not in *Zolhafah* or most of the Taphrosphyini (fig. 307).

Structures: The crista supraoccipitalis is best preserved in AMNH 29985, 30028, and 29987 in which it extends just posterior to the foramen magnum. However, it ends in a broken edge, so its total length is unknown. The supraoccipital forms the dorsal edge of the foramen magnum, as in most turtles. The cavum labyrinthicum can be seen in the CT scans and AMNH 29985.

EXOCCIPITAL (figs. 81, 87–89, 98–100)

Preservation: The exoccipital is present in the adult *Galianemys* specimens, AMNH 30040 and AMNH 30026, but not in MDEt 45.

Contacts: The exoccipital in *Galianemys* has the usual Pelomedusoides contacts: supraoccipital dorsally, opisthotic laterally, and basioccipital ventrally. The wide exoccipital-quadrate contact ventrolaterally is a bothremydid synapomorphy (fig. 308).

Structures: The condylus occipitalis in *Galianemys* is tripartite, with the exoccipitals and basioccipital making up one-third each. This is also the condition in *Kurmademys*, but in *Cearachelys* and all other bothremydids the basioccipital is excluded. There are two foramina nervi hypoglossi ventrolateral to the foramen magnum, as in *Cearachelys* and *Kurmademys*, with the upper one larger and the lower one close to or in the exoccipital-basioccipital suture.

The foramen jugulare posterius is closed laterally in AMNH 30037 (fig. 88, *G. emringeri*), AMNH 30028 (*G. whitei*), and AMNH 30027 (fig. 100, *G. whitei*) and on the left side of AMNH 30035 (fig. 87, *G. emringeri*), but never by the exoccipital. Rather, the opisthotic and quadrate (see Quadrate for discussion) meet to close it off. Nonetheless, the foramen jugulare posterius is not widely open in any of the specimens.

BASIOCCIPITAL (figs. 81, 82, 89, 90)

Preservation: The basioccipital is present in all the *Galianemys* skulls except the juvenile MDEt 45.

Contacts: As in other bothremydids, the basioccipital of *Galianemys* contacts the basisphenoid anteriorly, the quadrate laterally, and the exoccipital dorsally.

Structures: The basioccipital forms the ventral third of the condylus occipitalis in both species of *Galianemys*. The bone is wider than long, as in most other Pelomedusoides. The posterolateral corner of the basioccipital

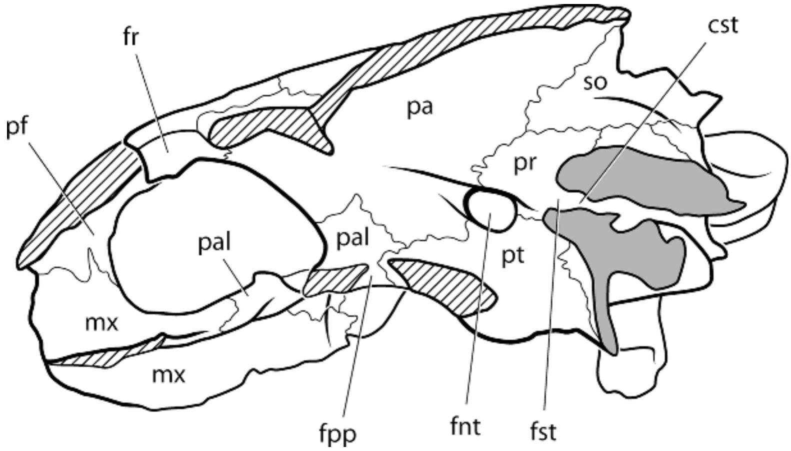

Fig. 97. *Galianemys whitei* Gaffney, Tong, and Meylan, 2002. AMNH 29986. Partially restored parasagittal section of left side of broken skull. [A. Venjara, del.]

is extended into a paired shelflike tuberculum basioccipitale, distinctly larger than those in *Cearachelys*. A shallow, median concavity lies between the tuberculum basioccipitale, as in *Cearachelys* and *Kurmademys*.

PROOTIC (figs. 81, 82, 86, 89, 94, 97, 277E)

Preservation: The prootic is present in all of the *Galianemys* specimens except MDEt 45.

Contacts: The usual suspects are the parietal medially, the quadrate laterally, the supraoccipital posterodorsally, and the pterygoid ventrally. Due to the supraoccipital-quadrate contact, there is no prootic-opisthotic contact, as in nearly all turtles except the Bothremydidae, the Baenidae, and *Annemys* (Sukhanov, 2000).

Structures: The blocklike prootic is exposed in the fossa temporalis where it forms the dorsolateral margin of the foramen nervi trigemini, as in other turtles. The prootic also forms the medial margin of the foramen stapedio-temporale, which is placed on the anterior face of the otic chamber, as in all other bothremydids except *Kurmademys*, where it is more dorsally placed. However, the foramen stapedio-temporale in *Galianemys* is not very close to the foramen nervi trigemini, as it is in the tribes Taphrosphyini and Bothremydini.

The prootic is exposed ventrally in *Galianemys emringeri* in the roof of the deep fossa pterygoidea (fig. 277E). The prootic forms the ventrally opening foramen nervi facialis, which can be traced dorsally into the fossa acustico-facialis in the CT scans and in the broken otic chamber of AMNH 29985.

OPISTHOTIC (figs. 81, 84, 87–89, 92, 98–100)

Preservation: The opisthotic is present in all the *Galianemys* except MDEt 45, but it is obscured by matrix and breakage in AMNH 30040.

Contacts: As in other turtles, the opisthotic contacts the supraoccipital anteromedially, the quadrate anterolaterally, the squamosal posterolaterally, and the exoccipital posteromedially. In contrast to most other turtles, there is no opisthotic-prootic contact. There is also a narrow, ventral contact with the quadrate dividing the fenestra postotica of some individuals.

Structures: The opisthotic forms much of the roof of the cavum acustico-jugulare and forms the dorsal margin of the fenestra postotica (see Quadrate) and foramen jugulare posterius (see Exoccipital). In *Galianemys* there is some variation in the subdivision of the fenestra postotica and the foramen jugulare posterius (see above), but there is still a common morphology that *Galianemys* shares with *Cearachelys*. The foramen jugulare posterius in all *Galianemys* is vertically compressed to form a horizontal slit extending laterally and is never closed by

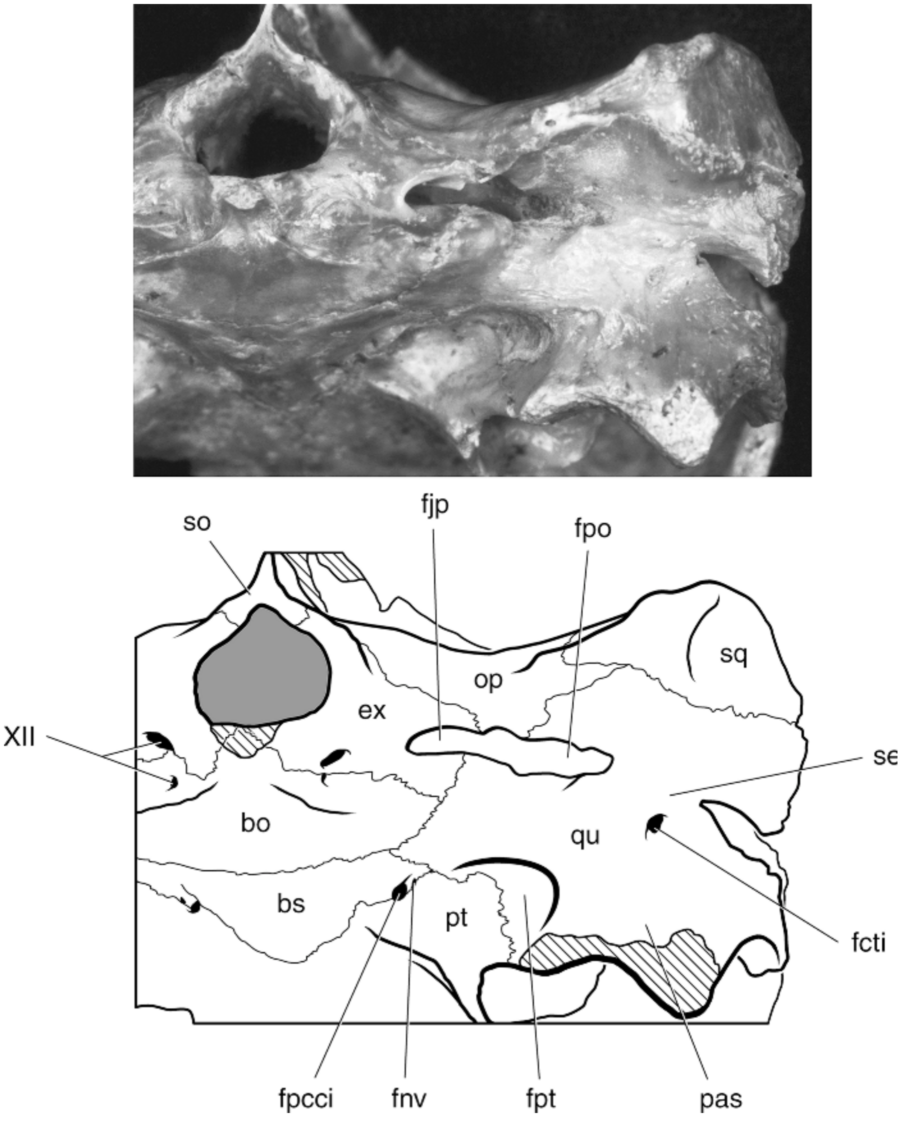

Fig. 98. *Galianemys whitei* Gaffney, Tong, and Meylan, 2002. AMNH 29986. Posterior oblique view. [A. Venjara and E.S. Gaffney, del.]

the exoccipital (figs. 87–89, 98–100). In all *Galianemys* the opisthotic variably constricts this slit by meeting or nearly meeting a similar process or ridge from the quadrate ventrally. In four *Galianemys* specimens the quadrate meets the opisthotic to close off the slit (see table 9), but in the others the foramen jugulare posterius communicates laterally with the fenestra postotica. In some *Galianemys* specimens, such as AMNH 30037, the opisthotic forms a thick wall between the foramen jugulare posterius and the fenestra postotica; in others there is only a thin separation, as in AMNH 30035.

The internal morphology of the cavum acusticojugulare can be seen in some of the specimens as well as the CT scans, and this will be dealt with in a future paper.

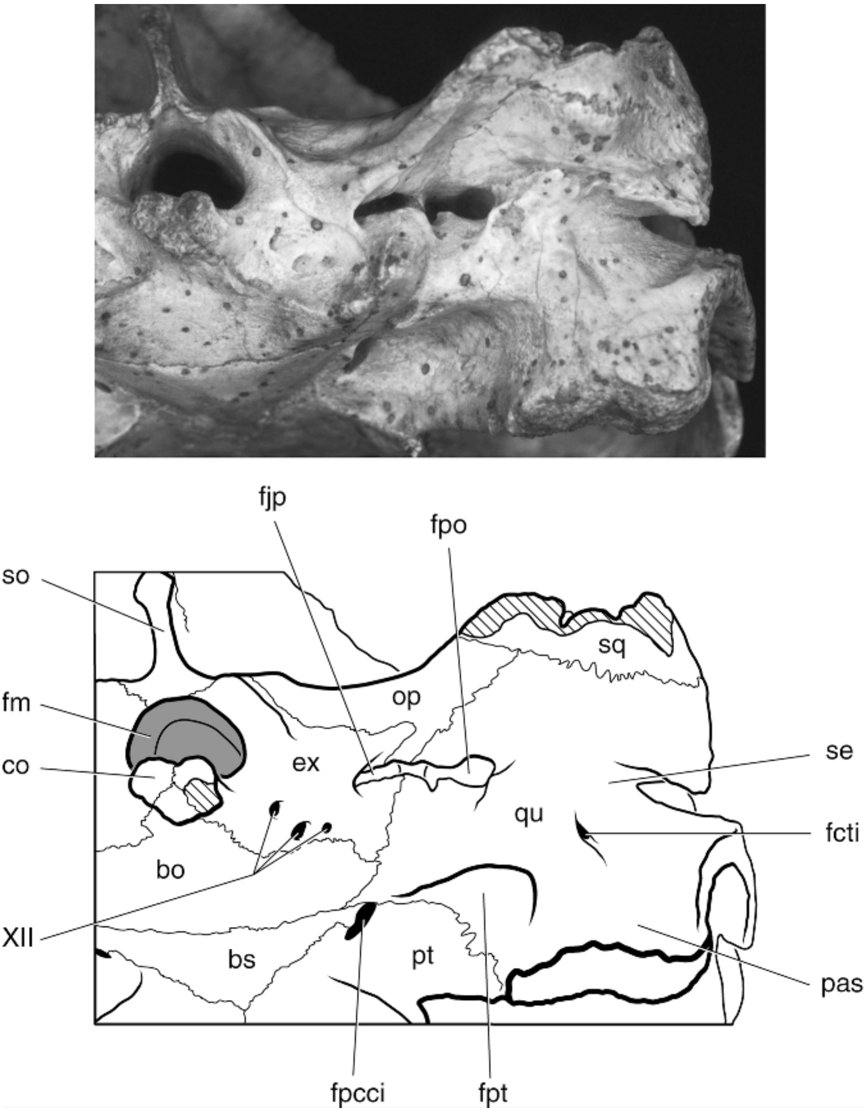

Fig. 99. *Galianemys whitei* Gaffney, Tong, and Meylan, 2002. AMNH 29987. Posterior oblique view [A. Venjara and E.S. Gaffney, del.]

Basisphenoid (figs. 81, 82, 89, 90, 277C, 277E)

Preservation: The basisphenoid is present in all of the *Galianemys* specimens except MDEt 45.

Contacts on ventral surface: The contacts of the basisphenoid common with other turtles are the pterygoid anterolaterally and the basioccipital posteriorly. All the Podocnemididae and Bothremydidae including *Galianemys* also have a broad lateral contact with the quadrate. In *G. emringeri* the basisphenoid contacts the prootic laterally, but in *G. whitei* the pterygoid-quadrate contact covers this. In both *Galianemys* species as well as all other turtles the prootic contacts the basisphenoid internally (visible in the medial view of a sectioned cavum cranii). The prootic-basisphenoid contact is exposed in *G. emringeri* by the deep fossa pterygoidea characteristic of that species (see Pterygoid, above). In *Kurmademys* the prootic and its associated foramen nervi facialis are exposed,

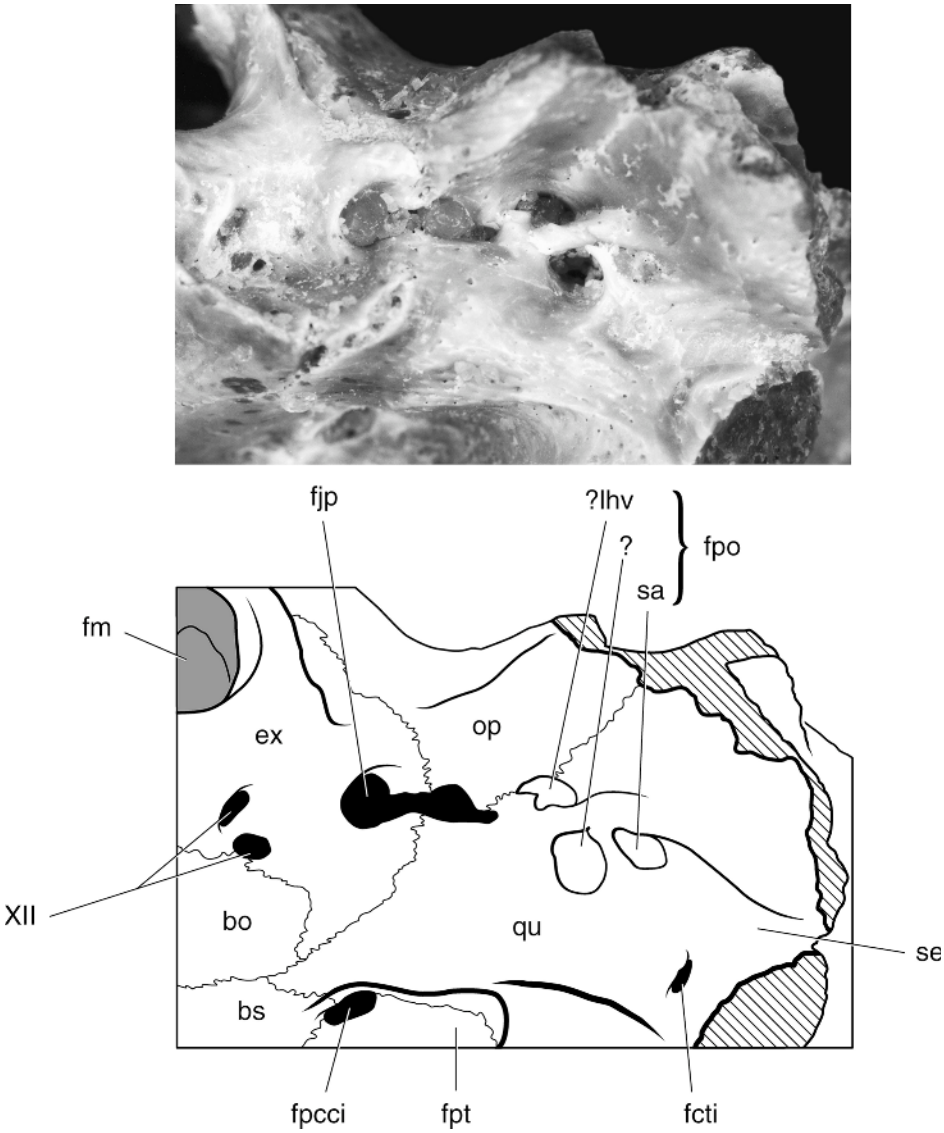

Fig. 100. *Galianemys whitei* Gaffney, Tong, and Meylan, 2002. AMNH 30027. Posterior oblique view. [A. Venjara and E.S. Gaffney, del.]

but not in *Cearachelys*. Thus, there is an exposed prootic-basisphenoid contact in *Kurmademys*.

Structures on ventral surface: The fossa pterygoidea is large in *Galianemys emringeri*, and the basisphenoid forms the medial wall of this depression. The basisphenoid also forms most of the foramen posterius canalis carotici interni, which is oriented nearly vertically in *G. emringeri* rather than nearly horizontal as in *G. whitei*.

Contacts on dorsal surface: As in other Pelomedusoides, the basisphenoid in *Galianemys* contacts the pterygoid anterolaterally, the prootic laterally, the palatine anteriorly, and the basioccipital posteriorly.

Structures on dorsal surface: The structures on the dorsal surface of the basisphenoid are visible in a number of *Galianemys* specimens of both species, particularly AMNH 29986 and 30026. There is a rodlike rostrum basisphenoidale without a dorsal ridge, an oval sella turcica with posterior, laterally placed foramen anterius canalis carotici interni, and a slightly overhanging dorsum sellae. The processus clinoideus is a distinct anterolateral process with the sulcus cavernosus lateral to it. There is no indication of a foramen caroticum laterale.

TRIBE BOTHREMYDINI
SUBTRIBE POLYSTERNONINA
Foxemys mechinorum

Although there are now a possible total of four skulls known for this taxon, this description is based almost entirely on only two of these; the remaining two were received too late to be incorporated into the manuscript as figures. The best skull, unassociated and nearly complete, is still PAM 511A. The smaller, type skull, MDEt 10, is partially crushed and lacks the left part of the palate, but it is associated with a shell and is the type of *Foxemys mechinorum*. An earlier description of this material is in Tong et al. (1998).

Two new skulls, consisting of a nearly complete but laterally crushed and distorted skull, MC M1734, and a partial posterior portion of skull, MC M2119, are now available but have not been included in this description except incidentally. MC M1734, the best new skull, differs from the two described skulls in having a distinct accessory ridge on the maxilla and premaxilla, a structure absent in PAM 511A and apparently absent in MDEt 10, although this skull has only a partial maxilla. MC M2119 lacks maxillae. It is possible that MC M1734 is a different taxon from *Foxemys mechinorum*, although there do not appear to be any other differences with PAM 511A. Alternatively, it could be a variant within the same species due to gender, age, or individual variation.

PREFRONTAL (figs. 101, 104)

Preservation: The prefrontal is present in both skulls, on both sides of PAM 511A and MDEt 10, but the ones on MDEt 10 are slightly damaged, particularly the left. The ventral surface is visible in MDEt 10. Sutures are discernable but not obvious on both skulls.

Contacts: As in other members of the tribe Bothremydini, the prefrontal in *Foxemys* contacts the maxilla anteroventrolaterally, the frontal posteriorly, and the other prefrontal medially. There is no palatine contact. The sutures agree in MDEt 10 and PAM 511A.

Structures: As in *Rosasia*, the prefrontal of *Foxemys* has a straight, transverse anterior edge, without a median process like that of *Chedighaii*, *Bothremys*, and *Araiochelys*. The anterior margin of the prefrontal is very close to the anterior margin of the premaxilla in *Foxemys*, not more posterior as in *Bothremys*, *Araiochelys*, and *Chedighaii*. The margins of the apertura narium externa are largely broken in *Polysternon* and *Zolhafah*.

FRONTAL (figs. 101, 103, 104)

Preservation: Both frontals are present in both *Foxemys* skulls, but there is breakage and missing bone in MDEt 10. Sutures are determinable in both skulls, however.

Contacts: As in the other taxa in the tribe Bothremydini, the frontal of *Foxemys* contacts the prefrontal anteriorly, the postorbital posterolaterally, the parietal posteriorly, and the other frontal medially. Due to damage in MDEt 10, the frontals have some shape differences between the skulls, but PAM 511A seems to be the least distorted and nearly original in shape.

Structures: The frontal in *Foxemys* forms the dorsal margin of the orbital edge and has about the same amount of exposure as in *Araiochelys*, *Polysternon*, and *Chedighaii*. *Bothremys* has less frontal exposure than in *Foxemys*, and the frontal is more exposed in *Rosasia*, although this may be due to damage.

On the ventral surface in MDEt 10, the sulcus olfactorius is very similar to that in *Bothremys*, lacking the ventral process of *Chedighaii hutchisoni*.

PARIETAL (figs. 101, 103, 104)

Preservation: Neither skull has a complete parietal, although both skulls have parts of both parietals preserved. The best parietal is the right one in PAM 511A that has much of the temporal margin, showing the amount of emargination. In MDEt 10, most of the right parietal is missing and much of the left one is damaged. Both parietals are preserved

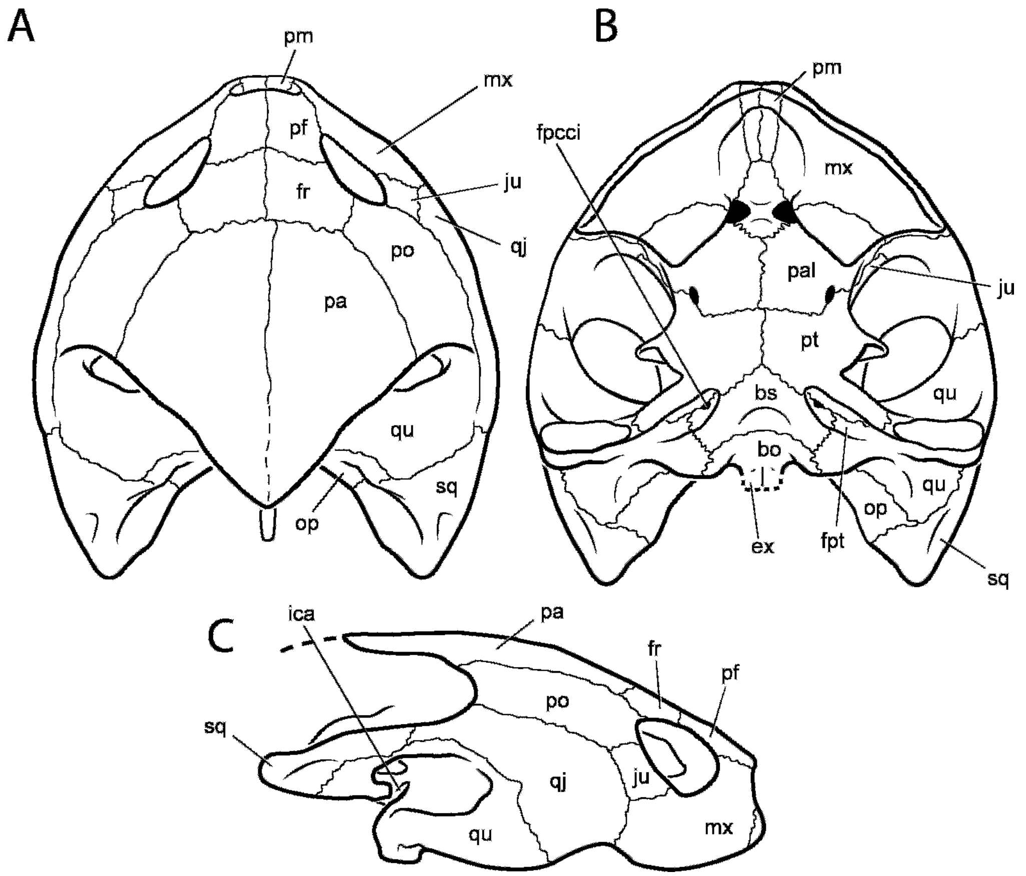

Fig. 101. *Foxemys mechinorum* Tong, Gaffney, and Buffetaut, 1998. Partially restored skull based on PAM 511A. **A**, dorsal; **B**, ventral; **C**, lateral. [R. Rogge, del.]

in MC M1734 and show the posterior edge of the temporal margin to be as restored in figure 101A.

Contacts of dorsal plate: As in the other tribe Bothremydini taxa, the parietal in *Foxemys* contacts the frontal anteriorly, the postorbital laterally, and the other parietal medially. Differences between MDEt 10 and PAM 511A are due to the poor preservation of the parietals in MDEt 10.

Structures of dorsal plate: The degree of temporal emargination in *Foxemys* is very similar to that in *Polysternon* and *Bothremys*. The parietal of *Araiochelys* is narrower but the emargination is similar. *Chedighaii* has a more extensive emargination; the emargination is not determinable in *Rosasia* and *Zolhafah*.

Contacts of processus inferior parietalis: The vertical part of the parietal is not visible in MDEt 10 and only partially in PAM 511A, where it is broken and lacks clear sutures.

Structures of processus inferior parietalis: The foramen nervi trigemini is present in PAM 511A but is poorly preserved.

JUGAL (figs. 101, 103, 104)

Preservation: The jugal in *Foxemys* is well preserved and undistorted on the left side of PAM 511A, but only partially preserved on the right. In MDEt 10 the left jugal is missing, and the bone is not clearly delimited on the right side.

Contacts of lateral plate: The jugal in *Foxemys* contacts the postorbital dorsally, the maxilla ventrally, and the quadratojugal posteriorly. In contrast to the tribe Cearachelyini, there is no postorbital-maxilla contact anterior to the jugal. All members

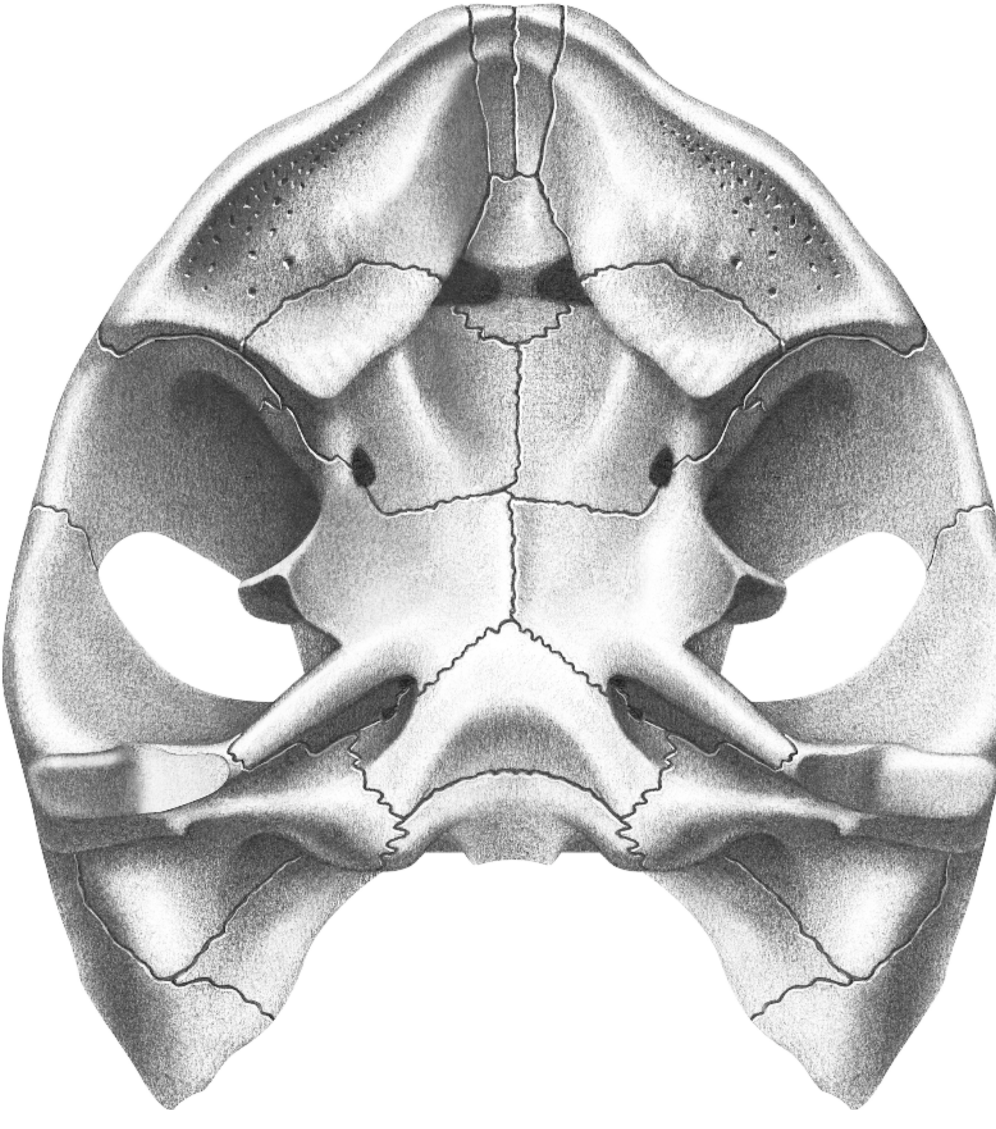

Fig. 102. *Foxemys mechinorum* Tong, Gaffney, and Buffetaut, 1998. Partially restored skull based on PAM 511A and MDEt 10 holotype. [F. Ippolito, del.]

of the tribe Bothremydini have the same contacts as *Foxemys*, where they can be determined.

Structures of lateral plate: As in most of the tribe Bothremydini, the jugal in *Foxemys* widely enters the orbital margin, in contrast to the narrow exposure in *Bothremys cooki* and *Kurmademys*. The jugal does not enter the orbital margin in the Cearachelyini. The jugal in *Foxemys* is excluded from the cheek margin by the quadratojugal-maxilla contact.

Contacts of medial process: The medial process of the jugal in *Foxemys* is visible only in PAM 511A, and it is best preserved on the left side. In the floor of the fossa orbitalis the jugal contacts the maxilla anterolaterally, the palatine medially, and the postorbital dorsomedially, as in other Bothremydini. In the posterior surface of the postorbital wall, the jugal contacts the maxilla ventrally, the palatine ventromedially, the pterygoid medially, and the postorbital dorsally, also as in other Bothremydini.

Structures of medial process: The jugal in *Foxemys* is exposed in the orbital floor much as in the other Bothremydini, even ones like *Bothremys* and *Zolhafah* that have pits formed by the jugal. The jugal in *Foxemys* does not enter the triturating surfaces as it does in the pitted Bothremydini, that is, the subtribe Bothremydina.

QUADRATOJUGAL (figs. 101, 103, 104)

Preservation: The quadratojugal is present on both sides of both specimens, but it is best seen in PAM 511A. However, MDEt 10 preserves enough to determine its size and its exposure on the cheek margin. Using both sides of PAM 511A allows a complete reconstruction of the bone.

Contacts: The quadratojugal of *Foxemys* contacts the postorbital dorsally, the jugal anterodorsally, the maxilla anteroventrally, the quadrate posteriorly, and the squamosal posterodorsally.

Structures: The quadratojugal of *Foxemys*, *Polysternon*, and *Chedighaii hutchisoni* differ from the other Bothremydini in being exposed on the ventral edge of the cheek rather than being excluded from the cheek by a maxilla-quadrate contact, as in *Bothremys*, *Rosasia*, and *Araiochelys* (fig. 4). The quadratojugal in *Foxemys* differs from *Polysternon* in being larger and more extensive anterodorsally.

The quadratojugal in *Foxemys* forms part of the lateral edge of the temporal emargination, as in *Bothremys*, *Polysternon*, and *Chedighaii*.

SQUAMOSAL (figs. 101, 103, 104)

Preservation: Both squamosals are preserved in both skulls, but the most complete is on the left side of PAM 511A. The sutures are clear in PAM 511A and discernable in MDEt 10.

Contacts: As in the other Bothremydini, the squamosal in *Foxemys* contacts the quadrate anteriorly, the opisthotic medially, and the quadratojugal anterodorsally.

Structures: The squamosal of *Foxemys* is similar to that in *Bothremys* (and probably in other Bothremydini but it is incomplete in most). As preserved, the squamosal is wider in *Foxemys* than in *Bothremys* and *Araiochelys*.

POSTORBITAL (figs. 101, 103)

Preservation: Postorbitals are preserved in both skulls, but the only nearly complete one is on the left side of PAM 511A; the right one is mostly missing. In MDEt 10 the right postorbital is complete enough to determine its limits, most of the left one is missing.

Contacts of lateral plate: As in the other Bothremydini, the postorbital of *Foxemys* contacts the frontal anteromedially, the jugal anteroventrally, the quadratojugal ventrolaterally, and the parietal posteromedially.

Structures of lateral plate: The postorbital in *Foxemys* forms the posterior orbital margin and extends posteriorly to form part of the temporal emargination, as in the other Bothremydini.

Contacts of medial process: In the posterior wall of the fossa orbitalis of PAM 511A, the postorbital contacts the palatine medially and the jugal ventrolaterally. Frontal or parietal contacts are not present as preserved. The posterior surface of the postorbital wall shows the postorbital bone contacting the jugal ventrolaterally and the pterygoid ventromedially.

Structures of medial process: The medial process in PAM 511A is largely covered by matrix posteriorly, but it forms part of the septum orbitotemporale lateral to the sulcus palatinopterygoideus, as in other Bothremydini. The postorbital, along with the jugal, palatine, and maxilla, forms the boundaries of the posterior extension of the fossa orbitalis, as in *Bothremys*, *Chedighaii*, *Zolhafah*, and *Rosasia*.

PREMAXILLA (figs. 101–104)

Preservation: Both premaxillae in *Foxemys* are preserved and nearly complete in PAM 511A. In MDEt 10 the premaxillae are missing. Sutures in PAM 511A are not obvious but they can be determined.

Contacts: As in other bothremydids, the premaxilla of *Foxemys* contacts the maxilla laterally, the vomer posteriorly, and the other premaxilla medially. Although it is not completely certain, and there is an obvious anterolateral crack, the maxilla-premaxilla suture is parasagittal in *Foxemys*, rather than trending anterolaterally, as in all the other Bothremydini (and as described in Tong et al., 1998).

Structures on dorsal surface: The floor of the fossa nasalis in *Foxemys* rises posteriorly from a flat anterior margin, as it does in *Rosasia*, distinctly different from *Bothremys*, which has a dorsal process and ridge beginning at the anterior margin of the premaxilla. The apertura narium externa of *Foxemys* is a simple oval, without the partial or complete subdivision seen in *Bothremys*, *Chedighaii*, and *Araiochelys*.

Structures on ventral surface: The premaxilla of *Foxemys* forms a relatively high and narrow labial ridge with a slight dorsal curve on the midline, as in *Bothremys* and in contrast to the straighter ridge in *Zolhafah*. The lingual ridge, forming the anterior margin of the midline concavity, is very close to the labial ridge in *Foxemys*, closer than in *Araiochelys* but similar to *Bothremys*. The midline concavity in *Foxemys* and *Polysternon* is wider than in the other Bothremydini. The foramen praepalatinum is not visible in PAM 511A. The anterior part of the skull of *Foxemys* is pinched near the premaxilla-maxilla suture, similar to the condition in *Bothremys* and *Rosasia* and distinct from *Araiochelys* and *Zolhafah*.

MAXILLA (figs. 101–104)

Preservation: Both maxillae are present and nearly complete in PAM 511A. In MDEt 10 the right maxilla is present but damaged anteriorly, the left one is only represented by fragments. Sutures are clear in PAM 511A.

Contacts of vertical plate: As in other Bothremydini, the maxilla of *Foxemys* contacts the premaxilla anteromedially, the jugal posterodorsally, the quadratojugal posteroventrally, and the prefrontal anterodorsally. There is no quadrate contact as in *Araiochelys*, *Bothremys*, and *Rosasia*.

Structures of vertical plate: As in *Bothremys*, the lower margin or rim of the fossa orbitalis in *Foxemys* is not separated from the outside surface of the maxilla by a distinct ridge; instead, it is a low, curved surface. *Araiochelys*, *Chedighaii*, and the other Bothremydini have a higher orbital rim. The dorsal process of the maxilla in *Foxemys* is slightly narrower than in *Bothremys* and *Chedighaii*.

Contacts of horizontal plate: The maxilla of *Foxemys* contacts the premaxilla anteromedially, the vomer medially, the palatine posteromedially, and the jugal posterodorsolaterally, as in *Polysternon*. There is no jugal contact on the triturating surface, and the jugal contact that is present is visible only on the posterior surface of the postorbital wall. There is no midline maxilla contact. The vomer contact is relatively broad (indeterminate in *Polysternon*), as in *Rosasia* and *Bothremys cooki*, in contrast to the narrow contact of *B. maghrebiana*, *Araiochelys*, and the absent or very small one in *Zolhafah*. In the floor of the fossa orbitalis, the maxilla contacts the palatine posteromedially and the jugal posterolaterally.

Structures of horizontal plate: The maxilla of *Foxemys* forms the anterior and lateral part of the triturating surface, with the palatine forming the posteromedial part, as in other Bothremydini. The triturating surface in *Foxemys*, along with that in *Polysternon* and *Chedighaii*, is relatively flat with no pit, as in other Bothremydini. The labial ridge in *Foxemys* and *Polysternon* is acute, as in *Araiochelys*, not blunt, as in *Zolhafah* and *Rosasia*. The ridge curves outward below the orbit and is slightly pinched more anteriorly, giving an outline similar to *Bothremys* and *Rosasia*. The labial ridge medial side curves smoothly into the triturating surface, giving that surface a shallow, concave margin, similar to that in *Polysternon* and *Chedighaii*. The lingual ridge in *Foxemys* is very shallow and barely recognizable, in contrast to the relatively sharp and well-defined lingual ridge in *Polysternon*. The width of the triturating surface in *Foxemys* is also greater than in *Polysternon*. The triturating surface width is similar in extent in *Bothremys*, *Rosasia*, and *Foxemys*, being less in the other Bothremydini.

Another skull that appears to be *Foxemys mechinorum*, MC M1734, agrees with PAM 511A and MDEt 10 except that it has a well-developed accessory ridge extending from the anterior midline concavity on the premaxilla, posterolaterally along the maxilla paralleling the labial ridge. Accessory ridges are nearly absent in bothremydids, being found only in *Sankuchemys* and the undescribed CNRST-SUNY 199. MC M1734 does not seem to

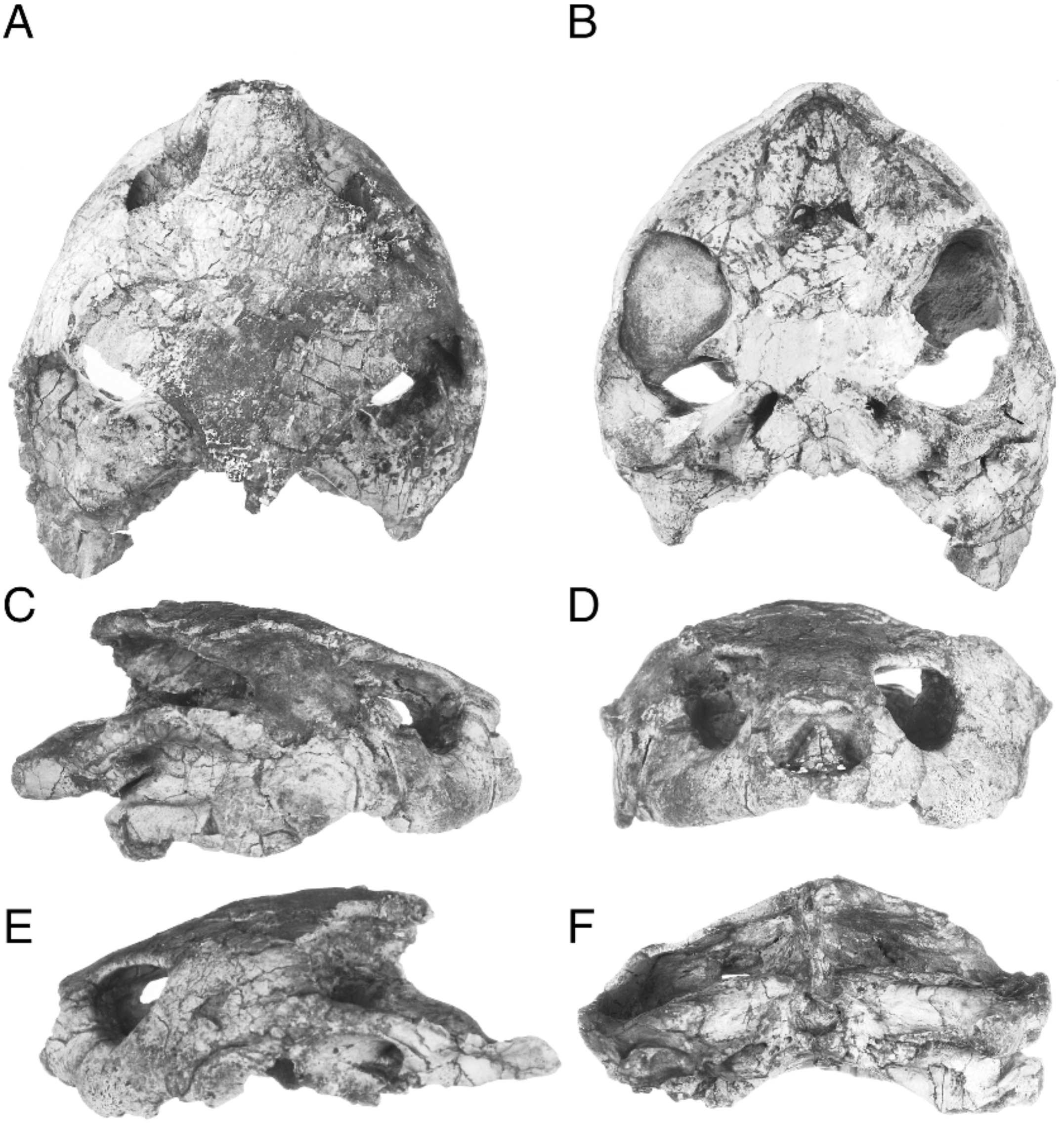

Fig. 103. *Foxemys mechinorum* Tong, Gaffney, and Buffetaut, 1998. PAM 511A. **A**, dorsal; **B**, ventral; **C**, right lateral; **D**, anterior; **E**, left lateral; **F**, posterior. [E. Heck, del.]

have other differences from the two described *Foxemys* skulls, so it is unclear whether it is best interpreted as individual variation or a different taxon.

The dorsal surface of the maxilla in *Foxemys* is visible in the floor of the fossa orbitalis.

VOMER (figs. 101–104)

Preservation: The vomer is complete but slightly damaged ventrally in PAM 511A. It is completely missing in MDEt 10.

Contacts: As in other bothremydids, the vomer of *Foxemys* contacts the premaxilla anteriorly, the maxilla anterolaterally, and the palatines posteriorly. The maxilla contact is broad, as in *Rosasia* and *Bothremys cooki*, not narrow, as in *B. maghrebiana*, *Araiochelys*, and *Zolhafah*.

Structures: The vomer of *Foxemys* is "stepped", with the anterior expansion sharply ventral to the interchoanal bar and the more dorsal posterior expansion. This is

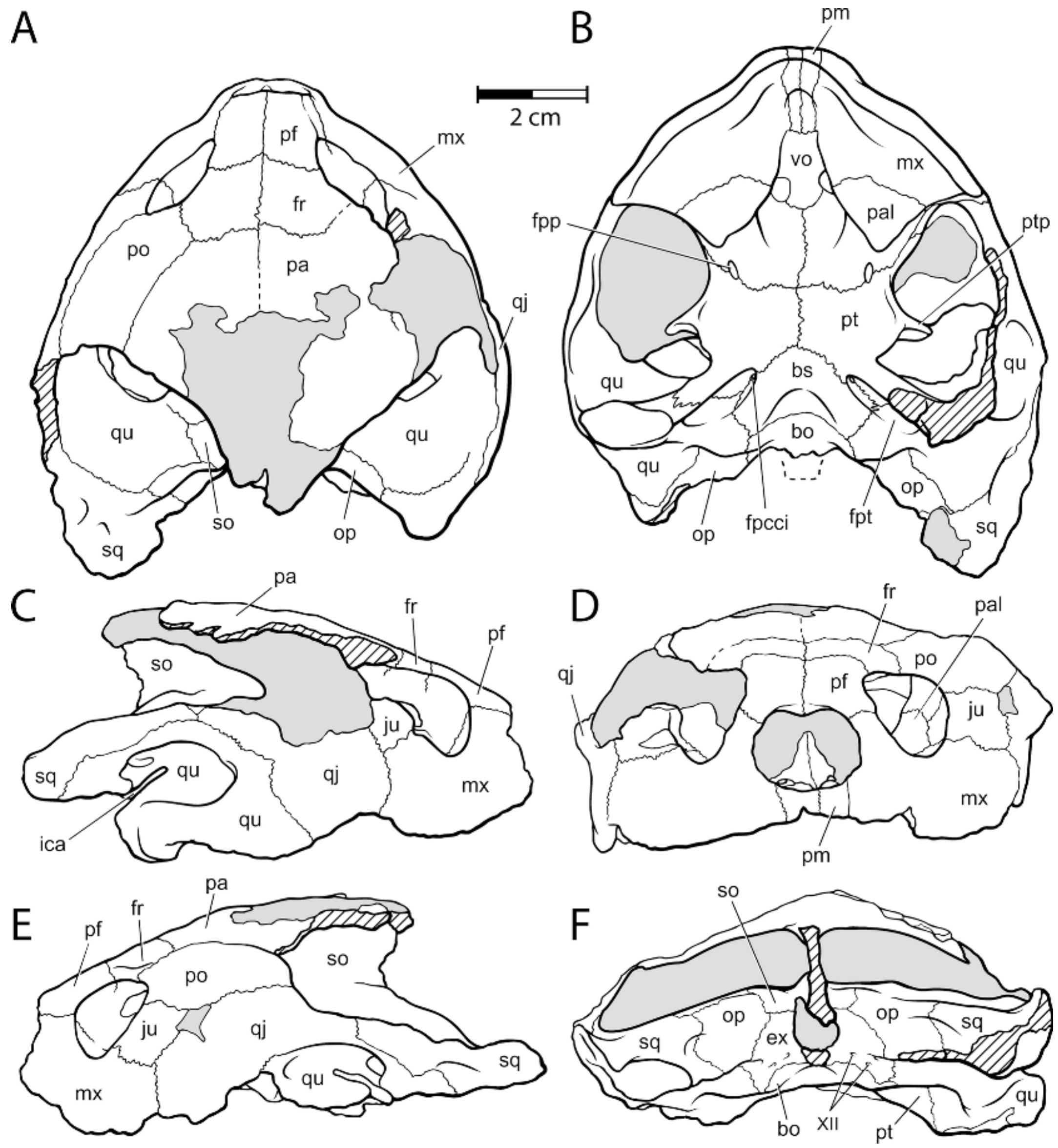

Fig. 104. *Foxemys mechinorum* Tong, Gaffney, and Buffetaut, 1998. PAM 511A. **A**, dorsal; **B**, ventral; **C**, right lateral; **D**, anterior; **E**, left lateral; **F**, posterior. [E. Heck, del.]

approached by *Bothremys* and *Araiochelys*, but distinct from the flat vomer of *Chedighaii*. The apertura narium interna in *Foxemys* is relatively wide, as in *Bothremys*, relative to that in *Rosasia*, but not as wide as in *Chedighaii*.

PALATINE (figs. 101–104)

Preservation: Both palatines are present in MDEt 10 but are broken anteriorly, so that only the right one retains the triturating surface portion of the palatine. In PAM 511A both palatines are preserved and are nearly complete with clear sutures.

Contacts: As in the other bothremydids, the palatine in *Foxemys* contacts the maxilla anterolaterally, the vomer anteromedially, the other palatine medially, and the pterygoid posteriorly. In the floor of the orbit, the palatine contacts the maxilla anterolaterally

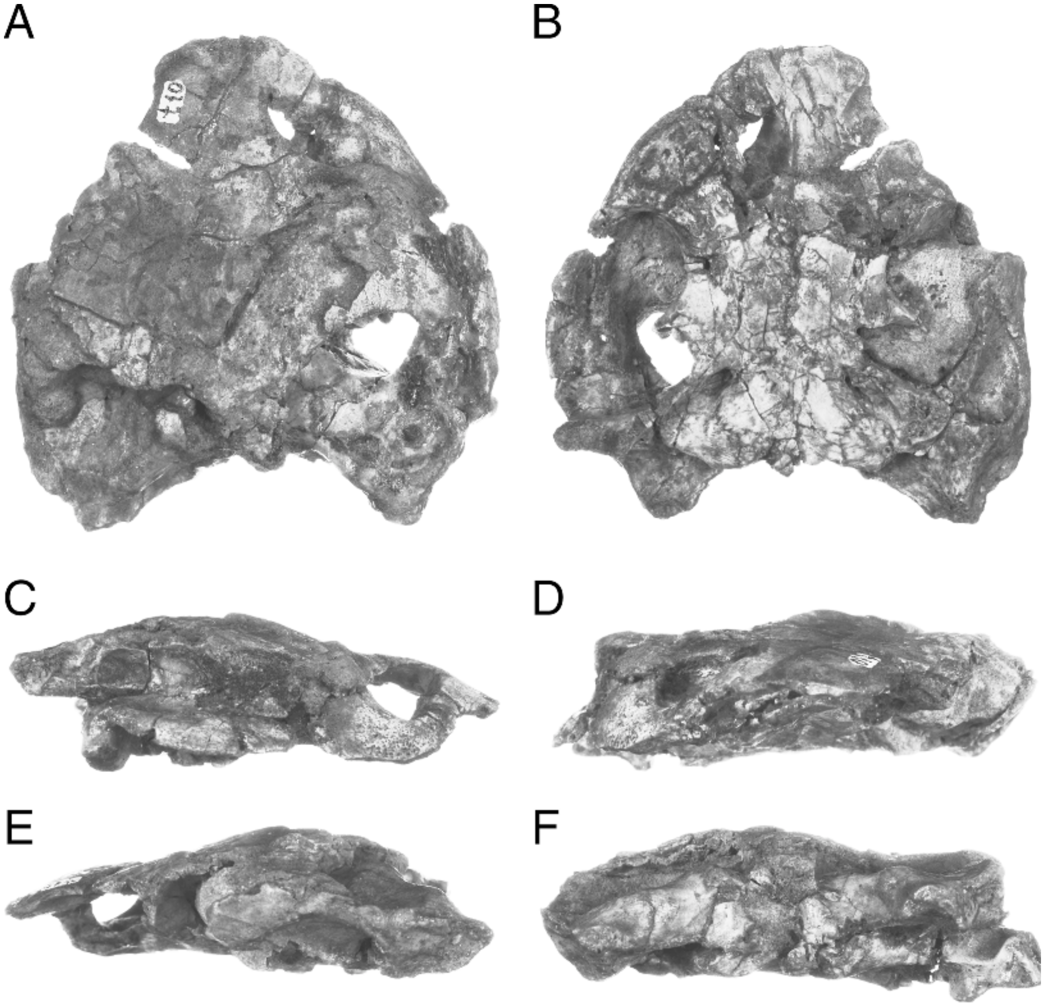

Fig. 105. *Foxemys mechinorum* Tong, Gaffney, and Buffetaut, 1998. MDEt 10 holotype. **A**, dorsal; **B**, ventral; **C**, right lateral; **D**, anterior; **E**, left lateral; **F**, posterior. [E. Heck, del.]

and the jugal laterally, as in other Bothremydini. Posterodorsally the palatine has a dorsal process that contacts the postorbital lateral to the sulcus palatinopterygoideus. On the posterior surface of the postorbital wall, the palatine only contacts the jugal and pterygoid and not the postorbital.

Structures on dorsal surface: The left orbit and sulcus palatinopterygoideus are prepared in PAM 511A, and the palatine is visible here. The palatine of *Foxemys* forms the medial part of the fossa orbitalis floor, as in other bothremydids. The palatine forms the anterior part of the sulcus palatinopterygoideus, also as in other bothremydids.

Structures on ventral surface: As in the other species in the tribe Bothremydini, the palatine in *Foxemys* forms the posteromedial part of the triturating surface. The surface is slightly curved, concave ventrally, but not to the degree seen in the pitted Bothremydini. The palatine forms most of the trough or choanal groove that leads into the apertura narium interna. In *Bothremys*, *Chedighaii*, and *Araiochelys*, the lingual ridge is a sharp demarcation separating the choanal groove from the triturating surface, but in *Foxemys* this is a more gradual change and the choanal groove is not so sharply defined. *Polysternon* also has an acute lingual ridge formed by the

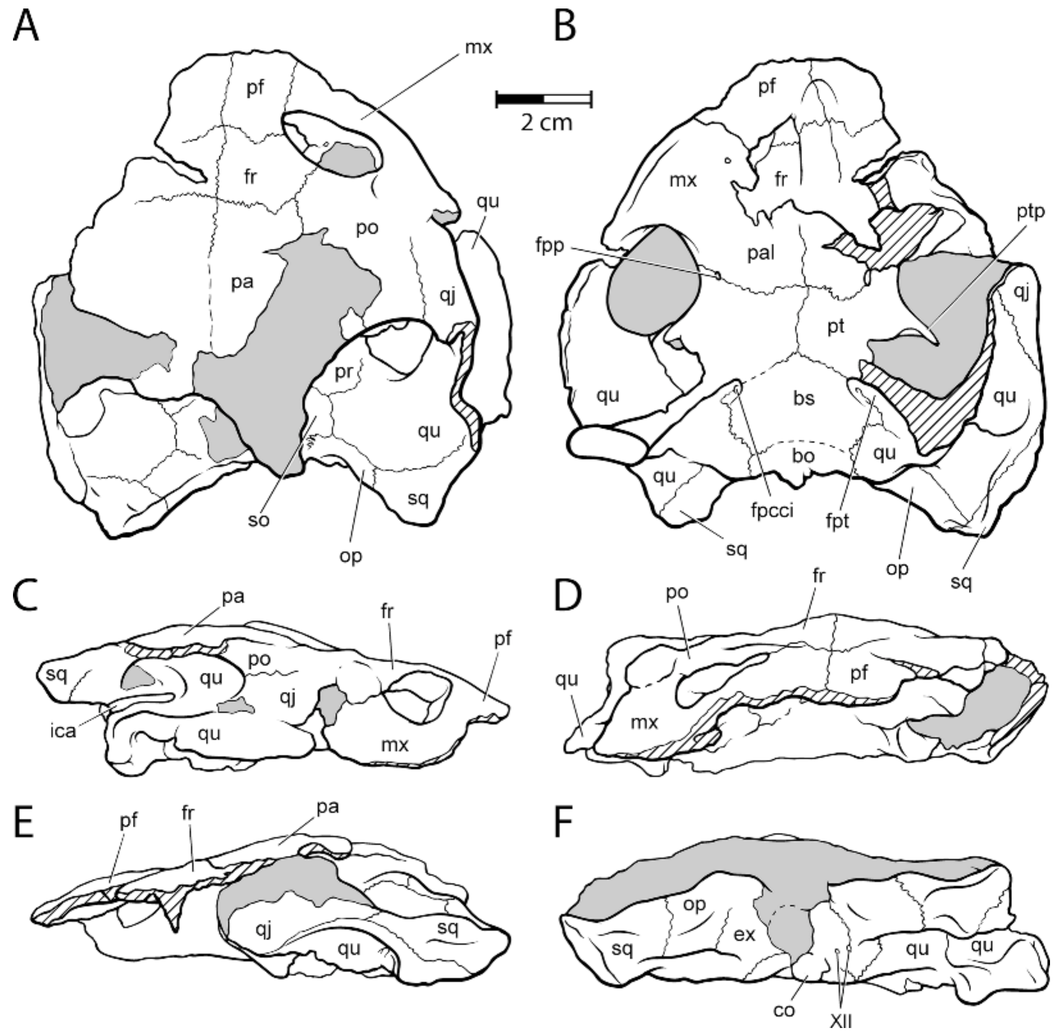

Fig. 106. *Foxemys mechinorum* Tong, Gaffney, and Buffetaut, 1998. MDEt 10 holotype. **A**, dorsal; **B**, ventral; **C**, right lateral; **D**, anterior; **E**, left lateral; **F**, posterior. [E. Heck, del.]

palatine, but the choanal passage is shallower, as in *Foxemys*, not deeper, as in *Bothremys*, *Araiochelys*, and *Chedighaii*. In *Rosasia* the lingual ridge is much closer to the midline, constructing the choanal passages. *Zolhafah* has a very shallow choanal passage.

QUADRATE (figs. 101, 104, 107)

Preservation: The quadrate is nearly complete on the right side of MDEt 10, but it is slightly distorted by dorsoventral crushing and is missing most of the ventral half on the left side. In PAM 511A the right quadrate is nearly complete on the right side, but the processus articularis is broken off on the left side. Sutures are clear in PAM 511A, but not completely discernable in MDEt 10.

Lateral surface contacts: As in *Polysternon*, *Chedighaii hutchisoni*, and the Cearachelyini, the quadrate of *Foxemys* has its anterior and anterodorsal edges contacting the large quadratojugal, in contrast to the quadratojugal plus maxilla contact seen in *Araiochelys*, *Rosasia*, and *Bothremys maghrebiana*. The universal posterolateral squamosal contact is present.

Lateral surface structures: *Foxemys* has the ventrolateral shelf formed below the cavum tympani, also seen in the other Bothremydini. The cavum tympani of *Fox-*

emys has a shape very similar in outline, depth, and extent to that in *Bothremys maghrebiana*. The cavum has no fossa precolumellaris.

The incisura columellae auris (figs. 103C, 107) in *Foxemys* is unusual within the Bothremydidae because it is not completely closed by bone to form a canal for the stapes. Rather, there is a thin slit from the sulcus eustachii to the incisura columellae auris. This open slit differs from that in the non-bothremydid Pelomedusoides, which also do not have the stapes in a bony canal, in that the slit in *Foxemys* is very narrow and is too narrow to contain the eustachian tube (for taxon distributions see figs. 303, 304). This is also the condition in *Polysternon*. The antrum postoticum in *Foxemys* is larger than that in *Bothremys*, *Araiochelys*, and *Chedighaii*. It is about the same size as in *Polysternon* and the Cearachelyini.

Dorsal and anterior surface contacts: The quadrate in *Foxemys* contacts the prootic anteromedially, the supraoccipital medially, the opisthotic posteromedially, and the squamosal posteriorly. The supraoccipital contact is common to all Bothremydidae except the Taphrosphyini and *Zolhafah*.

Dorsal and anterior surface structures: The foramen stapedio-temporale in *Foxemys* lies in the prootic-quadrate suture. The foramen lies on the anterior surface of the otic chamber and is not visible in dorsal view.

Contacts on ventral surface: The quadrate in *Foxemys* has the usual bothremydid contacts: the pterygoid anteromedially, the basisphenoid medially, and the basioccipital posteromedially. The basisphenoid contact in *Foxemys* and *Polysternon* is relatively broad, not narrow, as in *Bothremys*, *Araiochelys*, and *Chedighaii*.

Structures on ventral surface: The fossa pterygoidea is present and deep in *Foxemys*, as it is in *Polysternon*, uniquely among Bothremydini. There is a smaller fossa in *Rosasia*. The quadrate in *Foxemys* forms part of the fossa pterygoidea but does not participate in the foramen posterius canalis carotici interni (see Pterygoid). There is a small, posteriorly opening foramen in the quadrate just posterior to the pterygoid suture in the roof of the fossa pterygoidea. This seems to be the foramen chorda tympani superius.

The condylus mandibularis in *Foxemys* is just slightly anterior to the plane of the condylus occipitalis, as it is in *Bothremys*, *Zolhafah*, *Rosasia*, and *Chedighaii*. *Polysternon* has a condylus mandibularis well anterior to the condylus occipitalis, distinct from *Foxemys*.

Contacts on posterior surface: As in other Bothremydidae, the quadrate in *Foxemys* contacts the squamosal dorsolaterally, the opisthotic dorsomedially, the exoccipital medially, and the basioccipital ventromedially.

Structures on posterior surface: The fenestra postotica in *Foxemys* (fig. 107) is best seen in PAM 511A; in MDEt 10 the area is broken on the left side and filled with matrix on the right. The fenestra postotica is divided into two foramina, a more medial one for the lateral head vein (vena capitis lateralis) and a more lateral one for the stapedial artery (arteria stapedialis). The lateral one is formed by the quadrate completely, and the medial one has part of its dorsal edge formed by the opisthotic. A complete subdivision of the fenestra postotica does not occur in *Araiochelys*, *Bothremys maghrebiana*, *Chedighaii*, *Zolhafah*, *Rosasia*, or *Polysternon*.

PTERYGOID (figs. 101–104, 107)

Preservation: Both pterygoids are present and nearly complete in PAM 511A. In MDEt 10 they are both present but are broken posterolaterally.

Contacts on ventral surface: As in other bothremydids, the pterygoid of *Foxemys* contacts the palatine anteriorly, the other pterygoid anteromedially, the basisphenoid posteromedially, and the quadrate posterolaterally. There is a possible small prootic contact near the foramen posterius canalis carotici interni.

Structures on ventral surface: The processus trochlearis pterygoidei in *Foxemys* is nearly at right angles to the midline, similar to that in *Chedighaii* and *Polysternon*. In *Bothremys*, *Araiochelys*, and *Zolhafah* the processus is closer to the sagittal plane. The fossa pterygoidea (see Quadrate) is large and deep in *Foxemys*, and it is formed by the

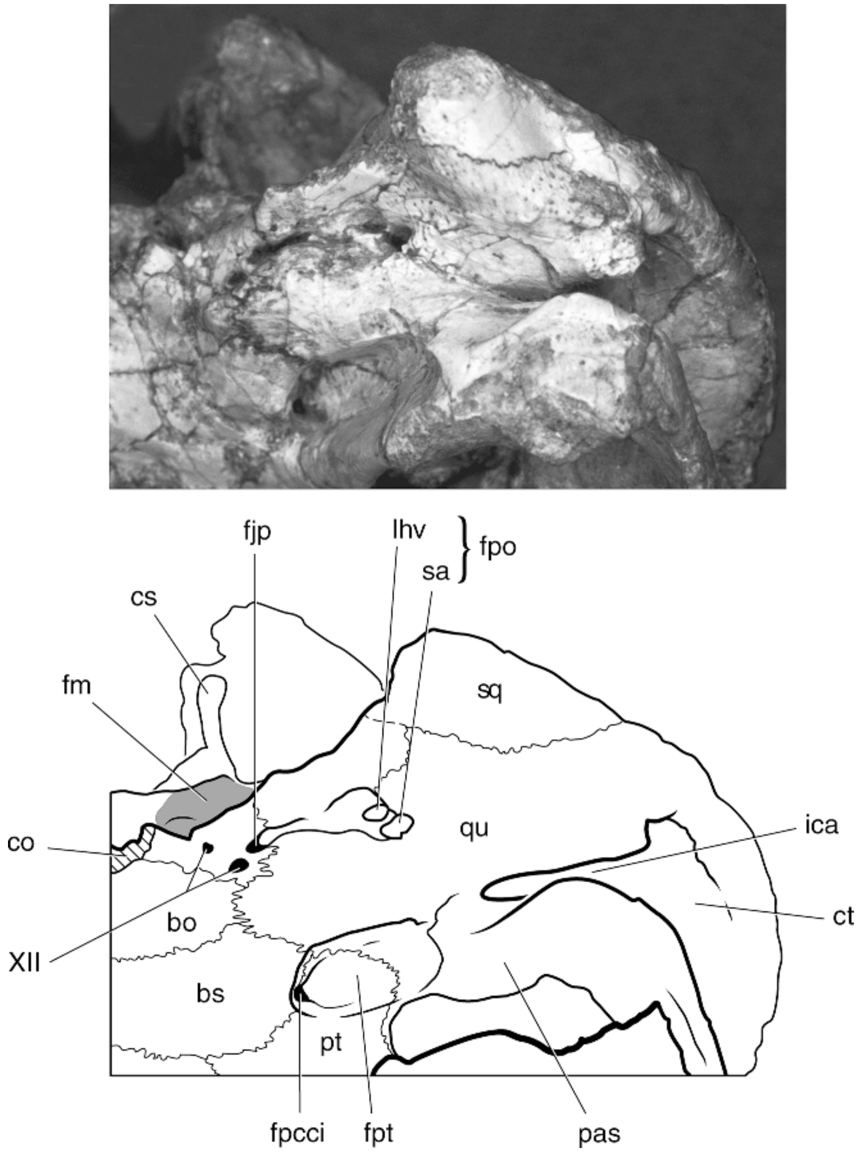

Fig. 107. *Foxemys mechinorum* Tong, Gaffney, and Buffetaut, 1998. PAM 511A. Posterior oblique view. [A. Venjara and E.S. Gaffney, del.]

pterygoid anteriorly and the basisphenoid and quadrate posteriorly. The foramen palatinum posterius lies in the palatine-pterygoid suture and is similar in size to that in *Bothremys*.

The foramen posterius canalis carotici interni is in the extreme anterodorsal part of the fossa pterygoidea roof. The lateral edge is formed by the pterygoid and the medial edge by the basisphenoid. The right foramen is more prepared in PAM 511A and seems to be divided into two canals; presumably the more medial is the canalis caroticus internus and the more lateral the canalis nervi vidiani. Just posterior to the anteromedially opening foramen posterius canalis carotici interni is another foramen, the foramen nervi facialis opening dorsally.

The prootic forms the foramen nervi facialis and is exposed around its margin, best seen on the right side. *Polysternon* also has the foramen posterius canalis carotici interni formed by the pterygoid and basisphenoid in the roof of the fossa pterygoidea, but the only known specimen is not well enough preserved to determine the presence of prootic sutures or the foramen nervi facialis position. It is likely that the exposure of the foramen nervi facialis and the prootic is related to the depth of the fossa pterygoidea (see *Kurmademys*: Basisphenoid, Pterygoid; *Galianemys*: Pterygoid, Quadrate; *Cearachelys*: Quadrate, Pterygoid). Among Bothremydini, *Rosasia* also has the foramen posterius canalis carotici interni formed by the pterygoid and basisphenoid. In *Zolhafah* the foramen is formed by pterygoid, basisphenoid, and quadrate, but in all other Bothremydini and all Cearachelyini, the foramen is formed by pterygoid and quadrate.

Contacts on dorsal surface: At the base of the processus trochlearis pterygoidei, the pterygoid in *Foxemys* has the usual bothremydid contacts, that is, the postorbital dorsolaterally, the jugal anterolaterally, and the palatine anteroventrally. There is no parietal contact here. The crista pterygoidea contacts that parietal dorsally and the prootic posterodorsally, but other contacts are obscured by matrix and breakage.

Structures on dorsal surface: The sulcus palatinopterygoideus is formed posteriorly by the pterygoid with the crista pterygoidea medially. The sulcus is similar to that in *Bothremys* and other Bothremydini.

SUPRAOCCIPITAL (figs. 101, 103)

Preservation: The supraoccipital in PAM 511A lacks the dorsal and some of the ventral part of the crista supraoccipitalis. In MDEt 10 nearly all of the dorsal part of the supraoccipital is missing, but the ventrolateral processes are present showing clear sutures.

Contacts: In *Foxemys* the supraoccipital contacts the parietal dorsally and anteriorly, the prootic anterolaterally, the quadrate laterally, the opisthotic posterolaterally, and the exoccipital posteroventrally.

Structures: The crista supraoccipitalis is not well preserved in *Foxemys* and its total length is unknown. As preserved it is about the same length and size as in *Bothremys maghrebiana*. The supraoccipital forms the dorsal margin of the foramen magnum and seems to lack the acute flange seen in *Bothremys maghrebiana* and *Araiochelys*.

EXOCCIPITAL (figs. 101, 104, 107)

Preservation: Both exoccipitals are present and nearly complete in MDEt 10, but breakage and matrix obscure some contacts. In MC M1734 both exoccipitals are present, nearly complete, with clear sutures; they are broken in PAM 511A.

Contacts: As in the other Bothremydini, the exoccipital in *Foxemys* contacts the supraoccipital dorsally, the opisthotic laterally, the quadrate ventrolaterally, and the basioccipital ventrally.

Structures: The rim of the foramen magnum is smooth in *Foxemys*, but in *Polysternon* and most Bothremydini there is a low ridge trending ventrolaterally from the supraoccipital. The condylus occipitalis has no basioccipital participating in the condyle. *Polysternon* and all the Taphrosphyini and Bothremydini have the exoccipital making up all of the condyle. The foramen nervi hypoglossi in *Foxemys* has two openings, as is usually the case in bothremydids.

The foramen jugulare posterius in *Foxemys* is nearly surrounded by the exoccipital. However, the lateral margin is open and there is no exoccipital-exoccipital contact closing the foramen laterally. *Polysternon* and the Cearachelyini also have this condition, but the remaining Bothremydini and all the Taphrosphyini have it closed.

BASIOCCIPITAL (figs. 101–104, 107)

Preservation: The basioccipital is present in MC M1734, but it is broken off at the base of the condylus occipitalis in PAM 511A, and more of the posterior margin is broken in MDEt 10. Sutures are discernable in MDEt 10, MC M1734, and clear in PAM 511A.

Contacts: The basioccipital in *Foxemys* contacts the basisphenoid anteriorly, the quadrates laterally, and the exoccipitals dorsally, as in other bothremydids. Whether the basioccipital enters the condylus mandibularis is not determinable.

Structures: The condylus occipitalis is missing in both *Foxemys* skulls. The tuberculum basioccipitale is similar in size and shape to that in *Bothremys maghrebiana*, *Polysternon*, and *Araiochelys*. It is larger than in the *Chedighaii hutchisoni*, but about the same as in *C. barberi*. There is a shallow, median concavity. as in most of the other Bothremydini.

PROOTIC (figs. 101, 104)

Preservation: The prootic is preserved on both sides in both skulls, but the medial structures and sutures are damaged or covered by matrix in both. Sutures on the ventral surface on the right side of PAM 511A are clear.

Contacts: The prootic in *Foxemys* contacts the parietal medially, the quadrate laterally, the supraoccipital posterodorsally, and the pterygoid ventrally. There is no opisthotic contact in either MDEt 10 or PAM 511A. On the ventral surface, the prootic contacts the pterygoid anterolaterally, the basisphenoid anteromedially, and the quadrate posterolaterally.

Structures: The foramen nervi trigemini in *Foxemys* lies between the prootic and parietal, but it is not well preserved in either skull.

It is possible that a small part of the prootic surrounding the foramen nervi facialis is exposed in the anterior roof of the fossa pterygoidea (see Pterygoid), but none of the specimens, including the two new skulls, MC M1734 and MC M2119, is well preserved in this area. It is likely that the exposure of the prootic and the foramen nervi facialis is correlated with the deep fossa pterygoidea. The exposure of the prootic in *Kurmademys* and *Sankuchemys* is similar.

OPISTHOTIC (figs. 101, 104, 107)

Preservation: Both opisthotics are preserved in both *Foxemys* skulls. Both skulls have a small amount of breakage along the posterior margins of each opisthotic.

Contacts: The opisthotic in *Foxemys* contacts the supraoccipital anteromedially, the quadrate anterolaterally, the squamosal posterolaterally, and the exoccipital posteromedially. There is no prootic contact (see Prootic, Supraoccipital).

Structures: The opisthotic does not form the lateral margin of the foramen jugulare posterius, but it comes very close to the open margin of the foramen and forms the horizontal groove that connects the foramen jugulare posterius and the fenestra postotica. The fenestra postotica is recessed into the occiput and divided into two foramina (see Quadrate). The more medial foramen, for the vena capitis lateralis, is formed dorsally by the opisthotic.

The posterior margin of the opisthotic is a horizontal flange, continuous with the squamosal, as seen in other Bothremydini. In *Foxemys* and the other Bothremydini, this flange lies ventral to a distinct step or concave indentation, formed on the vertical surface of the opisthotic.

BASISPHENOID (figs. 101–104)

Preservation: Both skulls have the basisphenoid preserved; the sutures in PAM 511A are clear, but in MDEt 10 they are not all distinct.

Contacts on ventral surface: The basisphenoid of *Foxemys* contacts the pterygoids anterolaterally, the prootic laterally, the basioccipital posteriorly, and the quadrate posterolaterally. The quadrate contact is broad in *Foxemys* and *Polysternon*, broader than in the other Bothremydini. The prootic contact is irregular and exposed in the roof of the fossa pterygoidea.

Structures on the ventral surface: The basisphenoid forms the medial part of the fossa pterygoidea in *Foxemys* (see Quadrate, Pterygoid). The foramen posterius canalis carotici interni is formed medially by the basisphenoid and laterally by the pterygoid (see Pterygoid). Just posterior to this foramen is an indentation where the prootic is exposed. Within the prootic is the foramen nervi facialis (see Prootic, Pterygoid).

Contacts and structures on dorsal surface: The dorsal surface of the basisphenoid is not visible in either *Foxemys* skull.

Polysternon provinciale

There is only one skull for this taxon. It is extensively fractured and not prepared internally, but most of the sutures are clear. The description below is modified from Tong and Gaffney (2000). The type of this species is a shell, and its association with this skull is based on its occurrence in the same quarry and at the same geological level as shells of

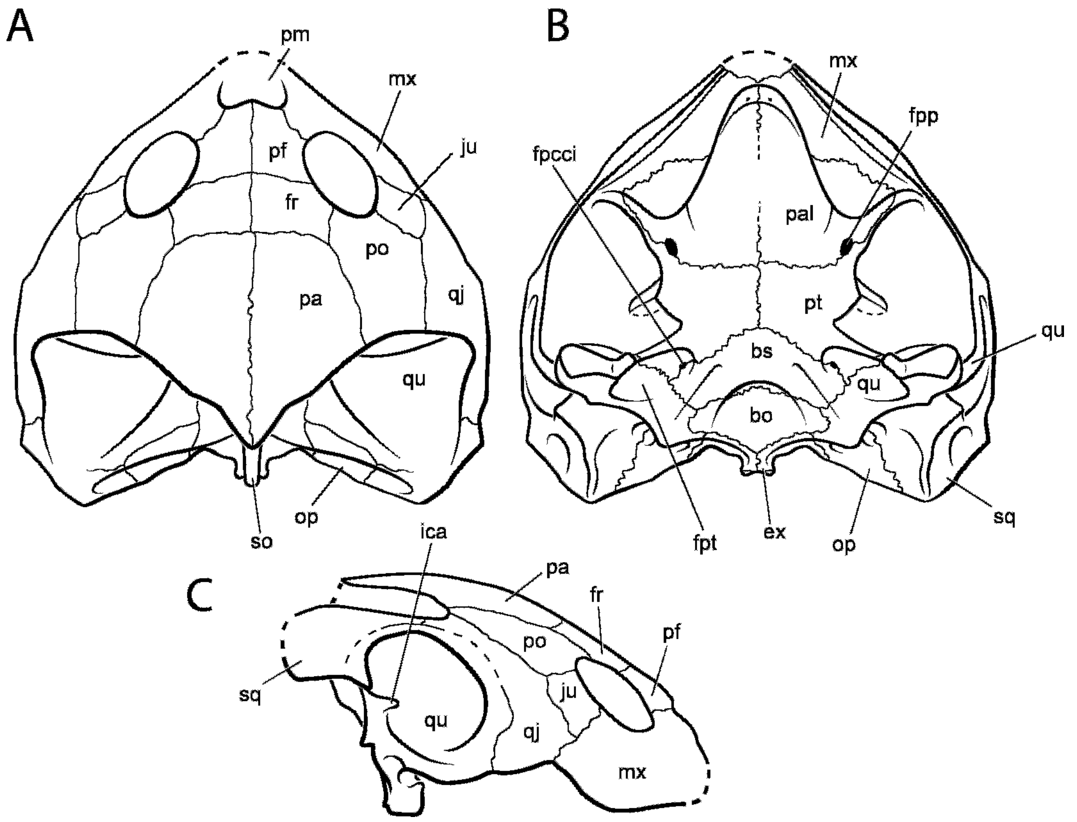

Fig. 108. *Polysternon provinciale* (Matheron, 1869). Partially restored skull based on AE 28. **A**, dorsal; **B**, ventral; **C**, lateral. [W.A. Recher, del.]

Polysternon. Polysternon and *Foxemys* are closely related based on quadrate and cheek characters.

PREFRONTAL (figs. 108, 111)

Preservation: Both prefrontals are present, but the maxilla contacts are broken areas of matrix. Only the dorsal surface is visible.

Contacts: As in *Foxemys*.

Structures: The prefrontals of *Polysternon* are very similar to those in *Foxemys*. The anterior edges are natural and are transverse with no projection. The contact with the dorsal process of the maxilla is broken on both sides, but the right one is better preserved. The internal portion of both prefrontals is covered by matrix. The orbits are slightly closer together in *Foxemys* than in *Polysternon*, so in the latter the prefrontals and the frontals are wider.

FRONTAL (figs. 108, 111)

Preservation: Both frontals are present; only the dorsal surface is visible.

Contacts: As in *Foxemys*.

Structure: The frontals are very similar to those in *Foxemys*.

PARIETAL (figs. 108, 111)

Preservation: The left parietal is nearly complete; the right one lacks a small part of the anterolateral margin. Only the dorsal surface is visible.

Contacts of dorsal plate: As in *Foxemys*.

Structures of dorsal plate: The parietal shape and the degree of temporal emargination in *Polysternon* are similar to those in the other Bothremydini, particularly *Foxemys* and *Bothremys*.

Contacts and structures of processus inferior parietalis: Covered by matrix.

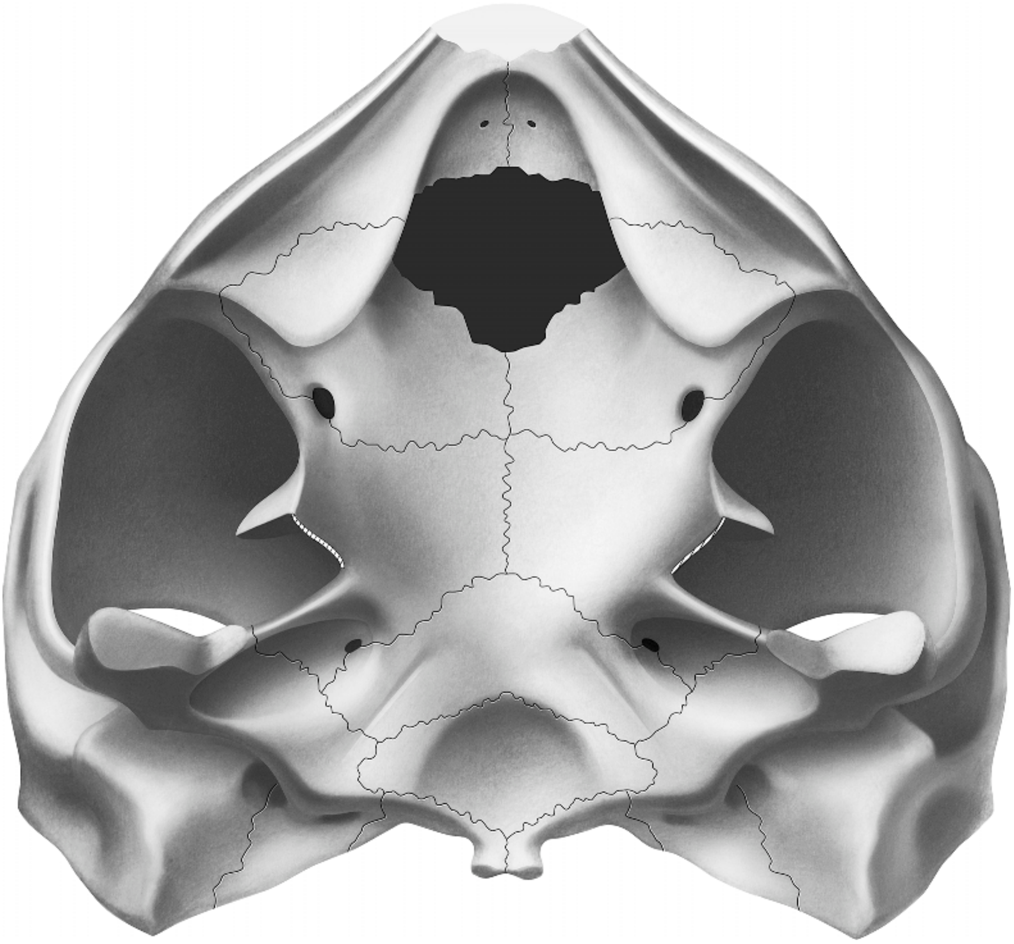

Fig. 109. *Polysternon provinciale* (Matheron, 1869). Partially restored ventral view based on AE 28. [W.A. Recher, del.]

JUGAL (figs. 108, 111)

Preservation: The jugals are preserved on both sides of AE 28.

Contacts of lateral plate: The jugal contacts the postorbital dorsally, the quadratojugal posteroventrally, and the maxilla anteroventrally, all as in *Foxemys* but in contrast to *Bothremys*, which has a small, dorsal quadratojugal.

Structures of lateral plate: The jugal does not reach the cheek margin, but it is exposed widely in the orbital margin, as in *Foxemys* and most other Bothremydini.

Contacts and structures of medial process: In ventral view, a small part of the medial process is visible in the anterior wall of the fossa temporalis that contacts the maxilla anteriorly, the palatine medially, and does not extend onto the triturating surface.

QUADRATOJUGAL (figs. 108, 111)

Preservation: The left quadratojugal in *Polysternon* is nearly complete, but the right one is only represented by its anterior part.

Contacts: As in *Foxemys*. The quadratojugal contacts the maxilla anteriorly, excluding the jugal from the cheek margin.

Structures: The quadratojugal in *Polysternon* agrees with *Foxemys* in the presence of a shallow cheek emargination that is longer than high. The quadratojugal forms a curved contact with the quadrate anterior to the cavum tympani of the quadrate in

Polysternon, as in *Foxemys*. In both *Polysternon* and *Foxemys* the quadratojugal forms the anterolateral corner of the temporal emargination, and a process extends posteriorly to contact the squamosal, preventing the quadrate from being exposed in the temporal margin. In the other Bothremydini (*Rosasia*, *Araiochelys*, *Bothremys*, *Chedighaii*) the quadratojugal is small and placed posterodorsally, allowing a quadrate-maxilla contact (fig. 4).

SQUAMOSAL (figs. 108, 111)

Preservation: The right squamosal is missing in AE 28 and the left one is damaged by crushing.

Contacts: As in *Foxemys*.

Structures: The squamosal in *Polysternon* lacks the posterior extension seen in *Foxemys* and other Bothremydini, but this is probably due to damage. The antrum postoticum is largely crushed and its internal structure is not visible.

POSTORBITAL (figs. 108, 111)

Preservation: The postorbital is complete on the left side; a small edge may be missing laterally on the right.

Contacts of lateral plate: As in *Foxemys*.

Structures of lateral plate: The postorbital in *Polysternon* is very similar to that in *Foxemys*, but it is slightly shorter. The postorbital-quadratojugal suture is slightly shorter in *Polysternon*, suggesting that the temporal emargination is slightly more extensive in *Polysternon* than in *Foxemys*.

Contacts and structures of medial process: Not visible due to matrix.

PREMAXILLA (figs. 108, 109, 111)

Preservation: The premaxillae in AE 28 are preserved but not complete; the anterior ends are missing.

Contacts: As in *Foxemys*.

Structures on dorsal surface: From the angle of the preserved portion it is likely that the snout of *Polysternon* was slightly more pointed than in *Foxemys*. Only the ventral surface of the premaxilla is visible; the dorsal surface is covered with matrix.

Structures on ventral surface: The midline suture is visible as well as the two foramina praepalatinum that are placed in the premaxillae, as in *Foxemys*, but unlike *Bothremys* in which these foramina are placed on the premaxilla-vomer suture.

The triturating surface on the midline at the anterior end of the skull was probably very narrow in *Polysternon*, as in *Foxemys*. Just posterior to the triturating surface, the premaxillae and maxillae form a midline depression in *Polysternon* that is much wider and more sharply defined than in *Foxemys*. The vomer in AE 28 is missing and the posterior edges of the premaxillae and anterior edges of the palatines are broken margins.

MAXILLA (figs. 108, 109, 111)

Preservation: All of both maxillae are preserved; the labial ridges have some minor breakage on their edges.

Contacts of vertical plate: As in *Foxemys*.

Structures of vertical plate: The maxilla depth from the orbit to the labial ridge edge varies from slightly shallower to significantly shallower than it is in the other Bothremydini. The labial ridge edge is acute, as in *Foxemys*. The apertura narium externa is inclined anteroposteriorly more than in *Foxemys*, but not as much as in *Zolhafah*.

Contacts of horizontal plate: As in *Foxemys*.

Structures of horizontal plate: The maxillae in *Polysternon* form most of the large triturating surfaces. Except for the premaxillary contact, the margins of the maxilla are clearly visible. Only its ventral and lateral surfaces in AE 28 are exposed; the dorsal surfaces are covered with matrix. The triturating surface in *Polysternon* is quite similar to *Foxemys*: it is strongly triangular, very narrow anteriorly, and wide posteriorly. The posterior part of the triturating surface is broader in *Foxemys* than in *Polysternon*, resulting in a distinctly narrower apertura narium interna in *Foxemys* than in *Polysternon*. Anteromedially the triturating surface of *Polysternon* has a low lingual ridge along the edge of the apertura narium interna that is sharper and more clearly defined than the very low one in *Foxemys*, and the labial ridge in *Polysternon* is clearly lower than that of *Foxemys*. The actual surface of the triturating area in *Polysternon* is flat, curving out to the labial ridge, but a low concavity can be seen on both sides in the region of the maxilla-palatine suture.

VOMER

Preservation: Not preserved.

PALATINE (figs. 108, 109, 111)

Preservation: Both palatines are present; some edges missing anteromedially.

Contacts: As in *Foxemys*.

Structures on dorsal surface: Covered by matrix.

Structures on ventral surface: The palatines in *Polysternon* are similar to those in *Foxemys*, differing primarily in the width of the apertura narium interna. Each foramen palatinum posterius is formed half by the palatine (anteriorly) and half by the pterygoid (posteriorly).

QUADRATE (figs. 108, 111, 112)

Preservation: The quadrate in AE 28 is largely missing on the right side and damaged to some extent on the left.

Contacts on lateral surface: The contacts are as in *Foxemys*: quadratojugal anteriorly and squamosal posterodorsally.

Structures on lateral surface: The quadrate in *Polysternon* has strong similarities to *Foxemys*, in contrast to other bothremydids. The incisura columellae auris of *Foxemys* is unusual among bothremydids in being open, with no complete bony bar separating the stapes from the eustachian tube. *Polysternon* as preserved clearly shows an open incisura columellae auris on the left quadrate, as in *Foxemys*. The dorsal margin of the incisura is broken and obscured by matrix holding some bone fragments, but the ventral margin and the posterior part of the dorsal margin are intact and clearly show smooth bone surfaces with no missing bone that could have closed the incisura. This is in contrast to the figure of *Polysternon* (AE 28) in Lapparent de Broin and Werner (1998: fig. 4h) that shows a closed incisura columellae auris in this same specimen.

The incisura columellae auris of *Polysternon* as preserved is widely open, much wider than in *Foxemys*. It is apparent, however, that the condylus mandibularis of the quadrate has been bent ventrally in this skull. Also, the dorsal margin of the incisura is absent, represented by a ridge of matrix and bone fragments. The base of the incisura seems to be well preserved and is relatively narrow, as in *Foxemys*, but the original extent of the rest of the incisura was probably narrower than preserved at present. Although the incisura columellae auris is open in *Polysternon*, it is likely that it was very narrow, nearly closed, as in *Foxemys*. Based on comparisons with other Pelomedusoides, it is likely that the eustachian tube was not present in the small, narrow incisura; rather, it was separated from the stapes, as in all other bothremydids. The pathway of the stapes and more medial and internal parts of the quadrate are not visible. The cavum tympani in AE 28 is cracked and slightly dislocated, but it is well enough preserved to show that there was no fossa precolumellaris. The cavum surface is smooth. This differs from *Foxemys*, which has a slight concavity but not a distinct fossa precolumellaris.

The antrum postoticum in *Polysternon* is crushed flat and its original extent is not completely determinable. However, there is enough of its dorsal edge present to show that at least a moderate antrum was present, not the extremely small or absent antrum seen in *Azabbaremys*. It is also clear that a large antrum postoticum of the sort seen in pelomedusids was not present in *Polysternon*. It is most likely that the antrum of *Polysternon* was the same as that in *Foxemys*.

Contacts on dorsal and anterior surface: The quadrates are visible on both otic chambers, although the left side is more complete. Sutures are not clear, but the opisthotic contact can be made out on both sides, and part of the squamosal suture is visible on the left side. As in *Bothremys*, *Rosasia*, and *Foxemys*, *Polysternon* has a well-developed quadrate-supraoccipital contact as seen on the right side of AE 28. All of both otic chambers are covered with matrix anteriorly.

Structures on dorsal and anterior surface: The foramen stapedio-temporale is not visible.

Contacts on ventral surface: As in *Foxemys*.

Structures on ventral surface: The fossa pterygoidea, formed by pterygoid and quadrate, is deep and narrow in both *Polysternon* and *Foxemys*. It is slightly deeper in *Poly-*

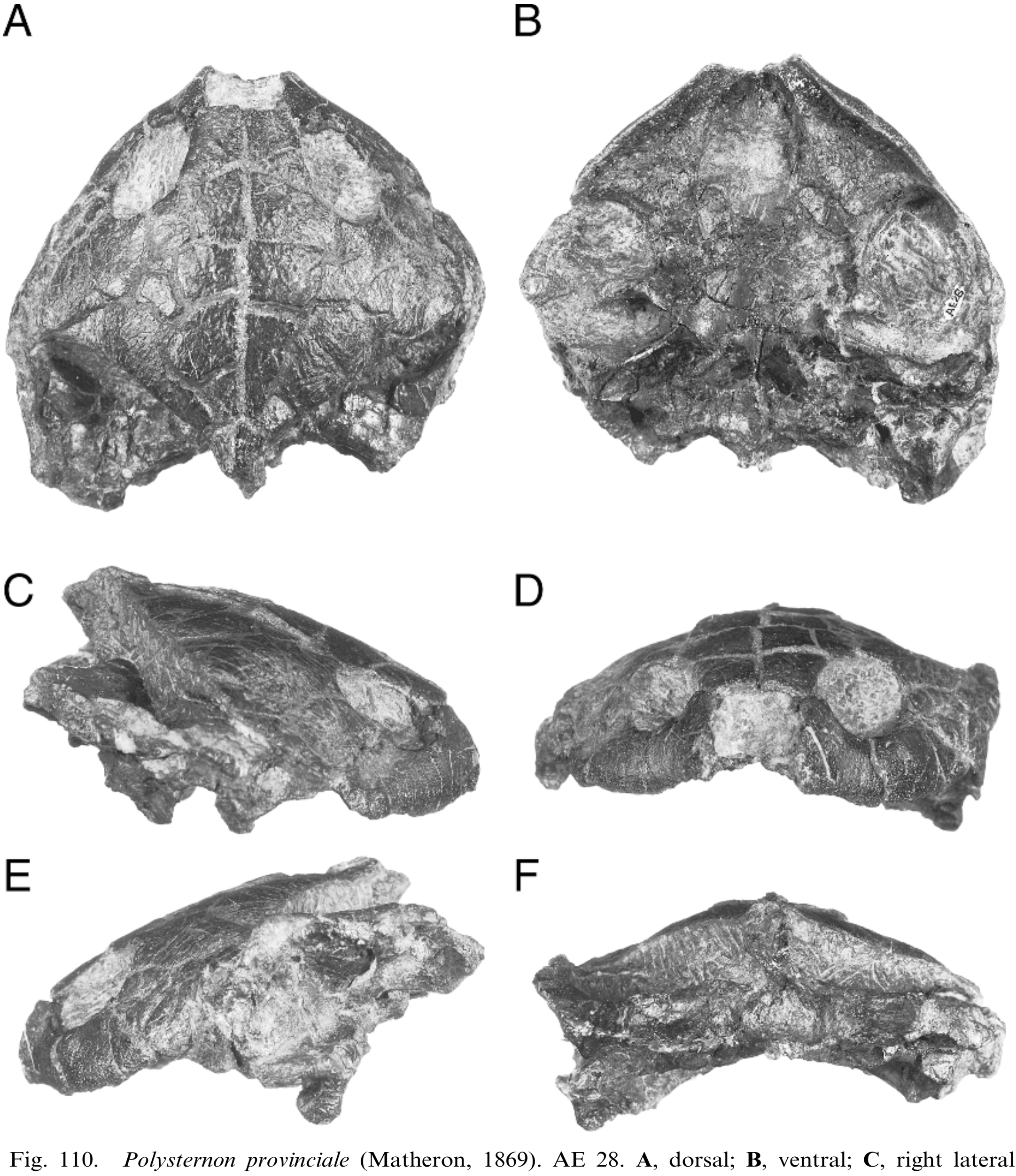

Fig. 110. *Polysternon provinciale* (Matheron, 1869). AE 28. **A**, dorsal; **B**, ventral; **C**, right lateral; **D**, anterior; **E**, left lateral; **F**, posterior (from Tong and Gaffney, 2000). [F. Ippolito, del.]

sternon than in *Foxemys*, although crushing may have affected this to some extent. The foramen posterius canalis carotici interni is formed by pterygoid and quadrate in both *Foxemys* and *Polysternon*.

A significant difference between *Polysternon* and *Foxemys* is the position of the processus articularis of the quadrate in relation to the occipital region of the skull. In *Polysternon* the condylus mandibularis and processus articularis of the quadrate are more anterior with respect to the condylus occipitalis, in contrast to *Foxemys* where they are more posterior, much closer to the condylus occipitalis. Although this area of the quadrate in AE 28 has been subjected to

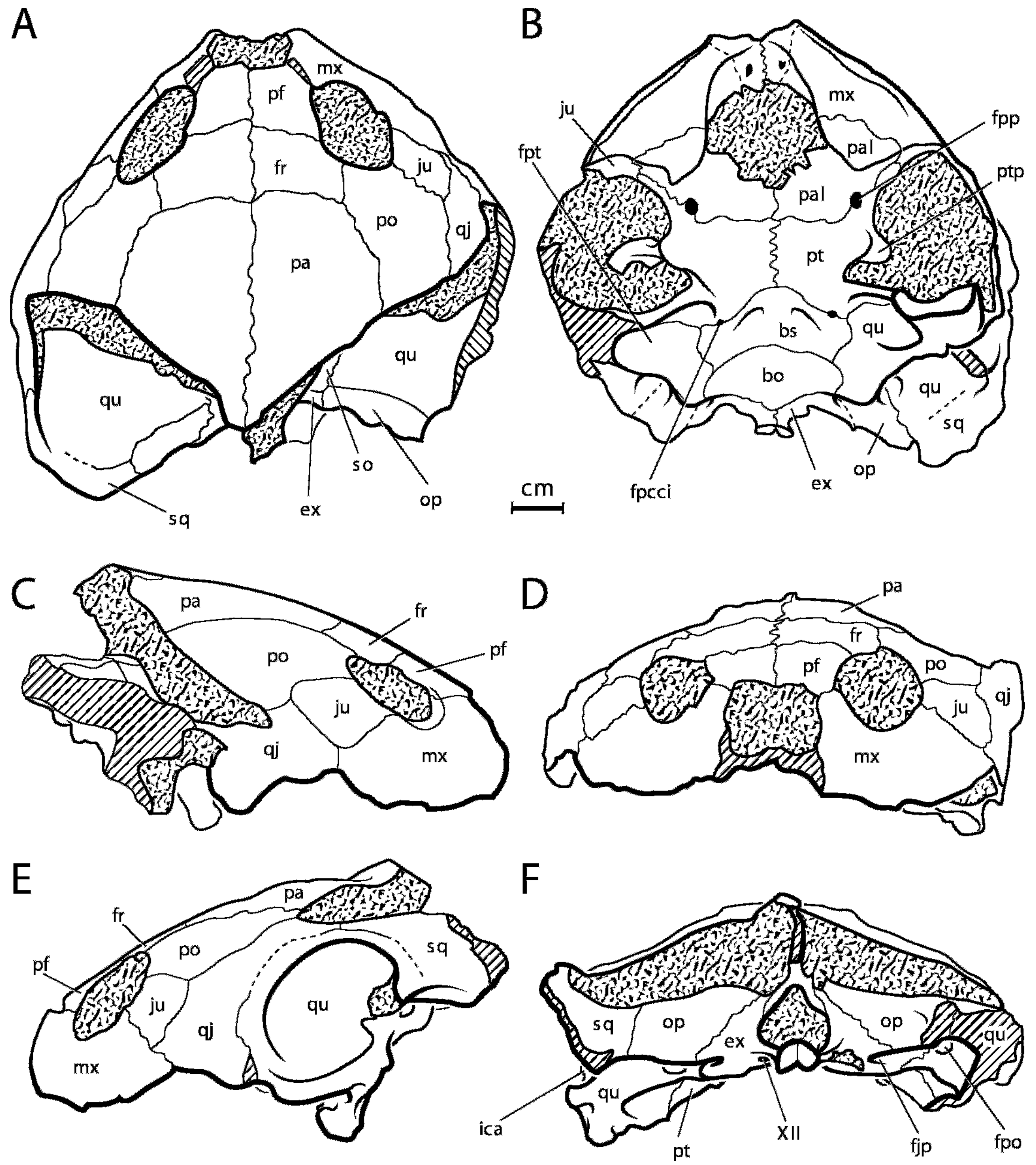

Fig. 111. *Polysternon provinciale* (Matheron, 1869). AE 28. **A**, dorsal; **B**, ventral; **C**, right lateral; **D**, anterior; **E**, left lateral; **F**, posterior (from Tong and Gaffney, 2000). [F. Ippolito, del.]

some postmortem displacement, it has not been moved very much in relation to the occiput.

Contacts on posterior surface: As in *Foxemys* and the other bothremydids, *Polysternon* has a well-developed quadrate-exoccipital contact, but it is more extensive in *Polysternon* than in *Foxemys*. The medial basioccipital contact is wider in *Polysternon* and *Foxemys* than it is in the other Bothremydini. The squamosal and opisthotic contacts are unclear.

Structures on posterior surface: The fenestra postotica is completely enclosed in

Polysternon and is partially subdivided, although the preservation on both sides is poor.

PTERYGOID (figs. 108, 109, 111)

Preservation: The pterygoids in AE 28 are both preserved, but visible only in ventral view. The edges of the processus trochlearis pterygoidei are broken in a few places.

Contacts on ventral surface: As in *Foxemys*.

Structures on ventral surface: The pterygoid in *Polysternon* is very similar to that in *Foxemys* except for the posterolateral process, the quadrate ramus. In *Foxemys* this process is directed more posteriorly and in *Polysternon* it is directed more anterolaterally in relation to the position of the processus articularis.

The fossa pterygoidea in *Polysternon* is shallower than in *Foxemys*, but some of this is due to breakage in AE 28. Similarly, the depression is wider in *Polysternon* than in *Foxemys*, presumably related to the more anterior position of the processus articularis in *Polysternon*. The processus trochlearis pterygoidei is present on both pterygoids. Its anterior surface is visible on the left side and its posterior face on the right side. The processus is at right angles to the skull midline, as in *Foxemys* and the other bothremydids.

Contacts and structures on dorsal surface: Covered by matrix and not visible.

SUPRAOCCIPITAL (figs. 108, 111)

Preservation: The supraoccipital in AE 28 is broken near its base, so the extent of the crista supraoccipitalis is not determinable. The ventral processes are slightly disarticulated and pushed ventrally, reducing the size of the foramen magnum. Only a small amount of the supraoccipital is exposed on the skull roof.

Contacts: The supraoccipital-quadrate contact is visible on the right side, and the exoccipital and opisthotic contacts are visible posteroventrally.

Structures: Very little of the crista supraoccipitalis is visible. The foramen magnum is as in *Foxemys*.

EXOCCIPITAL (figs. 108, 111, 112)

Preservation: The exoccipitals are preserved and nearly complete on both sides of AE 28 with most of their sutures visible.

Contacts: As in *Foxemys*.

Structures: The exoccipitals in *Polysternon* form all of the condylus occipitalis; none of the basioccipital even reaches the base of the condylus. The foramen jugulare posterius is open laterally on both sides, but it is better preserved on the right side, although it is broken on both. Only one foramen nervi hypoglossi is visible, and that is on the left exoccipital, because of crushing in the area of both exoccipitals. The exoccipital-quadrate suture and the exoccipital-opisthotic suture are both visible on both sides of the skull. The exoccipital as preserved is quite similar to that bone in *Foxemys*, except that in *Polysternon* the exoccipitals have a more extensive ventral exposure and present a longer ventral midline suture anterior to the occipital condyle. In *Foxemys*, the exoccipitals are less visible on the ventral side, with a shorter midline suture.

BASIOCCIPITAL (figs. 108, 109, 111, 112)

Preservation: The basioccipital is nearly complete in AE 28.

Contacts: The basioccipital in *Polysternon* is similar to that bone in *Foxemys*. Laterally it has well-developed contacts with the quadrates and posteriorly sends only a shallow, pointed process toward the condylus occipitalis and does not even reach the base of the condylus.

Structures: The basioccipitals of *Polysternon* and *Foxemys* show some important differences. In *Polysternon* the basioccipital is as wide as the basisphenoid and nearly as long. In *Foxemys* the basioccipital is narrower and much shorter. The condylus occipitalis (broken in *Foxemys*, but its bases show its position) is farther anterior in *Foxemys* than in *Polysternon* and the basioccipital is curved, concave posteriorly.

PROOTIC

Preservation: Probably present, but completely covered by matrix that fills the fossa temporalis. This is also the reason why the foramen stapedio-temporale is not determinable, as it is formed by the prootic in part.

OPISTHOTIC (figs. 108, 111, 112)

Preservation: Both opisthotics are preserved, but with some damage along their posterior edges. Ventral sutures are not clear.

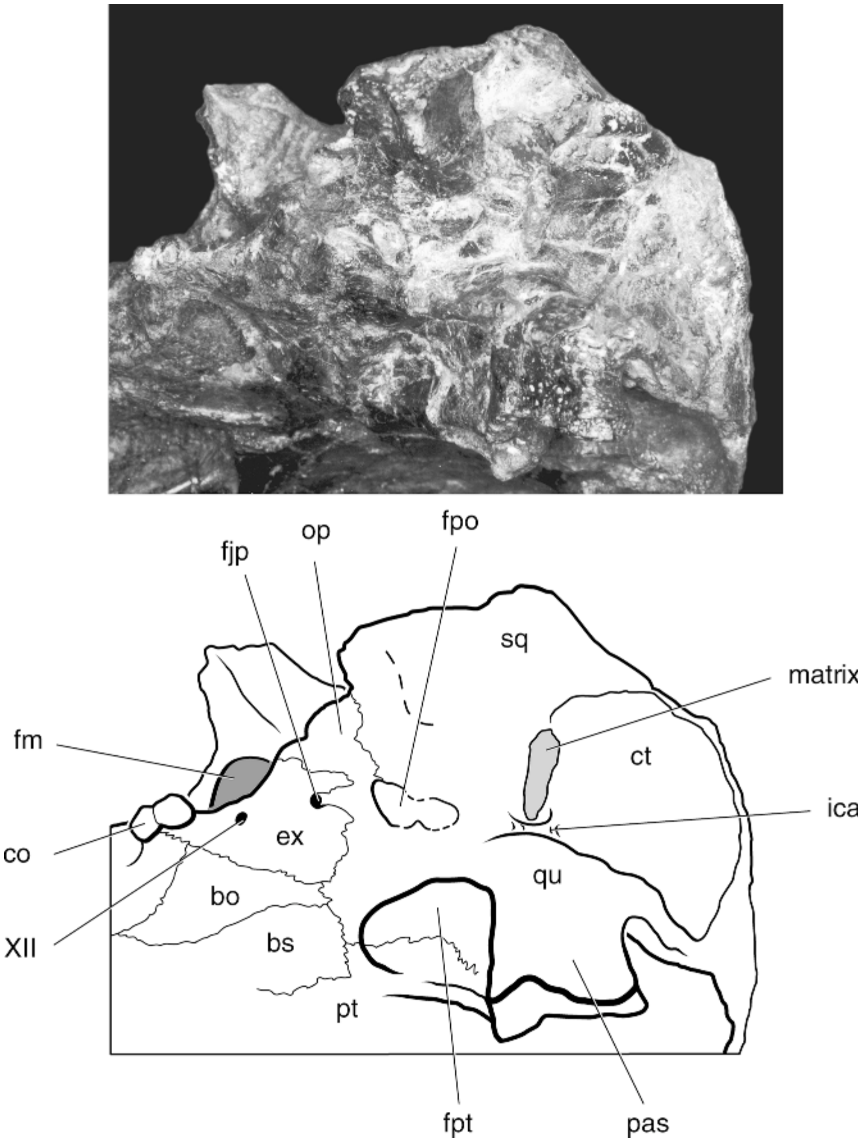

Fig. 112. *Polysternon provinciale* (Matheron, 1869). AE 28. Posterior oblique view reversed from left side. [A. Venjara and E.S. Gaffney, del.]

Contacts: Dorsally the opisthotic-quadrate suture is visible on both sides. Best preserved on the right otic chamber, the opisthotic does not reach the prootic due to the supraoccipital-quadrate contact.

Structures: The fenestra postotica is not well preserved on either side, but enough is available, particularly on the right, to show that the fenestra is closed laterally and medially as in *Bothremys* and all other Bothremydini.

BASISPHENOID (figs. 108, 109, 111, 112)

Preservation: The basisphenoid is nearly complete with generally clear sutures, but with some breakage laterally.

Contacts on ventral surface: The basisphenoid in *Polysternon* is triangular and very similar to that bone in *Foxemys*. The pterygoid and basisphenoid contacts are clear, but the lateral limits of the basisphenoid lie in regions of broken bone. Most of the quadrate-basisphenoid contact can be seen or extrapolated through cracks, except for the area where the quadrate-pterygoid-basisphenoid come together in the center of the fossa pterygoidea.

Structures on ventral surface: The foramen posterius canalis carotici interni is at the anterior end of the fossa pterygoidea, on the pterygoid-basisphenoid suture, as in *Foxemys*. This is in contrast to the position figured for the same specimen in Lapparent de Broin and Werner (1998: fig. 4d) in which this foramen is placed on the pterygoid-quadrate-basisphenoid contact.

Contacts and structures on dorsal surface: Not visible.

SUBTRIBE BOTHREMYDINA

Zolhafah bella

The single skull of this taxon is missing the cheeks and much of the skull roof. Most of its surface is eroded by blown sand. Nonetheless, enough is preserved to show that it is a Bothremydini related to *Rosasia* and outside the higher Bothremydini, *Bothremys* and *Chedighaii*. The skull roof is separate from the rest of the skull, which is free of matrix, so much of the internal areas are visible. A description of this skull with good photographs is in Lapparent de Broin and Werner (1998).

PREFRONTAL (figs. 113, 116)

Preservation: Both prefrontals are present but lack at least a third of their original length. The anterior margin is a rounded, eroded, irregular edge with an unknown amount missing. The dorsal surface is slightly eroded. The ventral surface is visible and free of matrix.

Contacts: As in other bothremydids, the prefrontal of *Zolhafah* contacts the maxilla anteroventrolaterally, the frontal posteriorly, and the other prefrontal medially. The prefrontal does not reach the palatine as it does in *Bothremys cooki*. As in other bothremydids, the frontal extends anteromedially beneath the prefrontal.

Structures: The anterior edge of the prefrontal in *Zolhafah* is a broken edge, and it is likely that at least a third or more of its original length is missing here. On the ventral surface, the prefrontal forms the roof of a large fossa nasalis that is clearly incomplete anteriorly. The apertura narium externa is wider than in the other Bothremydini, but most of its roof is probably missing.

As preserved, the fossa orbitalis has few original margins remaining, and none along its dorsal edge. The prefrontal and frontal are both eroded. However, it is likely that the prefrontal in *Zolhafah* only entered the margin of the orbit anterodorsally and did not form a significantly larger part of the margin, as in *Bothremys* and *Chedighaii*.

FRONTAL (figs. 113, 116)

Preservation: Both frontals are present in TUB Vb 173 but are eroded and missing bone along their lateral edges.

Contacts: As in other bothremydids, the frontal of *Zolhafah* contacts the parietal posteriorly, the prefrontal anteriorly, and the other frontal medially. There was probably a postorbital contact originally, but both postorbitals and lateral parts of both frontals are eroded away in TUB Vb 173.

Structures: The frontal of *Zolhafah* probably had a wide exposure in the orbital margin, as in *Rosasia*. Both frontals suffer from erosion and hence the orbits are larger postmortem than in life, but it is presumed that they still had a wide frontal exposure. The ventral surface shows a wide sulcus olfactorius defined by a parasagittal ridge that has an incomplete ventral edge on both sides.

PARIETAL (figs. 113, 116)

Preservation: Both parietals are present in *Zolhafah* but completely lack the temporal roof contribution and preserve only the roof over the cavum cranii. The processus inferior parietalis on both sides is badly eroded. The median section of the skull roof, consisting of prefrontals, frontals, and parietals, is detached from the rest of the skull. The contacts between the pieces are eroded and not fresh or close-fitting. The contacts that allow accurate placement of the skull roof piece are anteriorly, at the prefrontal-maxilla suture, and posteriorly, in a break within the parietal near the supraoccipital contact. On both sides fragments of the processus inferior parietalis contact the crista pterygoidea, but the walls of the processus on each side are mostly missing.

Contacts of dorsal plate: The parietal in TUB Vb 173 contacts the frontal anteriorly and the other parietal medially; the postorbitals and quadratojugals are missing.

Structures of dorsal plate: Nothing of the temporal roof or the sulcus palatinopterygoideus is preserved in *Zolhafah.*

Contacts of processus inferior parietalis: On both sides of the skull in *Zolhafah* a fragment of parietal remains in contact with the palatine anteroventrally and the pterygoid ventrally. More posteriorly the parietal contacts the prootic posteroventrally and the supraoccipital posteriorly.

Structures of processus inferior parietalis: The foramen nervi trigemini in *Zolhafah* has its usual parietal contribution anterodorsally, with the prootic dorsolaterally and the pterygoid ventrally. The margins of the foramen are eroded on both sides, but the positions of these elements can be reconstructed with some confidence.

JUGAL (figs. 113, 114, 116)

Preservation: Both jugals are present medially, but the lateral plates are represented only by small fragments on each side. The medial processes form part of the triturating surfaces, but the area is eroded dorsally and posteriorly on both sides.

Contacts of lateral plate: The lateral plate of the jugal on the right side in *Zolhafah* is only a small fragment showing sutural contact with the maxilla in what remains of the orbital margin. On the left side more of the jugal is preserved showing the maxilla contact. The dorsal tip of the eroded jugal fragment has what appear to be sutural interdigitations. If this is the case, then small fragments of the postorbital may be present in *Zolhafah.*

Structures of lateral plate: Despite the extensive breakage and erosion of the orbital margins, it is very likely that the jugal in *Zolhafah* enters the orbital margin, as described by Lapparent de Broin and Werner (1998).

Contacts of medial process: In the floor of the orbit in *Zolhafah*, the jugal contacts the maxilla anteriorly, anterolaterally, and anteromedially. It contacts the palatine posteromedially. In the postorbital wall the jugal has a long lateral suture with the maxilla. Posteriorly on the left side, there is an interdigitating suture with the palatine where the latter forms what is left of the septum orbitotemporale.

On the ventral surface the jugal forms a C-shaped contact with the maxilla anteriorly, and it contacts the palatine medially. These contacts vary slightly on each side, with the left one being more circular and the right one straightening out posteromedially. Contrary to the description and figure in Lapparent de Broin and Werner (1998: fig. 3a), the jugal is clearly exposed in the triturating surface on both sides (figs. 113, 114, 116B). The extent of exposure is similar to that in *Rosasia* and much less than in *Bothremys cooki.*

Structures of medial process: As in other bothremydids, the medial process of the jugal in *Zolhafah* forms part of the fossa orbitalis floor and the septum orbitotemporale. Due to extensive breakage neither septum orbitotemporale is complete enough to compare jugal exposure and contacts with other bothremydids.

On the triturating surface in *Zolhafah*, the jugal forms the dorsal part of the conical pit (figs. 113, 114, 116B), much as in *Rosasia.* Lapparent de Broin and Werner (1998: 141, fig. 3a) described the pit as being formed only by the palatine and maxilla, but there are clear jugal sutures present on each side showing a wide exposure of the jugal in each pit. The pit is cone-shaped, but as preserved it appears to be slightly asymmetrical, being shallower anteriorly where it grades into the maxillary surface. It is slightly steeper posteriorly where it forms the posterior wall of the pit. On both sides, the pit is eroded through dorsally, and the tip is absent. The left pit is more complete than the right one that lacks the posterior wall. The posterior wall in *Zolhafah* is thicker than in *Rosasia*, but not as thick and extensive as in *Bothremys.*

QUADRATOJUGAL

Preservation: It is likely that none of the quadratojugal is present in TUB Vb 173. The small fragment questionably identified as jugal or quadratojugal in Lapparent de Broin and Werner (1998: 145) is probably a piece of quadrate (see Quadrate).

SQUAMOSAL (figs. 113, 116)

Preservation: An anterior fragment of the squamosal is present on the left side in *Zolhafah*, but most of the bone is missing.

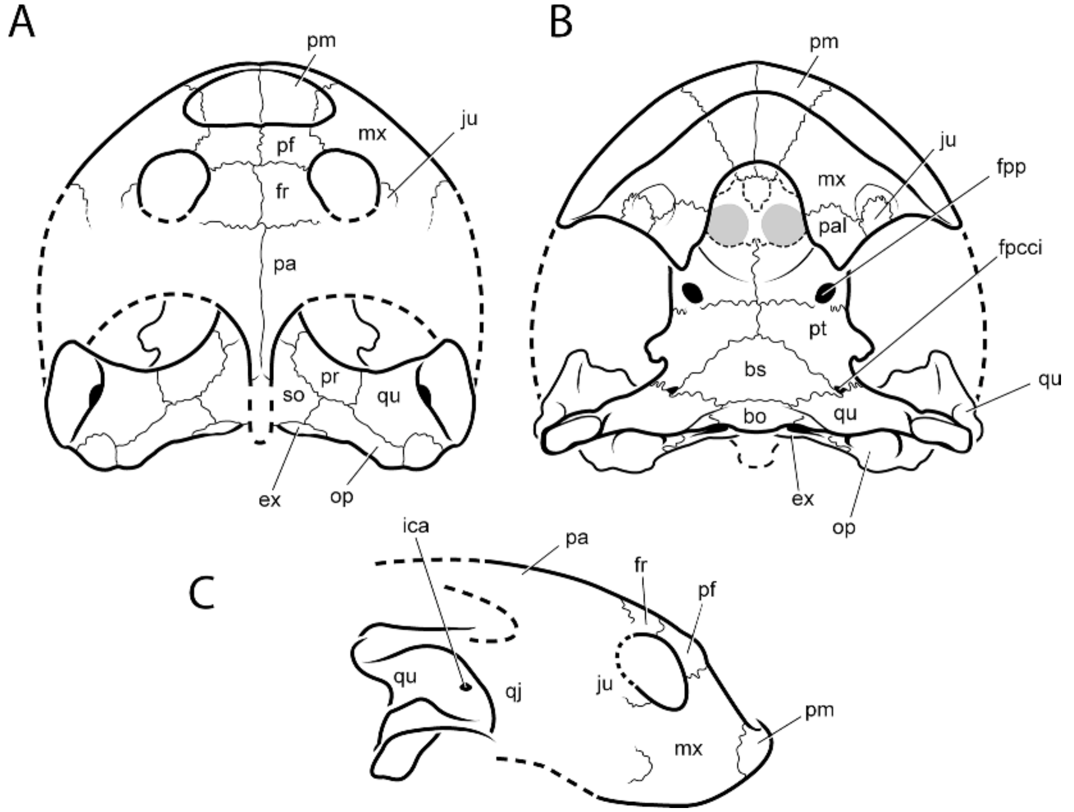

Fig. 113. *Zolhafah bella* Lapparent de Broin and Werner, 1998. Partially restored skull based on TUB Vb173 holotype. **A**, dorsal; **B**, ventral; **C**, lateral. [R. Rogge, del.]

Possibly a few fragments of squamosal are present in sutural interdigitations on the right side.

Contacts: The only contacts preserved in *Zolhafah* are with the quadrate anteriorly and with the opisthotic posteromedially.

Structures: Very little of the squamosal original surface is preserved in *Zolhafah*. Enough is preserved, however, to show that it is not inflated to form a large antrum postoticum, and a distinct ventral ridge is absent.

POSTORBITAL

Preservation: Except for a possible fragment on the left jugal, both postorbitals are missing in *Zolhafah*.

PREMAXILLA (figs. 113, 114, 116)

Preservation: Both premaxillae are present in *Zolhafah* and only seem to be missing some bone at their anteromedial margins on the dorsal surface. Thus, there was presumably more of an internarial division than is now present. Due to the complete absence of the anterior part of the prefrontals, it is possible that an extensive internarial separation was present.

Contacts: The premaxilla in *Zolhafah* is larger than in any other member of the Bothremydini, and the premaxilla suture is long and begins more posterolaterally than in other members of the Bothremydini. Posteriorly, the premaxillae narrow significantly to contact the vomer so that at the contact the bones are about the same width. As figured by Lapparent de Broin and Werner (1998: fig. 3a), it is likely that the maxilla and vomer met in the margin of the apertura narium interna, preventing exposure of the premaxilla in the apertura. On the left side the maxilla comes very close to meeting the vomer, but the edges are all broken, so an original contact was very likely.

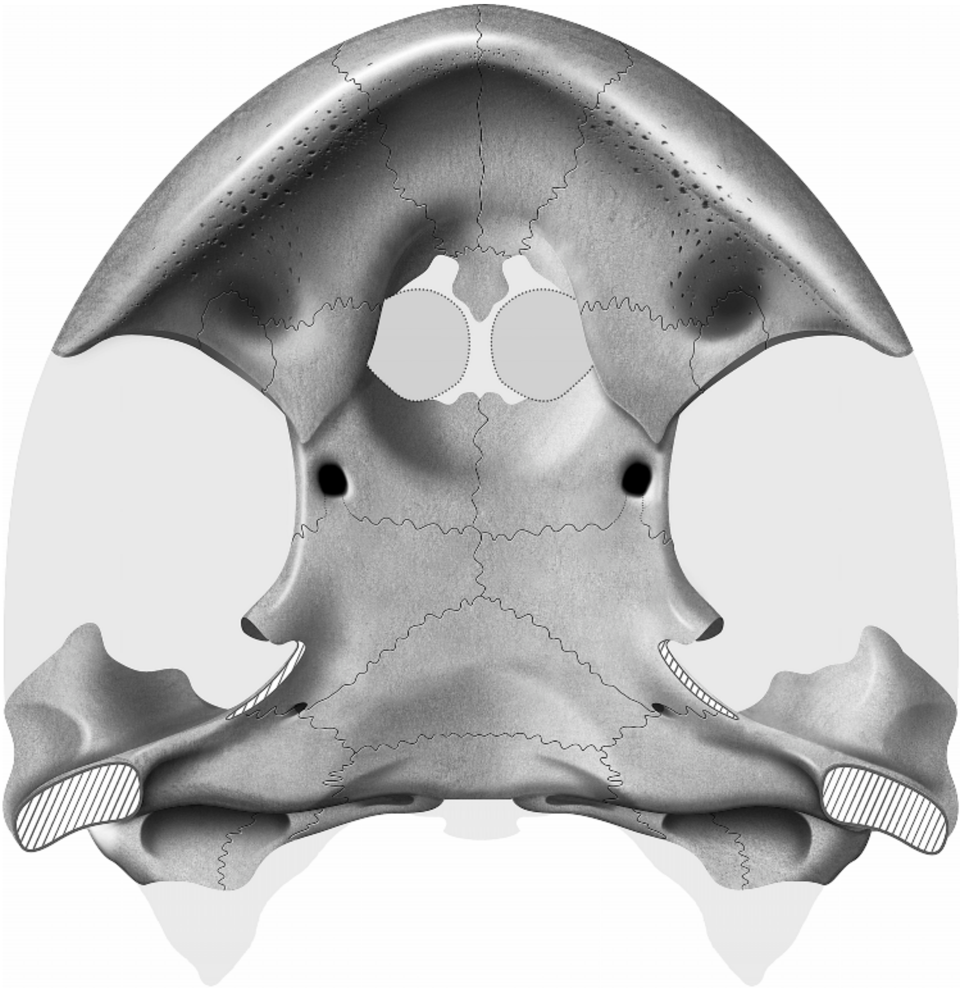

Fig. 114. *Zolhafah bella* Lapparent de Broin and Werner, 1998. TUB Vb173 holotype. Partially restored ventral view. [F. Ippolito, del.]

Structures on dorsal surface: The fossa nasalis and apertura narium externa in *Zolhafah* are very wide, relatively wider than in any other Bothremydini. The wide premaxillae form nearly all of the floor of the fossa nasalis. Each premaxilla has a low concavity separated from the anterior edge of the skull by a blunt ridge forming the apertura narium externa. This paired concavity is also in *Bothremys maghrebiana*. The concavity edge rises and widens posteriorly as it leads into the choanal passage and the apertura narium interna. The foramen praepalatinum is present on both sides just anterior to the vomer suture and is visible on both dorsal and ventral surfaces.

Structures on ventral surface: The labial ridge of *Zolhafah* is broad, low, and blunt, more so than in any other in the Bothremydini. The premaxillary part of the labial ridge continues the broad curve of the maxillary labial ridge in *Zolhafah*; there is no pinching or change in curvature as in *Rosasia* and *Bothremys*. There is also no upward curve on the midline of the labial ridge in *Zolhafah*, as in *Bothremys* and *Foxemys*. Posterior to the labial ridge, the triturating surface is a shallow concavity with a very indistinct lingual ridge sloping into the vomer. The area of the vague lingual ridge is usually a distinct median concavity in other bothremydids, but in *Zolhafah* it is only a shallow, sloping surface.

MAXILLA (figs. 113–116)

Preservation: Both maxillae are present in TUB Vb 173 and only lack their posterolateral and medial margins.

Contacts of vertical plate: As preserved, the maxilla in TUB Vb 173 contacts the prefrontal anterodorsally, the jugal posterodorsally, and the premaxilla anteromedially. A possible small fragment of the quadrate contact is preserved on the left side. This fragment is not really identifiable because the cheek is missing, but *Rosasia*, *Araiochelys*, and *Bothremys maghrebiana* have a quadrate contact in this position, and this is the basis for this identification. Lapparent de Broin and Werner (1998) questionably identified this as jugal or quadratojugal. A large quadratojugal that contacts the maxilla in this region is present in other Bothremydini taxa, namely *Chedighaii hutchisoni*, *Foxemys*, and *Polysternon*, so this cannot be discounted.

Structures of vertical plate: Most of the orbital margin is gone on the right side in TUB Vb 173. On the left side, the maxilla has what seems to be a slightly eroded ventral margin of the orbit. This is a high, acute ridge different from the low or absent ridge in other Bothremydini (see below). The maxilla of *Zolhafah* forms the lateral margin of the very wide apertura narium externa. The margin is a broadly rounded ridge, not acute and thin as in *Bothremys*.

Contacts of horizontal plate: he maxilla of *Zolhafah* has the usual bothremydid contacts: premaxilla anteromedially and palatine posteromedially. Additionally, there is the curved contact with the jugal posteriorly, as in *Rosasia*, *Bothremys*, and *Araiochelys*.

Structures of horizontal plate: The triturating surface of *Zolhafah* is broad and triangular, as in *Rosasia* and *Bothremys*. The labial ridge of the maxilla, as in the premaxilla, is unusually thick and obtuse with a low, rounded margin, not acute and thin as in the other Bothremydini species. The triturating surface is gently curved anteromedially and slopes into the pit, with the maxilla forming the anterior half of the cone-shaped depression and the jugal the dorsal part. The lingual ridge is low and indistinct, barely forming the median depression (see Premaxilla).

The medial edges of the maxilla are broken but form the margins of the apertura narium interna. The apertura is only slightly above the plane of the triturating surface in *Zolhafah*, not high above, as in *Bothremys* and *Araiochelys*. The medial processus of the maxilla are separated by the vomer-premaxilla contact, as in other Bothremydini species.

On the dorsal surface, the maxilla forms the fossa nasalis lateral wall and much of the choanal passage. In *Zolhafah* the choanal passage is as wide as the unusually wide fossa nasalis. In the vertical ridge separating the fossa nasalis and fossa orbitalis, a large foramen enters the main body of the maxilla that is probably the foramen supramaxillare. There is a concavity in the anterolateral part of the fossa orbitalis, beneath the orbital rim, not seen in any of the other Bothremydini. *Bothremys* and *Chedighaii* have a similar concavity but it is placed more posteriorly, in the postorbital wall.

VOMER (figs. 113–116)

Preservation: The anterior end of the vomer is preserved but the posterior two-thirds, the main body, is missing in *Zolhafah*. There is no sign of a suture on the palatine free edge, but it is likely that the free edges of the vomer have been eroded.

Contacts: The vomer meets the premaxilla anteriorly in *Zolhafah*. As preserved there is no maxilla contact, but as restored in Lapparent de Broin and Werner (1998: fig. 3a), if the broken edges are filled in, a vomer-maxilla contact would be present.

Structures: On the dorsal surface in *Zolhafah*, the anterior part of the vomer fragment bears the posterior edge of the median premaxillary ridge, with both premaxillae extending onto the vomer in a V-shaped suture. The ventral surface has no features and the surface is flat.

PALATINE (figs. 113–116)

Preservation: The left palatine is nearly complete; the right one is missing its edges posteriorly. Both have some breakage along the apertura narium interna margins.

Contacts: The palatine contacts the maxilla anteriorly, the jugal laterally, the pterygoid posteriorly, the other palatine medially, and, on the dorsal surface, the parietal posteromedially. These contacts also occur in *Bothremys* and *Rosasia*.

Structures on dorsal surface: Medially the palatine forms the lateral wall of the choanal passage leading into the apertura narium interna, which is formed laterally by palatine and maxilla, as in the other Bothremydini. The palatine forms the anterior floor of the sulcus palatinopterygoideus, the dorsal part of which is missing in TUB Vb 173. The palatine forms the posterior half of the fossa orbitalis, which is a shallow concavity.

The foramen palatinum posterius is a large, irregular opening in the palatine-pterygoid suture. It has broken edges around most of its perimeter, but the original margin shows that the foramen was much smaller, as in the other Bothremydini. There is a raised area on the palatine dorsal surface at its posterior edge that meets the processus inferior parietalis.

Structures on the ventral surface: The ventral surface of the palatine in *Zolhafah*, as in the other Bothremydini, bears a significant part of the triturating surface. The low and indistinct lingual ridge runs anteromedially to posterolaterally across the palatine. Anterolaterally the palatine slopes into the triturating surface pit before contacting the jugal.

QUADRATE (figs. 113–117)

Preservation: Both quadrates are present but damaged and missing significant portions. Both have had the surface areas eroded. The cavum tympani anterior and anterodorsal to the incisura columellae auris is missing on both sides.

Lateral surface contacts: Almost none of the lateral surface contacts is preserved. There is a probable quadrate fragment at the posterior edge of the maxilla (see Maxilla) on the left side, but the quadratojugal and postorbital are missing and the squamosal is extensively eroded.

Lateral surface structures: The cavum tympani is a deep, concave structure in *Zolhafah*, as it is in *Bothremys*, *Araiochelys*, *Rosasia*, and *Chedighaii*. There are the remnants of the horizontal shelf at the bottom of the cavum tympani found in all the other infrafamily Bothremydodda (the tribes Taphrosphyini and Bothremydini). The absence of the anterior part of the cavum tympani precludes determination of a fossa precolumellaris. The incisura columellae auris is a round opening, widely separated from the sulcus eustachii by bone. Due to erosion of the bone, the canal containing the stapes can be seen in TUB Vb 173, particularly on the right side, which is truly fascinating and brings tears to my eyes. The antrum postoticum is better preserved on the right side and is about the same size as in *Bothremys maghrebiana* (AMNH 30041), smaller than in *Galianemys*.

Dorsal surface contacts: *Zolhafah* has the usual pleurodire quadrate contacts: prootic anteromedially and opisthotic posteromedially. A fragment of the squamosal lies posterodorsally on the left quadrate. On both otic chambers there is a contact of the opisthotic and prootic, preventing a supraoccipital-quadrate contact. *Zolhafah* is unique among the Bothremydini in lacking a supraoccipital contact. In fact, the contact is present in all other Bothremydidae, that is, the tribes Kurmademydini, Cearachelyini, and Bothremydini, but not the tribe Taphrosphyini (fig. 307). The presence of the contact is probably primitive for the Bothremydidae and reversed independently in *Zolhafah* and the Taphrosphyini.

Dorsal and anterior surface structures: The foramen stapedio-temporale in *Zolhafah* is not completely preserved on either side due to erosion of the thin bone defining the foramen. However, it is clear from the position of the partially exposed canalis stapedio-temporalis that this foramen was completely on the anterior surface of the otic chamber at the medial limit of the quadrate. As in all other members of the tribes Bothremydini and Taphrosphyini, the foramen stapedio-temporale is close to the foramen nervi trigemini.

Contacts on ventral surface: As in all the other Bothremydidae, the quadrate in *Zolhafah* contacts the pterygoid anteromedially, the basisphenoid medially, and the basioccipital posteromedially. The degree of quadrate-basisphenoid contact is not as

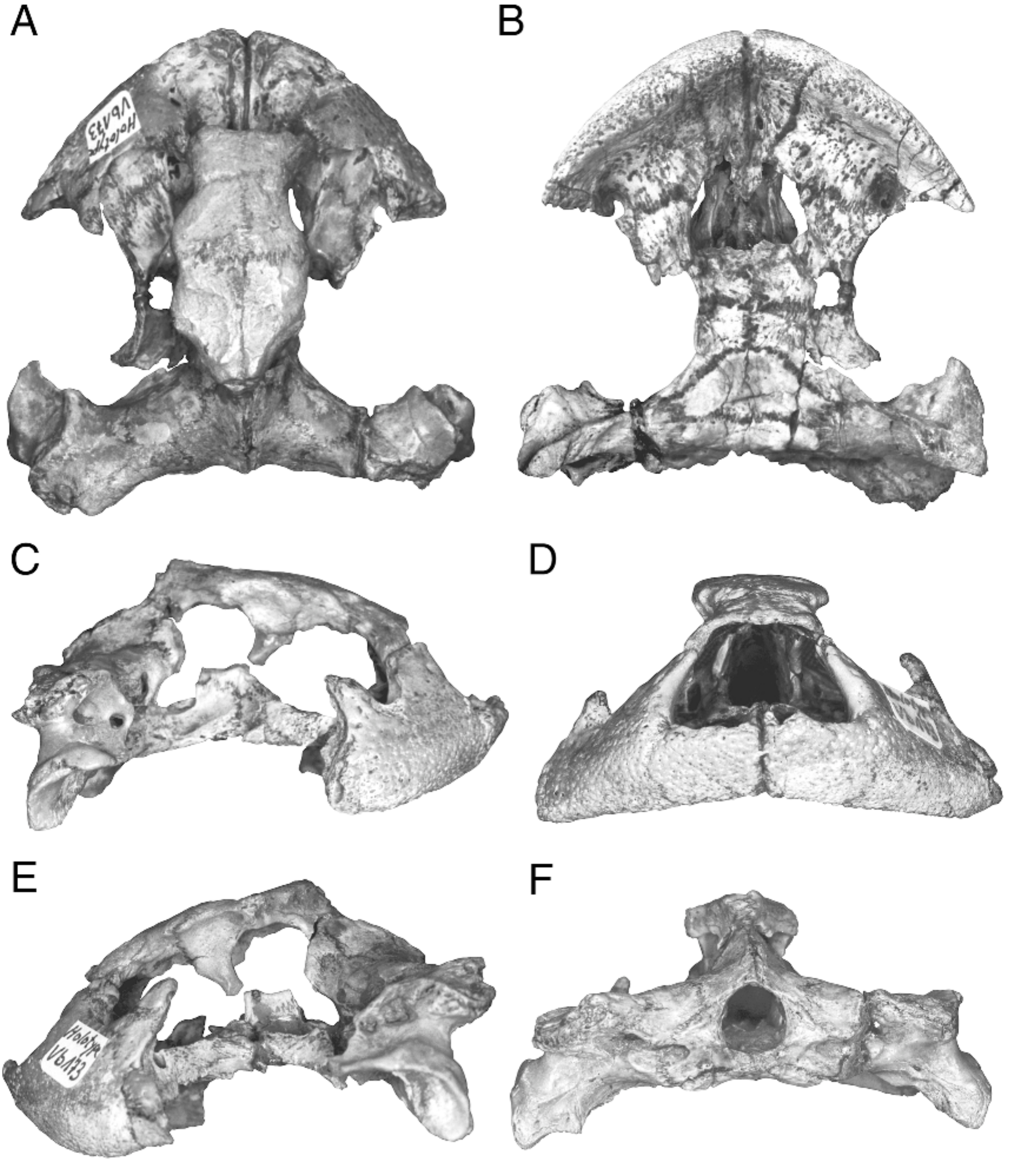

Fig. 115. *Zolhafah bella* Lapparent de Broin and Werner, 1998. TUB Vb173 holotype. **A**, dorsal; **B**, ventral; **C**, right lateral; **D**, anterior; **E**, left lateral; **F**, posterior. See also Lapparent de Broin and Werner (1998) for other figures. [E.S. Gaffney and C. Blik, del.]

narrow as in *Bothremys maghrebiana* and *Araiochelys*.

Structures on ventral surface: Although the ventral quadrate surface is damaged by erosion and breakage, particularly on the right side, enough is preserved on the left to show that no deep fossa pterygoidea was present. The quadrate shows no sign of any indentation or ridge in this area. The foramen posterius canalis carotici interni is formed by the pterygoid, basisphenoid, and quadrate (see Pterygoid). The quadrate has

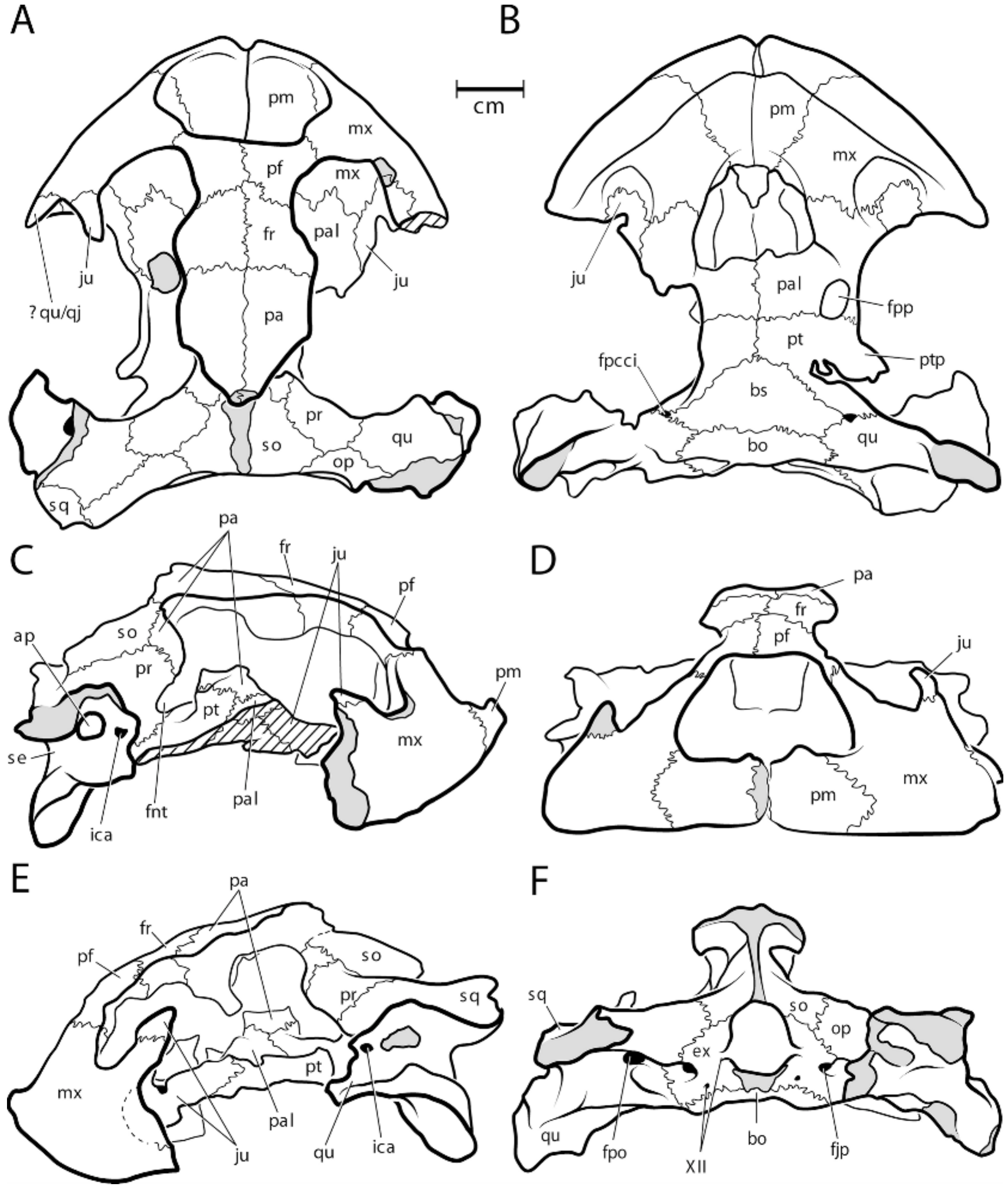

Fig. 116. *Zolhafah bella* Lapparent de Broin and Werner, 1998. TUB Vb173 holotype. **A**, dorsal; **B**, ventral; **C**, right lateral; **D**, anterior; **E**, left lateral; **F**, posterior. [A.M. Phillips, del.]

a groove that leads posterolaterally from the foramen. The condylus mandibularis in *Zolhafah* lies very close to the plane of the condylus occipitalis, as in the other Bothremydini, except *Polysternon* and *Araiochelys*.

Contacts on posterior surface: The quadrate in *Zolhafah* contacts the opisthotic dorsomedially, the exoccipital medially, the basioccipital ventromedially, and the small squamosal fragment dorsolaterally, all as in other Bothremydidae.

Structures on posterior surface: The fenestra postotica of *Zolhafah* is best seen on the left side (fig. 117), as it is present but damaged on the right. The quadrate forms the ventral margin of the fenestra postotica, with the opisthotic forming the dorsal half. The fenestra is completely enclosed medially and is separated from the foramen jugulare posterius by bone, as in the other Bothremydini. The fenestra postotica in *Zolhafah* is partially subdivided by low ridges on both quadrate and opisthotic into a more lateral opening (stapedial artery) and a more medial opening (lateral head vein). On the posterior surface of the quadrate is a low groove leading ventrally from the fenestra postotica. What this may be is unknown. Good grief. The foramen chorda tympani inferius is on the posterior surface of the quadrate below the sulcus eustachii.

PTERYGOID (figs. 113–116)

Preservation: Both pterygoids are present, having posterolateral damage. Most of the bone surface has been eroded. The dorsal surfaces of both pterygoids are visible.

Contacts on ventral surface: In *Zolhafah* the pterygoid contacts the palatine anteriorly, the other pterygoid anteromedially, the basisphenoid posteromedially, and the quadrate posterolaterally, all as in the other Bothremydidae. The medial pterygoid contact is about the same length as in *Rosasia*, longer than in *Bothremys* and *Araiochelys*, but not as long as in *Polysternon* and *Foxemys*.

Structures on ventral surface: The processus trochlearis pterygoidei is preserved on the left pterygoid, but it is eroded and damaged. As preserved, it is consistent with the angle and size of the processus in *Bothremys maghrebiana*. The ventral surface of the pterygoid has no indication of ridges or depressions. A fossa pterygoidea is absent. *Rosasia* has a distinct but not deep fossa, while *Polysternon* and *Foxemys* both have a deep fossa pterygoidea. The other Bothremydini lack a depression, as in *Zolhafah*.

The foramen posterius canalis carotici interni in *Zolhafah* (fig. 116B) is formed by quadrate, pterygoid, and basisphenoid (see Quadrate). Among the Bothremydini, only *Zolhafah* and *Bothremys kellyi* have these three bones forming the foramen (fig. 296B). In *Foxemys*, *Polysternon*, and *Rosasia*, the foramen is formed by basisphenoid and pterygoid, while in the remaining Bothremydini, the pterygoid and quadrate form the foramen. In all of the Bothremydini the pterygoid forms at least part of the foramen. This is probably primitive at the level of the family Euraxemydidae. The only other pleurodires with these three bones forming the foramen posterius canalis carotici interni are *Taphrosphys* and the as yet unnamed CNRST-SUNY 199.

The foramen palatinum posterius is in the suture between palatine and pterygoid (see Palatine). The pterygoid flange is broken away.

Contacts on dorsal surface: The dorsal surface of the pterygoids is preserved, but most of the septum orbitotemporale and dorsal part of the processus trochlearis pterygoidei are broken away, and only some of the sutural contacts remain. Similarly, some of the crista pterygoidea is missing.

Anteriorly, the pterygoid meets the palatine, and laterally, there is a thin process of the jugal reaching the base of the processus trochlearis pterygoidei. The crista pterygoidea contacts the parietal dorsally and the prootic posterodorsally. Posterolaterally the pterygoid reaches the quadrate, and medially it contacts the basisphenoid.

Structures on dorsal surface: The pterygoid forms the posterior floor of the sulcus palatinopterygoideus (see Palatine), as in the other Pelomedusoides. Medial to the crista pterygoidea is the sulcus cavernosus, formed by the pterygoid. Just lateral to the base of the processus clinoideus near the position of the foramen cavernosum is a paired foramen in the basisphenoid-pterygoid suture. Due to erosion of the otic chambers, the canal for the vidian nerve can be followed from the quadrate and prootic contact medially through the foramina and sulci leading to this foramen. Although the anterior exit of the vidian nerve is variable in turtles, it does not usually occur this far posteriorly, and in *Galianemys* it is known to exit more anteriorly near the foramen palatinum posterius, its usual position. It is possible that this foramen is the foramen caroticum laterale. In any case, in the other bothremydids in which this area is known, none has a foramen caroticum laterale and all have a foramen nervi vidiani that varies in position. For these reasons we identify it as the foramen nervi vidiani, but actually I don't give a rat's ass what it is.

Supraoccipital (figs. 113, 116, 117)

Preservation: The supraoccipital is missing the crista supraoccipitalis, and all of its surfaces are more or less eroded. The anterodorsal part of the contact with the parietal is mostly missing with eroded edges.

Contacts: The preserved contacts of the supraoccipital in *Zolhafah* are the parietal anteriorly, the prootic anterolaterally, the opisthotic posterolaterally, and the exoccipital posteroventrally, all as in other bothremydids. The quadrate contact is prevented by prootic-opisthotic contact (see Quadrate).

Structures: The crista supraoccipitalis is missing down to the main body of the supraoccipital, so there is no information on it in *Zolhafah*. The foramen magnum is eroded along its edges, but the supraoccipital clearly forms the upper part, as in other bothremydids.

Exoccipital (figs. 113, 116, 117)

Preservation: Both exoccipitals are present, eroded on their surfaces to expose the foramen nervi hypoglossi canals. A significant broken area is the condylus occipitalis, which is broken down to the base.

Contacts: As in other bothremydids, the exoccipital of *Zolhafah* contacts the supraoccipital dorsally, the opisthotic laterally, the quadrate ventrolaterally, and the basioccipital ventrally.

Structures: The foramen magnum in *Bothremys*, *Araiochelys*, *Chedighaii*, and *Foxemys* has a low, acute, posterior-facing ridge along the exoccipital margin. In *Zolhafah*, erosion has removed most of the original exoccipital surface (as well as supraoccipital and basioccipital surfaces) so that this ridge is absent and the occipital surface is flat compared with the other Bothremydini. This is probably an artifact of weathering.

The condylus occipitalis is broken off anterior to its neck (fig. 117). Even though the exoccipitals are broken off here, it looks like the basioccipital ends at this point and probably does not enter the condylus occipitalis, but this is not certain.

There are two foramina nervi hypoglossi on each exoccipital, with the dorsomedial one being larger than the more ventrolateral one. This is also the pattern in *Bothremys maghrebiana* and *Galianemys*. The foramen jugulare posterius is closed by a lateral meeting of the exoccipitals, as in the other Bothremydini with the important exceptions of *Foxemys* and *Polysternon*. The lateral margin of the foramen is more anterior than the medial margin, so the foramen faces more posterolaterally, as in *Bothremys maghrebiana*, but to a greater degree. This gives the foramen a superficial appearance of being open laterally, but this is not the case.

Basioccipital (figs. 113–117)

Preservation: Most of the basioccipital is present in TUB Vb 173, except for some erosion along the posterior margin.

Contacts: As in other bothremydids, the basioccipital of *Zolhafah* contacts the basisphenoid anteriorly, the quadrate laterally, and the exoccipitals dorsally.

Structures: The basioccipital is broken at the condylus occipitalis, but it looks like the basioccipital would not enter the condylus, although this is not certain (see Exoccipital). As preserved, there is only a slight raised indication of a tuberculum basioccipitale in *Zolhafah*, but this area is worn and eroded and its absence may be due to damage. There is a very shallow median concavity on the ventral surface of the basioccipital in *Zolhafah*. This area is worn and its subdued surface could be due to erosion.

Prootic (figs. 113, 116)

Preservation: Both prootics are present in TUB Vb 173 but have been eroded, exposing the canalis cavernosus anteriorly and removing the margins of the foramen nervi trigemini and foramen stapedio-temporale.

Contacts: As in other bothremydids, the prootic of *Zolhafah* contacts the parietal medially, the quadrate laterally, the supraoccipital posteromedially, and pterygoid ventrally. Contrary to all other bothremydids, except the tribe Taphrosphyini, there is also an opisthotic contact (see Supraoccipital and Quadrate).

Structures: Both prootics are eroded on their anterior surfaces. The canalis cavernosus is exposed, running medially from the

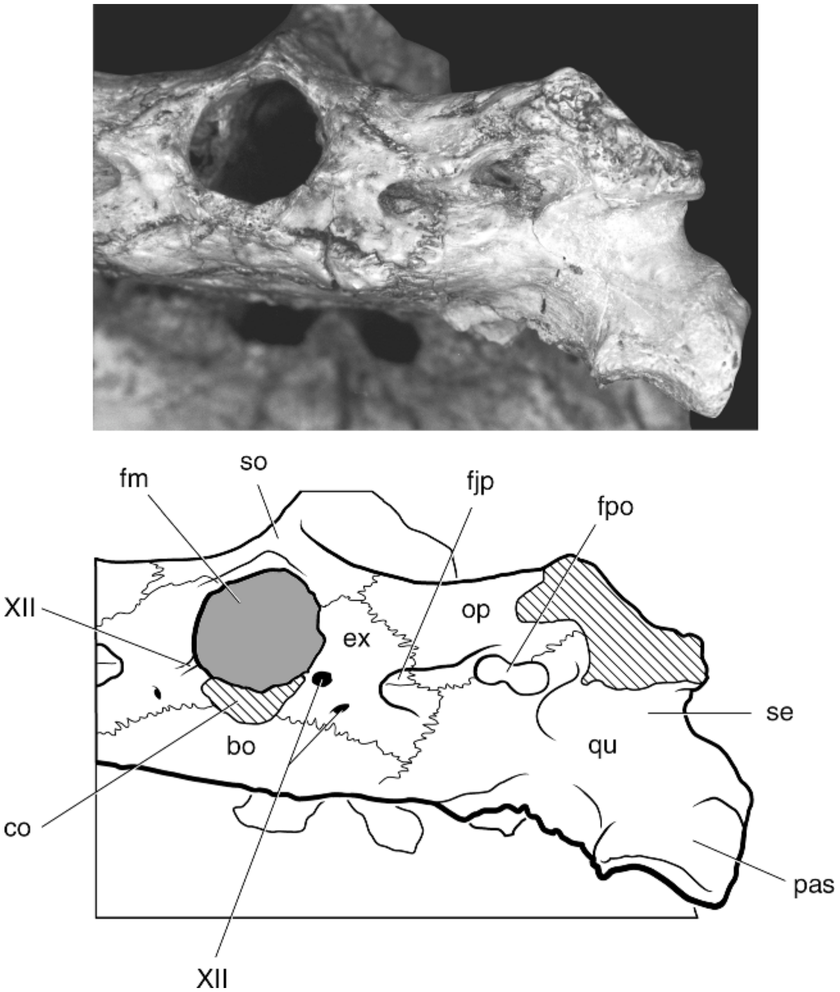

Fig. 117. *Zolhafah bella* Lapparent de Broin and Werner, 1998. TUB Vb173. Posterior oblique view reversed from left. [A. Venjara and E.S. Gaffney, del.]

quadrate. What seems to be the canalis nervi vidiani is exposed in the medial wall of the canalis cavernosus of the prootic, and probably communicates with a foramen in the pterygoid (see Pterygoid). The dorsal margin of the foramen nervi trigemini is formed by the prootic and is worn, but because of its greater thickness, it is still present, as opposed to the missing pterygoid and parietal parts of the foramen. The foramen stapedio-temporale margins are also eroded, but the canalis stapedio-temporalis (see Quadrate) can be seen, showing that the foramen stapedio-temporale was on the anterior surface of the otic chamber and was probably close to the foramen nervi trigemini.

Opisthotic (figs. 113, 116, 117)

Preservation: Both opisthotics are present in TUB Vb 173, but they are worn and eroded, particularly along the posterior edges.

Contacts: As in the other bothremydids, the opisthotic of *Zolhafah* contacts the supraoccipital anteromedially, the quadrate anterolaterally, the squamosal posterolaterally, and the exoccipital posteromedially on the occipital surface. In contrast to all other bothremydids except the tribe Taphrosphyini, *Zolhafah* has an anterior contact with the prootic.

Structures: The opisthotic of *Zolhafah*, as in all other bothremydids, forms the dorsal margin of the fenestra postotica. In *Zolhafah*, as in all of the tribes Taphrosphyini and Bothremydini, the fenestra is closed medially by opisthotic-quadrate contact (see Quadrate).

BASISPHENOID (figs. 113–116)

Preservation: The basisphenoid is present and with clear sutures. Both surfaces are worn and eroded. The dorsal surface is not completely prepared, and some damage has resulted from the preparation that has been done.

Contacts on ventral surface: As in other bothremydids, the basisphenoid of *Zolhafah* contacts the pterygoids anterolaterally (see Pterygoid), the quadrate posterolaterally, and the basioccipital posteriorly.

Structures on ventral surface: The foramen posterius canalis carotici interni is formed by pterygoid, quadrate, and basisphenoid (see Pterygoid, Quadrate).

Contacts on dorsal surface: As in the other Bothremydidae, the dorsal view of the basisphenoid of *Zolhafah* shows these contacts: pterygoid anteriorly and laterally, prootics posterolaterally, and basioccipital posteriorly.

Structures on dorsal surface: Among the Bothremydini, the dorsal surface of the basisphenoid can be seen in *Bothremys cooki* and *Bothremys maghrebiana*, as well as in *Zolhafah*. The rostrum basisphenoidale of *Zolhafah* is short and thick, as in both species of *Bothremys*. In contrast to *Bothremys*, however, the pterygoids extend medially to cover some of the rostrum in *Zolhafah*. The sulcus cavernosus is the same in all three species. The dorsum sellae in *Zolhafah* overhangs the sella turcica to a greater extent than in *Bothremys*. The edge of the sella turcica is broken and the sella was probably deeper and more enclosed than it is at present, also in contrast to *Bothremys*.

The foramen anterius canalis carotici interni cannot be seen, as the posterior part of the sella turcica is still filled with matrix. The processus clinoideus is broken on both sides, but the right one clearly shows that it was distinct, in contrast to the absent processus in *Bothremys*. The foramen nervi abducentis is visible on the left side but not on the right. The possible foramen nervi vidiani is discussed under Pterygoid.

Rosasia soutoi

The single skull (UNL uncataloged) representing this taxon lacks the occiput and much of the quadrate and right otic chamber. Otherwise, the skull is well preserved, uncrushed with clear sutures. It was described in Antunes and Broin (1988), who included stereophotographs as well as line drawings. *Rosasia*, along with *Zolhafah*, is outside the higher Bothremydini, *Bothremys* and *Chedighaii*.

PREFRONTAL (figs. 118, 121)

Preservation: Both prefrontals in UNL are present, nearly complete, and have clear sutures. Dorsal and ventral surfaces are visible. The anterior margin is slightly worn, but there are no broken edges.

Contacts: As in other bothremydids, the prefrontal in *Rosasia* contacts the maxilla anteroventrolaterally, the frontal posteriorly, and the other prefrontal medially. The maxilla contact is longer than in *Zolhafah* but shorter than in *Bothremys*. The frontal suture is transverse in *Rosasia*, not anteromedially trending, as in *Bothremys*.

Structures: The dorsal margin of the apertura narium externa is transverse in *Rosasia*, as in *Foxemys*, without the anterior projection seen in *Bothremys* and *Araiochelys*. There is some evidence of erosion here, but it is unlikely that much bone is missing. The prefrontal forms the anterodorsal orbital margin, as in other bothremydids. On its ventral surface, the prefrontal forms the roof of the fossa nasalis, a space that is much smaller in *Rosasia* than it is in *Zolhafah* and *Bothremys*, but is similar in size to *Foxemys*. The sulcus olfactorius is formed by a ridge on the prefrontal, similar to that in *Bothremys* and *Galianemys*.

FRONTAL (figs. 118, 121)

Preservation: Both frontals are present, nearly complete, and have clear sutures. Dorsal and ventral surfaces are visible. Some of the lateral margins are eroded away on both frontals.

Contacts: As in other bothremydids, the frontal of *Rosasia* contacts the prefrontal anteriorly, the parietal posteriorly, the postorbital posterolaterally, and the other frontal medially. The postorbital contact of *Rosasia*

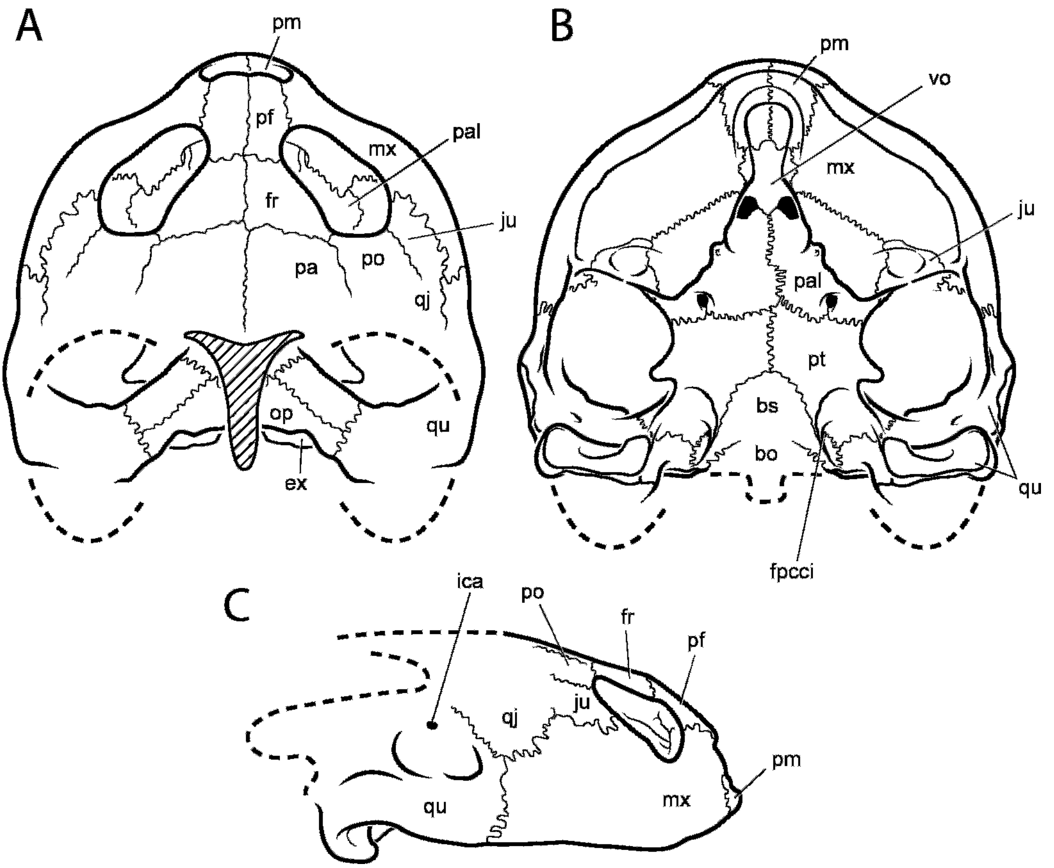

Fig. 118. *Rosasia soutoi* Carrington da Costa, 1940. Partially restored skull based on uncatalogued skull in Universidad Nova de Lisboa (UNL). **A**, dorsal; **B**, ventral; **C**, lateral. [R. Rogge, del.]

is much narrower than in other Bothremydini. However, all but the ventral orbital margins of UNL are eroded and missing bone, as noticed by Antunes and Broin (1988), and it is likely that the orbits were smaller originally. The very small postorbital-frontal contact is probably a postmortem artifact, and originally a more extensive contact would have been present.

Structures: As preserved, the frontal forms nearly all of the dorsal orbital margin in *Rosasia*, more so than in any other Bothremydini species. This may be due to erosion of the orbital margin; however, it is unlikely that the frontal had a very small orbital exposure as in *Bothremys maghrebiana*. The sulcus olfactorius is formed by a parasagittal ridge on the ventral surface of the frontal. It is similar in size and shape to that in *Bothremys*.

PARIETAL (figs. 118, 121)

Preservation: The anterior portion of both parietals is present, but the posterior part overlying the fossa temporalis and supraoccipital is missing. All of the posterior margins are broken edges. The processus inferior parietalis is preserved on both sides and is visible with clear sutures.

Contacts of dorsal plate: As in other bothremydids, the parietal in *Rosasia* contacts the frontal anteriorly, the postorbital laterally, and the other parietal medially. The presence or absence of a quadratojugal contact cannot be determined.

Structures of dorsal plate: The degree of temporal emargination cannot be determined, although the extreme emargination of the tribe Kurmademydini is unlikely.

Contacts of processus parietalis inferior: As in *Zolhafah* and other Bothremy-

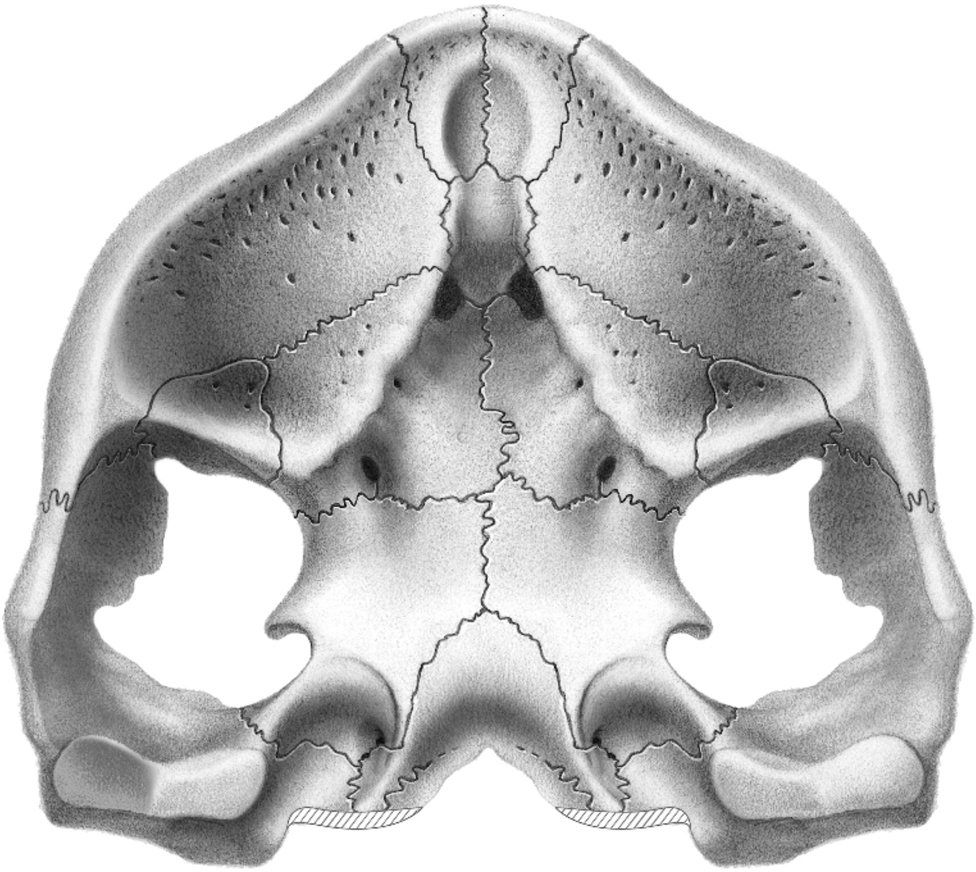

Fig. 119. *Rosasia soutoi* Carrington da Costa, 1940. UNL uncatalogued. Partially restored ventral view. [F. Ippolito, del.]

didae, the parietal in *Rosasia* contacts the palatine anteriorly, the pterygoid ventrally, the prootic posteroventrally, and the supraoccipital posteriorly.

Structures of processus inferior parietalis: The parietal forms part of the roof of the foramen interorbitale, which is relatively low in *Rosasia*, as in all other Bothremydini. The processus inferior parietalis of *Rosasia* is about the same size as in *Bothremys* and *Arenila*. At its posterior margin, the processus forms the anterodorsal margin of the foramen nervi trigemini, with the prootic and pterygoid forming the rest.

JUGAL (figs. 118, 119, 121)

Preservation: The anterior and medial part of the jugal is present on both sides, but its posterior edge is a broken margin on the right side and partially on the left. Sutures are clear.

Contacts of lateral plate: The jugal of *Rosasia* contacts the maxilla ventrally, the postorbital dorsally, and the quadratojugal posteriorly. Even though the posterodorsal margin is a broken edge, the possibility of another bone contact is unlikely.

Structures of lateral plate: The jugal of *Rosasia* forms more of the orbital margin than it does in *Bothremys cooki*, but it is similar to that in *Foxemys*. The jugal is widely separated from the cheek margin by a broad expanse of maxilla.

Contacts of medial process: In the orbital floor the jugal of *Rosasia* contacts the maxilla anteriorly and the palatine medially. In the postorbital wall the jugal contacts the postorbital dorsomedially and the pterygoid ventromedially. The jugal medial process is exposed on the triturating surface where it contacts the palatine anteromedially and the maxilla anterolaterally. The jugal exposure is more than in *Zolhafah* but less than in *Bothremys cooki*.

Structures of medial process: The jugal forms part of the fossa orbitalis floor, about as in *Zolhafah*. The septum orbitotemporale also contains some jugal laterally.

The jugal forms most of the pit on the triturating surface in *Rosasia*. The pit is a concavity that, uniquely among bothremydids with pits, lacks its posterior wall and is only partially complete compared to *Bothremys*, *Araiochelys*, and *Zolhafah*, which have deeper, more complete pits with higher posterior walls. The pit in *Zolhafah* and *Rosasia* is placed more posteriorly, closer to the edge of the triturating surface, than it is in *Bothremys* and *Araiochelys*.

QUADRATOJUGAL (figs. 118, 121)

Preservation: The quadratojugal is present only on the left side in UNL, and it is incomplete dorsally and posteriorly. Sutures are discernable but not clear on the external surface, but the internal surface sutures are clearer.

Contacts: The quadratojugal of *Rosasia* contacts the jugal anteriorly, the maxilla anteroventrally, and the quadrate posteroventrally. In Antunes and Broin (1988) and Lapparent de Broin and Werner (1998) the quadratojugal was described as extending ventrally to the cheek margin, completely separating maxilla and quadrate. We have found that the quadratojugal does not extend ventrally and that it is widely separated from the cheek margin by a broad maxilla-quadrate contact (fig. 121E). These sutures are identified on both the internal and external surfaces of the cheek. One factor leading to this reinterpretation is the more recent identification of a maxilla-quadrate contact and dorsally retracted jugal in a number of the Bothremydidae (e.g., *Bothremys*, *Araiochelys*, *Azabbaremys*, *Labrostochelys*, *Taphrosphys*) that were unknown when Antunes and Broin (1988) were describing *Rosasia*. All the Pelomedusoides known at that time had a large quadratojugal and no quadrate-maxilla contact.

Structures: The quadratojugal in *Rosasia* is located high on the skull, well above the cheek margin. This is also the condition in *Bothremys* but not in *Chedighaii*, *Polysternon*, and *Foxemys*, which have "normal" quadratojugals that extend ventrally to the cheek margin. Whether the quadratojugal in *Rosasia* reaches the temporal margin cannot be determined.

SQUAMOSAL

Preservation: Neither squamosal is preserved in *Rosasia*.

POSTORBITAL (figs. 118, 121)

Preservation: The anterior and medial parts of both postorbitals are preserved in *Rosasia*. Their posterior margins are broken edges. Sutures are clear. There is some breakage and bone loss along the anterior margin.

Contacts of lateral plate: The postorbital of *Rosasia* contacts the frontal anteromedially, the jugal ventrolaterally, and the parietal medially. The very narrow frontal contact may be smaller than originally present (see Frontal).

Structures of lateral plate: The postorbital actually forms the posterior margin of the orbit! The orbital margin has been eroded on both sides, particularly the postorbitals, making the orbits as preserved larger than they were in life. Nonetheless, the orbits of *Rosasia* probably were larger in life than in any other Bothremydini species (they are incomplete in *Zolhafah*).

Contacts of medial process: As in other Bothremydini species, the septum orbitotemporale in *Rosasia* is large and thick, constricting the sulcus palatinopterygoideus. The contacts with the postorbital in anterior view are the palatine ventrally and the jugal ventrolaterally. In posterior view the postorbital contacts the pterygoid ventromedially, the jugal ventrolaterally, and the parietal medially.

Structures of medial process: The postorbital forms the dorsolateral margin of the sulcus palatinopterygoideus (see Parietal, Palatine) and part of the septum orbitotemporale. The sulcus palatinopterygoideus in *Rosasia* is smaller than in other species, such as *Cearachelys*, but it is not low, as in *Bothremys* and *Chedighaii hutchisoni*. *Rosa-*

sia, along with *Bothremys*, *Araiochelys*, and *Chedighaii*, has a posterior enlargement of the fossa orbitalis, increasing the size of this space. The dorsal part of this space is covered by the postorbital.

PREMAXILLA (figs. 118–121)

Preservation: Both premaxillae are present in the UNL specimen and are complete and visible on all sides, but with some cracking.

Contacts: The premaxilla contacts the maxilla posterolaterally, the other premaxilla medially, and the vomer posteriorly. The maxilla suture trends anterolaterally, making the premaxilla much wider anteriorly than posteriorly, as in *Bothremys*, *Zolhafah*, and *Araiochelys*, but in contrast to the parasagittal suture of *Foxemys*.

Structures on dorsal surface: The premaxilla forms part of the floor of the fossa nasalis, relatively small in *Rosasia*, in contrast to *Zolhafah* and *Bothremys*. A low midline ridge, very similar to that in *Foxemys*, leads into the choanal passages.

Structures on ventral surface: The labial ridge on the premaxilla in *Rosasia* is blunt and rounded, like the maxillary labial ridge. It is thick, like in *Bothremys*, but not thinner, as in *Foxemys*. The median concavity is very narrow and extends anteriorly nearly to the labial ridge in *Rosasia*. It is narrower than in *Foxemys*, *Polysternon*, *Bothremys arabicus*, *B. kellyi*, and *Zolhafah*, but it is similar to *Bothremys cooki, B. maghrebiana*, and *Araiochelys*. The horizontal part of the triturating surface is very narrow on the midline in *Rosasia*, similar to *Foxemys* and in contrast to the wide area in *Zolhafah*. The labial ridge in anterior view in *Rosasia* shows a slight dorsal curve, similar to *Bothremys* and *Foxemys*.

MAXILLA (figs. 118–121)

Preservation: Both maxillae are present, nearly complete, with clear sutures. The right maxilla lacks its posteroventral end.

Contacts of vertical plate: The maxilla of *Rosasia* contacts the premaxilla anteriorly, the prefrontal anterodorsally, the jugal dorsally, the quadratojugal posterodorsally, and the quadrate posteriorly. In Antunes and Broin (1988) and Lapparent de Broin and Werner (1998) there was no maxilla-quadrate contact described, but this contact is now well supported by our observations (see Quadratojugal).

Structures of dorsal plate: The dorsal process of the maxilla in *Rosasia* is shorter than in *Araiochelys* and *Bothremys* and about the same as in *Foxemys*. It is wider than in *Zolhafah* (see Prefrontal). The maxilla forms the ventral margin of the orbit, which is blunt in *Rosasia* and most Bothremydini, not acute, as in *Cearachelys*. The foramen orbitonasale in *Rosasia* is similar in size and position to that in *Bothremys*. The apertura narium externa is relatively small in *Rosasia*, as it is in *Foxemys*, not wide, as in *Zolhafah* and *Bothremys* (see Prefrontal).

Contacts of horizontal plate: The maxilla in *Rosasia* contacts the premaxilla anteromedially, the vomer medially, the palatine posteromedially, and the jugal posteriorly. There is no midline contact of the maxillae.

Structures of horizontal plate: The maxilla in *Rosasia* is wide, similar to *Foxemys*, slightly narrower than in *Bothremys*, and wider than in *Araiochelys*. Its lateral margin and the labial ridge are broadly convex laterally, with a slight pinching near the premaxilla suture, as in *Foxemys* and *Bothremys*. *Zolhafah* is slightly convex distally and lacks the pinching. The triturating surface of *Rosasia* is broadly concave ventrally, as in *Bothremys* and *Araiochelys*. Despite the pits, most of the rest of the triturating surface in *Zolhafah* is nearly flat.

VOMER (figs. 118–121)

Preservation: The vomer in the UNL specimen is intact and unbroken anteriorly, but its posterior end has been broken and slightly displaced dorsally from the anterior half. Some telescoping of the two parts seems to have taken place. The posterior sutures are obscured by a mix of glue and broken bone.

Contacts: The vomer of *Rosasia* contacts the premaxillae anteriorly, the maxillae laterally, and the palatines posteriorly. As in *Bothremys cooki* and *Foxemys*, the maxilla contact is relatively long in *Rosasia*, not short, as in *Bothremys maghrebiana* and *Araiochelys*, or absent, as in *Zolhafah* and *Chedighaii hutchisoni*. The posterior contact with the palatine is unclear but narrow as

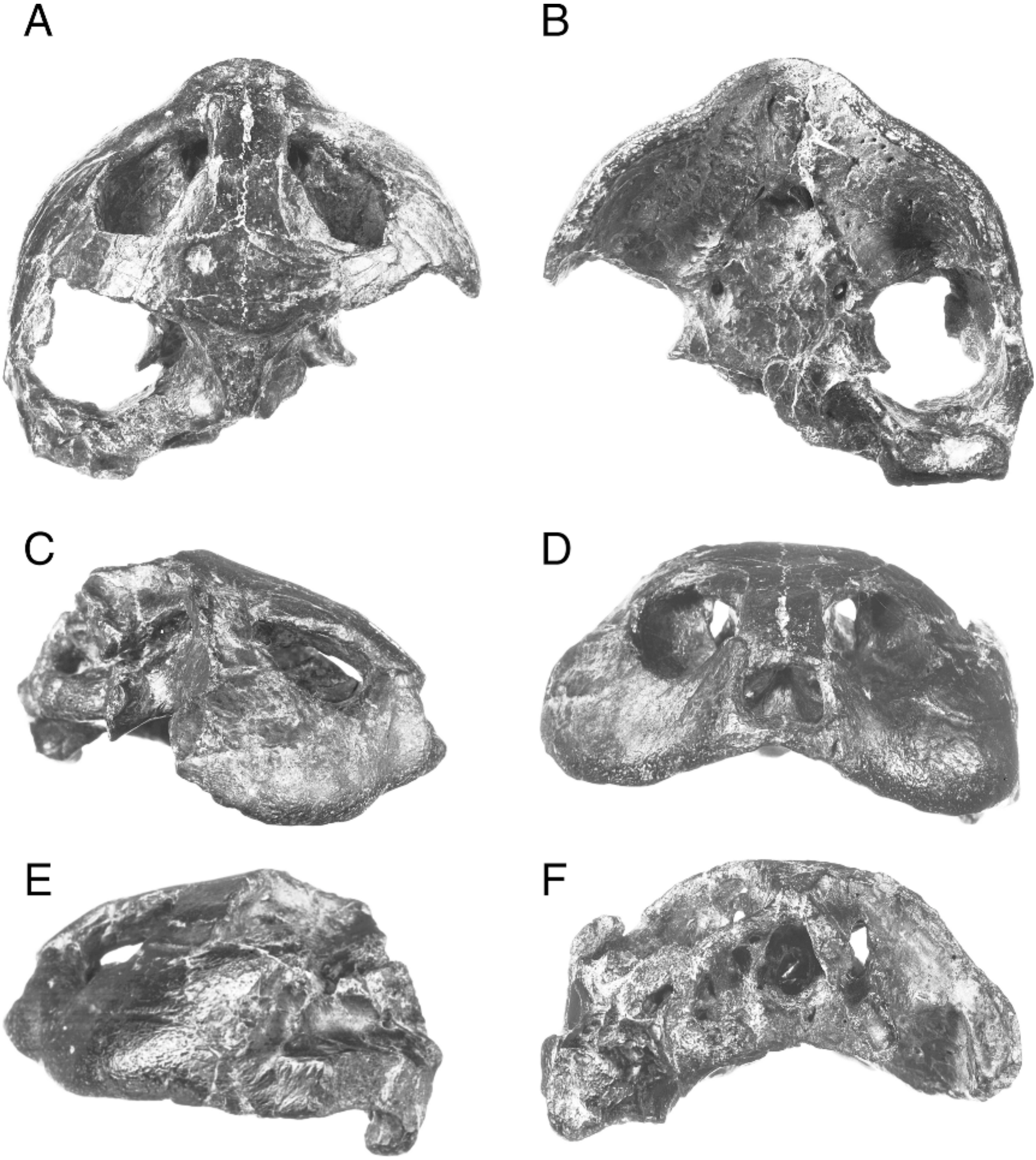

Fig. 120. *Rosasia soutoi* Carrington da Costa, 1940. UNL uncatalogued. **A**, dorsal; **B**, ventral; **C**, right lateral; **D**, anterior; **E**, left lateral; **F**, posterior. See also Antunes and Broin (1988) for other figures. [E. Heck, del.]

preserved, although restoring the telescoped portion would increase its contact area.

Structures: The vomer of *Rosasia* has a relatively horizontal, anterior half and a sharply angled, nearly vertical posterior half. The posterior half is narrower than the anterior half, and it completely separates the apertura narium interna on the midline. The apertura narium interna in *Rosasia* is relatively small, as in *Bothremys cooki*. It opens posteromedially, as in *Foxemys*, rather than more ventrally, as in other Bothremydini.

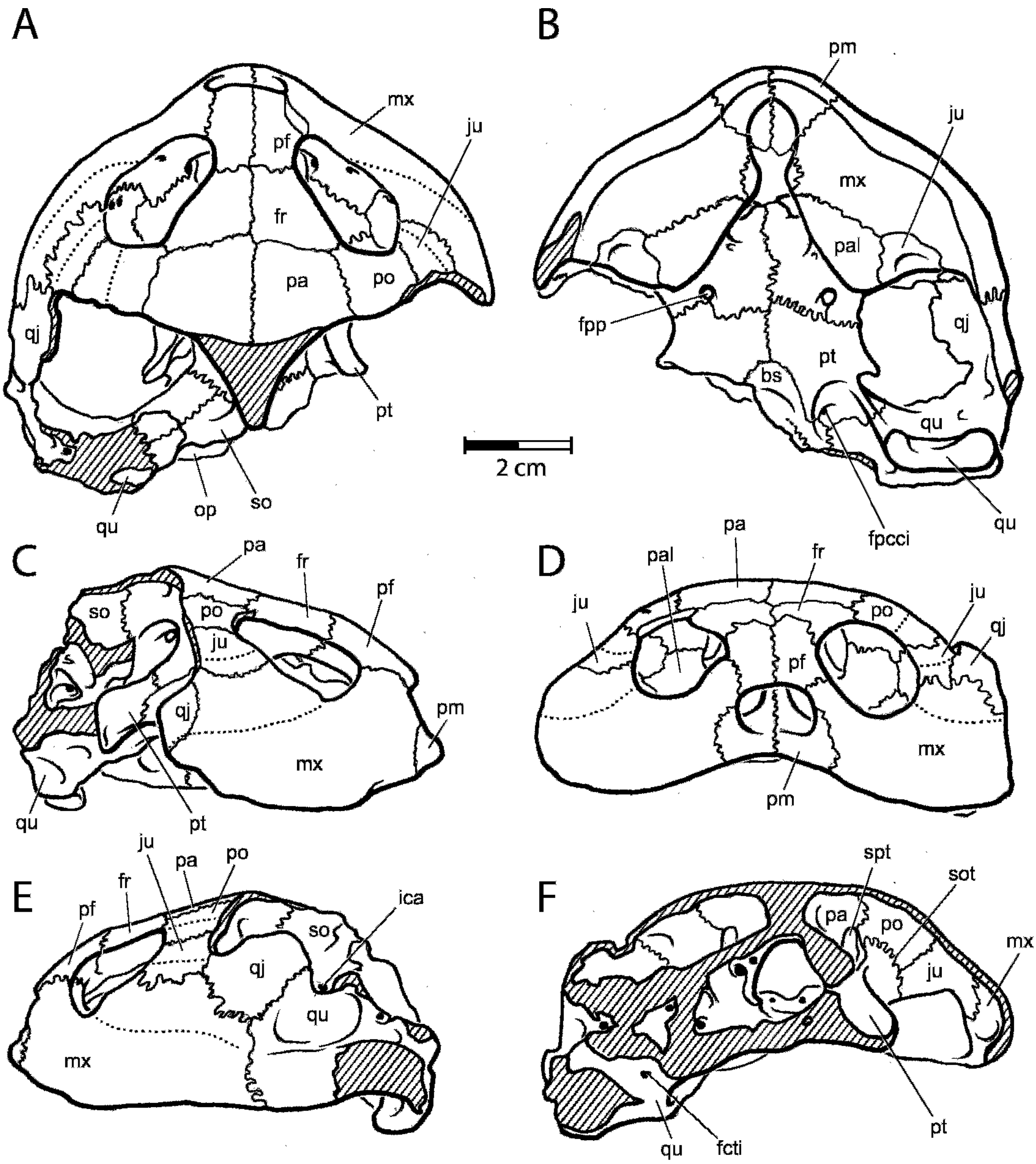

Fig. 121. *Rosasia soutoi* Carrington da Costa, 1940. UNL uncatalogued. **A**, dorsal; **B**, ventral; **C**, right lateral; **D**, anterior; **E**, left lateral; **F**, posterior. Dotted lines are scale impressions. [F. Ippolito, del.]

The apertura narium interna is largely hidden in ventral view by the medial expansion of the palatine and maxilla and by the anterior part of the vomer.

Palatine (figs. 118–121)

Preservation: Both palatines are present and only lack a small part of their anterior margin in the apertura narium interna. Sutures are clear and both surfaces are visible.

Contacts: On the ventral surface, the palatine of *Rosasia* contacts the maxilla anteriorly, the vomer anteromedially, the other palatine medially, the pterygoid posteriorly, and the jugal laterally. On the dorsal surface, in the floor of the fossa orbitalis, the palatine contacts the maxilla anteriorly, the jugal laterally, the postorbital posterodorsally, and the pterygoid posteriorly.

Structures on dorsal surface: The palatine forms the medial part of the floor of the fossa orbitalis and the anterior part of the sulcus palatinopterygoideus, all as in other bothremydids. The palatine has a dorsal, parasagittal ridge about as high as the crista pterygoidea, meeting the processus inferior parietalis, as in *Cearachelys*.

Structures on ventral surface: The palatine forms a significant part of the triturating surface, as in the other Bothremydini and in Cearachelyini. The palatine bears the lingual ridge and the choanal passage, which is placed dorsally well above the level of the triturating surface, in contrast to *Zolhafah*, which has them closer to the same plane. The foramen palatinum posterius is formed completely by the palatine, near the pterygoid suture, rather than within the suture, as in most Bothremydini.

QUADRATE (figs. 118–121)

Preservation: Only an incomplete left quadrate is present in the UNL specimen. The posterior and dorsal region of the left quadrate is missing and the margins are broken surfaces.

Lateral surface contacts: As preserved, the quadrate of *Rosasia* contacts the quadratojugal anterodorsally and the maxilla anteroventrally, in contrast to the description of Antunes and Broin (1988) of no quadrate-maxilla contact (see Quadratojugal, Maxilla).

Lateral surface structures: There is no cheek emargination in *Rosasia*. Below the cavum tympani can be seen the anterior part of the quadrate shelf found in the other Bothremydini, which is broken off posteriorly. Only the anteroventral part of the cavum tympani remains in the UNL specimen. Most of the portion of the quadrate above and behind the incisura columellae auris is missing. As preserved, the UNL specimen agrees with *Bothremys maghrebiana*. There is no fossa precolumellaris, and the incisura columellae auris is contained in a canal and widely separated by bone from the sulcus eustachii.

Contacts in dorsal view: The quadrate contacts the prootic anteromedially. Although much of the posterior part of the otic chamber is missing, a small part of the supraoccipital contact is preserved. Antunes and Broin (1988: fig. 3) showed only the prootic contact extending posteriorly to the edge of the bone. However, a clear prootic-supraoccipital suture can be followed laterally into the damaged area on the dorsal surface where it runs into the quadrate (fig. 121A). Most bothremydids have a supraoccipital-quadrate contact, except for *Zolhafah* and the Taphrosphyini.

Structures in dorsal view: The foramen stapedio-temporale is present on the left otic chamber in *Rosasia*, in the prootic-quadrate suture, as in all turtles. The foramen faces anteriorly and is close to the foramen nervi trigemini, as in all other infrafamily Bothremydodda.

Contacts on the ventral and posterior surfaces: In ventral view the quadrate in *Rosasia* contacts the pterygoid anteromedially and the basisphenoid medially, as in other bothremydids. The basioccipital is mostly broken off, but a very narrow contact with the quadrate remains posteromedially. There are small fragments of sutural surfaces with bone on the posterior surface of the quadrate that are identified as opisthotic by Antunes and Broin (1988). These are not as extensive as they indicate, but parts of the opisthotic may be present.

Structures on the ventral and posterior surfaces: On the ventral surface of the quadrate the condylus mandibularis is not preserved, but the surrounding structures and the preserved part of the basioccipital show that it was at about the same level as the condylus occipitalis, as in *Zolhafah*, *Chedighaii*, and *Bothremys*. On the occipital surface, the quadrate is mostly a broken surface. The sulcus eustachii wraps around from the lateral surface and provides an area of original bone surface trending ventromedially. The foramen chorda tympani inferius, as described by Antunes and Broin (1988), is on the posterior quadrate surface. The margins of the fenestra postotica are not preserved, but the aditus canalis stapedio-temporalis is still present.

Pterygoid (figs. 118–121)

Preservation: The right pterygoid in the UNL specimen is complete, but the left one only consists of its anterior half. Fracturing has disturbed the bone, and some is missing around the margins of the processus trochlearis pterygoidei. Sutures are clear. Only the external part of the dorsal surface is visible.

Contacts on ventral surface: As in other bothremydids, the pterygoid of *Rosasia* contacts the palatine anteriorly, the other pterygoid anteromedially, the basisphenoid posteromedially, and the quadrate posterolaterally. The basisphenoid suture makes an anterolateral jog, forming an indentation into the pterygoid, not found in any other bothremydid. This was not shown in Antunes and Broin (1988).

Structures on ventral surface: The processus trochlearis pterygoidei is relatively small and at an acute angle to the midline, as in *Zolhafah* and *Bothremys* and in contrast to the more obtuse angle in *Polysternon* and *Foxemys*. A shallow fossa pterygoidea is present in *Rosasia*, formed by both pterygoid and basisphenoid. Among the other Bothremydini, *Foxemys* and *Polysternon* have a deep and narrow fossa pterygoidea, but none of the other Bothremydini has a pterygoid depression except *Rosasia*.

The foramen posterius canalis carotici interni in *Rosasia* is formed by the pterygoid laterally and the basisphenoid medially, in the anterior and deepest part of the fossa pterygoidea, as described and figured by Antunes and Broin (1988). A small foramen in the pterygoid-basisphenoid suture posterior to the foramen posterius canalis carotici interni is probably the foramen nervi facialis. The foramen palatinum posterius in *Rosasia* is formed almost entirely by the palatine with only a small contribution to its margin by the pterygoid on the right side.

Contacts on dorsal surface: The base of the processus trochlearis pterygoidei contacts the postorbital dorsolaterally and the jugal anterolaterally. There is no parietal contact, although the parietal comes close to the pterygoid on the dorsal edge of the sulcus palatinopterygoideus. The crista pterygoidea in *Rosasia* contacts the parietal dorsally, the palatine anteriorly, and the prootic posterodorsally, as in other bothremydids. The pterygoid forms the anteroventral margin of the foramen nervi trigemini.

Structures on dorsal surface: The floor of the sulcus palatinopterygoideus is largely formed by the pterygoid. The sulcus in *Rosasia* is similar to that in *Bothremys* and *Zolhafah.*

Supraoccipital (figs. 118, 121)

Preservation: The anterior part of the supraoccipital is preserved in the UNL specimen, particularly on the left side, but most of it is missing on the right, and the crista supraoccipitalis is gone.

Contacts: The parietal contact can be seen anteriorly and dorsally. Anterolaterally the complete prootic contact is preserved on the left otic chamber. In the broken area along the posterior edge of the left otic chamber, there is a narrow supraoccipital-quadrate contact (see Quadrate), as in all the other Bothremydidae except the Taphrosphyini and *Zolhafah.*

Structures: The crista supraoccipitalis is broken off and all margins of the foramen magnum are gone. The recessus labyrinthicus supraoccipitalis is visible on the left side.

Exoccipital

Preservation: Antunes and Broin (1988) identified a few small portions of the exoccipital on the broken posterior edge of the skull. Although the area is broken and open to various interpretations, we cannot confirm that these pieces are exoccipital. In any case, all of these structures are missing: foramen magnum, condylus occipitalis, foramen nervi hypoglossi, foramen jugulare posterius, and foramen jugulare anterius.

Basioccipital (figs. 118, 121)

Preservation: Very little of the basioccipital is left in the UNL specimen. Only a small part of the anterior and left lateral margins are present in the eroded area at the posterior edge of the skull.

Contacts: Some of the basisphenoid contact is visible along the left anterior edge of the basioccipital. It is likely that a small part of the left lateral quadrate contact is also preserved.

Structures: Not enough of the basioccipital is present to show the tuberculum basioccipitale, condylus occipitalis, foramen magnum, or median concavity.

PROOTIC (figs. 118, 121)

Preservation: Most of the left prootic and the medial part of the right prootic are present. Both show some erosion and surface damage.

Contacts: As in other bothremydids, the prootic of *Rosasia* contacts the parietal medially, the quadrate laterally, the supraoccipital posterodorsally, and the pterygoid ventrally. In contrast to the description of Antunes and Broin (1988), we find that there is no prootic-opisthotic contact due to the supraoccipital-quadrate contact (see Quadrate).

Structures: The prootic forms the posterodorsal margin of the foramen nervi trigemini and the medial edge of the foramen stapedio-temporale. The two foramina are separated more than they are in *Bothremys*, but they are still close together compared with *Kurmademys* and the Cearachelyini. Between the two foramina is a trough, as in *Zolhafah* and the other Bothremydini. The amount of separation of the foramen nervi trigemini and foramen stapedio-temporale is about the same in *Rosasia* and *Zolhafah.*

Some of the cavum labyrinthicum formed by the prootic is visible on the left side. The fenestra ovalis anterior rim, recessus labyrinthicus prooticus, canalis semicircularis horizontalis, and hiatus acusticus are preserved and have been identified in Antunes and Broin (1988: fig. 8).

OPISTHOTIC

Preservation: The posterior margin of the UNL specimen is a broken, eroded edge that has some fragments of bone with sutural surfaces. Some of these may be fragments of opisthotic. We have reinterpreted most of the large area identified as opisthotic by Antunes and Broin (1988: figs. 3, 8) as quadrate (see Quadrate).

BASISPHENOID (figs. 118–121)

Preservation: The basisphenoid in the UNL specimen is missing its posterolateral third on the right side, and most of its posterior margin is eroded and lacks the original bone surface. Sutures are clear and much of the dorsal as well as ventral surfaces are visible.

Contacts on ventral surface: As in other bothremydids, the basisphenoid of *Rosasia* contacts the pterygoid anterolaterally, the quadrate posterolaterally, and the basioccipital posteriorly. The pterygoid suture has an indentation (see Pterygoid), so the suture is not straight or slightly curved as in other bothremydids. The basioccipital suture is fragmentary but shows a convex anterior curve in contrast to the straight transverse suture of *Zolhafah.*

Structures on ventral surface: The foramen posterius canalis carotici interni lies in the pterygoid-basisphenoid suture close to the quadrate contact. The foramen is at the top of the fossa pterygoidea. In most of the Bothremydini the foramen is between the pterygoid and quadrate, but in *Rosasia*, *Foxemys*, and *Polysternon* it is between the pterygoid and basisphenoid. In *Zolhafah* and *Bothremys kellyi* the foramenis formed by all three bones: quadrate, pterygoid, and basisphenoid.

There is a slight median concavity on the basisphenoid and it forms the lateral part of the moderately developed fossa pterygoidea (see Pterygoid).

Contacts and structures on dorsal surface: Only a few sutures can be seen on the basisphenoid inside the cavum cranii. These are between the prootic and basisphenoid. The dorsum sellae and sella turcica are visible and are similar to those in *Bothremys cooki.*

Araiochelys hirayamai

A single, nearly complete skull (THUg 3338) represents this taxon. Some of the cheek and posterior skull roof are damaged. *Araiochelys* is the sister taxon to *Bothremys* + *Chedighaii.* The possibility of *Araiochelys* being a narrow-jawed morph of *Bothremys maghrebiana*, which also occurs in the Moroccan Paleocene phosphates, is discussed in the Systematics section under *Araiochelys.*

PREFRONTAL (figs. 122, 125)

Preservation: Both prefrontals are present in THUg 3338: the preservation is good, sutures are clear, and the internal surface is not visible. The anteromedial projection seems damaged.

Contacts: Contacts are as in *Bothremys* and other Bothremydini, with one exception.

The anteromedial process of the prefrontal nearly contacts the dorsal process of the premaxilla, and probably contacted it originally. As preserved, the bones are only separated by a narrow band of matrix in an area that is damaged by ventrally directed crushing. As restored, the prefrontal contacts the premaxilla. This contact does not usually occur in *Bothremys*, although the bones come close to one another in some specimens of *B. maghrebiana*.

Structures: The prefrontal in *Araiochelys* is narrower than in *Bothremys*. It is constricted anteriorly by the maxilla (see Maxilla) and it has an internarial, median process. The dorsal process of the premaxilla forms most of the internarial division (see Premaxilla), but the anteromedial process of the prefrontal in *Araiochelys* is longer and more acute than in *Bothremys* or *Chedighaii*. *Rhothonemys*, a taphrosphyine with unusually large nares, and *Bothremys kellyi* also have divided nares.

FRONTAL (figs. 122, 125)

Preservation: Both frontals are present in THUg 3338 and are well preserved with clear sutures.

Contacts: The frontal of *Araiochelys* has the same contacts as in *Bothremys*.

Structures: The frontal in *Araiochelys* is roughly wider than long or rectangular, as in most bothremydids, but it is narrower than the frontal in *Bothremys maghrebiana*. The frontal of *Araiochelys* also has a greater orbital exposure than in *B. maghrebiana*.

PARIETAL (figs. 122, 125)

Preservation: Both parietals are present in THUg 3338, but the left one is lacking the temporal margin except for displaced fragments. The right parietal seems to preserve the original edge of the temporal emargination.

Contacts: The contacts of the dorsal plate of the parietal in *Araiochelys* are the same as in *Bothremys*. The processus inferior parietalis is not visible.

Structures: The dorsal plate of the parietal in *Araiochelys* is similar in size and shape to others in the Bothremydini. The degree of temporal emargination is about the same as in *Bothremys maghrebiana*, and a little less than in *Chedighaii hutchisoni*. The parietal of *Araiochelys* is slightly narrower than in *B. maghrebiana*, but about the same as in *C. hutchisoni*.

JUGAL (figs. 122–125)

Preservation: The jugal is preserved in THUg 3338 on the palate, in the right fossa orbitalis, and on both cheeks. The posterior and ventral limits are probably only represented by broken edges on both sides. The posteroventral edge of the jugal is not known, and it is shown as incomplete in the restoration.

Contacts: The jugal in *Araiochelys* has a complex contact pattern. On the ventral surface the jugal contacts the maxilla anterolaterally and the palatine medially. There is a narrow posteromedial contact with the pterygoid. In *Bothremys*, *Zolhafah*, and *Rosasia*, the jugal is also exposed on the palate between maxilla and palatine, but the degree of exposure varies. In *B. cooki* the jugal is widely exposed, with the maxilla and palatine being widely separated posterior to the jugal. In *B. maghrebiana* the jugal has its smallest exposure; it is present only in the dorsal tip of the triturating surface pit, and a broad palatine-maxilla contact is present posterior to the jugal. *Araiochelys* has an intermediate condition with the jugal exposed in the pit and in a narrow band from the pit to the edge of the fossa temporalis inferior. The palatine and maxilla are separated by the jugal, but not to the extent seen in *B. cooki*. In *Zolhafah* and *Rosasia* the pit is not as completely conical as in *Bothremys* and *Araiochelys*, even though the top of the pit is still formed by the jugal at its tip. In both there is no palatine-maxilla contact and the jugal is closer to the fossa temporalis inferior than it is in *Bothremys* and *Araiochelys*.

On the lateral surface of the skull in *Araiochelys*, the jugal contacts the maxilla anteroventrally and the postorbital dorsally. Its likely contact with the quadrate and/or quadratojugal is not determinable due to damage. In the floor of the fossa orbitalis the jugal contacts the palatine medially and the maxilla anterolaterally.

Structures: The jugal forms part of the triturating surface and part of the cheek. The triturating surface is dominated by the large

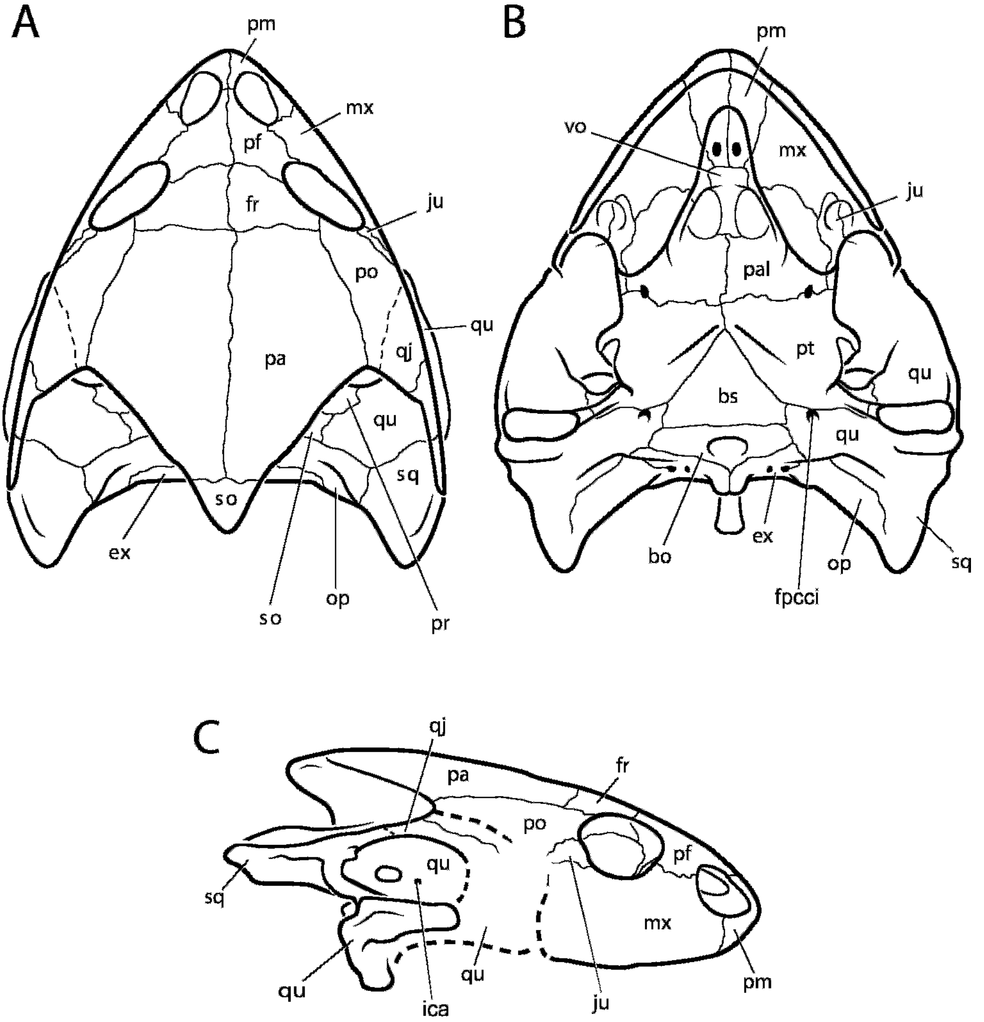

Fig. 122. *Araiochelys hirayamai*, n. gen. et sp. THUg 3338 holotype. Partially restored views of skull. **A**, dorsal; **B**, ventral; **C**, lateral. [R. Rogge, del.]

conical pit formed by jugal, maxilla, and palatine. The upper part of the pit and part of the wall between the pit and the fossa temporalis inferior are formed by the jugal. In contrast to *Araiochelys*, the jugal in *Bothremys cooki* forms all of the pit and the wall, and in *B. maghrebiana* the jugal forms only the dorsal tip of the pit.

The cheek in THUg 3338 is not well preserved. The jugal lies at the posteroventral corner of the orbital margin, and this part of the jugal is well preserved, particularly on the right side. As in other Bothremydini, it lies between the postorbital and maxilla. The cheek in other Bothremydini is not preserved either. It is missing in *Bothremys cooki* and *Zolhafah*. It is preserved in *B. maghrebiana*, but the jugal-quadratojugal sutures are indistinct. In *Rosasia* the jugal contacts the quadratojugal and not the quadrate, being placed relatively high in the cheek. In *Araiochelys* the jugal is small, as in the other Bothremydini, and may not have contacted the quadrate. The extent of the cheek in *Araiochelys* can be restored, showing that the jugal was probably separated from the cheek margin by a quadrate-maxilla contact, as in *B. maghrebiana* and *Rosasia*.

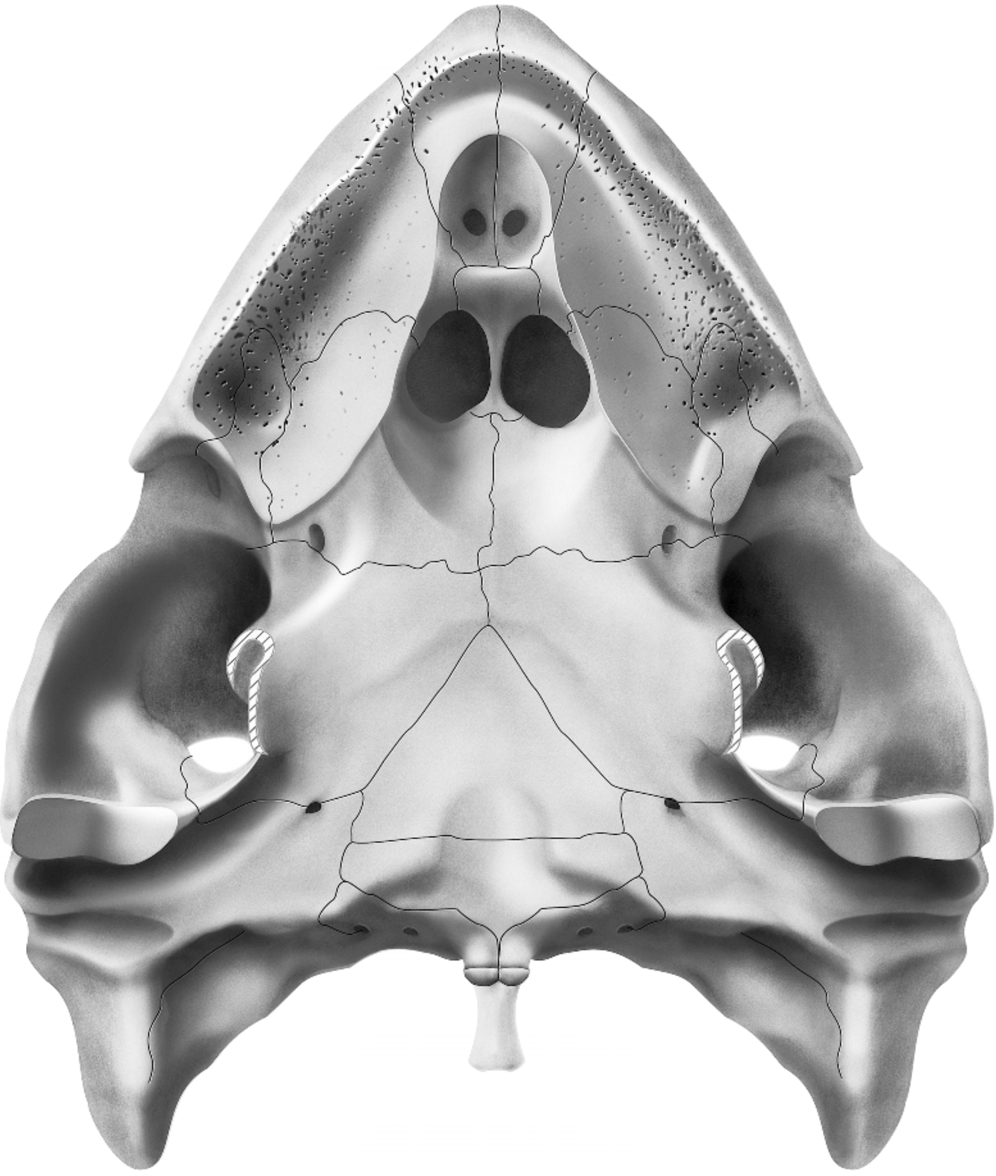

Fig. 123. *Araiochelys hirayamai*, n. gen. et sp. THUg 3338 holotype. Partially restored ventral view. [M. Stalcup and F. Ippolito, del.]

QUADRATOJUGAL (figs. 122, 125)

Preservation: The quadratojugal in THUg 3338 is poorly preserved. It is missing on the left side and indistinct on the right. What appears to be the quadratojugal-postorbital suture is in an area of minute breakage, but the quadrate-quadratojugal suture is clear.

Contacts and structures: The quadratojugal is a long flat element as interpreted here, with an exposure posteriorly on the temporal emargination between the postorbital and quadrate. The medial contact with the postorbital runs slightly laterally as it extends anteriorly. The quadrate contact is the usual curved suture roughly paralleling the cavum tympani. The anterior contact of the quadratojugal is missing, but it may have contacted the jugal and maxilla, as in *Rosasia*. The quadratojugal did not extend ventrally to reach the cheek margin as in *Foxemys* and *Polysternon*, due to the quadrate-maxilla contact (see Quadrate).

SQUAMOSAL (figs. 122, 125)

Preservation: The squamosals in THUg 3338 are present on both sides, but the edges have been damaged. The left one is more complete, but it is supported by matrix ventrally and has some missing areas dorsally.

Contacts: The squamosal contacts in *Araiochelys* are the same as in *Bothremys maghrebiana*, as far as can be determined.

Structures: The squamosal in *Araiochelys* agrees closely with that bone in *Bothremys maghrebiana*. Unfortunately, complete squamosals are rare in the tribe Bothremydini; *B. cooki* has none, and squamosals are missing posteriorly in *Zolhafah*, *Rosasia*, and *Chedighaii hutchisoni*. In *B. maghrebiana* and *Chedighaii barberi*, the squamosal has a posterior process that has a low ridge ventrally and a low trough on its dorsal surface, nearly identical to the squamosal of *Araiochelys*.

POSTORBITAL (figs. 122, 125)

Preservation: The postorbital is nearly complete on the right side of THUg 3338, but only its anterior end is present on the left side.

Contacts and structures: As in *Bothremys maghrebiana*, the lateral plate of the postorbital of *Araiochelys* contacts the frontal anteromedially, the jugal anterolaterally, the quadratojugal posterolaterally, and the parietal medially. The medial process of the postorbital is mostly covered by matrix in THUg 3338, but the jugal contact can be seen in the anterior wall of the fossa temporalis inferior.

PREMAXILLA (figs. 122–125)

Preservation: Both premaxillae are present and well preserved with clear sutures in THUg 3338.

Contacts: The premaxilla of *Araiochelys* contacts the maxilla posterolaterally, the other premaxilla on the midline, and the vomer posteriorly.

Structures in dorsal view: The premaxilla forms the anterior part of the fossa nasalis and apertura narium externa. In *Araiochelys* the fossa and apertura are relatively large, as in *Bothremys* and *Chedighaii* and in contrast to the smaller apertura and fossa in *Foxemys* and *Rosasia*. The orientation of the opening is more lateral in *Araiochelys* than in the other members of the Bothremydini. *Araiochelys* also differs in having a completely divided or almost completely divided apertura rather than the partially divided or figure eight-shaped apertura in *Bothremys cooki* and *Chedighaii*. Each premaxilla in *Araiochelys* has a dorsal process adjacent to the midline that together form the lower part of the nasal division. The base of the process is thick and is similar to the lower dorsal process in *Bothremys maghrebiana*. Both *Chedighaii* and *B. cooki* are damaged or lack a premaxilla. However, *B. cooki* has enough of the premaxilla preserved to show that some midline process was present, although its extent is not determinable. The premaxillary dorsal process in *Araiochelys* is continuous with a posterior midline ridge on the floor of the fossa nasalis. A similar, but lower ridge is present in *B. maghrebiana* and probably *B. cooki*. The anterior margin of the premaxilla in *Araiochelys* protrudes well anteriorly to the prefrontal in dorsal view, as in *Bothremys* and *Chedighaii* but in contrast to *Rosasia* and *Foxemys*.

Structures in ventral view: The premaxilla forms the anteromedial part of the triturating surface and consists of a more vertical labial ridge with a more horizontal plate posteriorly. In *Araiochelys* the labial ridge has a slight median upturn to form a shallow notch similar to *Bothremys* but in contrast to *Foxemys*. *Chedighaii* is not preserved in this area, although *C. barberi* shows a ventral curve on the portion of premaxilla preserved. The labial ridge in *Araiochelys* has a sharp edge but a broad base, as in *Bothremys*. However, the labial ridge is thinner and has a more acute angle in *Araiochelys* than in *Bothremys*.

The premaxillary triturating surface behind the labial ridge in *Araiochelys* forms a relatively deep midline concavity, similar to that in *Bothremys* but slightly narrower. The lingual ridge forms the anterior and lateral margin of the concavity and marks the edge of the foramina-rich triturating surface. The ridge is higher and more distinct in *Araiochelys* and *Bothremys maghrebiana* than it is in *B. cooki*, which has a low ridge and shallow midline concavity. The premaxilla in *Araiochelys* forms all of the foramen praepalatinum, which lies in the midline concavity near the vomer suture, as in *Bothremys*.

MAXILLA (figs. 122–125)

Preservation: Both maxillae are present in THUg 3338. They are complete and well preserved except for the posterolateral limits on the cheek, which are represented by broken edges on both maxillae.

Contacts: The maxilla contacts in *Araiochelys* for both the vertical and horizontal plates are the same in *Araiochelys* and *Bothremys* except for the area around the triturating surface pit. In *Araiochelys* and *Bothremys cooki* there is no maxilla-palatine contact posterior to the pit, while in *Bothremys maghrebiana* there is a contact. On the cheek, there is no posterior contact of the maxilla with anything as preserved. However, on the right side the quadrate has a long anterior process with a broken anterior margin that nearly reaches the maxilla with a broken posterior margin. It is very difficult to see how any of the other cheek elements could have extended between the quadrate and maxilla to separate them. It is possible that a narrow space was present between them, but this seems unlikely, and the restoration has been done with a quadrate-maxilla contact as in *Bothremys maghrebiana*.

Structures of vertical plate: The dorsal process of the maxilla is wider in *Bothremys* and narrower in *Araiochelys* and *Chedighaii*. For *Araiochelys* this is a function of the large apertura narium externa, while in *Chedighaii* the orbits are closer to the apertura.

The maxilla forms the lower margin of the fossa orbitalis, and in most bothremydids this is a narrow ridge. In *Bothremys* this ridge is either absent (*B. cooki* and *B. maghrebiana* AMNH 30561) or very low (*B. maghrebiana* AMNH 30041, AMNH 30522, MHNL 20-268370, and AMNH 30234). In *Araiochelys* it is a distinct raised ridge clearly separating cheek from fossa orbitalis. The fossa orbitalis itself is comparatively larger and faces more laterally in *Araiochelys* than in *Bothremys* and *Chedighaii*.

The vertical plate of the maxilla forms the suborbital part of the cheek and the labial ridge. In dorsal view the external surface of this plate is a nearly straight, more vertical sheet in *Araiochelys*. In *Bothremys* the maxilla is convex anterolaterally, forming a curved margin. The degree of swelling is greater in *Bothremys* than in any of the other bothremydids. However, the two species of *Chedighaii* have expanded maxillae, with *C. barberi* being relatively straight, although the skull is wide in contrast to *Araiochelys*. In *C. hutchisoni* the maxilla edge is broken and it may have been curved. The maxillary plate below the orbit is unusually deep in *Bothremys* and *Chedighaii*, but in *Araiochelys* it is shallower.

The labial ridge in *Araiochelys* is acute along its edge, as in *Bothremys* and *Chedighaii barberi* (missing in *C. hutchisoni*), but in *Bothremys* the bone thickens dorsally more than in *Araiochelys*. The entire maxillary plate in *Bothremys* is thicker than in *Araiochelys*. *Chedighaii hutchisoni* is thick, as in *Bothremys*, but *C. barberi* is thinner, as in *Araiochelys*.

Structures of horizontal plate of maxilla: The maxilla of *Araiochelys* is relatively narrow compared to *Bothremys* and *Chedighaii hutchisoni* (fig. 123). The shape is not as triangular as in the other Bothremydini. The apertura narium interna is slightly narrower in *Araiochelys* than in *Bothremys maghrebiana*, but not as narrow as in *B. cooki*. The apertura in both *Araiochelys* and *B. maghrebiana* is larger than in *B. cooki*.

The triturating surface of *Araiochelys* is defined medially by a low lingual ridge. In common with *Bothremys* but in contrast to *Chedighaii*, there is a well-developed pit in the posterior part of the triturating surface. The maxilla forms the anterior and lateral cone-shaped surface that forms the outer part of the pit; the tip is formed by the jugal (see Jugal). This part of the maxilla in *Araiochelys*, the area between the pit and the labial ridge, is much narrower than in *Bothremys*. The differences in this part of the triturating surfaces between *Araiochelys* and *Bothremys* might be compared with

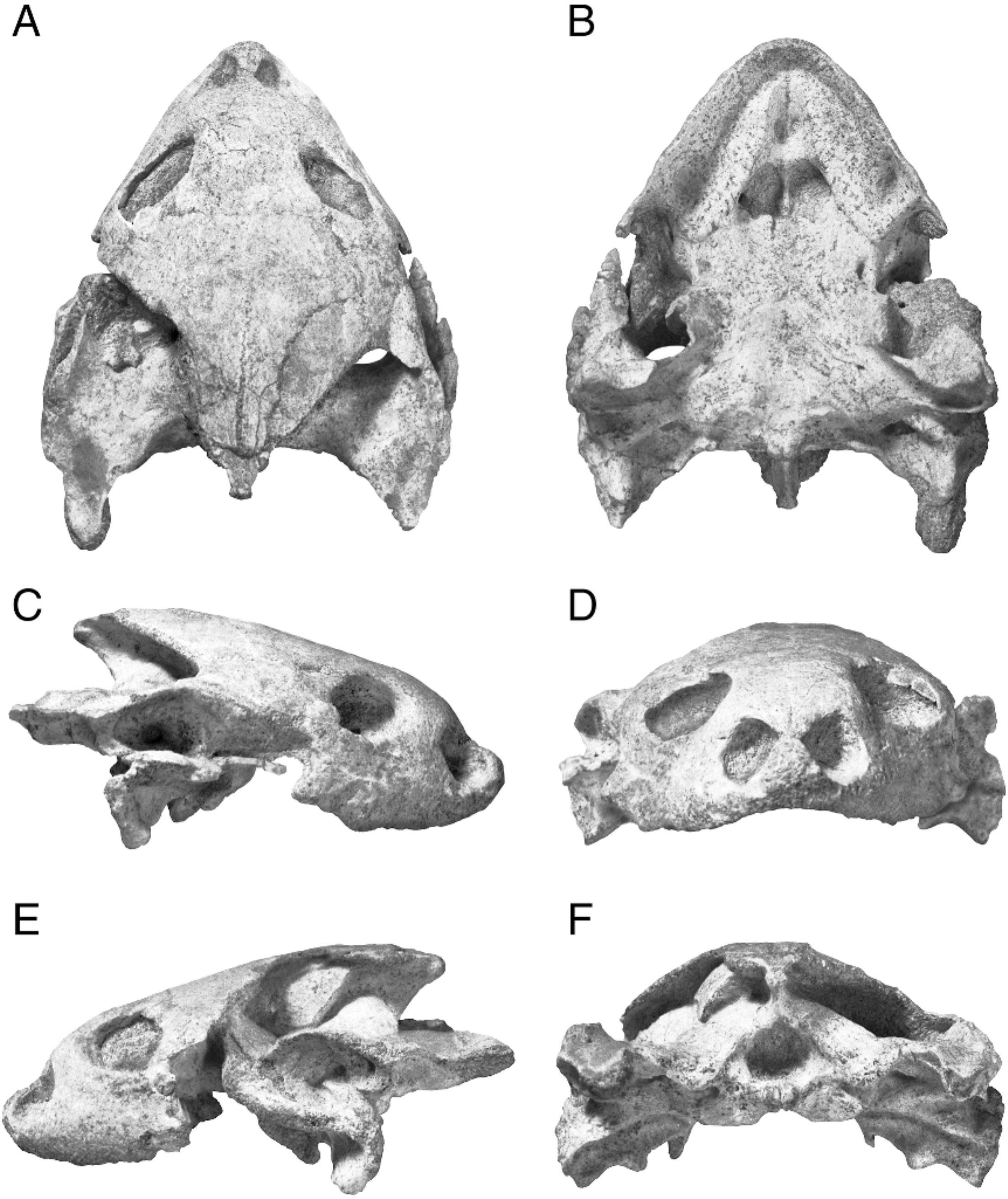

Fig. 124. *Araiochelys hirayamai*, n. gen. et sp. THUg 3338 holotype. **A**, dorsal; **B**, ventral; **C**, right lateral; **D**, anterior; **E**, left lateral; **F**, posterior. [M. Stalcup, del.]

differences found between males and females in *Graptemys* (Lindeman, 2000), *Emydura* (Cann, 1998), and trionychids (Dalrymple, 1977) (see Discussion in Systematics). In *Bothremys* there is also an expansion of the palatine part of the triturating surface medial to the pit. The more anterior part of the triturating surface in *Araiochelys* has a low lingual ridge medial to a shallow trough.

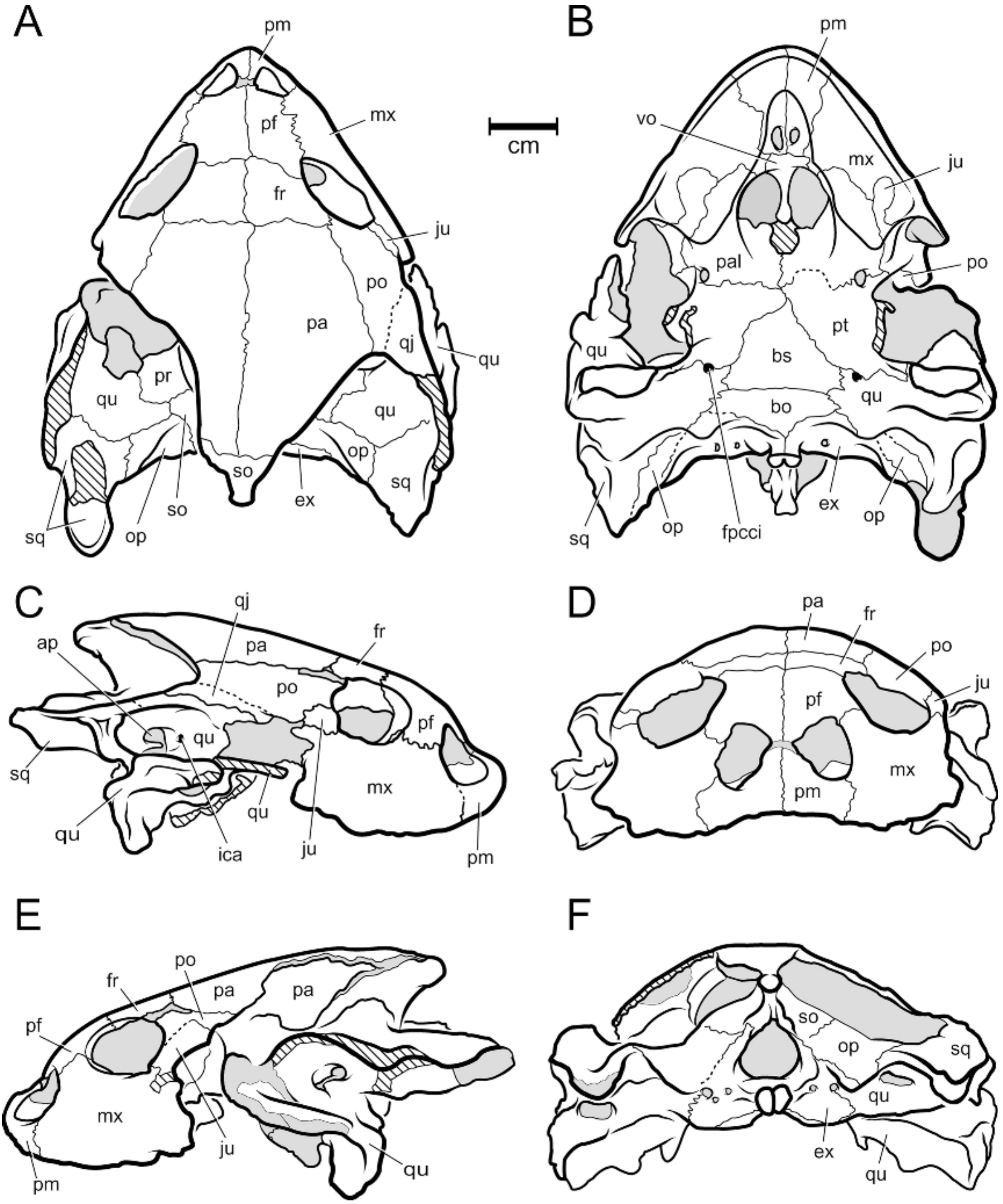

Fig. 125. *Araiochelys hirayamai*, n. gen. et sp. THUg 3338 holotype. **A**, dorsal; **B**, ventral; **C**, right lateral; **D**, anterior; **E**, left lateral; **F**, posterior. [M. Stalcup, del.]

Most of the dorsal surface of the maxilla is covered by matrix, but some is visible in the floor of the right fossa orbitalis. The maxilla only forms a narrow part of the fossa, lateral to the palatine.

VOMER (figs. 122–125)

Preservation: The vomer in THUg 3338 is nearly complete; the posterior contact with the palatines is damaged.

Contacts: The vomer contacts in *Araiochelys* are as in *Bothremys*: premaxilla anteriorly, maxilla anterolaterally, and palatine posteriorly. *Chedighaii hutchisoni* lacks the maxilla contact. The anterior end has a short maxilla contact, as in *B. maghrebiana*, rather than the long one in *B. cooki*.

Structures: The vomer in *Araiochelys* is dumbbell shaped as in *Bothremys*. Only its ventral surface is visible. The vomer separates the paired apertura narium interna, as in *Bothremys* and *Chedighaii* (see Maxilla).

PALATINE (figs. 122–125)

Preservation: Both palatines are present in THUg 3338. They are only damaged where they form the posterior margin of the apertura narium interna, and only a small amount of bone seems to be missing. Only the ventral surface of the palatine is visible.

Contacts: The contacts of the palatine in *Araiochelys* are the usual bothremydid ones: maxilla anteriorly, vomer anteromedially, palatine medially, and pterygoid posteriorly. In addition, *Araiochelys* has a lateral jugal contact beginning in the triturating surface pit and extending posteriorly to the usual palatine-jugal contact. In contrast to *Bothremys maghrebiana*, there is no palatine-maxilla contact posterior to the pit (see Maxilla, Jugal).

Structures on ventral surface (dorsal surface obscured by matrix): The triturating surface in *Araiochelys* has a significant contribution from the palatine, which forms the posteromedial part of the surface and the posterior part of the lingual ridge (see Maxilla). This portion of the palatine is narrower in *Araiochelys* than in *Bothremys* and *Chedighaii*. The palatine forms the posterior and posterolateral margins of the apertura narium interna. It is very similar in *Araiochelys* and *Bothremys maghrebiana*. The foramen palatinum posterius is formed by both palatine and pterygoid, as in *Bothremys* and *Chedighaii*. The degree of palatal arching and choanal formation is very similar in *Araiochelys*, *Bothremys*, and *Chedighaii*.

QUADRATE (figs. 122, 125, 126)

Preservation: Both quadrates are present in THUg 3338, but both are incomplete on their anterior margins in the cheek. Both have also been crushed slightly dorsoventrally.

Contacts in lateral view: The quadrate in *Araiochelys* contacts the squamosal posterolaterally, as in the other Bothremydini. There is probably a quadrate-maxilla contact on the cheek (see Maxilla) on the right side, as seen in *Bothremys*. Anterodorsally the postorbital contacts the quadrate but the suture in unclear (see Postorbital). Although unlikely, a jugal contact is possible due to the poor condition of the cheek in THUg 3338 (see Jugal). The dorsal margin of the quadrate is a broken edge on both sides in THUg 3338, so that the presence or absence of a squamosal-quadratojugal contact is indeterminate. Thus, the exposure of the quadrate on the temporal emargination as it is preserved is unlikely to have been its original condition.

Structures in lateral view: The cavum tympani in *Araiochelys* is similar to that in *Bothremys maghrebiana*. The incisura columellae auris is completely closed, as in other taxa in the subtribe Bothremydina, and the stapes lies in a bony canal. As in *B. maghrebiana*, *Araiochelys* has a low ridge extending posteriorly from the incisura to the sulcus eustachii. The sulcus is a deep cleft in *Araiochelys* and *Bothremys* (it is not well preserved in *Chedighaii*) with a lateral overhang made up of quadrate and squamosal and a ventrolateral shelf formed by the quadrate. The antrum postoticum in *Araiochelys* is very similar to that in *B. maghrebiana*, although there is some variation in size of the antrum among the four specimens of that species. The antrum postoticum of *Araiochelys* faces anterolaterally, as in *B. maghrebiana*, and it is about the same size as in AMNH 30561, a little larger than in AMNH 30234, and smaller than in AMNH 30041.

The cavum tympani in *Araiochelys* is a deep cone, becoming shallower anteriorly, with a large lateral shelf ventrally, all as in *Bothremys* (it is not completely preserved in *Chedighaii*). The cavum in THUg 3338 is partly distorted by dorsoventral crushing so that the shelf now forms a pocket at the bottom of the cavum tympani, but this pocket is due to crushing, and the shelf was like that in *Bothremys maghrebiana* (AMNH 30041). There is no fossa precolumellaris.

Contacts and structures in dorsal view: In *Araiochelys* the quadrate contacts in dorsal view on the otic chamber are as in the other Bothremydini (except for *Zolhafah*): prootic anteromedially, opisthotic posteromedially, supraoccipital medially, and squamosal posteriorly. The foramen stapedio-temporale lies on the anterior face of the otic chamber and, as in other Bothremydini, is not visible in dorsal view.

Contacts in ventral and posterior view: As in the other Bothremydidae, *Araiochelys* has these contacts: pterygoid anteromedially, basisphenoid medially, basioccipital posteromedially, exoccipital posteromedially behind the basioccipital, and squamosal posterolaterally.

Structures in ventral and posterior view: The foramen posterius canalis carotici interni in *Araiochelys* is formed in the pterygoid-quadrate suture, as in *Bothremys* and *Chedighaii*. As in those genera, the quadrate forms more of the foramen and has an anteromedially trending trough that leads into the foramen.

The fenestra postotica in *Araiochelys* is an oval opening (fig. 126), separated laterally from the foramen jugulare posterius by a broad sheet of quadrate, exoccipital, and opisthotic, as in *Bothremys* and *Chedighaii*. The fenestra postotica is not divided but is figure eight-shaped with a more ventrolateral channel and a more dorsomedial one. The opisthotic forms the dorsomedial part of the fenestra postotica.

On the posterior surface of the processus articularis of the quadrate is a posteriorly directed ridge or flange running roughly horizontally ("quadrate pocket" in fig. 126). This flange is downturned along its posterior margin to enclose a trough or pocket on the back of the quadrate. This area is the attachment for the M. depressor mandibulae in other turtles, so presumably this pocket contained at least part of the attachment for this muscle. *Bothremys maghrebiana* and *Chedighaii barberi* both have a distinct ridge in this position, but not the downturned edge making it a partially enclosed pocket. *B. cooki* and *C. hutchisoni* lack this area, and AMNH 29444, *B. cooki*, has the same ridge as in *C. barberi*. In the roof of this quadrate pocket in *Araiochelys* is the posterior opening for the chorda tympani, the foramen chorda tympani inferius, completely hidden in posterior view as well as in the oblique view of the ear.

The internal cavum acustico-jugulare and aditus canalis stapedio temporalis are not visible due to matrix. The condylus mandibularis is slightly anterior to the condylus occipitalis, as in *Bothremys* and *Chedighaii*; it is not anterior to the main body of the basisphenoid, as in *Polysternon*.

PTERYGOID (figs. 122–125)

Preservation: Both pterygoids are present in THUg 3338 with the dorsal and most of the lateral surfaces covered by matrix. Only the proximal part of the pterygoid flange remains, but all (left) and nearly all (right) of the processus trochlearis pterygoidei are present.

Contacts in ventral view: *Araiochelys* has the usual contacts of the Bothremydini: palatine anteriorly, pterygoid anteromedially, basisphenoid posteromedially, and quadrate posterolaterally. *Araiochelys* lacks the pterygoid-maxilla contact posterior to the triturating pit seen in *B. maghrebiana*, also present in the other *Bothremys* species. Nearly all of the dorsal and lateral surfaces of the pterygoid are covered by matrix in THUg 3338, but at the base of the processus trochlearis pterygoidei in the postorbital wall can be seen the jugal and postorbital contacts of the pterygoid.

Structures on ventral surface: The pterygoid in *Araiochelys* is very similar to that in *Bothremys*. The processus trochlearis pterygoidei is well preserved in *Araiochelys* and agrees closely with that in *Bothremys*. The quadrate ramus bears the pterygoid flange (preserved only in *B. maghrebiana*). There is no fossa pterygoidea in *Araiochelys*, *Bothremys*, or *Chedighaii* as occurs in *Foxemys* and *Polysternon*. The foramen posterius canalis

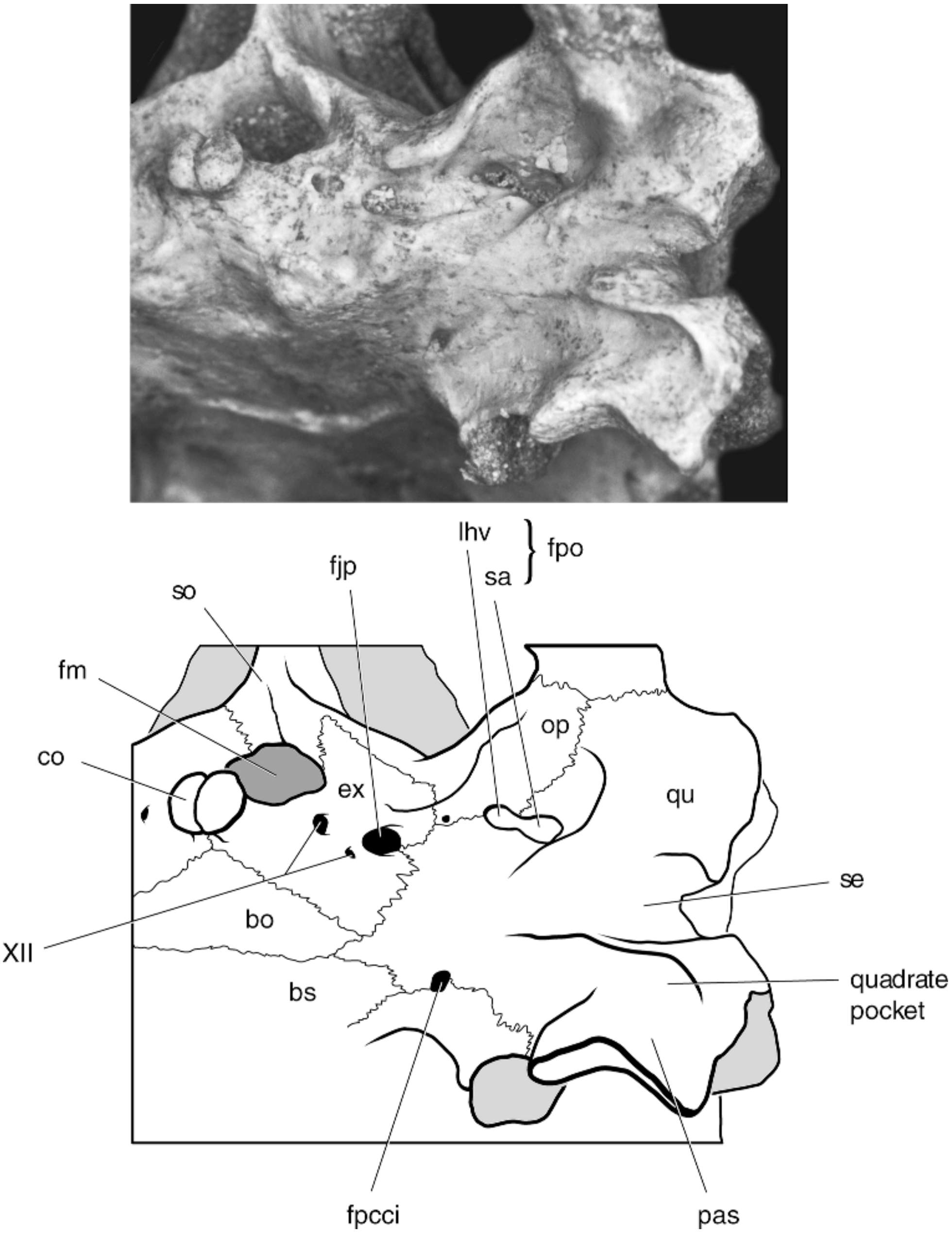

Fig. 126. *Araiochelys hirayamai*, n. gen. et sp. THUg 3338 holotype. Posterior oblique view reversed from left side. [A. Venjara and E.S. Gaffney, del.]

carotici interni has the pterygoid forming its anterior edge, as in *Bothremys* and *Chedighaii* (see Quadrate). The foramen palatinum posterius is formed by palatine and pterygoid (see Palatine). The pterygoid of *Araiochelys* has a narrow ridge paralleling the pterygoid-basisphenoid suture. This is seen in *B. maghrebiana* but not in *Chedighaii* or *B. cooki*.

SUPRAOCCIPITAL (figs. 122, 125)

Preservation: The supraoccipital in THUg 3338 is complete and not obscured by matrix.

Contacts: As in the other Bothremydini, the supraoccipital of *Araiochelys* contacts are parietals anterodorsally, the prootic anterolaterally, the quadrate laterally, the opisthotic posterolaterally, and the exoccipital posteroventrally. These contacts in *Araiochelys* are very similar to those in *Bothremys* and *Chedighaii.*

Structures: The crista supraoccipitalis in *Araiochelys* is short and relatively shallow, similar to that in *Bothremys maghrebiana* and *Chedighaii hutchisoni*. In *Araiochelys*, however, the ventral margin of the crista is thin, while in *Bothremys* and *Chedighaii* there is a swelling along its ventral edge that is thicker than the plate itself. As in everything, the supraoccipital forms the top of the foramen magnum.

EXOCCIPITAL (figs. 122, 125, 126)

Preservation: Both exoccipitals in THUg 3338 are preserved and are complete with the sutures clear.

Contacts: As in the other Bothremydini, the exoccipital of *Araiochelys* contacts the supraoccipital dorsally, the opisthotic laterally, the quadrate ventrolaterally, and the basioccipital ventrally.

Structures: The foramen magnum and condylus occipitalis are very similar in *Araiochelys* and *Bothremys maghrebiana* (missing in *B. cooki*). The condyle is formed entirely by exoccipital, with the basioccipital not even entering the neck of the condyle.

The foramen nervi hypoglossi are nearly the same in position in *Araiochelys*, *Chedighaii*, *Bothremys maghrebiana*, and *B. cooki* (AMNH 29444). Two foramina are present, with the medial one being larger and more dorsal and the lateral one being smaller and more ventral. The foramen jugulare posterius is also very similar in the three genera, except that it is larger in AMNH 29444 than in *Araiochelys*, *B. maghrebiana*, and *Chedighaii.* The foramen is completely closed, with the exoccipital being prevented from meeting itself by a small process of opisthotic. Above the foramen jugulare posterius, the exoccipital forms the medial portion of an overhanging ridge, similar to that in *Bothremys maghrebiana* but much larger (see Opisthotic).

BASIOCCIPITAL (figs. 122, 125, 126)

Preservation: The basioccipital in THUg 3338 is complete with clear sutures. Only its ventral surface is visible.

Contacts: As in the other Bothremydini, the contacts of the basioccipital in *Araiochelys* are the basisphenoid anteriorly, the quadrate laterally, and the exoccipitals dorsally.

Structures: The condylus occipitalis completely excludes the basioccipital, which has only a small process at the exoccipital median suture. There is a low, blunt tuberculum basioccipitale in *Araiochelys*, as in *Bothremys maghrebiana*, AMNH 29444, and *Chedighaii.* Also as in these taxa, *Araiochelys* has a shallow median concavity ahead of the condylus occipitalis. The basioccipital in *Araiochelys* is very short and wide, as in *Bothremys* and *Chedighaii.*

PROOTIC (figs. 122, 125)

Preservation: Both prootics are presumably present and complete in THUg 3338 but are mostly covered by matrix. Both are visible in dorsal view, and the right one has its anterior surface exposed.

Contacts: As exposed, the prootic in *Araiochelys* contacts the quadrate laterally, the parietal medially, and the supraoccipital posterodorsally, all as in *Bothremys* and *Chedighaii.* All three lack a prootic-opisthotic contact.

Structures: Few prootic structures are visible. The foramen stapedio-temporale lies on the anterior surface of the prootic, but the medial margin and the foramen nervi trigemini are covered by matrix. No internal surfaces are visible.

OPISTHOTIC (figs. 122, 125, 126)

Preservation: Both opisthotics are present in THUg 3338 and are complete with most sutures clear, although the most lateral sutures are difficult to make out.

Contacts: As in the other Bothremydini, the opisthotic of *Araiochelys* contacts are the supraoccipital anteromedially, the quadrate anterolaterally, the squamosal posterolaterally, and the exoccipital posteromedially. There is no prootic contact.

Structures: The opisthotic barely enters the margin of the foramen jugulare posterius (see Exoccipital). The opisthotic forms the dorsomedial part of the fenestra postotica (see Quadrate). In *Araiochelys*, the opisthotic and exoccipital form an overhanging ridge above the foramen jugulare posterius and fenestra postotica. This ridge appears to be the same as that seen in *Chedighaii hutchisoni* (broken in *C. barberi*) and *Bothremys*.

BASISPHENOID (figs. 122–125)

Preservation: The basisphenoid in THUg 3338 is complete with clear sutures; only its ventral surface is visible.

Contacts: As in the other Bothremydini, the basisphenoid of *Araiochelys* contacts are the pterygoids anteriorly, the quadrate laterally, and the basioccipital posteriorly. As in *Bothremys maghrebiana*, *B. cooki* (AMNH 29444), and *Chedighaii*, the pterygoid contact is long and the quadrate contact very short.

Structures: The basisphenoid in *Araiochelys* is totally flat and featureless.

Bothremys cooki

The skull of *Bothremys cooki* is the original bothremydid skull from the (probably) Late Cretaceous of New Jersey that was first described by Leidy (1865) (see fig. 19). It lacks the otic chambers and the occiput, but the remaining areas are well preserved, free of matrix, with visible internal areas. The basisphenoid is separate and its dorsal surface is visible. An otic chamber from North Carolina (AMNH 29444) is referred to this species, although there is only a very slight morphologic overlap, the size agrees, and it belongs in this group. The otic chamber is described and figured in this section but it is not used in the reconstructions except for the additional side view (fig. 127D). The skull of *Bothremys cooki* was described in detail in Gaffney and Zangerl (1968), in the senior author's first paper. I hope I get it right this time.

PREFRONTAL (figs. 127, 130)

Preservation: The right prefrontal is nearly complete; the left one is missing its anterior portion.

Contacts: The prefrontal in *Bothremys cooki* has the usual Bothremydini contacts: the maxilla anteroventrolaterally, the other prefrontal medially, and the frontal posteriorly. There is no anteroventral contact with the premaxilla as in *Araiochelys* and *B. kellyi*. The ventral process of the prefrontal has a broad contact with the palatine in the orbital floor. The dorsal process of the maxilla extends anteromedially to restrict the exposure of the prefrontal in *B. cooki* and *B. maghrebiana*.

Structures: The dorsal margin of the apertura narium externa has the midline protrusion or process seen in the other *Bothremys* species and most bothremydids. The interorbital distance in *Bothremys cooki* is less than in *B. kellyi* and about the same as in *B. maghrebiana*.

FRONTAL (figs. 127, 130)

Preservation: Both frontals are present and nearly complete.

Contacts: As in the other *Bothremys*, the frontal of *B. cooki* contacts the prefrontal anteriorly, the parietal posteriorly, the postorbital posterolaterally, and the other frontal medially. The frontal in *B. cooki* is slight longer and slightly narrower than in *B. maghrebiana*, but it is very similar to *B. kellyi*.

Structures: The frontal in *Bothremys* is only narrowly exposed in the orbital margin, in contrast to *Rosasia* and *Zolhafah*, although the degree of exposure is only slightly less than in *Araiochelys*, *Polysternon*, and *Foxemys*. The sulcus olfactorius (see Gaffney and Zangerl, 1968: fig. 21, for endocast) is similar in all *Bothremys* and is lower and wider than in forms like *Galianemys*.

PARIETAL (figs. 127, 130)

Preservation: Both parietals are present, but they lack the entire posterolateral emargination. The processus inferior parietalis is present and visible internally and externally on both sides of the skull. The right one is nearly complete, but both parietals have some breakage along their lower margins.

Contacts of dorsal plate: As in *B. maghrebiana*. The ventral process of the parietal lateral to the sulcus palatinopterygoideus (fig. 278B) contacts the postorbital laterally and probably the pterygoid ventrally. Although the contact is missing, the space would have been filled by the parietal.

Structures of dorsal plate: The degree of temporal emargination is not determinable in *B. cooki*. The ventral process of the parietal that forms the roof for the sulcus palatinopterygoideus is unusually deep in the other species of *Bothremys*, and this is apparent in *B. cooki*, resulting in a low sulcus palatinopterygoideus. The parietal has a ventrolateral process lateral to the sulcus palatinopterygoideus that descends alongside the postorbital. The ventral end of the process is broken off on both sides, but on the right side the pterygoid has a suture as its dorsal margin, and only the parietal would have filled the space and reached the pterygoid (Gaffney and Zangerl, 1968: 211, fig. 13). This process and contact also occur in *Chedighaii hutchisoni*, *Bothremys maghrebiana*, and *Bothremys arabicus*.

Contacts of processus inferior parietalis: The processus contacts the palatine anteroventrally, the pterygoid ventrally, the prootic posteroventrally, and the supraoccipital posteriorly, as in other bothremydids.

Structures of processus inferior parietalis: The foramen interorbitale is low in *Bothremys cooki*, as it is in *B. maghrebiana* (fig. 144), *Chedighaii hutchisoni*, *Araiochelys*, *Rosasia*, and *Foxemys*. The foramen nervi trigemini has the usual bones forming it: parietal anterodorsally, prootic dorsolaterally, and pterygoid ventrally.

JUGAL (figs. 127, 128, 130, 133)

Preservation: The jugal is present and missing its posterior margin on both sides.

Contacts of lateral plate: The jugal plate in *Bothremys cooki* contacts the maxilla anteroventrally in a long, interdigitating suture. The postorbital contact is along the upper edge of the jugal, but the postorbital sends a small process ventrally along the anterodorsal margin of the jugal in the orbital rim. The ventral edge of the jugal entirely contacts the maxilla. The posterior edge is broken, so the contact is indeterminate.

Structures of lateral plate: The jugal forms a small part of the orbital margin, less of it in *Bothremys cooki* than in *B. maghrebiana* and *B. kellyi*. *B. cooki* has a low ridge but no acute rim marking the ventral orbital margin. This is the condition in *B. maghrebiana* also, but both *B. kellyi* and *Bothremys arabicus* have a distinct rim with an acute ridge.

Contacts of medial process: On the ventral surface, the jugal in *B. cooki* is broadly exposed on the triturating surface, contacting the maxilla anteriorly, the palatine medially, and the pterygoid posteromedially. The broad pterygoid contact on the ventral surface is unique to *B. cooki*. The jugal in *B. maghrebiana* has a much smaller exposure; the palatine-maxilla contact prevents jugal exposure along the fossa temporalis margin as seen in many other Bothremydini.

The postorbital wall in posterior view shows the jugal forming its lower half, contacting the postorbital dorsally and the pterygoid medially. The postorbital wall in anterior view shows less jugal, as it lies primarily in the fossa orbitalis floor, contacting the postorbital dorsally and the palatine medially.

Structures of medial process: The jugal in *Bothremys cooki* is unique among bothremydids in its extensive exposure on the palate (figs. 128, 133). It forms most of the characteristic pit and extends posteromedially, forming most of the wall between the fossa temporalis and the pit (Gaffney and Zangerl, 1968: fig. 20). As in the other pitted bothremydids, the jugal forms the roof of the pit and is exposed on the dorsal surface near the orbit directly above the pit, as in the nonpitted forms. So the pit development does not involve the relative movement of the jugal onto the triturating surface, it perchance is the result of exposure of the overlying jugal by removal of maxilla and palatine.

QUADRATOJUGAL

Preservation: Not preserved.

SQUAMOSAL

Preservation: Not preserved.

POSTORBITAL (figs. 127, 130)

Preservation: The anterior part of both postorbitals are present, but the posterior part of the lateral plates that make up the temporal roof are gone.

Contacts of lateral plate: The postorbital contacts the jugal anteroventrally, the frontal anteromedially, and the parietal posteromedially, as in the other *Bothremys* species. The jugal contact has a narrow, anteroventral process that extends along the orbital margin, not seen in other Bothremydini.

Structures of lateral plate: The postorbital in *B. cooki* forms more of the orbital

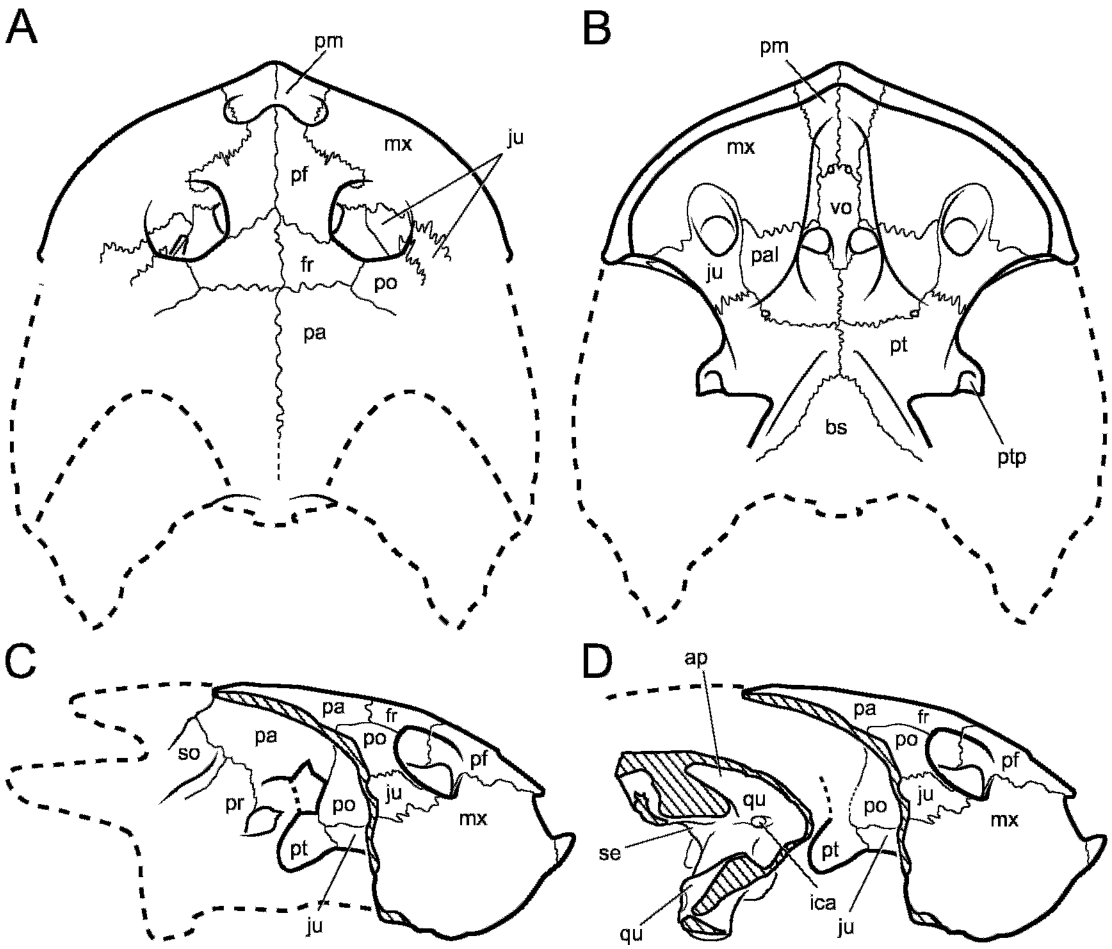

Fig. 127. *Bothremys cooki* Leidy, 1865. Partially restored skull based on AMNH 2521 holotype, outline from *Bothremys maghrebiana*. **A**, dorsal; **B**, ventral; **C**, lateral as preserved with outline from *B. maghrebiana*; **D**, lateral with quadrate added from AMNH 29444. [F. Ippolito, del.]

margin than in *B. maghrebiana* and *B. kellyi*, comparable to that in *Rosasia*.

Contacts of medial process: In the posterior wall of the fossa orbitalis, the postorbital of *B. cooki* contacts the palatine anteromedially, the jugal anterolaterally, and the parietal medially, as in *B. maghrebiana*. In the anterior wall of the fossa temporalis, the postorbital contacts the jugal ventrolaterally, the parietal medially, the maxilla ventrally, and the pterygoid ventromedially. There does not appear to be a palatine contact as in *B. maghrebiana*.

Structures of medial process: The medial postorbital process in *B. cooki* forms part of the roof and lateral wall of the sulcus palatinopterygoideus (fig. 279B), which in *Bothremys* and *Chedighaii* is lower than in other Bothremydini. The posteroventral part of the fossa orbitalis is enlarged in *Bothremys*, *Chedighaii*, *Araiochelys*, and *Rosasia*, in contrast to remaining Bothremydini.

PREMAXILLA (figs. 127, 128, 130)

Preservation: Parts of both premaxillae are present in AMNH 2521. The right one is nearly complete except for an area missing along the midline suture. The left one is missing more of the medial area.

Contacts: As in *Bothremys maghrebiana*.

Structures on dorsal surface: The fossa nasalis and apertura narium externa in *B.*

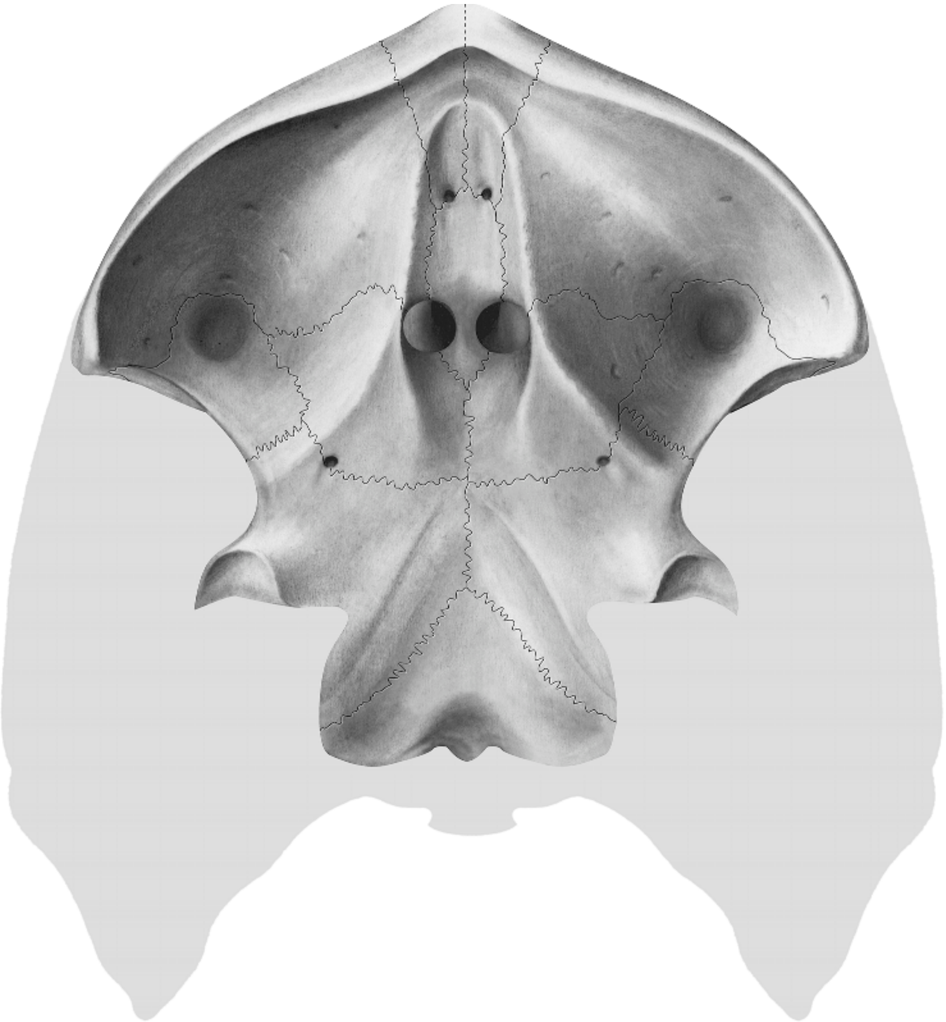

Fig. 128. *Bothremys cooki* Leidy, 1865. AMNH 2521 holotype. Partially restored ventral view of skull, outline from *Bothremys maghrebiana*. [L. Meeker and F. Ippolito, del.]

cooki are very similar to those in *B. maghrebiana*. Although not completely preserved, the premaxilla in *B. cooki* has a dorsal process partially dividing the apertura, as in *B. maghrebiana*. The anterior surface of the premaxilla slopes anterodorsally in both so that the rim of the apertura narium externa is anterior to the labial ridge. The ventral margin of the apertura is also well anterior to the prefrontal as well.

Structures on ventral surface: The labial ridge in *Bothremys cooki* is very similar to that in *B. maghrebiana*. It is blunt, not as blunt as in *Zolhafah*, but more obtuse than the acute ridge of *Foxemys*. Actually, all of this crap is pretty obtuse in my opinion. The labial ridge in *B. kellyi* is slightly thicker than in *B. cooki* and *B. maghrebiana*; the ridge is not preserved in *Bothremys arabicus*. The snout of *B. cooki* is slightly pinched, as it is in *B. kellyi*, *B. maghrebiana*, *Rosasia*, *Polysternon*, and *Foxemys*.

The midline concavity formed by the lingual ridge on the palate is very similar in both *B. cooki* and *B. maghrebiana*. It is shallower in *B. cooki* than in *B. maghrebiana*. The concavity is narrower in these two species, along with *Rosasia* and *Araiochelys* (and probably *Chedighaii barberi*), in contrast to the other Bothremydini. The foramen

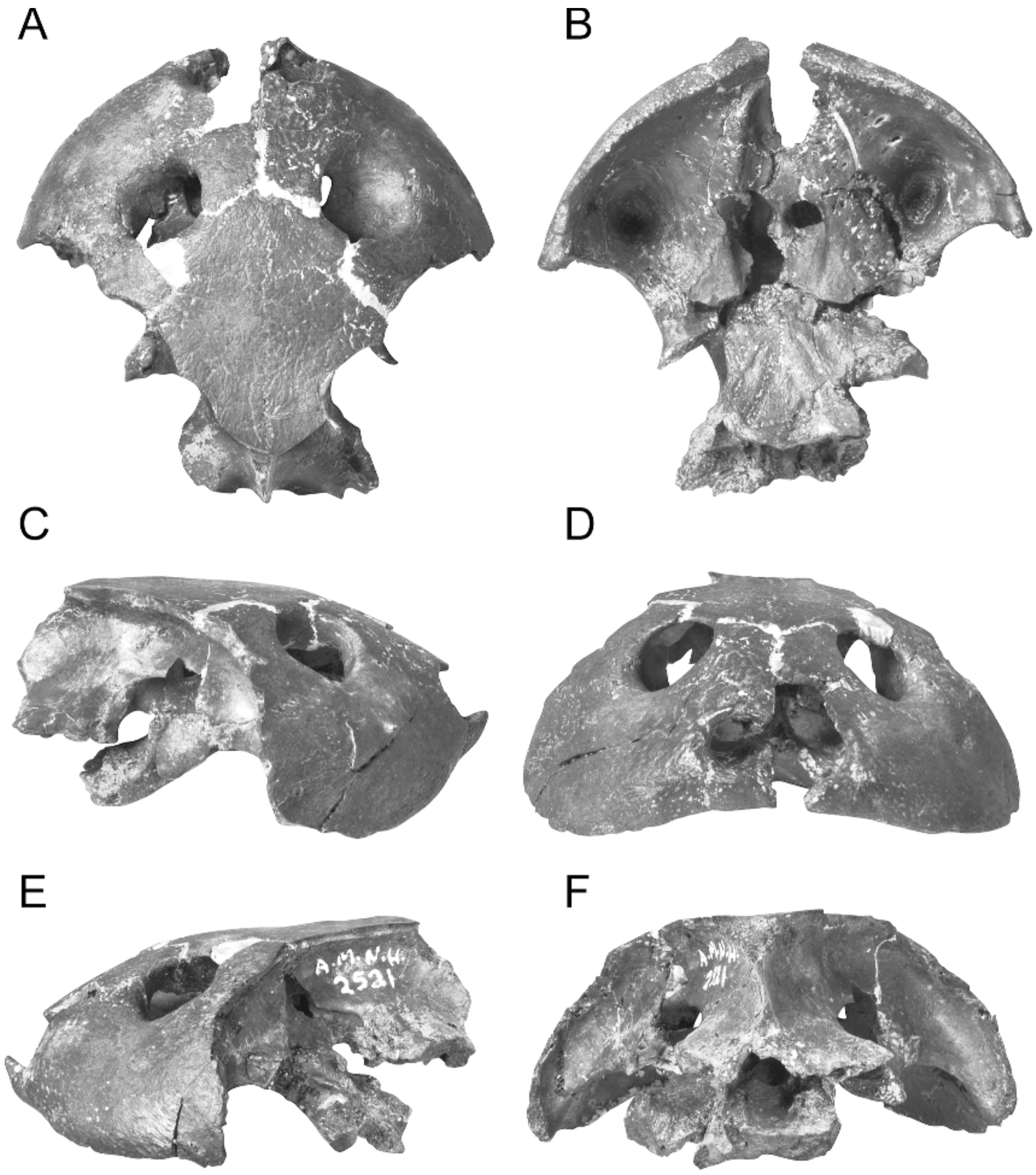

Fig. 129. *Bothremys cooki* Leidy, 1865. AMNH 2521 holotype. **A**, dorsal; **B**, ventral; **C**, right lateral; **D**, anterior; **E**, left lateral; **F**, posterior. [F. Ippolito, del.]

praepalatinum is close to and may be within the premaxilla-vomer suture.

MAXILLA (figs. 127, 128, 130, 133)

Preservation: Both maxillae are present in AMNH 2521, and they are complete except for their posterolateral margins, which are broken edges.

Contacts of vertical plate: The maxilla contacts the premaxilla anteromedially, the jugal posterodorsally, and the prefrontal anterodorsally. The quadrate and quadratojugal contacts are not determinable.

Structures of vertical plate: The maxilla forms the lower margin of the orbit, which in *Bothremys cooki* and *B. maghrebiana* is a low,

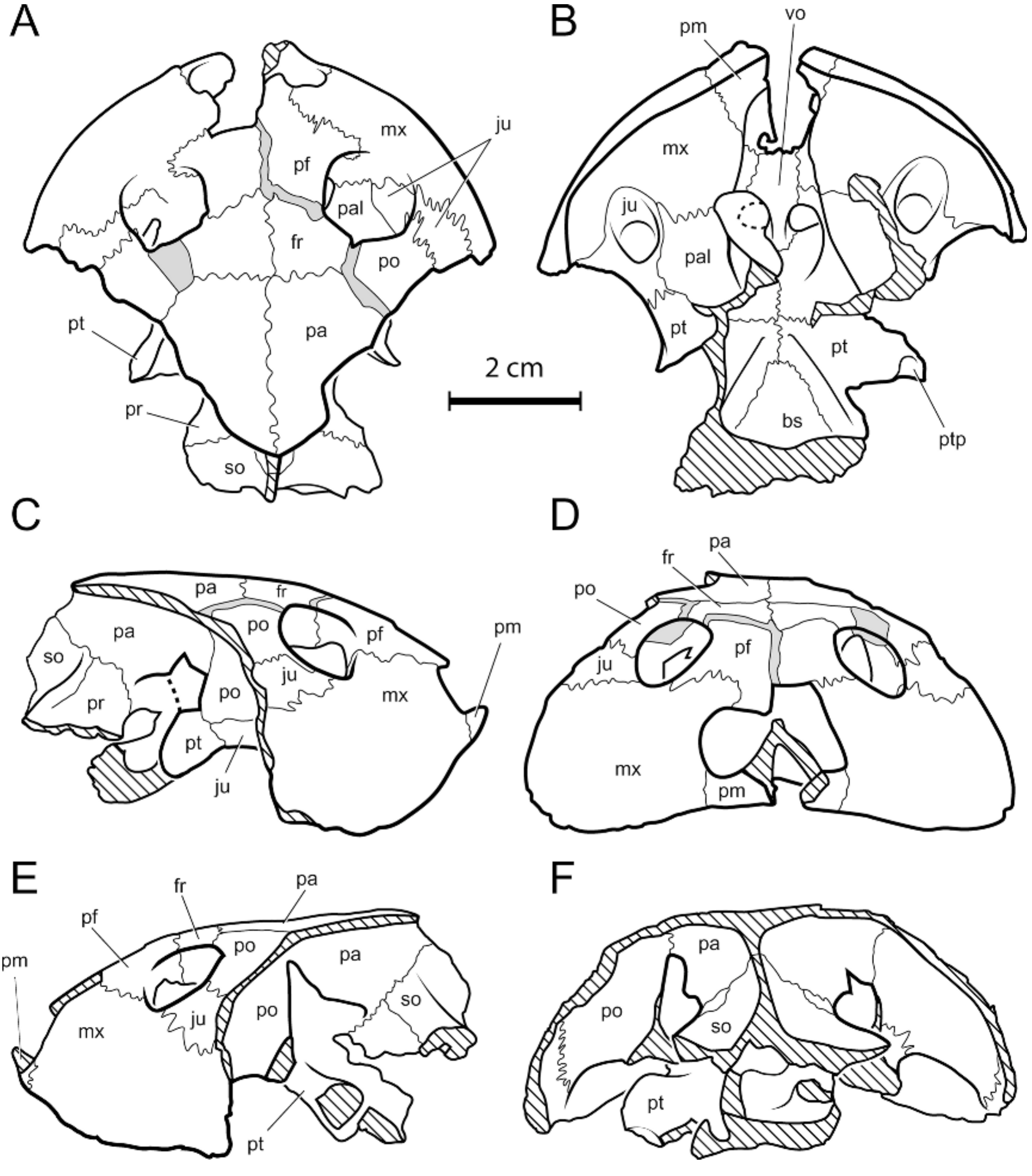

Fig. 130. *Bothremys cooki* Leidy, 1865. AMNH 2521 holotype. **A**, dorsal; **B**, ventral; **C**, right lateral; **D**, anterior; **E**, left lateral; **F**, posterior. [F. Ippolito, del.]

rounded surface, not an acute ridge, as in *B. kellyi*. The fossa nasalis and choanal passages in *B. cooki* are the same size and shape as in *B. maghrebiana*. There is no indication of a cheek emargination. *B. cooki* differs slightly from both *B. maghrebiana* and *B. kellyi* in having a slightly deeper maxilla below the orbit. The dorsal process of the maxilla is broad in *B. cooki*, *B. maghrebiana*, *B. kellyi*, and probably *Bothremys arabicus*, in contrast to the narrower process in other Bothremydini.

Contacts of horizontal plate: The maxilla contacts the premaxilla anteromedially, the vomer medially, the palatine posteromedially, and the jugal posterolaterally. There is no midline contact of the maxillae. *Bothremys cooki* differs from *B. maghrebiana* in lacking a maxilla-palatine contact posterior to the jugal. The vomer-maxilla contact is much wider in *B. cooki* than in *B. maghrebiana*.

Structures of the horizontal plate: The maxilla of *B. cooki* is dominated by the large pit formed by maxilla, jugal, and palatine (fig. 133). Nearly all of the triturating surface is sloping into the pit, as in *B. maghrebiana*, *B. kellyi*, and *Bothremys arabicus*, in contrast to *Araiochelys*, in which the anterior part of the surface is flat or slopes away from the pit. The dorsal surface of the horizontal plate forms the floor of the fossa orbitalis, as in *B. maghrebiana*, and part of the postorbital wall.

VOMER (figs. 127, 128, 130)

Preservation: A nearly complete vomer, possibly missing some of its anterior margin, is preserved in AMNH 2521.

Contacts: The vomer contacts the premaxilla anteriorly, the maxilla anterolaterally, and the palatine posteriorly. The maxilla contact is relatively wide, uniquely so among Bothremydini. The vomer has an elongated anterior end followed by a narrow bar separating the apertura narium interna (not the apertura narium externa as stated incorrectly in Gaffney and Zangerl, 1968: 219). *Foxemys* and *Rosasia* also have a wide maxilla-vomer contact, but it is short in *Araiochelys*, *Zolhafah*, and *B. maghrebiana*. There does not seem to be a vomer-maxilla contact in *Chedighaii hutchisoni*.

Structures: The vomer is higher than wide in cross section and has a shallow groove, the sulcus vomeri, running along its dorsal surface. The posterior half of the vomer rises dorsally above the level of the median concavity on the palate.

PALATINE (figs. 127, 128, 130)

Preservation: Both palatines are present. The right one is missing some bone medially, and the left one is damaged along its lateral and ventrolateral edge. Both are damaged posteriorly. This breakage can be seen in the 1865 figures of Leidy (pl. 18. fig. 7; reproduced as fig. 19 in this paper).

Contacts: The palatine in *Bothremys cooki* contacts the maxilla anterolaterally, the jugal laterally, the pterygoid posteriorly, and the vomer anteromedially. The palatine of *B. cooki* does not contact the maxilla posterior to the pit as it does in *B. maghrebiana*. In the floor of the fossa orbitalis the palatine contacts the maxilla anteriorly, the jugal laterally, the postorbital posterolaterally, and the pterygoid in the floor of the sulcus palatinopterygoideus.

Structures on dorsal surface: The floor of the fossa orbitalis in *B. cooki* has the posteroventral pocket also seen in *Chedighaii* and the other *Bothremys* species. The palatine sends a low process dorsally to meet the anterior part of the processus inferior parietalis and has a dorsal process in the lateral wall of the sulcus palatinopterygoideus that meets the postorbital. The sulcus is continuous with the medial part of the fossa orbitalis.

Structures on ventral surface: The palatine forms the posteromedial part of the triturating surface, agreeing with *B. maghrebiana* and *B. kellyi* (see *B. maghrebiana* and *B. kellyi* for description). The lingual ridge is nearly the same in all three, with nearly all of the triturating surface sloping into the pit. The palatine forms the lateral margin of the apertura narium interna. The apertura in *B. cooki* is a nearly circular, paired opening, while in *B. maghrebiana*, the apertura is more elongate and slightly larger. Part of the apertura edges are damaged in *B. kellyi*. In *Bothremys arabicus* the apertura is also circular but larger.

QUADRATE (figs. 132, 135)

Preservation: The quadrate is not known in the type skull, only in AMNH 29444. This otic chamber has most of the quadrate but lacks all of the lateral sutural edges with the cheek bones, as well as some of the anterior cavum tympani. The antrum postoticum is broken open along both quadrate and squamosal, revealing its extent. The medial and ventral parts of the quadrate in AMNH 29444 are complete.

Contacts on lateral surface: Only the posterodorsal contact with the squamosal is preserved.

Structures on lateral surface: The lateral structures consist of the cavum tympani and associated features and the condylus mandibularis, all of which agree closely with

Bothremys maghrebiana. The incisura columellae auris is a canal completely encased by bone, opening at the most medial part of the cavum tympani. The sulcus eustachii is a broad groove extending posteriorly, not a narrow, deep channel as in *B. kellyi.* The antrum postoticum is slightly larger than in *B. maghrebiana*, about as large as in *B. kellyi.*

Contacts on dorsal and anterior surface: As in *Bothremys maghrebiana.*

Structures on dorsal and anterior surface: The foramen stapedio-temporale is placed well anterior and medial on the otic chamber, just lateral to the foramen nervi trigemini. The quadrate only enters the ventrolateral part of the foramen stapedio-temporale in AMNH 29444. The anterior surface of the otic chamber is nearly vertical in AMNH 29444, but in *Bothremys kellyi* the otic chamber is greatly enlarged anteriorly, above the level of the condylus mandibularis. Most of this is formed by quadrate. *B. maghrebiana* has a slight enlargement, greater than in AMNH 29444, but nothing like that in *B. kellyi.*

Contacts on ventral surface: As in *Bothremys maghrebiana.*

Structures on ventral surface: There is no fossa pterygoidea, although there is a slight depression around the foramen posterius canalis carotici interni. The foramen is formed between the pterygoid and quadrate, as in *B. maghrebiana*, *Araiochelys*, and *Chedighaii*, but in contrast to *B. kellyi* in which the foramen posterius canalis carotici interni is formed by the basisphenoid as well as pterygoid and quadrate. The condylus occipitalis in AMNH 29444 is nearly on the plane of the condylus occipitalis, as in all the other Bothremydini except *Polysternon.*

Contacts on posterior surface: As in *Bothremys maghrebiana.*

Structures on posterior surface: As in *Bothremys maghrebiana* except for the bony subdivision of the fenestra postotica in AMNH 29444. The more dorsomedial part, for the stapedial artery, of the fenestra postotica is separated by bone from the more ventrolateral part, for the lateral head vein, in AMNH 29444, in contrast to *B. maghrebiana* in which they are not separated by bone.

PTERYGOID (figs. 127, 128, 130, 132, 134)

Preservation: In AMNH 2521, the type skull, parts of both pterygoids are preserved. The left one is more complete; it is missing the quadrate ramus and has breakage along the anterior margin and processus trochlearis pterygoidei. The right one consists only of the medial part and the base of the processus trochlearis pterygoidei. The right otic chamber, AMNH 29444, has the quadrate ramus of the pterygoid preserved.

Contacts on ventral surface: The type skull, AMNH 2521, has the pterygoid contacts with the palatine anteriorly, the basisphenoid posteromedially, and the other pterygoid anteromedially. AMNH 29444 shows the quadrate contact.

Structures on ventral surface: The processus trochlearis pterygoidei in *Bothremys cooki* has the same morphology as in *B. maghrebiana.* The quadrate ramus (AMNH 29444) is also as in *B. maghrebiana.* There is no fossa pterygoidea (AMNH 29444), but there is a slight depression around the foramen posterius canalis carotici interni. In AMNH 29444, the foramen posterius canalis carotici interni is formed by the pterygoid anteriorly and the quadrate posteriorly, as in *B. maghrebiana*, *B. arabicus*, *Chedighaii*, and *Araiochelys*, but in contrast to *B. kellyi*, which has the basisphenoid in the margin. The foramen palatinum posterius in *B. cooki* is only on the right side and is the same as in *B. maghrebiana.*

Contacts on dorsal surface: The pterygoid at the base of the processus trochlearis pterygoidei contacts the postorbital dorsolaterally, the parietal (see Parietal) dorsomedially, and the jugal dorsolaterally, all as in *B. maghrebiana*, *Chedighaii*, and *B. arabicus.* The crista pterygoidea contacts the processus inferior parietalis dorsally and anteriorly and the prootic posteriorly, as seen in AMNH 2521. In AMNH 29444, the more posterior contacts with the prootic posterodorsally and the quadrate posterolaterally are visible.

Structures on dorsal surface: The pterygoid forms the floor of the sulcus palatinopterygoideus, as in the other bothremydids. There is no indication of the foramen nervi vidiani, but this area is not perfectly preserved. The crista pterygoidea is similar in

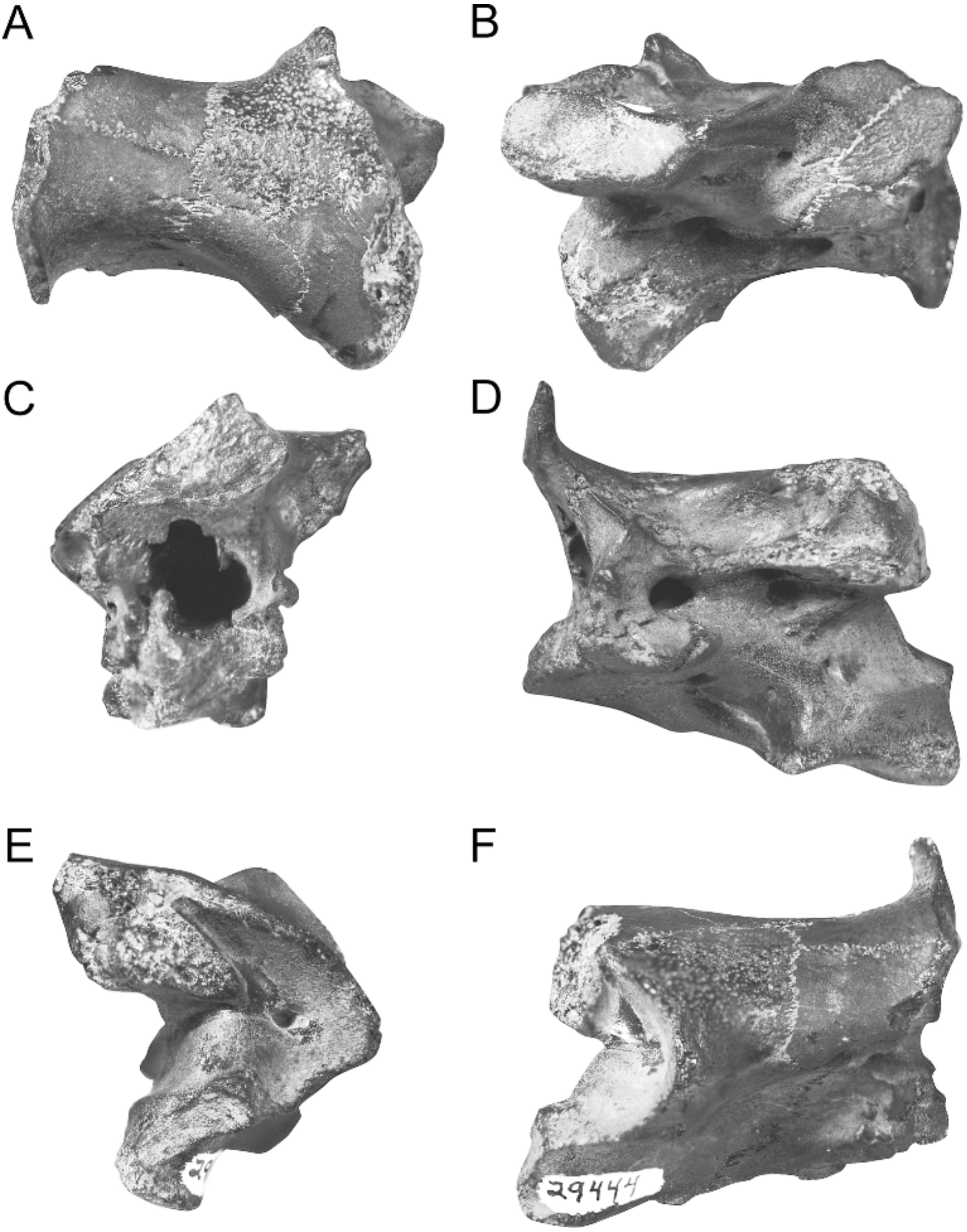

Fig. 131. *Bothremys cooki* Leidy, 1865. AMNH 29444. Right otic chamber. **A**, dorsal; **B**, ventral; **C**, medial; **D**, posterior; **E**, lateral; **F**, anterior. [F. Ippolito, del.]

size and shape to that in *B. maghrebiana*. The foramen nervi trigemini has the usual formation: parietal dorsally, pterygoid ventrally and anteroventrally, and prootic posterodorsally.

SUPRAOCCIPITAL (figs. 127, 130, 132)

Preservation: Only the anterior part of the supraoccipital is present in the type skull, AMNH 2521. In AMNH 29444 the right lateral process is preserved.

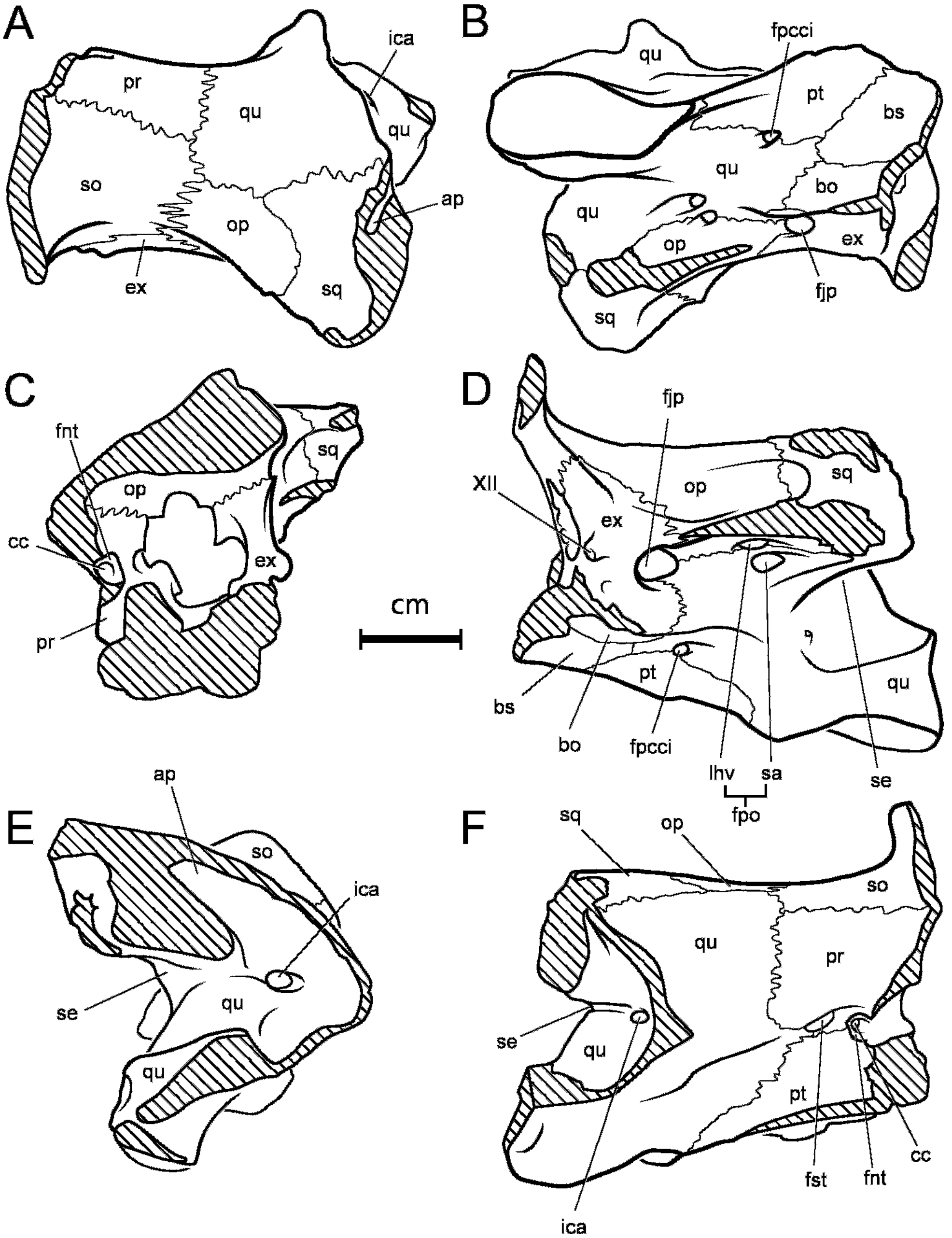

Fig. 132. *Bothremys cooki* Leidy, 1865. AMNH 29444. Right otic chamber. **A**, dorsal; **B**, ventral; **C**, medial; **D**, posterior; **E**, lateral; **F**, anterior. [F. Ippolito, del.]

Contacts: In AMNH 2521 the supraoccipital contacts the parietals dorsally and anteriorly, as in other bothremydids. It contacts the prootic anterolaterally, but other contacts are lost due to breakage. In AMNH 29444 the supraoccipital contacts the prootic anterolaterally, the quadrate laterally, the opisthotic posterolaterally, and the exoccipital posteroventrally, as in *Bothremys maghrebiana*.

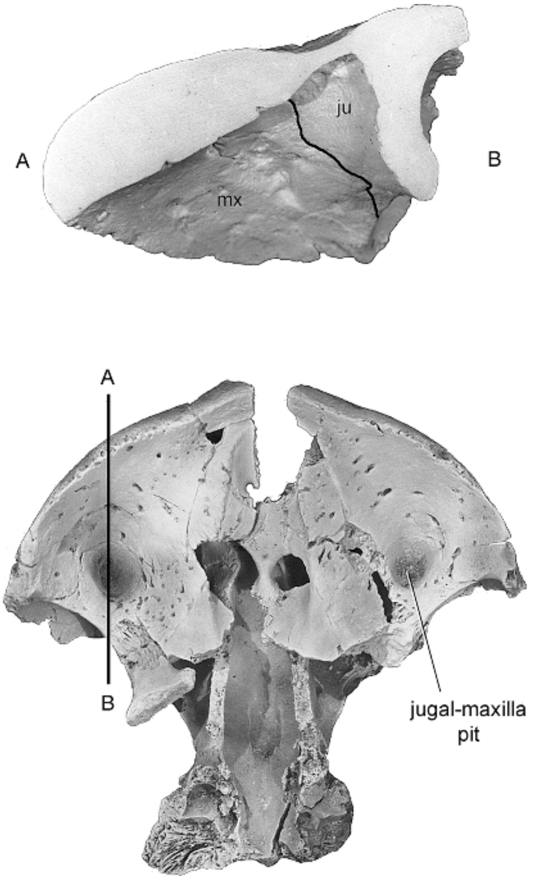

Fig. 133. *Bothremys cooki* Leidy, 1865. AMNH 2521 holotype. Upper, section through cast of right cheek region showing pit morphology. Lower, ventral view of skull, A–B shows line of section in upper figure. Modified from Gaffney and Zangerl (1968). [E.S. Gaffney, del.]

Structures: The crista supraoccipitalis is represented only by a short broken edge in AMNH 2521, but it agrees with *B. maghrebiana*. The ventral surface shows only a small part of the foramen magnum and some of the cavum labyrinthicum (see Gaffney and Zangerl, 1968: fig. 16). The other specimen, AMNH 29444, shows most of the foramen magnum on the right side and part of the base of the crista supraoccipitalis. These agree with *B. maghrebiana*.

Exoccipital (figs. 132, 135)

Preservation: The exoccipital is not preserved in the type of *Bothremys cooki*, AMNH 2521, but it is partially present on the right side of AMNH 29444. This exoccipital is complete except for the ventromedial area and the condylus occipitalis.

Contacts: The exoccipital contacts the supraoccipital dorsally, the opisthotic laterally, the quadrate ventrolaterally, and the basioccipital ventrally, all as in *B. maghrebiana* and other Bothremydini.

Structures: The foramen magnum is the same as in *B. maghrebiana*. The condylus occipitalis is missing, and not enough of it or the basioccipital is preserved to determine the composition of the missing condylus occipitalis. All of the posterior surface of the exoccipital is in the same vertical plane in *B. cooki*, AMNH 29444, but in *B. maghrebiana* the lower part is inclined anteroventrally, and in *B. kellyi* it is concave, similar to *Chedighaii hutchisoni*.

The foramen nervi hypoglossi in AMNH 29444 appear to be three in number, with a large medial one and two small ventrolateral ones, as in *Araiochelys* and some *B. maghrebiana*. The foramen jugulare posterius is formed by the exoccipital except laterally, where it is closed by the opisthotic and quadrate. The foramen is relatively large, larger than in *B. kellyi*, *B. maghrebiana*, *Bothremys arabicus*, and *Araiochelys*, but similar to that in *Chedighaii*.

Basioccipital (figs. 132, 135)

Preservation: The type skull of *Bothremys cooki*, AMNH 2521, lacks the basioccipital. AMNH 29444 has the right half of one, with the posterior edge having a broken surface.

Contacts: The basioccipital in AMNH 29444 contacts the basisphenoid anteriorly, the quadrate laterally, in a contact that is much wider than in *B. kellyi* and *B. maghrebiana*, and the exoccipitals posterodorsally.

Structures: The condylus occipitalis in AMNH 29444 is broken away, and the broken surface does not allow the extent of the basioccipital to be determined. There is no tuberculum basioccipitale and no ventral median concavity; the ventral surface of the basioccipital is flat. The bone is a bit longer than in the other species of *Bothremys*.

Prootic (figs. 132)

Preservation: Parts of both prootics are preserved in the type skull of *Bothremys*

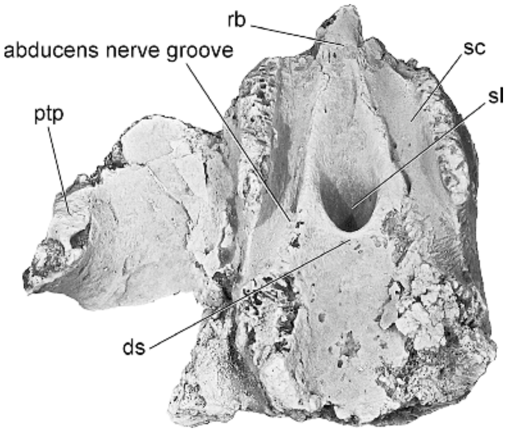

Fig. 134. *Bothremys cooki* Leidy, 1865. AMNH 2521 holotype. Dorsal view of basisphenoid and left pterygoid. [E.S. Gaffney, del.]

cooki, AMNH 2521. The right one consists of most of the upper part of the bone and its anterior surface. The left one is less preserved laterally and is more damaged by pyrite. The otic chamber, AMNH 29444, has the right prootic nearly complete, lacking only its medial edge.

Contacts: The prootic in AMNH 2521 contacts the parietal dorsomedially, and the pterygoid ventrally on its anterior surface. On its dorsal surface it contacts the supraoccipital posterodorsally, but the other contacts are missing. In AMNH 29444, the prootic shows all the contacts seen in *Bothremys maghrebiana* except for the parietal, which is broken away.

Structures: Both prootics show a close similarity to the prootic of *B. maghrebiana*. They lack the dorsal ridge and strong anterior overlap seen in *B. kellyi*, *Chedighaii*, and some *B. maghrebiana*. The foramen nervi trigemini has the usual formation of parietal anterodorsally, prootic dorsally, and pterygoid posteroventrally. The foramen is preserved in both AMNH 2521 and AMNH 29444, and it is the same size and position in both. In AMNH 29444 the foramen cavernosum lies on the posteroventral margin of the foramen nervi trigemini, showing where the canalis cavernosus becomes the sulcus cavernosus. The foramen nervi trigemini and the foramen stapedio-temporalis are close together, separated only by a narrow bar of prootic.

The medial surface of the prootic in AMNH 29444 preserves part of the hiatus acusticus and the cavum labyrinthicum. The hiatus has the foramen nervi acustici, which is single as preserved, but the posterior part of the hiatus is missing. The foramen nervi facialis is also preserved.

OPISTHOTIC (figs. 132, 135)

Preservation: The opisthotic is not preserved in the type of *Bothremys cooki*, AMNH 2521. A nearly complete right opisthotic is preserved in AMNH 29444. This opisthotic is missing a small part along its posterior edge.

Contacts: The opisthotic in AMNH 29444 has the same contacts as in *Bothremys maghrebiana.*

Structures: The foramen jugulare posterius in AMNH 29444 is larger than in most other Bothremydini. It is closed laterally by both opisthotic and quadrate joining to form the margin. The fenestra postotica is completely closed and subdivided by a narrow but complete bony separation into a more dorsomedial foramen for the stapedial artery and a more ventrolateral foramen for the lateral head vein. On the dorsal surface, the opisthotic has a broad, posteriorly facing concavity formed by the opisthotic and squamosal that occurs in *B. kellyi* and *Chedighaii* and, to a lesser extent, in most Bothremydini.

BASISPHENOID (figs. 127, 130, 134)

Preservation: The type skull of *Bothremys cooki*, AMNH 2521, has most of the basisphenoid preserved, but it is a bit chewed up along its posterior margin. It is also missing some of the posterolateral edges. AMNH 29444 has only the posterolateral third or so of the bone preserved.

Contacts on ventral surface: The basisphenoid of *B. cooki* has the usual contacts as seen in *B. maghrebiana*. The quadrate contact is narrow, as in *B. maghrebiana*, but not as narrow as in *B. kellyi.*

Structures on ventral surface: The foramen posterius canalis carotici interni is not formed by the basisphenoid in AMNH 29444, as it is in *B. kellyi*. The surface is flat, with no concavities or depressions.

Contacts on dorsal surface: The dorsal surface is visible in AMNH 2521 (Gaffney

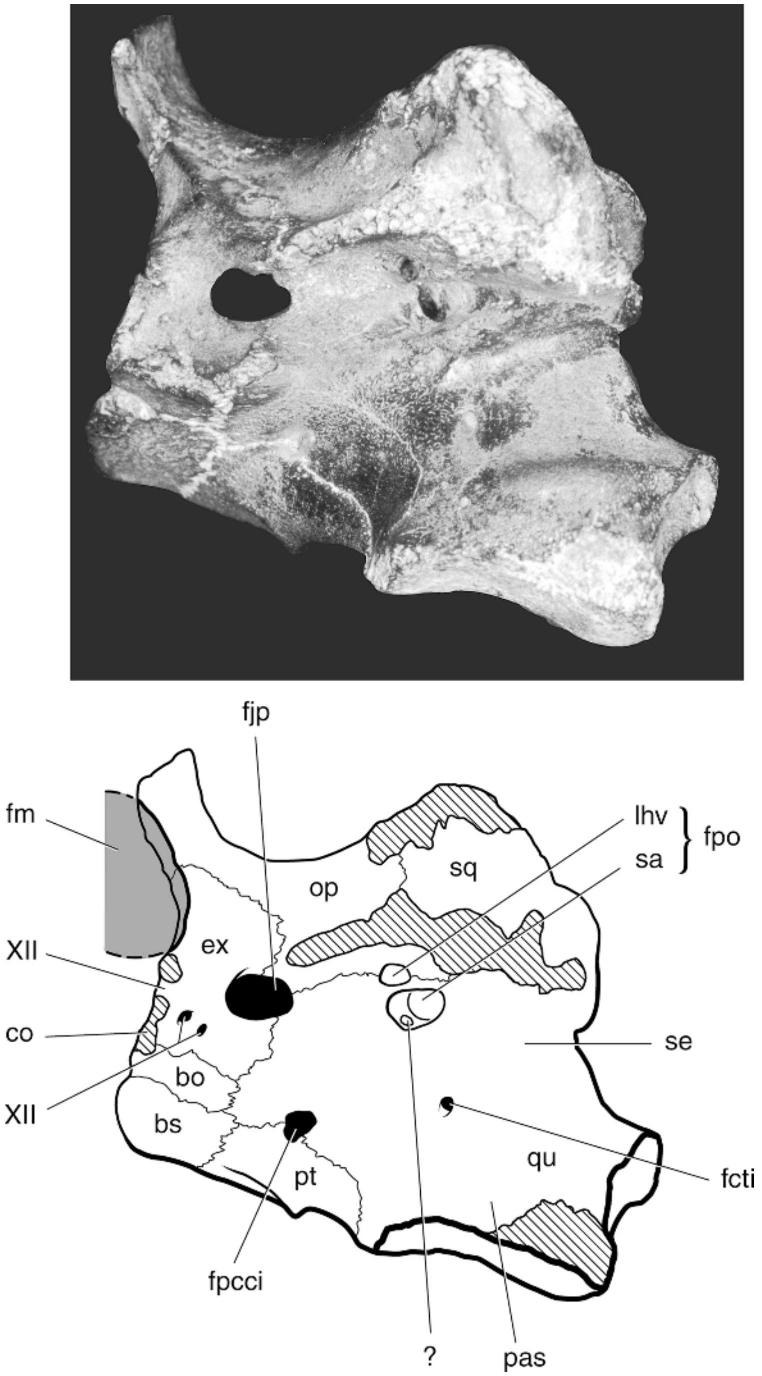

Fig. 135. *Bothremys cooki* Leidy, 1865. AMNH 29444. Posterior oblique view. [A. Venjara and E.S. Gaffney, del.]

and Zangerl, 1968: fig. 19). The crista pterygoidea contacts the processus inferior parietalis, but not the frontal. There is no palatine contact, but the basisphenoid overlaps the pterygoids anteriorly, as in nearly all turtles.

Structures on dorsal surface: The rostrum basisphenoidale in *Bothremys cooki* (fig. 134) is rodlike but fairly short, very similar to that in *Chedighaii barberi*, YPM PU 12951, an endocast (fig. 167). The dorsum sellae and sella turcica are also very similar, with the dorsum sellae overhanging the sella turcica and forming a teardrop-shaped opening. The foramen anterius canalis carotici interni is visible at the posterolateral corner of the sella turcica. The processus clinoideus is absent, as in *Chedighaii* (it is indeterminate in the other *Bothremys*). The foramen nervi abducentis seems to be absent as a fully formed canal, also as in *Chedighaii barberi*.

Bothremys maghrebiana

There are five good skulls of *Bothremys maghrebiana*, making it morphologically the best known taxon in the tribe Bothremydini, and the more extensive description and figures reflect this. There is some individual variation, particularly with MHNL 20-268370, and this is noted in the description. There are four species in *Bothremys* at present. *B. maghrebiana* is most similar to *B. cooki*, although the analysis only weakly supports a sister-taxon relationship (fig. 288).

PREFRONTAL (figs. 136, 143)

Preservation: At least parts of the prefrontal are present in all five *Bothremys maghrebiana* skulls, but it is most complete in AMNH 30041, AMNH 30561, and MHNL 20-268370.

Contacts: The prefrontal of *Bothremys maghrebiana* has the same contacts as in *Bothremys cooki* and the other bothremydids: maxilla anteroventrolaterally, frontal posteriorly, and other prefrontal medially.

Structures: The prefrontal in *Bothremys maghrebiana* has an anterior projection on the midline that is also present in *B. cooki* and *Chedighaii*. In all the *Bothremys* species this helps form the distinctive figure eight-shaped apertura narium externa. In *Chedighaii* the lower margin is missing. *Foxemys* and *Polysternon*, as well as *Cearachelys*, have a transverse, not protruding margin to the apertura.

The sulcus olfactorius of *Bothremys maghrebiana* is slightly shallower than in *B. cooki* and is much shallower than in *Chedighaii.* It is very variable among the bothremydids.

FRONTAL (figs. 136, 143)

Preservation: The frontals are preserved in all five *Bothremys maghrebiana* skulls, although there is some damage to them in both AMNH 30234 and AMNH 30041.

Contacts: The frontal in *Bothremys maghrebiana* has the usual bothremydid contacts: prefrontal anteriorly, postorbital posterolaterally, parietal posteriorly, and frontal medially. The frontal in *B. maghrebiana* differs from the other bothremydids in being much wider than long. In *B. cooki* the frontal is nearly square, and in the others the frontal is relatively narrower than in *B. maghrebiana.*

Structures: The size and position of the orbits in the Bothremydini are variable. *Bothremys* and *Chedighaii* have unusually small and upward-facing orbits. In *Rosasia* and *Zolhafah* the orbits are larger, while in *Polysternon* and *Foxemys* the orbits are largest. To a certain extent this size difference is subjective, and *Zolhafah* has incomplete orbits. Also, the orientation of the orbits is distinctly dorsally facing in *Bothremys* and *Chedighaii hutchisoni.* In the other Bothremydidae there is usually a more lateral component to the orbital orientation.

PARIETAL (figs. 136, 143, 278B)

Preservation: The parietal is present at least in part in all five *Bothremys maghrebiana* specimens, but its posterior margin is complete only in AMNH 30234 and MHNL 20-268370. In AMNH 30041 the dorsal plate of the right parietal is completely missing, revealing the cavum cranii. AMNH 30234 is probably missing a small part near the midline at its posteriormost limit.

Contacts of dorsal plate: As in the other Bothremydinae, the parietal of *Bothremys maghrebiana* contacts the frontal anteriorly, the postorbital laterally, and the other parietal medially. There is no parietal-quadratojugal or squamosal contact.

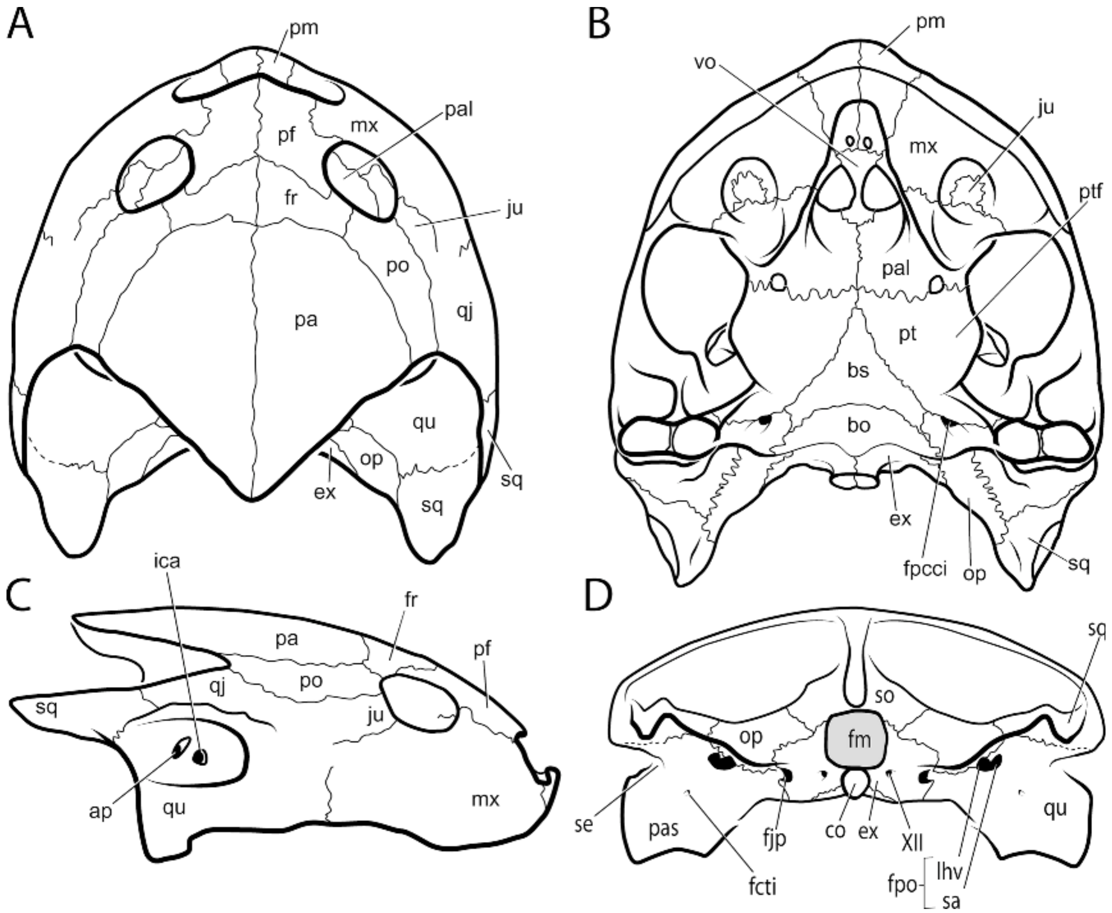

Fig. 136. *Bothremys maghrebiana*, n. sp. Partially restored views of skull based on AMNH 30234 with additions from AMNH 30041 and AMNH 30561 holotype. **A**, dorsal; **B**, ventral; **C**, lateral; **D**, posterior (based primarily on AMNH 30561 holotype and AMNH 30234). For more detailed view of area around foramen posterius canalis carotici interni, see figure 277**B**. [A.M. Phillips, del.]

Structures of dorsal plate: Among the Bothremydini the complete temporal roof is known in *Polysternon*, *Foxemys*, *Araiochelys*, and *Chedighaii*. The extent of the roof is very similar in *Bothremys maghrebiana* and *Foxemys*; it is slightly more extensive than in *Polysternon*. However, in *Chedighaii* it is more emarginate than in these three, completely exposing the otic chamber rather than partially exposing it. However, the difference is not great and could very well be within individual variation of some or all of these taxa.

The ventral surface of the parietal lateral to the sulcus palatinopterygoideus has a ventral process in *Bothremys maghrebiana*. In other bothremydids and pleurodires in general the parietal forms the roof of the sulcus, actually a tunnel-shaped structure in most Pelomedusoides, but not part of the lateral wall. In both *B. maghrebiana* and *B. cooki* there is a well-developed ventral process attached to the medial edge of the postorbital (fig. 278B). In *B. maghrebiana* it reaches the palatine (on the anterior surface, not on the posterior surface, which is shown in fig. 278); in *B. cooki* it is more extensive posteriorly and contacts the pterygoid. The process is best seen in the anterior view of the postorbital wall of the fossa orbitalis in *B. maghrebiana*, AMNH 30041, and in the posterior view of

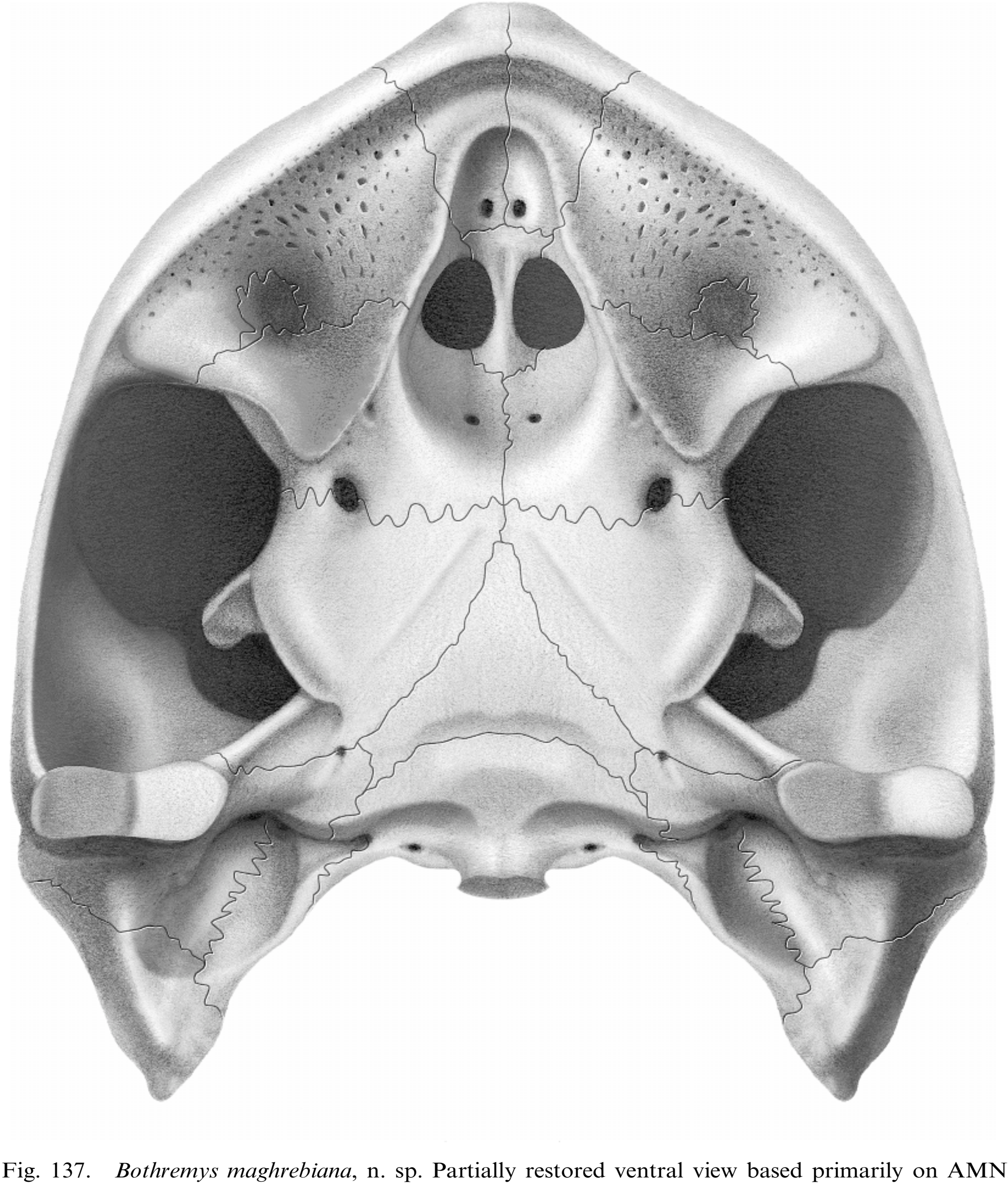

Fig. 137. *Bothremys maghrebiana*, n. sp. Partially restored ventral view based primarily on AMNH 30234 with additions from AMNH 30041 and AMNH 30561 holotype. [F. Ippolito, del.]

the postorbital wall in *B. cooki*, AMNH 2521.

Contacts of processus inferior parietalis: The processus is clearly visible only in AMNH 30041, although its anterior margin is revealed in AMNH 30234. Sutures are clear on the right processus inferior parietalis of AMNH 30041, although there is some fragmentation due to crushing. The contacts are the usual in Bothremydinae: palatine anteroventrally, pterygoid ventrally, prootic posteroventrally, and supraoccipital posteriorly.

Processus inferior parietalis: The foramen interorbitale (fig. 144) in *Bothremys maghrebiana* is nearly the same as in *B. cooki*, although some crushing in *B. maghrebiana* makes close comparisons difficult.

The foramen is longer in *Bothremys* (not known in *B. kellyi*) than in *Chedighaii*, but it is very similar in *Rosasia* and *Foxemys*.

The foramen nervi trigemini in *B. maghrebiana* is formed by the usual bones seen in other Bothremydinae: parietal anterodorsally, prootic dorsolaterally, and pterygoid ventrally. The foramen nervi trigemini in *B. maghrebiana* is very close to the foramen stapedio-temporale.

JUGAL (figs. 136, 137, 139, 143, 278B)

Preservation: The jugal is present in all five *Bothremys maghrebiana* specimens, but it is complete only in AMNH 30234, and sutures are not entirely clear in this skull. Sutures are clear in AMNH 30041 and 30561, which are lacking parts of the lateral plate of the jugal.

Contacts of lateral plate: In *B. maghrebiana* the laterally exposed portion of the jugal contacts the maxilla anteroventrally and the postorbital dorsally. In AMNH 30041 and 30561, which have clear sutures, the jugal ends posteriorly in a broken edge. In AMNH 30234 the sutures are obscured by cracking and poor preservation. It is likely that the quadratojugal-jugal suture lies above the maxilla-quadrate suture and that the jugal does not contact the quadrate. This condition would be nearly the same as in *Rosasia*. In *Chedighaii*, *Polysternon*, and *Foxemys* there is no maxilla-quadrate contact. In *B. cooki* and *Zolhafah* the cheek is missing.

Structures of lateral plate: The jugal in *Bothremys maghrebiana* is exposed in the posterior wall of the orbit and forms part of its margin. There is no cheek emargination in *B. maghrebiana*, and the jugal does not reach the cheek margin.

Contacts of medial process: The orbital floor of *Bothremys maghrebiana* is best seen in the left orbit of AMNH 30041. The contacts are with the maxilla anteriorly and laterally and with the palatine medially, as in the other Bothremydini. At least some of the jugal is exposed in the orbital floor in all five skulls, but sutures are clearly visible only in AMNH 30041 and 30522. They show contact laterally with the maxilla, ventromedially with the palatine, and dorsomedially with the postorbital. On the triturating surface the jugal contacts the maxilla anteriorly and the palatine posteriorly.

Structures of medial process: The jugal is a complex element that forms part of three surfaces. Its dorsal surface forms part of the floor of the fossa orbitalis, and in *Bothremys maghrebiana* its ventral surface is exposed in the tip of the pit formed on the triturating surface (figs. 136, 137). This condition is best seen in AMNH 30041, on the left side, and in AMNH 30561, also on the left side. The dorsal sutures are clear, but the ventral ones are harder to interpret. However, both AMNH 30561 and AMNH 30041 have the pits broken through by a hole into the orbit that makes identification easier. The bone at the tip of the pit is very thin (as it is in *Bothremys cooki*) and easily broken. In both skulls the jugal on the dorsal surface can be followed into the broken edge and onto the ventral surface in the pit apex. The sutural contact with maxilla and palatine is irregular in both skulls and obscured by nutrient foramina and fusion, but the general position of the jugal forming the apex of the pit is clear.

In *Bothremys cooki* the pit is formed almost entirely by the jugal, which is broadly exposed along the edge of the fossa temporalis inferior. In *Zolhafah* and *Rosasia* much of the pit is also formed by the jugal, which is also exposed along the fossa temporalis inferior margin, although not to the extent seen in *B. cooki*. Thus, *B. maghrebiana* differs from all these in having no exposure of the jugal on the margin of the fossa temporalis inferior due to broad contact of the maxilla and palatine. *Cearachelys* and *Galianemys whitei* also have exposure of the jugal along this margin, but exposure on the triturating surfaces is slight. In *Chedighaii* there are no pits and no exposures of the jugal.

The third area of jugal exposure is on the posterior surface of the septum orbitotemporale in the fossa temporalis superior (fig. 278B). The jugal here is bound by the maxilla laterally and the postorbital dorsomedially. On the right side of AMNH 30041 the palatine contacts the jugal ventromedially, but on the left side it seems that the palatine does not extend laterally to reach the jugal, although it is not entirely clear. On both sides of this specimen, however, there is a clear ventral suture of the jugal showing that it does not extend anteriorly to meet the jugal exposed in the pit.

QUADRATOJUGAL (figs. 136, 141)

Preservation: The quadratojugal is missing in AMNH 30041 and 30561. It is present but not clearly defined by sutures in AMNH 30234, AMNH 30522, and MHNL 20-268370.

Contacts: The quadratojugal in *Bothremys maghrebiana* contacts the quadrate ventrally and the postorbital medially, as seen on the right side of AMNH 30234. On the left side can be seen a narrow, posterolateral contact with the squamosal. The definite maxilla-quadrate contact preserved in AMNH 30561, 30522, and 30041 shows that a C-shaped quadratojugal extending to the cheek margin could not be present in *B. maghrebiana*. The quadratojugal is restricted to the area above the quadrate, as in *Rosasia* and *B. kellyi*. The jugal-quadratojugal suture is not clearly discernable although it is likely in the area posterior to the maxilla-quadrate contact, in which case there would be no quadratojugal-maxilla contact.

Structures: The quadratojugal of *Bothremys maghrebiana* forms part of the temporal roof and is exposed on the edge of the skull roof. There is no cheek exposure of the quadratojugal in *B. maghrebiana*.

SQUAMOSAL (figs. 136, 139)

Preservation: The squamosal is present in all five skulls, but it is most complete in AMNH 30234 in which only a small part of the temporal margin seems to be missing. Sutures are visible in all five skulls, but they are best seen in AMNH 30561 and 30041.

Contacts: The squamosal contacts the quadrate anteriorly, the opisthotic medially, and the quadratojugal anterodorsally.

Structures: The squamosal of *Bothremys maghrebiana* is a cone-shaped bone fitting around the relatively well-developed antrum postoticum of the quadrate. The bone is not preserved in *B. cooki*, *B. arabicus*, and *Rosasia*, and it is only partially preserved in *Chedighaii*, *Zolhafah*, and *Polysternon*. *Foxemys*, along with *B. maghrebiana*, has the best preserved squamosals among the Bothremydini. The bone has a low ventral ridge in all the taxa with it preserved, in contrast to the deep ridge seen in some Taphrosphyini.

POSTORBITAL (figs. 136, 141, 278B)

Preservation: The anterior part of the postorbital is present in AMNH 30561 and 30041, but only AMNH 30234 has the bone nearly complete. Sutures are clear in AMNH 30561, 30041, and 30234.

Contacts of lateral plate: The postorbital of *Bothremys maghrebiana* contacts the frontal anteromedially, the jugal anteroventrally, the quadratojugal posteroventrally, and the parietal medially.

Structures of lateral plate: The postorbital has a wide exposure in the posterior orbital margin in *B. maghrebiana*, as in the other bothremydines. The postorbital of *B. maghrebiana* is slightly narrower than that bone in *Foxemys*, *Polysternon*, and *Chedighaii*. It is incomplete or missing in *B. cooki*, *Rosasia*, and *Zolhafah*. The postorbital forms part of the posterior margin of the temporal roof in *B. maghrebiana*, as in the other Bothremydini.

Contacts of medial process: The medial process of the postorbital in *Bothremys maghrebiana* is preserved in all three skulls but is clearest in AMNH 30041. The postorbital is exposed in the fossa orbitalis and the posterior surface of the postorbital wall (fig. 278B). In the fossa orbitalis the postorbital contacts the jugal laterally, the palatine anteroventrally, and the parietal medially. In *B. maghrebiana* there is a descending process of the parietal between the postorbital and the sulcus palatinopterygoideus, as in *B. cooki*. In the posterior view of the postorbital wall the postorbital contacts the jugal laterally, the palatine and maxilla ventrally, the pterygoid medially, and the parietal dorsomedially.

Structures of medial process: The postorbital bone in *Bothremys maghrebiana* makes up part of the roof and lateral wall of the sulcus palatinopterygoideus, as in other pleurodires, but in *Bothremys* the descending process of the parietal covers much of the postorbital exposure. The postorbital wall in both *Bothremys* and *Rosasia* is placed more posteriorly in comparison to other bothremydids. The sulcus palatinopterygoideus (fig. 144) is therefore shorter in

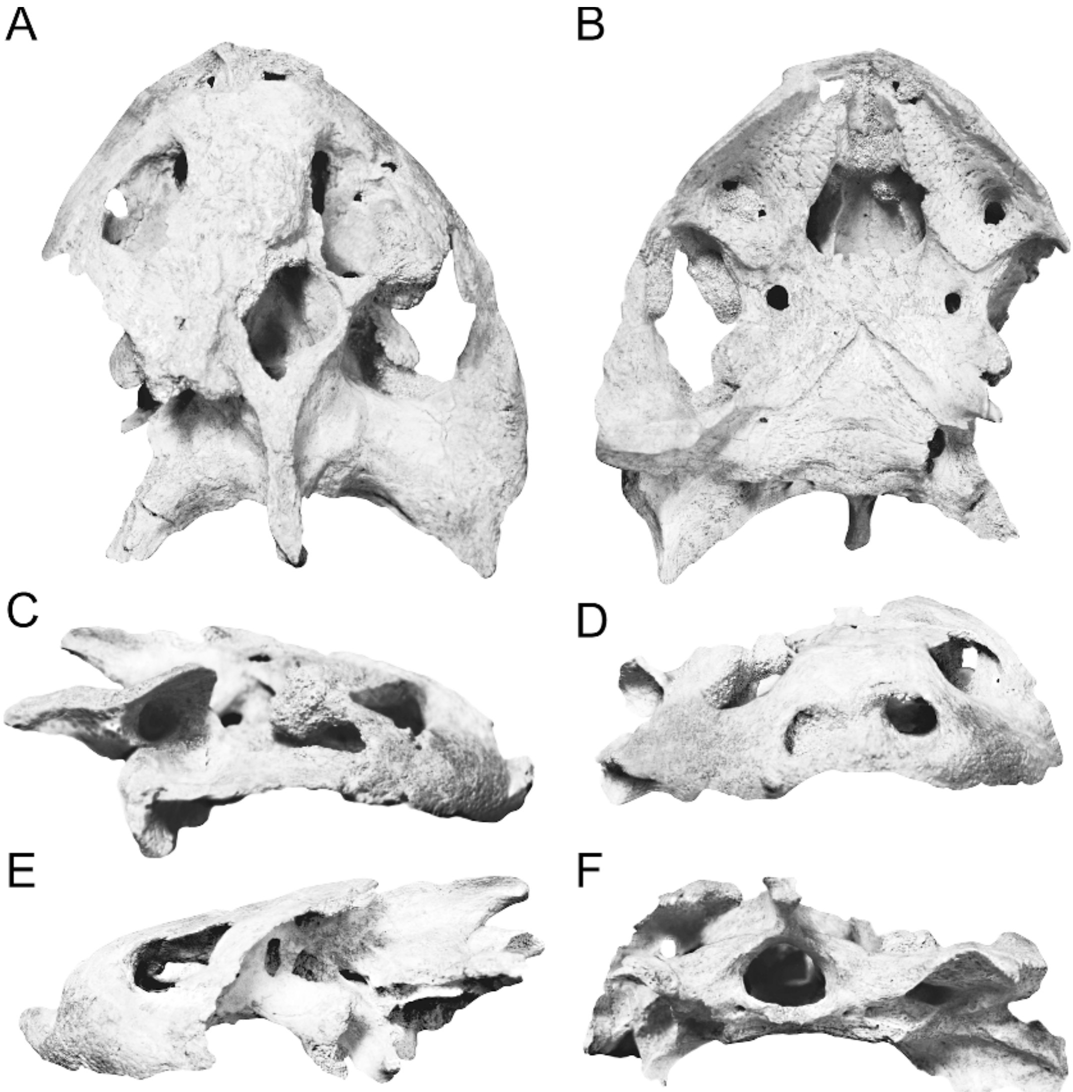

Fig. 138. *Bothremys maghrebiana*, n. sp. AMNH 30041. **A**, dorsal; **B**, ventral; **C**, right lateral; **D**, anterior; **E**, left lateral; **F**, posterior. [A.M. Phillips, del.]

Bothremys than in the other bothremydids. The postorbital forms part of the dorsal pocket of the fossa orbitalis, characteristic of bothremydids (character 27).

PREMAXILLA (figs. 136, 137, 143)

Preservation: At least some of the premaxilla is present in all five *Bothremys maghrebiana* skulls; sutures are visible in AMNH 30041, 30522, and 30561.

Contacts: The premaxilla in *B. maghrebiana* contacts the maxilla posterolaterally, the other premaxilla medially, and the vomer posteriorly. These contacts are very similar in the other *Bothremys* species.

Structures in dorsal view: The premaxilla in *Bothremys maghrebiana* is very similar to that in *B. cooki*. They both are distinctly protuberant, extending anteriorly past the anterior limit of the prefrontal at the dorsal margin of the apertura narium externa. A protuberance of the premaxilla is also present in *Rosasia*. The condition in *Chedighaii* and *Zolhafah* is not determinable.

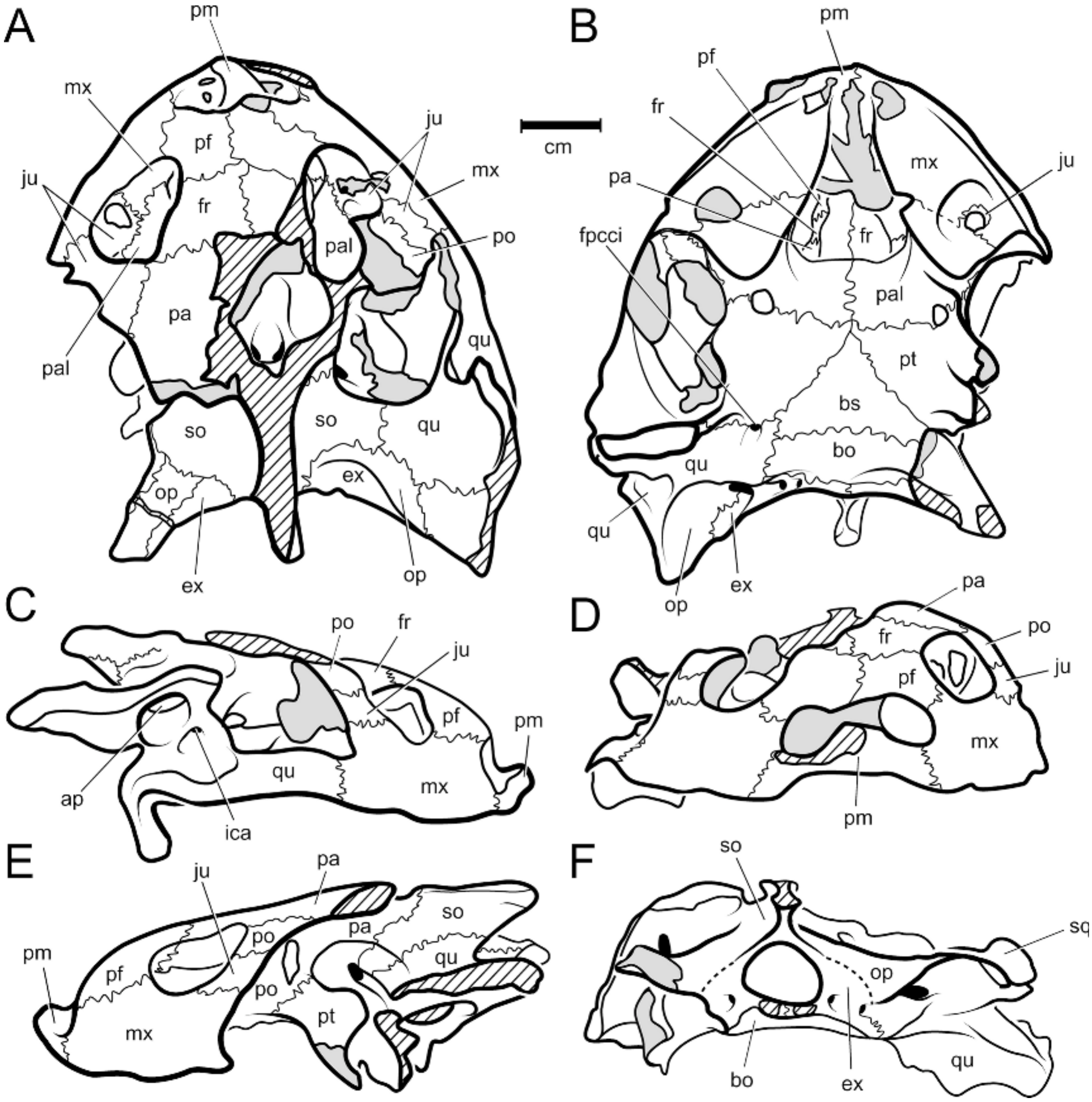

Fig. 139. *Bothremys maghrebiana*, n. sp. AMNH 30041. **A**, dorsal; **B**, ventral; **C**, right lateral; **D**, anterior; **E**, left lateral; **F**, posterior. [A.M. Phillips, del.]

Structures in ventral view: The premaxilla in all species of *Bothremys* is very wide anteriorly and triangular in shape. This is also the condition in *Chedighaii*, *Rosasia*, and *Zolhafah*, but not in *Foxemys*, where it is more parallel-sided. In ventral view the premaxilla of *Bothremys maghrebiana* is very similar to that bone in *B. cooki*. The labial ridge is blunt but not as blunt as in *Zolhafah*, and it is more blunt than the acute ridge of *Foxemys*. All *Bothremys* species have an anterior profile of the premaxillae with a shallow rise on the midline of the labial ridge, comparable to that in *Foxemys*, but not flat, as in *Kurmademys*. All *Bothremys* species have a similar midline concavity developed on the premaxillae, vomer, and maxillae. This concavity is defined anteriorly and laterally by the lingual ridge and is a surface that lacks the highly vascularized texture of the triturating surface. It is typically distinct and deep in most but not all bothremydids. In *B. maghrebiana* and *B. cooki* it is relatively narrow, in contrast to *B. kellyi, B. arabicus, Foxemys*, and *Polysternon*. It is much narrower in *Rosasia*.

The foramen praepalatinum is best preserved in *Bothremys maghrebiana* in AMNH 30561. This paired foramen is almost completely formed by the premaxilla at its posterior limit, close to but not within the vomer-premaxilla suture. It is situated in a very similar position in *B. cooki*.

MAXILLA (figs. 136, 137, 143)

Preservation: At least one nearly complete maxilla is present in all five *Bothremys maghrebiana* specimens. It is best preserved with clearest sutures in AMNH 30561, but good sutures are visible also in AMNH 30041, 30234, and 30522. Only the right maxilla is well preserved in MHNL 20-268370.

Contacts of vertical plate: The more vertical or lateral portion of the maxilla in *Bothremys maghrebiana* contacts the premaxilla anteromedially, the jugal posterodorsally, the quadrate posteriorly, and the prefrontal anterodorsally. The posterodorsal sutures are not clear in AMNH 30234, which is the only specimen to preserve this area. It is likely that there is a small maxilla-quadratojugal contact as in *Rosasia*, but this is ambiguous. In common with *Rosasia*, the maxilla in *B. maghrebiana* contacts the quadrate posteriorly without the quadratojugal intervening, as in *Polysternon*, *Foxemys*, and *Chedighaii*, among the Bothremydini.

Structures of vertical plate: The relations of the dorsal process of the maxilla do not vary much among the Bothremydini. In *Bothremys maghrebiana* the suture between the maxilla and prefrontal extends from the dorsolateral corner of the apertura narium externa to the anterior margin of the orbit, as it does in other Bothremydini. The length of the suture, which reflects the width of the dorsal process, however, does vary among these. In the *Bothremys* species this process is wider than in any of the other Bothremydini. *Chedighaii* also has a wide process, wider than in other Bothremydini except for *Bothremys*.

The maxilla forms the lateral margin of the apertura narium externa. In *Bothremys* the narium is relatively wide, as it is in most Bothremydini except *Rosasia*, *Foxemys*, and *Polysternon*. The extent of the maxilla from the orbit to the lower cheek margin is great in all species of *Bothremys* and in *Chedighaii*, more so than in other Bothremydini. The labial ridge in *Bothremys maghrebiana* is broadly curved as in *B. cooki*; both are very similar in shape laterally and ventrally.

Contacts of horizontal plate: In *Bothremys maghrebiana* the maxilla contacts the premaxilla anteromedially, the vomer medially, the palatine posteromedially, and the jugal posteriorly. The vomer contact in *B. maghrebiana* is short in contrast to *B. cooki*, which has a long vomer-maxilla contact that is related to the longer anterior portion of the vomer and greater separation of the apertura narium interna from the front of the snout. The jugal contact in *B. maghrebiana* is also significantly different from that in *B. cooki* and is related to the way in which the triturating pits are formed (see below). In *B. maghrebiana* the jugal (see Jugal) is visible on the left side of AMNH 30041 and both sides of AMNH 30561. The jugal has an irregular, circular contact with the maxilla except for its posterior margin where it contacts the palatine. The maxilla also contacts the jugal dorsomedially in the posterior surface of the postorbital wall.

Structures of horizontal plate: In *Bothremys maghrebiana* as in *B. cooki* and the other Bothremydini, except *Araiochelys*, the maxilla horizontal plate is very wide and triangular, forming most of the distinctive triturating surface.

The triturating surface in *Bothremys maghrebiana* is most similar to that in *B. cooki* and *B. kellyi* among the Bothremydini, but there are important differences. The shape of the labial ridge is quite similar in *B. cooki* and *B. maghrebiana*, differing from *Rosasia* in being more acute and not as curved anteriorly. The ridge in *Zolhafah* is very blunt and much straighter than in any of the other Bothremydini. The labial ridge margin is missing in *Chedighaii hutchisoni* but it is acute in *C. barberi*. The medial and more horizontal surface of the triturating surface in *B. maghrebiana* is broadly curved, forming the outer parts of the surface leading into the pit, so that most of the pit is formed by the maxilla in *B. maghrebiana*. Only the tip is formed by the jugal. In the other species of *Bothremys* much more of the pit is formed by the jugal. However, the area of the triturating surface formed by the jugal in *B. cooki* is formed mostly by the palatine in *B. maghrebiana*, so the maxilla itself is similar in extent in these two species. The maxilla in both species reaches the edge of the temporal fossa to form part of the postorbital wall. This part of the triturating surface is also similar to that in *Rosasia* and *Zolhafah*; both of these have the jugal making up the tip of the pit, but the pit is shallower and lies closer to the temporal fossa edge, lacking the well-developed posterior wall seen in other *Bothremys* species. The maxilla in *B. maghrebiana* between the pit and the premaxilla is much less extensive than it is in *B. cooki*. *Chedighaii* lacks the triturating surface pits and lacks any exposure of the jugal on the triturating surface.

Medially the maxilla in *Bothremys maghrebiana* forms part of the lingual ridge, much as in the other Bothremydini. The lingual ridge is not a ridge in the Bothremydini; rather, it forms a raised margin where the triturating surface is separated from the depressed area around the apertura narium externa. This area is very similar in the other *Bothremys* species.

On the dorsal surface, the maxilla forms part of the floor of the fossa orbitalis and the orbital margin. The maxilla in *B. maghrebiana* forms the lateral edge of the foramen orbitonasale and the anterior part of the fossa orbitalis, as in *B. cooki* and the other Bothremydini. The maxilla in *Bothremys maghrebiana* forms a small part of the posterior surface of the postorbital wall. The maxilla forms part of the ventral pocket in the posterior part of the fossa orbitalis (fig. 144).

VOMER (figs. 136, 137, 143)

Preservation: In *Bothremys maghrebiana* the vomer is present in AMNH 30234, 30522, and 30561. It is well preserved with clear sutures in AMNH 30561 and 30522.

Contacts: The contacts of the vomer in *Bothremys maghrebiana* are with the premaxillae anteriorly, the maxillae anterolaterally, and the palatines posteriorly, as in other Bothremydidae.

Structures: The vomer in *Bothremys maghrebiana* is dumbbell-shaped, widened at each end with a narrow central bar. In *B. cooki* the anterior expansion is much more extensive and the maxillary contact is longer than in *B. maghrebiana*. *Zolhafah* also has a small or absent vomer-maxilla contact, but *Rosasia* has an anteriorly expanded vomer. *Chedighaii* has a vomer that lacks an anterior expansion of the sort seen in *B. cooki*, but the degree of maxilla contact is unclear.

The vomer forms the medial margin of each apertura narium interna. In *Bothremys maghrebiana* the apertura is slightly larger than in *B. cooki* and is placed more anteriorly. The shape of the apertura is circular in *B. cooki* but oblong in *B. maghrebiana*. The foramen praepalatinum in *B. maghrebiana* is formed almost completely by the premaxilla.

PALATINE (figs. 136, 137, 143)

Preservation: Most of both palatines are missing in MHNL 20-268370, but the remaining four have the bone nearly complete on one or both sides. Sutures are clearest in AMNH 30561 and 30522.

Contacts: The palatine in *Bothremys maghrebiana* contacts the maxilla in a long, roughly transverse suture trending anteromedially to posterolaterally with a short interruption in the middle for the jugal. This is in strong contrast to *B. cooki*, which has only the anteromedial part of the contact, as the larger jugal prevents more lateral contact with the maxilla. The anteromedial corner of the palatine has a short contact with the vomer. There is a long midline contact with the other palatine and a nearly transverse posterior contact with the pterygoid.

On the dorsal surface of the palatine in *B. maghrebiana* there is the usual parasagittal contact with the processus inferior parietalis of the parietal. In the floor of the orbit the palatine contacts the maxilla anterolaterally, the jugal laterally, and the postorbital posterolaterally.

Structures on dorsal surface of palatine: The orbital floor in *Bothremys maghrebiana* is exposed clearly in AMNH 30561 and 30041. The palatine exposure in *B. maghrebiana* is much as in *B. cooki*; there is not a great deal of variation within the

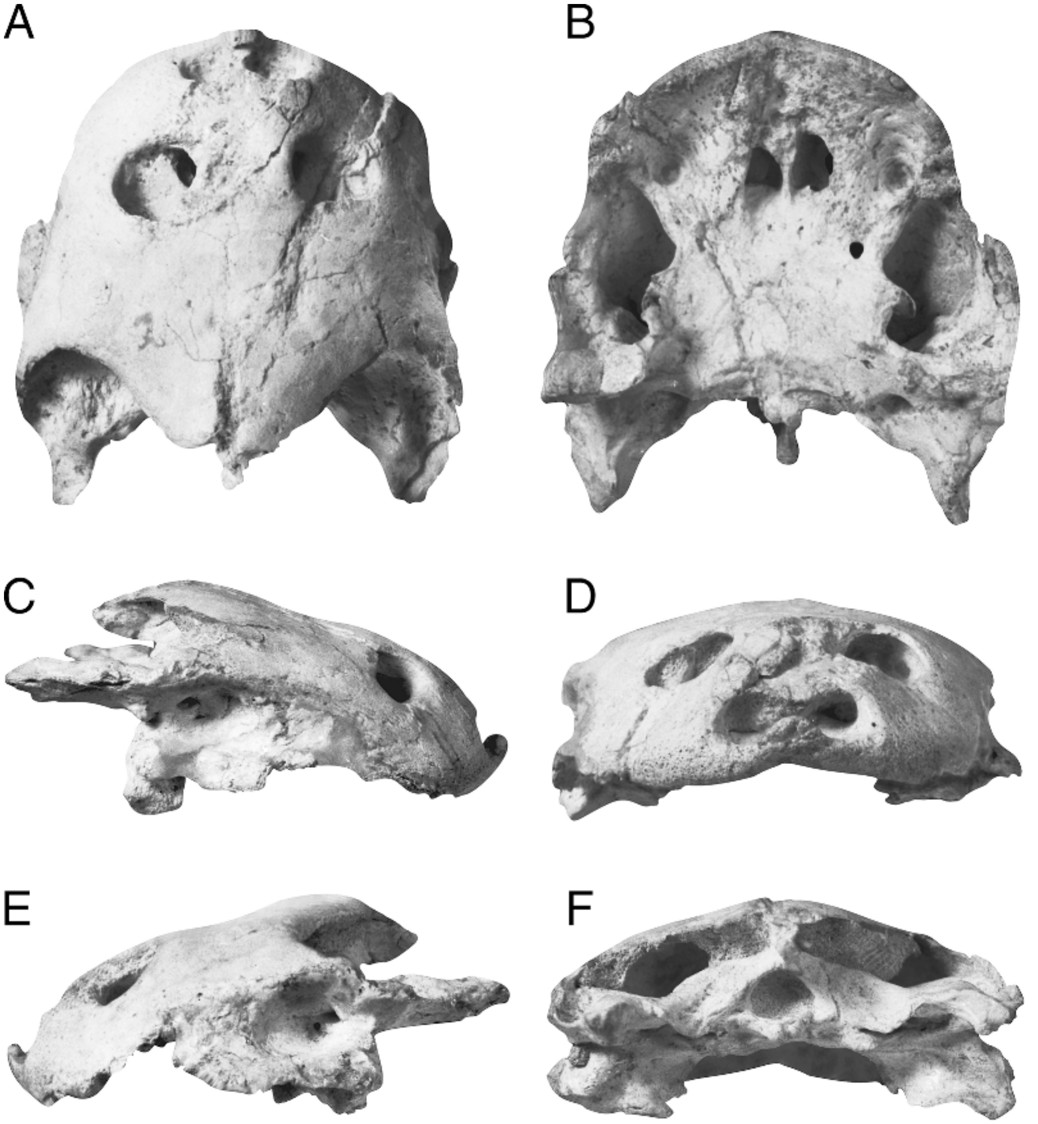

Fig. 140. *Bothremys maghrebiana*, n. sp. AMNH 30234. **A**, dorsal; **B**, ventral; **C**, right lateral; **D**, anterior; **E**, left lateral; **F**, posterior. [A.M. Phillips, del.]

Bothremydini in any case. The foramen orbitonasale is also similar in the other *Bothremys* species. There is no dorsal process of the palatine on either anterior or posterior postorbital wall surfaces.

Structures on ventral surface of palatine: The palatine of *Bothremys maghrebiana* forms a significant part of the triturating surface, the posteromedial third, as in the other Bothremydini. This part of the palatine is broadly curved, forming the posteromedial part of the pit on the triturating surface. The triturating surface area of the palatine has the characteristic nutrient foramina up to the low lingual ridge that roughly trends anteromedially to posterolaterally, as in *B. cooki*.

The palatine forms the dorsal and lateral walls of the apertura narium interna and the broadly curved choanal passage leading into it. This area is very similar in *Bothremys maghrebiana* and *B. cooki*.

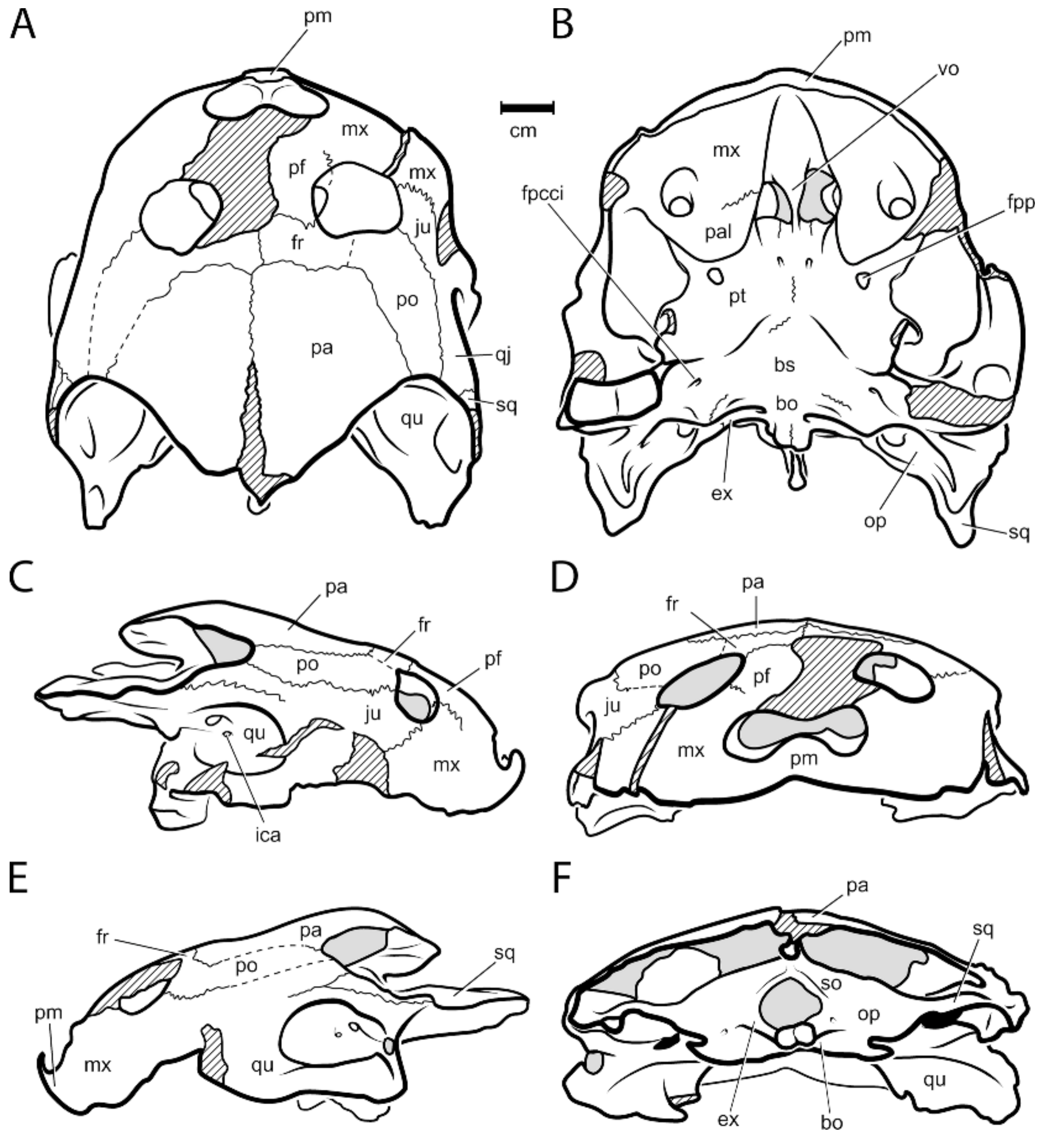

Fig. 141. *Bothremys maghrebiana*, n. sp. AMNH 30234. **A**, dorsal; **B**, ventral; **C**, right lateral; **D**, anterior; **E**, left lateral; **F**, posterior. [A.M. Phillips, del.]

QUADRATE (figs. 136, 137, 139, 145, 286B)

Preservation: The quadrate is present on both sides in AMNH 30234, AMNH 30561, and MHNL 20-268370, but it is missing on the right side of AMNH 30041 and is damaged on the right side of AMNH 30522. All five skulls show sutures.

Contacts in lateral view: The quadrate in *Bothremys maghrebiana* contacts the maxilla anteriorly, the quadratojugal dorsally, and the squamosal posterodorsally.

Structures in lateral view: The cheek in *Bothremys maghrebiana* is completely lacking any emargination and is very similar to *Rosasia* in this feature. *Zolhafah* and *B. cooki* do not have the cheek area preserved, and *Chedighaii hutchisoni* has a shallow emargination.

The cavum tympani in *Bothremys maghrebiana* is similar to that in the other Bothremydini in which it is known (fig. 286B). Unfortunately, it is missing in the type specimen of *B. cooki*, although it is preserved in AMNH 29444, which is probably *B. cooki*. *Rosasia* and *Zolhafah* have only part of it preserved, so *B. maghrebiana* represents one of the best preserved ears in the Bothremydini! Only *Polysternon* and *Foxemys* have good ear regions preserved and they differ significantly from *B. maghrebiana* and the other Bothremydini in having an open incisura columellae auris (fig. 281).

The cavum tympani of *Bothremys maghrebiana* is a deep, hemispherical cone, as is typical of the infrafamily Bothremydodda, which have a nearly horizontal, shelflike platform forming its ventral edge. This area is not preserved in the type skull of *B. cooki*, but AMNH 29444 does have this shelf. The cavum tympani in *B. maghrebiana* has no fossa precolumellaris, a structure lacking in the other Bothremydidae except *Kurmademys*. As in all other Bothremydidae, *B. maghrebiana* has an extensive bony separation between the stapes and eustachian tube. There is a distinct groove and notch for the eustachian tube in *B. maghrebiana*, as in AMNH 29444 and both species of *Chedighaii*.

The antrum postoticum in *Bothremys maghrebiana* shows some variation among the five skulls. In AMNH 30234, AMNH 30522, MHNL 20-268370, and AMNH 30561, the antrum is smaller than in AMNH 30041, the smallest skull. The smaller size of the antrum in the larger skulls suggests that it may be growth related, as in many living turtles. The antrum postoticum is often relatively larger in the juveniles of a species than in the adults, and the small condition in the larger skulls of *B. maghrebiana* may be the adult condition of this species. It is somewhat subjective to discriminate between "moderate" and "small" character states in the size of the antrum postoticum in bothremydids. However, the interpreted adult condition of *B. maghrebiana* is the same size as in the other *Bothremys* species and *Chedighaii*, but it is distinctly smaller than in *Polysternon* and *Foxemys*. The smallest *B. maghrebiana* skull, AMNH 30041, however, has an antrum postoticum about the same relative size as in these latter genera.

Contacts in dorsal view: The quadrate in *Bothremys maghrebiana* has the usual contacts of most Bothremydini: prootic anteromedially, supraoccipital medially, opisthotic posteromedially, and squamosal posteriorly and posterolaterally.

Structures in dorsal view: The only varying structure here is the position of the foramen stapedio-temporale. In *Bothremys maghrebiana* it is in the advanced bothremydid position on the anterior face of the otic chamber.

Contacts in ventral view: The quadrate in turtles is a complex element that in bothremydids typically contacts nine bones (basisphenoid, basioccipital, pterygoid, opisthotic, prootic, supraoccipital, maxilla, quadratojugal, and squamosal; see fig. 136). These contacts are all present in *Bothremys maghrebiana*, and seven are visible in ventral view (all of the above except the supraoccipital and prootic). The medial process of the quadrate contacts the pterygoid anteromedially, the basisphenoid medially, and the basioccipital posterodorsally. These contacts are very similar in *B. cooki* (AMNH 29444) and *Zolhafah*. The basisphenoid suture is longer in *Foxemys* and *Polysternon* and much shorter in *Chedighaii*. Most of the basioccipital suture in *Rosasia* is eroded, but the basisphenoid suture seems similar in length to that in *B. maghrebiana*.

Structures in ventral view: In ventral view the quadrate of *Bothremys maghrebiana* shows only the slightest imprint of the pterygoideus musculature, in strong contrast to the deep fossa pterygoidea seen in *Foxemys* and *Polysternon*. This concavity is also absent in *Chedighaii*, *Zolhafah*, and *B. cooki* (AMNH 29444), but a moderately developed one is present in *Rosasia*.

The foramen posterius canalis carotici interni is formed between the quadrate and pterygoid in *Bothremys maghrebiana* (fig. 277B), as in *B. cooki* (AMNH 29444), *Chedighaii*, and *B. arabicus*, but in contrast to *B. kellyi*. The foramen is best preserved on the right side of AMNH 30041 and on the left side of AMNH 30234.

The condylus mandibularis is at about the level of the basioccipital, just anterior to the condylus occipitalis, as in *Foxemys*, *Chedighaii*, *Zolhafah*, and *B. cooki* (AMNH 29444). It is distinct from the much more anterior placement seen in *Polysternon*.

Contacts in posterior view: In *Bothremys maghrebiana* the quadrate contacts the squamosal dorsolaterally, the opisthotic dorsomedially, and the exoccipital medially. These are the usual contacts found in all the other Bothremydini.

Structures in posterior view: The fenestra postotica of *Bothremys maghrebiana* is a single opening, partially divided by a shallow, dorsal ridge into a more medial and a more lateral portion (fig. 145). The dorsomedial part of the fenestra (fig. 145) is formed by the opisthotic, as in the other Bothremydini. In *B. cooki* (AMNH 29444, fig. 135), the fenestra is completely subdivided by bone into two openings, but its size is very similar to that in *B. maghrebiana*. The foramen chorda tympani inferius (fig. 145) is preserved on the posterior surface of the processus articularis of the quadrate in all *B. maghrebiana* specimens.

PTERYGOID (figs. 136, 137, 139, 277B)

Preservation: The pterygoid is present on both sides in all five skulls, with AMNH 30041, 30522, and 30561 showing clear sutures.

Contacts on ventral surface: In *Bothremys maghrebiana* the pterygoid contacts the palatine anteriorly, the other pterygoid anteromedially, the basisphenoid posteromedially, and the quadrate posterolaterally. These contacts are as in the other Bothremydini, but the anteromedial pterygoid contact is very short in *B. maghrebiana*, shorter than in any other Bothremydini, but closest to *B. cooki*.

Structures on ventral surface: The processus trochlearis pterygoidei is present on both sides in all five *Bothremys maghrebiana* skulls, and it appears to be nearly complete and undamaged in AMNH 30041. It is angled posterolaterally at about 45°, more posterior than the process in *Foxemys*, *Polysternon*, and *Chedighaii*, but about the same as in *B. cooki*, *Zolhafah*, and *Rosasia*. Compared with *Podocnemis*, the processus in *B. maghrebiana* is relatively small, but compared with *Pelusios* and *Pelomedusa* it is about the same size. In comparison with the Pelomedusidae, however, the processus in those Bothremydini that have it well preserved show its position to be significantly closer to the otic chamber than in the Pelomedusidae. The web or flange of bone extending ventrally between the processus trochlearis pterygoidei and the quadrate ramus of the pterygoid is at least partially preserved in AMNH 30234, which shows it to be relatively extensive, as in the Pelomedusidae. The attachment margin of the pterygoideus muscle is marked in *B. maghrebiana* only by a low ridge or step extending transversely along the quadrate ramus of the pterygoid.

The foramen posterius canalis carotici interni is formed anteriorly by the pterygoid (for description see Quadrate). The foramen palatinum posterius is in the suture between the pterygoid and palatine, which tends to be more transverse in *Bothremys maghrebiana* than in *B. cooki* and *Foxemys*. The foramen is slightly larger in *B. maghrebiana* than in *B. cooki*, which has a foramen smaller than other Bothremydini.

Contacts on dorsal surface: The base of the processus trochlearis pterygoidei in *Bothremys maghrebiana* contacts the postorbital dorsolaterally, the parietal dorsally (see Parietal), and the palatine ventrolaterally (AMNH 30041). The crista pterygoidea, visible internally and externally in AMNH 30041, contacts the processus inferior parietalis dorsally, the prootic posterodorsally, and the quadrate posterolaterally.

Structures on the dorsal surface: The sulcus palatinopterygoideus is formed between the processus trochlearis pterygoidei laterally and the processus inferior parietalis medially (fig. 144). In *Bothremys maghrebiana* this structure is completely enclosed by the pterygoid and parietal, but not the postorbital as in most other Bothremydini (fig. 278B). The sulcus enclosure is relatively short in *B. maghrebiana* as it is in *B. cooki* and the *Chedighaii* endocast (fig. 167), but in contrast to the Podocnemididae, which have a longer, more tunnel-like sulcus palatinopterygoideus. Although the sulcus in *Bothremys* is short, it is preceded anteriorly by an enlarged space in the posterior portion of the fossa orbitalis (see Postorbital). This space seems to be missing in the *Chedighaii*

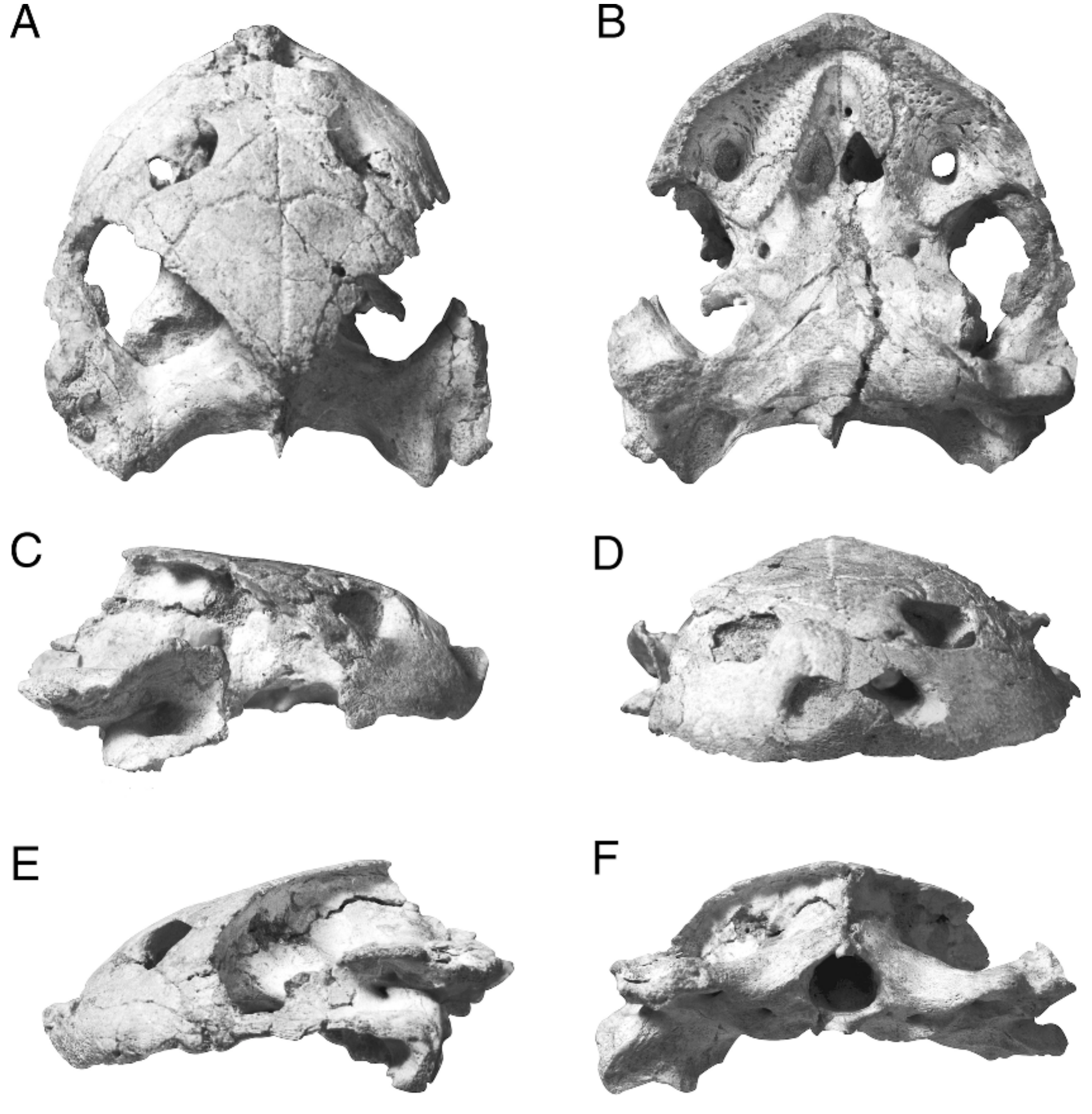

Fig. 142. *Bothremys maghrebiana*, n. sp. AMNH 30561 holotype. **A**, dorsal; **B**, ventral; **C**, right lateral; **D**, anterior; **E**, left lateral; **F**, posterior. [A.M. Phillips, del.]

endocast, which shows a distinct ridge separating the nearly spherical fossa orbitalis from the sulcus palatinopterygoideus.

The foramen palatinum posterius lies in the posterior floor of the sulcus palatinopterygoideus. It is slightly larger than in *Bothremys cooki* and much larger than the one in the *Chedighaii* endocast, AMNH 12951.

The foramen nervi trigemini in *Bothremys maghrebiana* is formed by the pterygoid for its ventral length with the parietal entering it anterodorsally and the prootic posterodorsally. This is the same as in *Bothremys cooki* and *Zolhafah*. The pterygoid forms the floor of the sulcus/canalis cavernosus, which lies between the foramen nervi trigemini laterally and the processus clinoideus of the basisphenoid, with the foramen cavernosum just medial to the posterior margin of the foramen nervi trigemini. In *B. maghrebiana* the foramen stapedio-temporale is very close to the foramen nervi trigemini, as it is in most

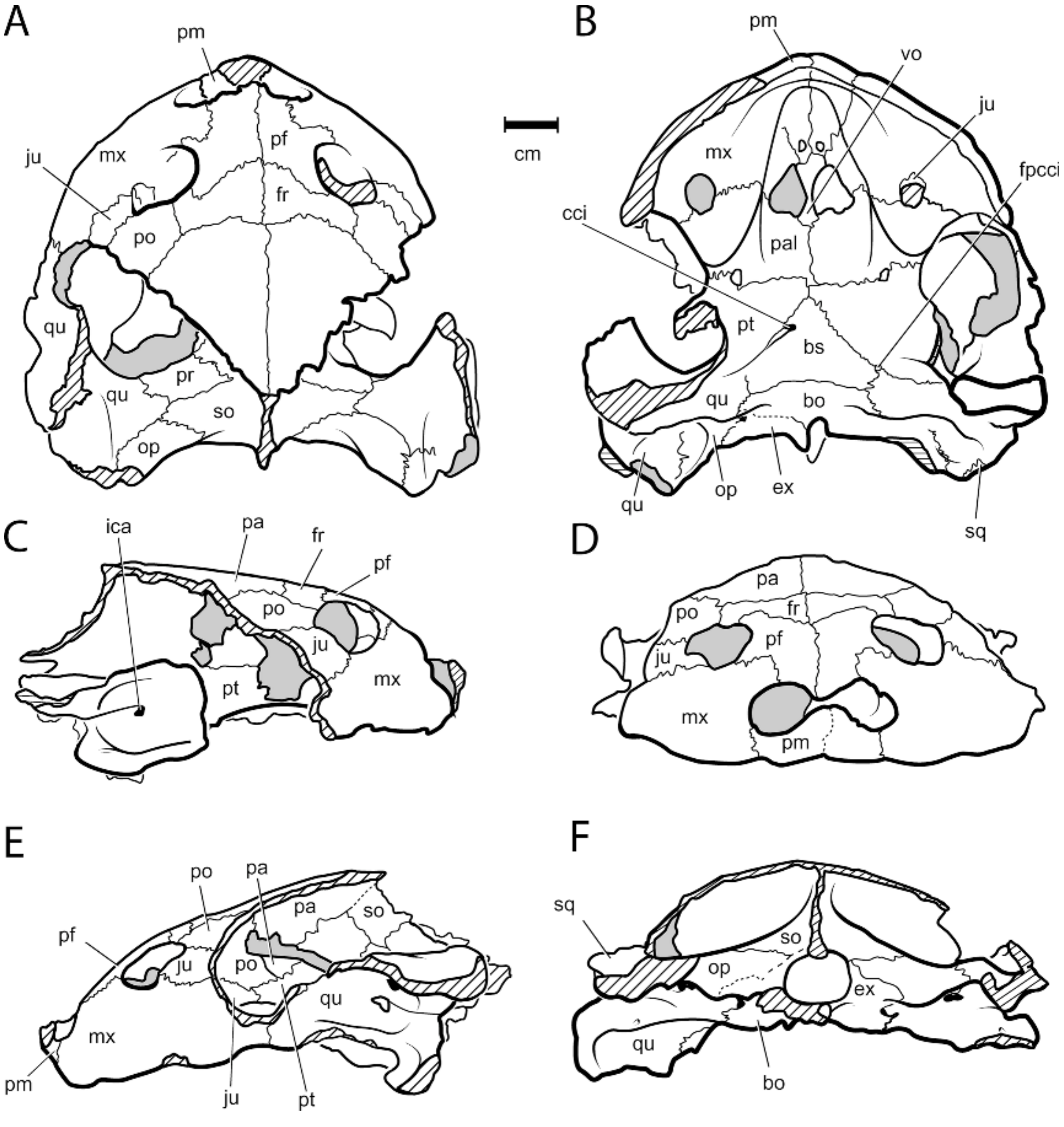

Fig. 143. *Bothremys maghrebiana*, n. sp. AMNH 30561 holotype. **A**, dorsal; **B**, ventral; **C**, right lateral; **D**, anterior; **E**, left lateral; **F**, posterior. [A.M. Phillips, del.]

Bothremydini. The wall between the foramen stapedio-temporale and the foramen cavernosum is thinner in *B. maghrebiana* than it is in *B. cooki* (AMNH 29444). It is not preserved in the type skull of *B. cooki*. In *Zolhafah* it is completely eroded, exposing the canalis cavernosus as well as the canalis stapedio-temporalis.

SUPRAOCCIPITAL (figs. 136, 139)

Preservation: The occipital part of the supraoccipital is preserved in all five skulls, but the more posterior crista supraoccipitalis is complete in MHNL 20-268370 and AMNH 30041. AMNH 30561 is missing nearly all of the crista, and it is partially present in the others.

Contacts: The supraoccipital contacts in *Bothremys maghrebiana* are with the parietals dorsally and anteriorly, the prootic anterolaterally, the quadrate laterally, the opisthotics posterolaterally, and the exoccipitals posteroventrally (seen best in AMNH 30561 and 30041). The quadrate-supraoccipital contact is found in all Bothremydini except *Zolhafah* and in all other Bothremydidae except the Taphrosphyini.

Structures: The crista supraoccipitalis in *Bothremys maghrebiana* is relatively short, thickened along its ventral edge, and not projecting very far beyond the edge of the skull roof. The foramen magnum is formed by the supraoccipital dorsally, as in other pleurodires. The cavum labyrinthicum is not exposed in any of the *B. maghrebiana* skulls.

EXOCCIPITAL (figs. 136, 145)

Preservation: Both exoccipitals are present in all five *Bothremys maghrebiana* skulls; the best sutures are in AMNH 30561, although most sutures can be seen in all of them.

Contacts: As in the other Bothremydini, the exoccipital of *Bothremys maghrebiana* contacts the supraoccipital dorsally, the opisthotic laterally, the quadrate ventrolaterally, and the basioccipital ventrally.

Structures: The foramen magnum in *Bothremys maghrebiana* is formed laterally and ventrally by the exoccipital. The condylus occipitalis is formed entirely by the exoccipitals; the basioccipital does not extend posteriorly as in *Cearachelys*.

There is only one foramen nervi hypoglossi in *Bothremys maghrebiana*, as in *Polysternon* and in contrast to *Zolhafah*, *Chedighaii*, *Foxemys*, and *B. cooki* (AMNH 29444), all of which have two. The single foramen of *B. maghrebiana* is placed close to the positions of the paired foramina in the other taxa, between the condylus occipitalis and the foramen jugulare posterius.

The foramen jugulare posterius in *Bothremys maghrebiana* is fully enclosed. In AMNH 30561 it can be seen that the exoccipital forms the medial, dorsal, and ventral margins with the quadrate, with a very narrow edge of the opisthotic filling it in laterally. This is the same as in *Zolhafah*. In *Chedighaii hutchisoni* the opisthotic does not enter the foramen, but otherwise it is also the same. In *B. cooki* (AMNH 29444) the opisthotic does enter the foramen, but in NCSM 18650, a possible *Chedighaii*, it does not. The type skulls of *B. cooki* and *C. barberi* are indeterminate. In *B. maghrebiana* the foramen jugulare posterius has its lateral margin placed more anteriorly than the medial margin and it is overhung by the opisthotic. The size of the foramen jugulare posterius varies among the Bothremydini. In *B. cooki* (AMNH 29444) and NCSM 18650 it is much larger than in *B. maghrebiana* and the other Bothremydini. Among the *B. maghrebiana* specimens, the foramen jugulare posterius is smaller in AMNH 30234 than in the other skulls.

BASIOCCIPITAL (figs. 136, 137, 277)

Preservation: The basioccipital is present in all five skulls; sutures are best in AMNH 30561, 30522, and 30041.

Contacts: The basioccipital in *Bothremys maghrebiana* agrees with those in other Bothremydini. It contacts the basisphenoid anteriorly, the quadrate laterally, and the exoccipitals dorsally.

Structures: The basioccipital of *Bothremys maghrebiana* does not contribute to the condylus occipitalis or its neck. There is a paired tuberculum basioccipitale that is quite low, as in *Zolhafah* and *Polysternon* but in contrast to *Foxemys* and *Chedighaii*. The ventral surface of the basioccipital in *B. maghrebiana* has a shallow concavity similar to that seen in most other Bothremydini.

PROOTIC (figs. 136, 143)

Preservation: Both prootics are present in all five skulls, but the bone is best seen with clear sutures in AMNH 30561 and especially AMNH 30041, where preparation is most extensive.

Contacts: The prootic of *Bothremys maghrebiana* has the usual Bothremydini contacts: the parietal medially, the quadrate laterally, the supraoccipital posterodorsally, and the pterygoid ventrally.

Structures: The prootic of *Bothremys maghrebiana* contains the foramen stapedio-temporale, which is formed in the suture between the prootic and quadrate. The sutures around the foramen stapedio-temporale clearly show that, as in nearly all turtles,

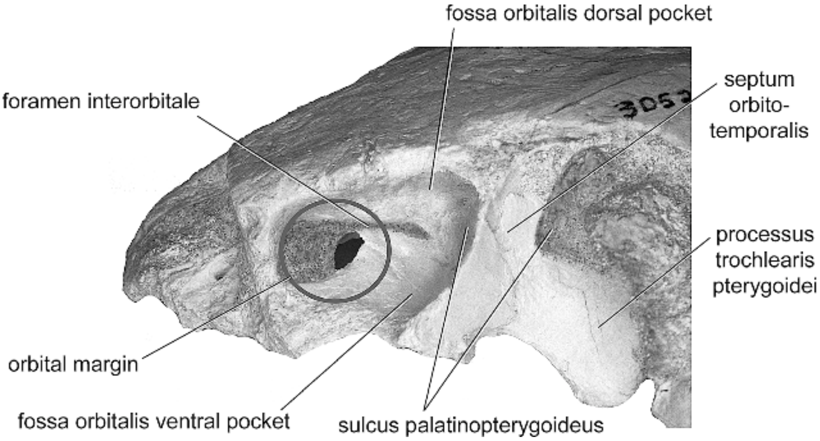

Fig. 144. *Bothremys maghrebiana*, n. sp. AMNH 30522. Parasagittal view of left fossa orbitalis with position of orbital margin shown by circle. [E.S. Gaffney, del.]

the quadrate and prootic make up the foramen. However, it is possible that a small part of the pterygoid enters it because the quadrate-pterygoid suture cannot be clearly seen in the region of the foramen stapedio-temporale. A groove connects the foramen stapedio-temporale medially with the lateral edge of the foramen nervi trigemini. The bar of bone between the two foramina seems to be the prootic, but this is also uncertain as the prootic-pterygoid suture is unclear and some of the bar could be pterygoid. The only other Bothremydini specimen that is well preserved in this area is *B. cooki* (AMNH 29444), and it shows the prootic nearly surrounding the foramen stapedio-temporale with only a small area of quadrate at its ventrolateral border (fig. 132). The bar of bone separating the two foramina in this specimen is entirely prootic.

On the left side of AMNH 30041 the quadrate is missing along the prootic suture. This shows the path of the canalis stapedio-temporalis, the canalis cavernosus, and the cavum labyrinthicum.

OPISTHOTIC (figs. 136, 143, 145)

Preservation: The opisthotic is present on both sides of all five skulls. Sutures are clearest in AMNH 30561, but the absence of the quadrate in AMNH 30041 makes the internal area of the opisthotic visible.

Contacts: The opisthotic contacts in *Bothremys maghrebiana* are as in other Bothremydini: supraoccipital anteromedially, squamosal posterolaterally, quadrate anterolaterally, and exoccipital posteromedially. In the cavum cranii, the opisthotic is visible in AMNH 30041, and the opisthotic does not seem to contact the basioccipital or basisphenoid, but this is not certain.

Structures: In posterior view the opisthotic forms a horizontal ridge from the exoccipital to the squamosal in *Bothremys maghrebiana* and most Bothremydini. Ventral to the ridge at the lateral edge of the opisthotic, this bone forms the dorsomedial margin of the fenestra postotica, most of which is formed by the quadrate (see Quadrate).

In AMNH 30041 the roof of the cavum acustico-jugulare can be seen, largely made of opisthotic. The fenestra ovalis is visible medially, formed posteriorly by the (mostly missing) opisthotic and anteriorly by the prootic, as in all turtles. Much of the cavum labyrinthicum is also visible, also agreeing with other turtles.

BASISPHENOID (figs. 136, 137, 139, 277B)

Preservation: The basisphenoid is present in all five skulls. Sutures are best seen in AMNH 30561, 30522, and 30041. The dorsal surface is visible in AMNH 30041.

Contacts in ventral view: The basisphenoid of *Bothremys maghrebiana* has the usual contacts of the Bothremydini: pterygoid anterolaterally, basioccipital posteriorly, and quadrate posterolaterally.

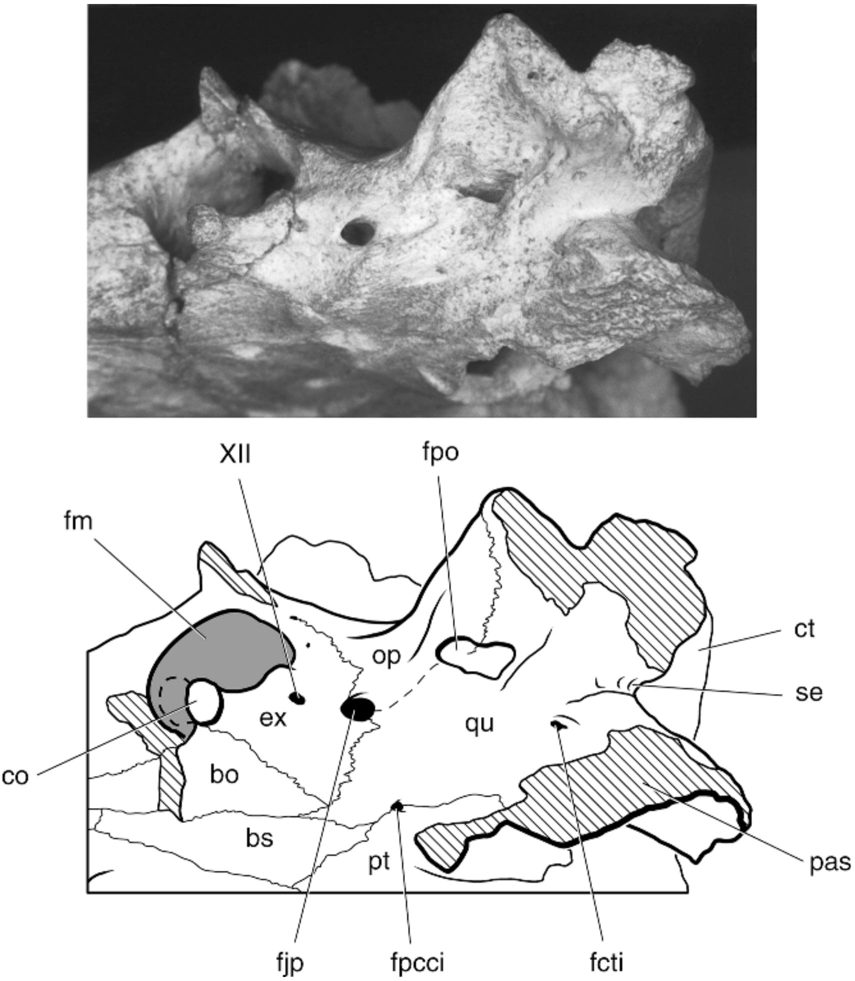

Fig. 145. *Bothremys maghrebiana*, n. sp. AMNH 30561 holotype. Posterior oblique view of skull. [A. Venjara and E.S. Gaffney, del.]

Structures in ventral view: The basisphenoid of *Bothremys maghrebiana* is nearly triangular with a sharp apex that almost completely separates the pterygoids and nearly reaches the palatines. *B. cooki* is similar but not as extreme, while the other Bothremydini have longer midline pterygoid contacts.

Contacts in dorsal view: The basisphenoid of *Bothremys maghrebiana* completely separates the pterygoid and reaches the palatines on the dorsal surface, in the floor of the cavum. The other contacts are as in turtles generally: prootic laterally and basioccipital posteriorly.

Structures in dorsal view: The rostrum basisphenoidale in *Bothremys maghrebiana* and the other Bothremydini is fused into a midline process similar to that seen in *Pelusios* (fig. 23). The rostrum of *B. cooki*, *Chedighaii barberi*, and the *Chedighaii* endocast, YPM PU 12951 (fig. 167), are longer and narrower, as in *Podocnemis* (Gaffney, 1979a: fig. 54). The sella turcica in *B. maghrebiana* is slightly wider than in *B. cooki* so that the paired foramen anterius canalis carotici interni are visible in dorsal view. The dorsum sellae does not overhang the sella turcica in *B. maghrebiana* to the extent it does in *B. cooki* or YPM PU 12951. The basisphenoid in *Zolhafah* is not well preserved or completely prepared, but the rostrum is short, as in *B. maghrebiana*.

The processus clinoideus in nearly all turtles is penetrated at or near its base by the canal for the abducens nerve (Gaffney, 1979a). In *Bothremys maghrebiana*, *B. cooki*, *Chedighaii* endocast, YPM PU 12951, and probably *Chedighaii barberi*, the processus clinoideus is absent and the canalis nervi abducentis is a groove (Gaffney, 1977a: fig. 3). The distribution of this character is hard to determine, but it may be unique to *Bothremys* + *Chedighaii*.

Bothremys kellyi

Known from one relatively well-preserved skull, this taxon is allied (although weakly, see fig. 288) with the other large Bothremydini, *Bothremys arabicus*, from the Late Cretaceous of Jordan. The basicranium is damaged but the remaining parts of the skull are intact and the sutures are clear.

PREFRONTAL (figs. 146, 149)

Preservation: Both prefrontals are nearly complete.

Contacts: The prefrontal in *Bothremys kellyi* has the usual Bothremydini contacts: the maxilla anteroventrolaterally, the other prefrontal medially, and the frontal posteriorly. There is also an anteroventral contact on the midline with a dorsal process of the premaxilla, as in *Araiochelys* but in contrast to all other Bothremydini.

Structures: The dorsal margin of the apertura narium externa has a midline protrusion formed by the prefrontal in *B. kellyi*, other *Bothremys*, and most Bothremydini. The dorsal margin of the orbit is widely separated from the midline in *B. kellyi*, slightly more than in other *Bothremys* species. The sulcus olfactorius is slightly wider in *B. kellyi* than in other *Bothremys* species. Although the area is damaged on both sides, it is highly likely that there is a wide prefrontal-palatine contact in the anterior part of the fossa orbitalis, as in *B. maghrebiana*.

FRONTAL (figs. 146, 149)

Preservation: Both frontals are present and complete.

Contacts: As in *Bothremys cooki*. The frontal of *B. kellyi* is slightly wider than in *B. cooki*, but about the same as in *B. maghrebiana*.

Structures: The frontal in *B. kellyi* is very similar to that in *B. cooki* and *B. maghrebiana*.

PARIETAL (figs. 146, 149)

Preservation: Both parietals are present in AMNH 30553. The dorsal plate is complete in both, except for some breakage along the left temporal edge. The processus inferior parietalis is completely covered by matrix on both sides.

Contacts of dorsal plate: The contacts of the parietal are the same in all *Bothremys* species (see *B. maghrebiana*). The supraoccipital contact seems larger in *B. kellyi* than in *B. maghrebiana*, although it is not well preserved in the latter. The area is missing in *B. arabicus* and *B. cooki*.

Structures of dorsal plate: The temporal emargination in *B. kellyi* is nearly identical to that in *B. maghrebiana* in size and extent. The area is missing in *B. cooki* and *B. arabicus*.

Contacts and structures of processus inferior parietalis: The processus is entirely covered by matrix in AMNH 30553.

JUGAL (figs. 146, 147, 149)

Preservation: Parts of both jugals are present, although both are damaged on the external surface. The left jugal retains enough of the lateral plate to see its contacts, but the right one is missing almost all of its ventral edge.

Contacts of lateral plate: Despite some damage, the jugal in *Bothremys kellyi* is one of the few in the Bothremydini that allows determination of all contacts. The jugal contacts the postorbital dorsally, the quadratojugal posteriorly, the maxilla anteroventrally, and, although preserved only in fragments, the quadrate posteroventrally. The quadrate contact is dotted in the reconstruction (fig. 146), not because there may not be one, but because its length and shape are not definite.

Structures of lateral plate: The jugal in *Bothremys kellyi* forms more of the ventral rim of the orbit than it does in *B. cooki* and *B. maghrebiana*. The rim is a distinct, acute ridge in *B. kellyi*, in contrast to the low, rounded margin in *B. cooki*, *B. maghrebiana*, and *B. arabicus*.

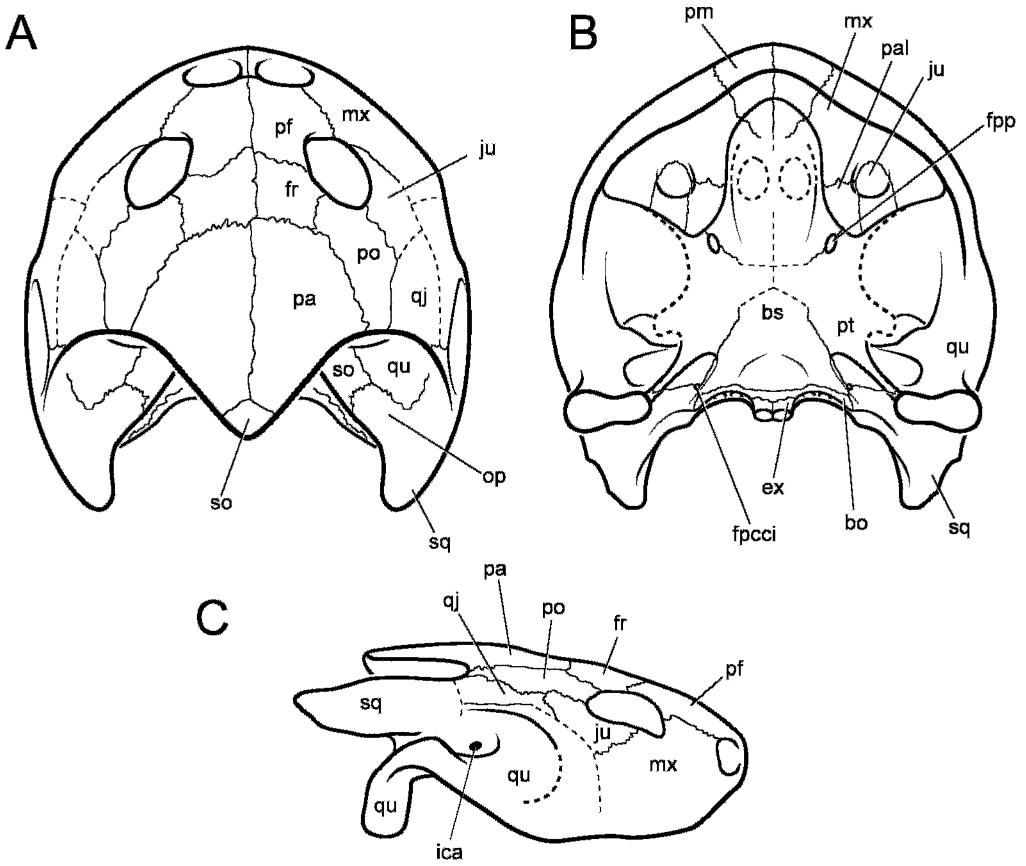

Fig. 146. *Bothremys kellyi*, n. sp. AMNH 30553 holotype. Partially restored skull. **A**, dorsal; **B**, ventral; **C**, lateral. [F. Ippolito, del.]

Contacts of medial process: The jugal is not clearly exposed on the floor of the fossa orbitalis or in the septum orbitotemporale, although it contacts the maxilla laterally and the palatine medially at least. In ventral view, the jugal is exposed in the triturating surface, forms the top of the pit, and lies between maxilla and palatine, as in *Bothremys arabicus* and *Araiochelys*. This differs from *B. cooki*, in which the jugal extends to the pterygoid, and from *B. maghrebiana*, in which the jugal is restricted to the top of the pit, allowing a wide maxilla-palatine contact.

Structures of medial process: The jugal in AMNH 30553 is not clearly visible in the septum orbitotemporale, but it does participate in the formation of this structure. The jugal forms the apex and posterior wall of the large and well-defined pit in *Bothremys kellyi*, as it does in *B. cooki*. In *B. maghrebiana* the posterior wall is formed by maxilla and palatine and the jugal is restricted to the pit apex.

QUADRATOJUGAL (figs. 146, 149)

Preservation: Parts of both quadratojugals are present in AMNH 30553, but they are damaged. The right one is more complete and the left one retains anterior contacts but is missing the posterior area.

Contacts: The quadratojugal in *Bothremys kellyi* contacts the quadrate ventrally, the squamosal posteriorly, the postorbital medially, and the jugal anteriorly. The quadratojugal of *B. kellyi* is similar to that in *B. maghrebiana* and *Araiochelys* (to the extent the bone is preserved in *Araiochelys*) in that it lacks the ventral extension seen in more primitive bothremydids and in *Chedighaii hutchisoni*, *Foxemys*, and *Polysternon*.

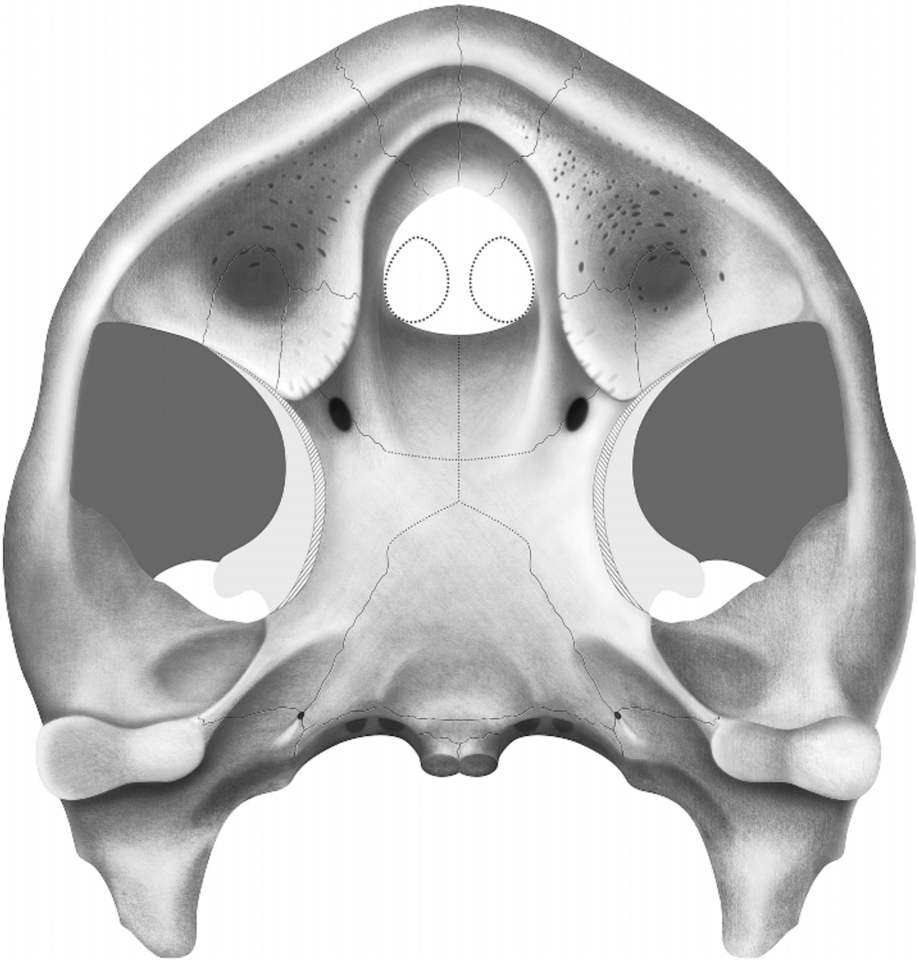

Fig. 147. *Bothremys kellyi*, n. sp. AMNH 30553 holotype. Partially restored ventral view. [C. Blik, del.]

Structures: The quadratojugal forms the lateral part of the temporal roof and enters the temporal margin between the postorbital and the squamosal, as in *Bothremys maghrebiana*.

SQUAMOSAL (figs. 146, 149, 285)

Preservation: Both squamosals are present and only missing some of the lateral edges.

Contacts: As in *Bothremys maghrebiana*. The squamosal in *B. kellyi* extends more anteromedially along the quadrate suture than in *B. maghrebiana* and in AMNH 29444, a probable *B. cooki* otic chamber (see *B. cooki* Discussion).

Structures: The squamosal in *Bothremys kellyi* has lost much of the usual cone shape of this bone in other turtles; instead, it has some features differentiating it from all other pleurodires (fig. 285). The antrum postoticum (see Quadrate) is similar in size and shape to that in *B. maghrebiana*. On the posterodorsal surface of the otic chamber, the squamosal and opisthotic are raised into an anteromedial-posterolateral trending ridge that dominates the otic chamber, a feature that is unique to *B. kellyi*. Presumably this large ridge is related to muscle attachment sites. The other bothremydids usually have a low shelf along the posterior edge of the otic chamber that seems to be the homolog of the large ridge in *B. kellyi*.

The squamosal in *B. maghrebiana* and other bothremydids lies above the cavum tympani and the sulcus eustachii, with the broad groove trending posteriorly from the cavum tympani. In *B. kellyi* the sulcus eustachii is greatly constricted (fig. 285) by dorsal and ventral ridges that bend to come close to each other and reduce the sulcus to a narrow channel, unique to this species. The squamosal, as well as the quadrate, forms the upper ridge of this channel. On the ventral surface of the squamosal, *B. kellyi* has the same low ridge seen in *B. maghrebiana*.

POSTORBITAL (figs. 146, 149)

Preservation: Most of both postorbitals are present, but they are slightly damaged along the quadratojugal suture.

Contacts of lateral plate: The postorbital contacts the frontal anteromedially, the jugal anterolaterally, the quadratojugal posterolaterally, and the parietal medially, all as in *B. maghrebiana*. Both *B. maghrebiana* and *B. kellyi* differ from *B. cooki* in lacking the small anteroventral process along the orbital rim found in the latter species.

Structures of lateral plate: In *Bothremys kellyi* the postorbital forms the upper part of the orbital margin and a small part of the posterior temporal margin, all the same as in *B. maghrebiana*. The postorbital in *B. maghrebiana* and *B. kellyi* is long but narrower than in *Foxemys*, *Polysternon*, and *Chedighaii hutchisoni*; the postorbital is incompletely known in the other Bothremydini.

Contacts and structures of medial process: Not visible due to matrix and crushing.

PREMAXILLA (figs. 146–149)

Preservation: Both premaxillae are present in AMNH 30553 and are nearly complete, although slightly chewed on. The right one is disarticulated along its sutures and slightly displaced from its natural position.

Contacts: The premaxilla contacts are as in *B. maghrebiana* except that the vomer is missing and there is a dorsomedial contact with the prefrontal. The apertura narium externa is slightly compressed in AMNH 30553, and the dorsal premaxillary process is slightly bent inward on both sides. There is a contact on the right side, although the left one is slightly damaged and separated by matrix.

Structures on dorsal surface: As in the other *Bothremys* species, the premaxilla anterior surface slopes anterodorsally so that it lies well anterior to the labial ridge. The premaxilla protrudes beyond the prefrontal. The apertura narium externa in *B. kellyi* is divided on the midline by a contact of the premaxillary dorsal process and the prefrontal. The premaxilla dorsal process is short in all the other Bothremydini, except *Araiochelys*, which has a long process contacting the prefrontal and dividing the apertura narium externa. The fossa nasalis of *B. kellyi* agrees with that in *B. cooki* and *B. maghrebiana*.

Structures on ventral surface: The labial ridge of *Bothremys kellyi* agrees with that in *B. cooki* and *B. maghrebiana*, except that it is slightly thicker (fig. 147). The snout does not appear to be pinched, as in *B. cooki* and *B. maghrebiana*. The median concavity in *B. kellyi* is wide, wider than in *B. cooki* and *B. maghrebiana*, but about as wide as in *B. arabicus*.

MAXILLA (figs. 146–149)

Preservation: Both maxillae are preserved. The left one is complete except for damage along its posterolateral margin. The right one is missing the ventrolateral area of the vertical plate.

Contacts of vertical plate: The maxilla in *Bothremys kellyi* contacts the premaxilla anteromedially, the jugal posteromedially, and the prefrontal anterodorsally. The posterolateral margins of both maxillae do not show a sutural edge, but on the left side the maxilla is separated only by a narrow space, so it is very likely that there was a quadrate-maxilla contact, as in *Rosasia*, *Araiochelys*, and *B. maghrebiana*.

Structures of vertical plate: The vertical plate of the maxilla in *Bothremys kellyi* is very similar to that in *B. cooki* and *B. maghrebiana*. It is slightly more inflated anterolaterally and more robust. The maxilla has a distinct, acute ridge for the orbital rim, in contrast to *B. cooki* and *B. maghrebiana*, which lack this. The fossa nasalis and choanal passages are nearly the same as in *B. cooki* and *B. maghrebiana*. There is no cheek emargination.

Contacts of horizontal plate: The maxilla in *B. kellyi* contacts the premaxilla anteromedially, the palatine posteromedially, and the jugal posteriorly. The jugal separates palatine and maxilla posterior to the pit so that there is no contact as in *B. maghrebiana*. Medially, the vomer is missing and the area is too damaged to see if the maxilla had a long or short suture with the vomer.

Structures of horizontal plate: The labial ridge in *B. kellyi* is slightly thicker than in *B. cooki* and *B. maghrebiana*, and the ventral margin goes from a narrow angle anteriorly to a rounded edge posteriorly (fig. 147). In *B. cooki* and *B. maghrebiana* the edge is a narrow angle its entire length. Also as in the other *Bothremys*, nearly all of the triturating surface of the maxilla is on a slope into the prominent pit.

The dorsal surface of the maxilla forms part of the fossa orbitalis floor.

VOMER

Preservation: Not preserved.

PALATINE (figs. 146–149)

Preservation: Both palatines are present but damaged medially and a little chewed up along the apertura narium interna.

Contacts: The palatine in *Bothremys kellyi* contacts the maxilla anterolaterally and the pterygoid posteriorly, as in *B. maghrebiana*. The vomer is missing and the median contact of palatine and vomer is not determinable. The basisphenoid has been crushed dorsally above the level of the pterygoids, forcing them, and to some extent the palatines, apart. The midline palatine-palatine contact is damaged, so the extent of palatine contact and the possibility of basisphenoid contact are unclear. Anterolaterally, the palatine contacts the jugal.

Structures on dorsal surface: The palatine floors much of the fossa orbitalis, but the contacts are unclear. The rest is covered by matrix or disturbed by crushing.

Structures on ventral surface: The palatine forms the roof and lateral margin of the apertura narium interna, which is very similar in *Bothremys kellyi*, *B. cooki*, and *B. maghrebiana*. The palatine bears the posterior part of the lingual ridge, which runs posteriorly from the margin of the median concavity on the premaxilla, along the edge of the apertura narium interna, turning posterolaterally and then anterolaterally as it edges between the pit and the fossa temporalis inferior. The surface on the palatine slopes into the pit. The foramen palatinum posterius is at the posterolateral margin of the palatine, within the palatine-pterygoid suture, as in the other *Bothremys*.

QUADRATE (figs. 146–149, 285)

Preservation: Most of both quadrates in AMNH 30553 are preserved, but both have varying amounts of damage to the anterior lateral margin. The left one is damaged but is more complete anteriorly than the right one. The left quadrate also has some damage to the cavum tympani, but the right one is nearly complete.

Contacts on lateral surface: The quadrate in *Bothremys kellyi* contacts the squamosal posterodorsally, the quadratojugal dorsally, the jugal anterolaterally, and the maxilla anteriorly. Neither the jugal or quadrate contacts are well preserved, but the positions of the jugal and maxilla leave no other interpretation. The quadrate-maxilla contact occurs in *Rosasia*, *Araiochelys*, and *B. maghrebiana*, as well as in *B. kellyi*.

Structures on lateral surface: The cavum tympani in *B. kellyi* differs from all other Bothremydidae in having the sulcus eustachii a deep channel, with a lateral flange of the quadrate extending around the sulcus and, along with a similar process of the squamosal and quadrate, above, nearly enclosing the sulcus eustachii (fig. 285). This flange continues anteriorly and is continuous with the large shelf that forms the lower margin of the cavum tympani. The antrum postoticum in *B. kellyi* is slightly larger than in *B. maghrebiana*.

Contacts on dorsal and anterior surface: The sutures here are not entirely clear, but the quadrate contacts the prootic anteromedially, the opisthotic posteromedially, the supraoccipital medially, and the squamosal posteriorly.

Structures on dorsal and anterior surface: The anterior surface of the otic chamber is usually flat or rounded in bothremydids, but in *Bothremys kellyi* the quadrate and prootic are swollen or expanded into a horizontal, rounded ridge, not too different from that seen in cryptodires as the processus trochlearis oticum. In this case, the

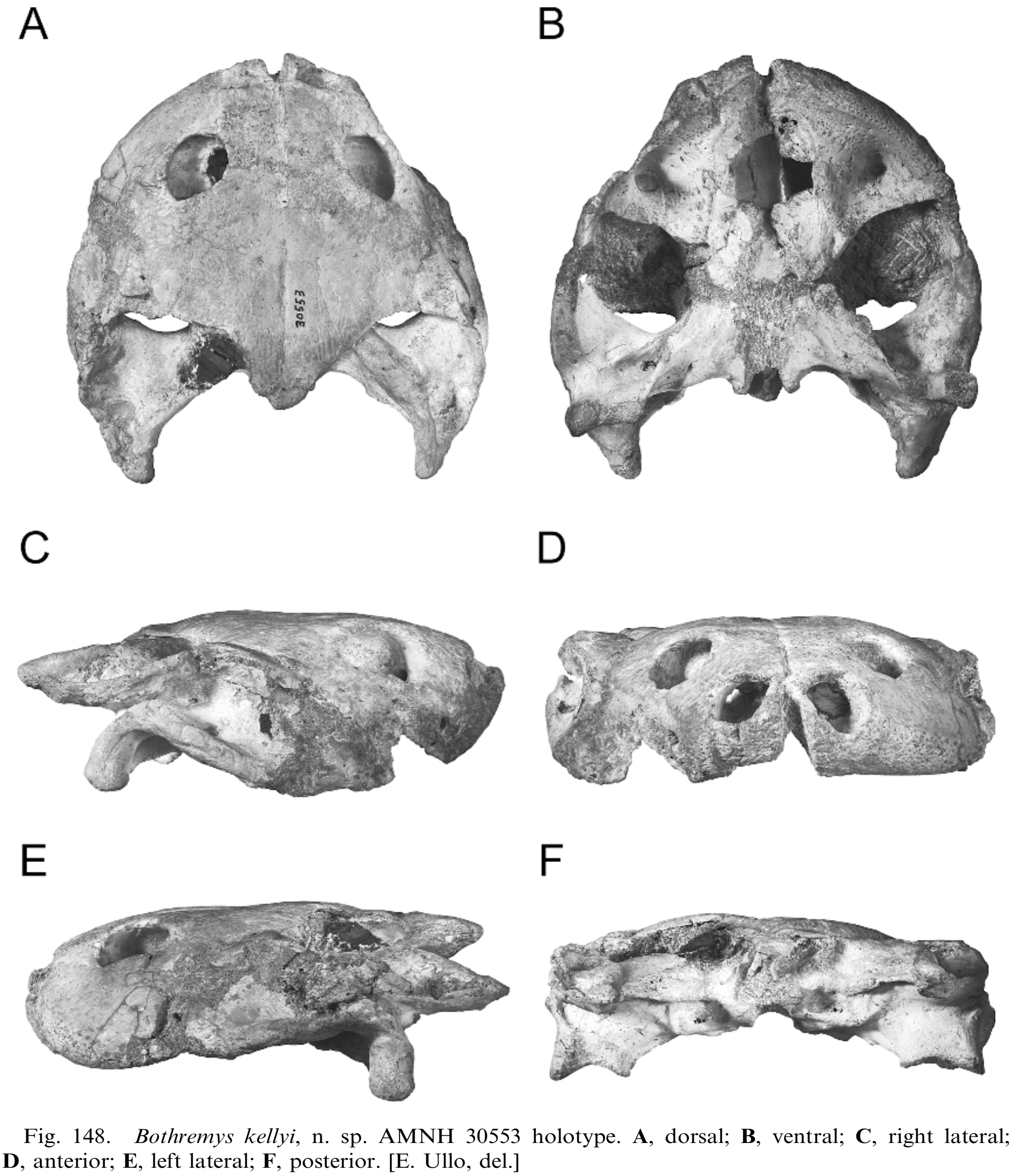

Fig. 148. *Bothremys kellyi*, n. sp. AMNH 30553 holotype. **A**, dorsal; **B**, ventral; **C**, right lateral; **D**, anterior; **E**, left lateral; **F**, posterior. [E. Ullo, del.]

ridge is actually thicker than in cryptodires; it is wider laterally and medially rather than in its center. It is smooth, not rugose. *B. maghrebiana* has a much smaller ridge in this place, as do the two species of *Chedighaii*; however, *B. arabicus* and *Araiochelys* do not. The enlarged otic chamber seems to be related to the relatively large and deep cavum tympani in these forms, rather than to a change in jaw musculature.

The foramen stapedio-temporale is visible only on the right side of *B. kellyi*. It is ventral to the horizontal enlargement and on the medial end of the otic chamber. The foramen nervi trigemini is covered by matrix, but the foramen stapedio-temporale must be very

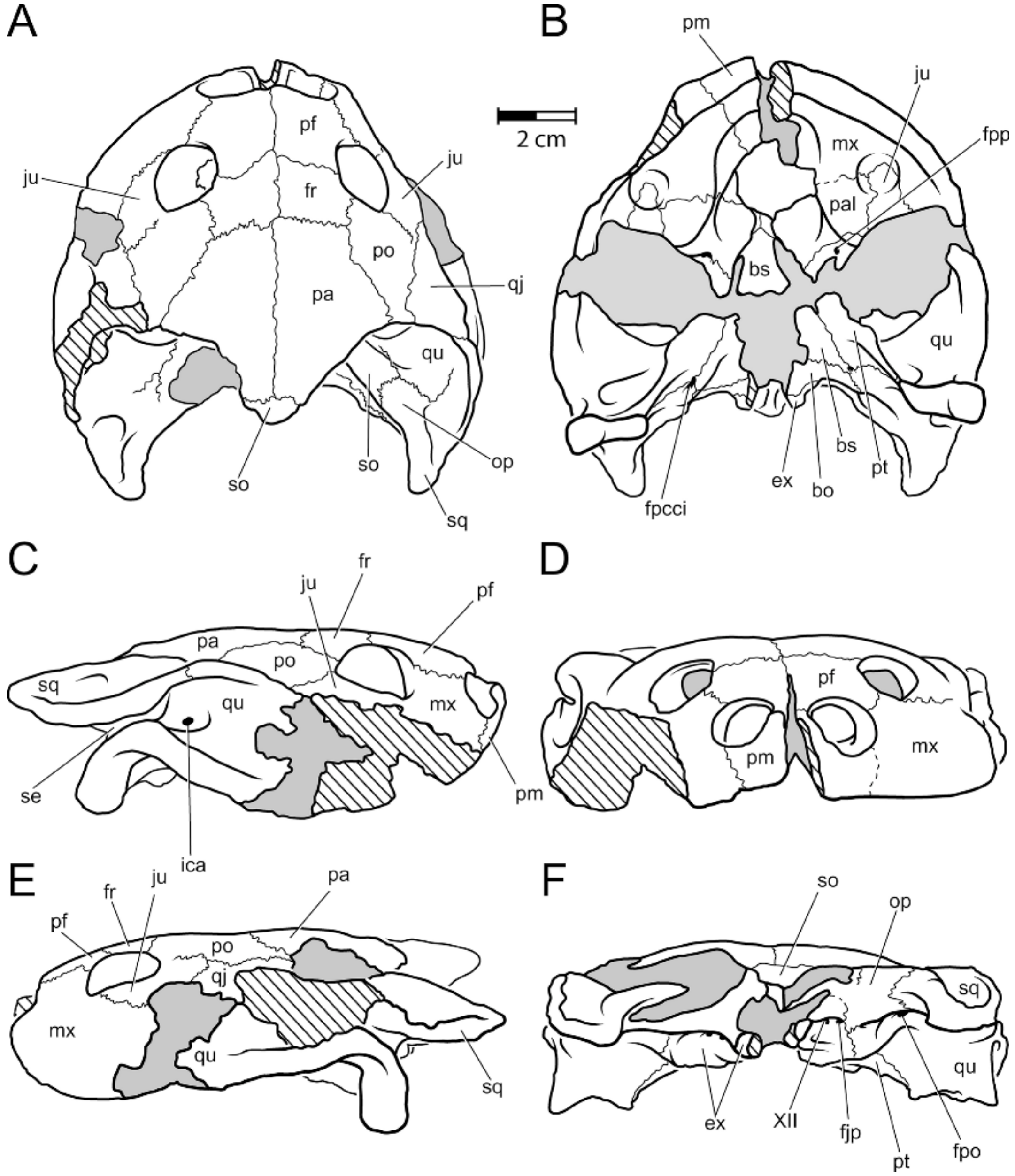

Fig. 149. *Bothremys kellyi*, n. sp. AMNH 30553 holotype. **A**, dorsal; **B**, ventral; **C**, right lateral; **D**, anterior; **E**, left lateral; **F**, posterior. [E. Ullo, del.]

close to it as there is very little room for any other position.

Contacts on ventral surface: As in *Bothremys maghrebiana*.

Structures on ventral surface: *B. kellyi* is unique among the higher Bothremydini (i.e., *Bothremys*, *Chedighaii*, *Araiochelys*) in having the foramen posterius canalis carotici interni formed by the basisphenoid as well as the usual pterygoid and quadrate. However, this is not as much of a difference as it may sound: the foramen is very close to the basisphenoid even when that bone does not enter its margin. There is no fossa pterygoidea and no depression around the foramen posterius canalis carotici interni, as in AMNH 29444, a likely *Bothremys cooki* ear.

The condylus mandibularis is level with the condylus occipitalis in *B. kellyi* as in other Bothremydini except *Polysternon.*

Contacts on posterior surface: The occipital region of AMNH 30553 is crushed and the sutures are unclear. The medial contacts of the quadrate are partly determinable: squamosal dorsolaterally, opisthotic dorsomedially, and basioccipital ventromedially.

Structures on posterior surface: The fenestra postotica is fully enclosed and seems to be a single foramen without subdivisions, but neither fenestra is well preserved. The foramen chorda tympani inferius is present on the posterior surface of the processus articularis.

PTERYGOID (figs. 146–149)

Preservation: Although parts of both pterygoids are present, the bones are badly damaged. The posterior parts and anterior margins are present, but the centers, with the processus trochlearis pterygoidei, are largely missing.

Contacts on ventral surface: The pterygoid in *Bothremys kellyi* contacts the palatine anteriorly, the basisphenoid posteromedially, and the quadrate posterolaterally. The median contact with the other pterygoid is unclear; the anterior part of the basisphenoid has been crushed dorsally and anteriorly to force the pterygoids apart. It is possible that there was no midline contact, because as preserved, what appears to be part of the basisphenoid completely separates the pterygoids. When the degree of crushing is compensated for, and when broken edges are moved into what is now matrix, it seems more likely that the pterygoids did have at least a narrow contact.

Structures on ventral surface: There is no sign of either processus trochlearis pterygoidei in AMNH 30553. The entire left and most of the right foramen palatinum posterius are preserved and are in about the same position as in *Bothremys maghrebiana.* The quadrate ramus is present on both sides. There is no fossa pterygoidea and no depression around the foramen posterius canalis carotici interni. Although much of the pterygoid is poorly preserved, the foramen posterius canalis carotici interni is well preserved on both sides. The foramen posterius canalis carotici interni in *B. kellyi* is formed by basisphenoid anteromedially, pterygoid anterolaterally, and quadrate posteriorly. This is in contrast to the other *Bothremys* species, *Chedighaii*, and *Araiochelys*, all of which lack a basisphenoid contribution to the foramen. The basisphenoid is very close to the foramen in these taxa, however.

Contacts on dorsal surface: The pterygoid contact with the jugal anterolaterally in the posterior wall of the fossa temporalis is visible, but none of the other contacts in this area is visible due to matrix. The pterygoid-quadrate contact leading ventrolaterally from the foramen stapedio-temporale can also be seen. These are the same as in *Bothremys maghrebiana* as far as can be determined.

Structures on dorsal surface: None are visible.

SUPRAOCCIPITAL (figs. 146, 149)

Preservation: The supraoccipital is present and probably complete, but it is badly broken around the foramen magnum by dorsoventral crushing. On the lateral side, the bone is obscured by what appears to be a large blood clot, but I suppose it is just a hematite crystal or something else.

Contacts: The supraoccipital in *Bothremys kellyi* contacts the parietals anteriorly on the dorsal surface. Laterally it contacts the quadrate; only a small part of the anterolateral prootic contact is visible. Posterolaterally the supraoccipital contacts the opisthotic and ventrally it contacts the exoccipital.

Structures: The foramen magnum in *Bothremys kellyi* is largely obscured by crushing, but it is better preserved on the left side and seems similar to that in *B. maghrebiana.* The crista supraoccipitalis is broken along its ventral edge, but it seems to be about as extensive as in *B. maghrebiana*, reaching posterior to the condylus occipitalis, but well anterior to the posterior margin of the squamosals. The posterodorsal part of the supraoccipital is a flat, horizontal plate that forms the posteromedial part of the skull roof, as in *Araiochelys* and to some extent in *B. maghrebiana*.

The supraoccipital of *B. kellyi* forms the medial part of the large, rounded ridge extending along the top of the otic chamber that is unique to *B. kellyi* (see Squamosal, Opisthotic).

EXOCCIPITAL (figs. 146, 149)

Preservation: Both exoccipitals are preserved in AMNH 30553, but dorsoventral crushing has broken the dorsal part of the right one and distorted some features on the left. Both exoccipitals have been disarticulated on their midline suture and separated, along with the basioccipital, which has been split down the middle.

Contacts: The exoccipital in *Bothremys kellyi* contacts the supraoccipital dorsally, the opisthotic dorsolaterally, the quadrate ventrolaterally, and the basioccipital ventrally, although the latter suture is unclear.

Structures: The foramen magnum in *Bothremys kellyi* is the same as in *B. maghrebiana*. The condylus occipitalis is formed entirely by the exoccipitals; the basioccipital does not enter the neck. There are two foramen nervi hypoglossi, equal in size, rather than two or three with one being much larger, which is seen more commonly. The lower surface of the exoccipital forms a concavity facing posteriorly, with a low ridge running horizontally just dorsal to the foramen nervi hypoglossi and foramen jugulare posterius that forms the upper margin of the concavity. The lower margin is a shelf, narrow at the base of the condylus occipitalis, running laterally onto the quadrate. A similar concavity is in *Chedighaii* and *Bothremys arabicus*, but *B. maghrebiana* and the *B. cooki* otic chamber, AMNH 29444, lack it. The foramen jugulare posterius lies ventral to the strong shelf forming the upper edge of the concavity. The foramen is completely closed and seems to be closed by contact of the exoccipital laterally without opisthotic or quadrate, in contrast to *B. cooki* (AMNH 29444) and *B. maghrebiana*.

BASIOCCIPITAL (figs. 146, 149)

Preservation: The basioccipital in AMNH 30553 is broken and separated along its midline, with more than a centimeter of matrix between the two parts. Although some bone is missing along the fractured edges, the basioccipital seems otherwise intact.

Contacts: The basioccipital in *Bothremys kellyi* contacts the basisphenoid anteriorly, the quadrate laterally in a very narrow suture, and the exoccipitals posterodorsally.

Structures: The basioccipital is entirely absent from the condylus occipitalis; the exoccipital suture is visible on both sides. There is no tuberculum basioccipitale, although the ventral shelf defining the exoccipital concavity is partially basioccipital and may be homologous to the tuberculum in other turtles. There is a shallow median concavity, slightly deeper than in *Bothremys maghrebiana*. As in other *Bothremys* species, *Chedighaii*, and *B. arabicus*, the basioccipital in *B. kellyi* is relatively narrow.

PROOTIC (figs. 146, 149)

Preservation: Both prootics in AMNH 30553 are present and probably complete, but they are almost completely covered by matrix and the ventrally crushed skull roof.

Contacts: The lateral contact with the quadrate in *Bothremys kellyi* is visible on both sides on the anterior surface, and on the right side, the pterygoid contact can also be seen, but the other contacts are covered by matrix.

Structures: The prootic in *Bothremys kellyi* is extended anteriorly into a large overhang, continuing the broad anterior ridge from the quadrate (see Quadrate), as in *Chedighaii*. Under the overhang is the foramen stapedio-temporale laterally and the foramen nervi trigemini medially, both with their dorsal margin formed by the prootic. Both foramina are close together, as in other Bothremydini. On the dorsal surface, the prootic supports part of the large dorsal ridge on the otic chamber.

OPISTHOTIC (figs. 146, 149)

Preservation: Both opisthotics in AMNH 30553 are preserved and are nearly complete. The sutures are hard to make out on the left opisthotic due to surface damage.

Contacts: The contacts in *Bothremys kellyi* are as in *B. maghrebiana*.

Structures: The foramen jugulare posterius is relatively small and has little or none of the opisthotic entering it. The fenestra postotica in *Bothremys kellyi* is a completely enclosed foramen with no apparent sign of subdivision, although matrix may obscure one. Overhanging the fenestra postotica is a thin, horizontal flange, similar to the one in *Chedighaii hutchisoni.*

BASISPHENOID (figs. 146–149)

Preservation: The basisphenoid in AMNH 30553 has been rent asunder by forces beyond comprehension. The bone is in three pieces: an anterior triangular piece with no clear sutural margins, possibly displaced anteriorly, thrust between the palatines, and two lateral pieces separated on the midline, missing at least some bone.

Contacts on ventral surface: The anterior contacts in *Bothremys kellyi* are dubious. As preserved, the basisphenoid completely separates palatines and pterygoids, but this seems unlikely. In the restoration I moved this section posteriorly, but it may have the anterior width too great. The basisphenoid contacts the pterygoid anterolaterally, the basioccipital posteriorly, and, in a very narrow contact, the quadrate posterolaterally.

Structures on ventral surface: The foramen posterius canalis carotici interni has its anteromedial margin formed by the basisphenoid (in addition to pterygoid and quadrate) in contrast to the other *Bothremys* species, *Chedighaii*, and *Araiochelys*, which have only pterygoid and quadrate making up the margin. The ventral surface of the basisphenoid seems to be flat, but as it is badly damaged this is not certain.

Bothremys arabicus

This taxon is represented by a large skull lacking much of the skull roof, but the ventral surface is well preserved. *Bothremys arabicus* seems to be related to the other large African Bothremydina, *B. kellyi*. *Bothremys arabicus* is described by Zalmout, Mustafa, and Wilson (2005).

PREFRONTAL (figs. 150, 153)

Preservation: What looks like a short length of suture on the left side of the apertura narium externa separates a fragment of the left prefrontal from the maxilla. Otherwise, both prefrontals are missing in *Bothremys arabicus*.

FRONTAL

Preservation: Both frontals are missing, possibly overlain by a mixture of bone hash and matrix.

PARIETAL (fig. 153)

Preservation: Some of the dorsal plate of what is presumed to be parietal can be seen on the broken surface on the left side of the dorsal part of the skull. Elsewhere, bone bits mixed with matrix prevent identification of useful sutures, and even midline sutures are not visible.

Contacts of dorsal plate: None preserved, except as described below.

Structures of dorsal plate: The extent of broken bone in *Bothremys arabicus* suggests a skull roof with very limited emargination, as in *B. maghrebiana*, and not an emarginate one, as in *Kurmademys*. The left side preserves part of the lateral wall of the sulcus palatinopterygoideus. This shows a ventral process of the parietal (fig. 153E) that runs posterior to the postorbital and reaches the pterygoid, as in *B. cooki*, *B. maghrebiana*, and *Chedighaii hutchisoni*.

Contacts of processus inferior parietalis: None visible.

Structures of processus inferior parietalis: On the left side in *Bothremys arabicus* a badly broken area medial to the sulcus palatinopterygoideus represents the processus inferior parietalis (fig. 153E). The foramen nervi trigemini is not discernable due to breakage. The parietal can also be seen on the left side forming the braincase wall posteriorly to the supraoccipital, although a parietal-supraoccipital suture is not visible.

JUGAL (figs. 150–153)

Preservation: The lateral plate of the jugal in *Bothremys arabicus* is preserved in part on the left side. Both jugals are preserved in the palate.

Contacts of lateral plate: Only the ventral contact with the maxilla is preserved.

Structures of lateral plate: The lateral plate in *Bothremys arabicus* forms the posteroventral orbital margin and is widely exposed in the orbit, more so than in *B. maghrebiana* and much more than in *B. cooki*. The jugal and maxilla together make up half of the entire orbital margin, with each forming nearly equal amounts.

Contacts of medial process: The floor of the orbit in *Bothremys arabicus* is covered by matrix. In the posterior surface of the postorbital wall, the jugal contacts the postorbital dorsomedially, the pterygoid posteriorly, the palatine ventromedially, and the maxilla anterolaterally. In palatal view the jugal contacts the maxilla anteriorly and the palatine medially.

Structures of medial process: The jugal forms the anteroventral part of the septum orbitotemporale in *Bothremys arabicus* and widely extends into the triturating pit (fig. 151), as in *B. kellyi* and *B. cooki* but in contrast to *B. maghrebiana*. The width of the jugal in *B. arabicus* is less than that in *B. cooki* and there is no jugal-pterygoid contact in the triturating surface as in *B. cooki*. The jugal forms the tip of the pit, as in *B. maghrebiana* and the other Bothremydini with pits, and the dorsal part of the pit, as in *B. cooki*. In the wall of the fossa temporalis the jugal contacts the postorbital dorsally in an indistinct suture partially obscured by cracks. Posteromedially the jugal contacts the pterygoid just above the more ventral contact with the palatine. Some of this contact is obscured by resin and cracks.

QUADRATOJUGAL

Preservation: Not preserved.

SQUAMOSAL (fig. 153)

Preservation: A small fragment of what is probably squamosal lies above the quadrate on the left side in *Bothremys arabicus*. Most of both squamosals have been removed by overpreparation.

Contacts and structures: Only some sutures and small fragments remain: quadrate-squamosal on the right side above cavum tympani, and quadrate-squamosal-opisthotic on the left side.

POSTORBITAL (figs. 150, 153)

Preservation: None of the lateral plate remains in *Bothremys arabicus*, but the medial process on the left side is partially preserved.

Contacts and structures: The damaged medial process is present in the anterior wall of the septum orbitotemporale where it contacts the parietal dorsomedially (the suture is unclear), the pterygoid ventromedially, and the jugal ventrolaterally. The postorbital does not contact the palatine.

PREMAXILLA (figs. 150–153)

Preservation: Both premaxillae are present, but their anterior margins and the labial ridge are broken away.

Contacts: The premaxilla in *Bothremys arabicus* can be seen on the external skull surface on the right side where it contacts the maxilla and forms the floor of the fossa nasalis. Sutures inside the fossa nasalis are not clear and the vomer contact is not determinable. A piece of matrix covered by bone lies on top of the left premaxilla and the medial part of the right one. As preserved, the premaxilla-maxilla contact in *B. arabicus* lies closer to the lateral edge of the apertura narium externa than it does in *B. maghrebiana*. The premaxillae in *B. arabicus* are very wide, much wider than in *Foxemys* and *Rosasia*.

Structures on dorsal surface: The fossa nasalis in *Bothremys arabicus* is slightly larger than in other Bothremydini, and the apertura narium externa probably is larger as well, although it is imperfectly preserved. The midline process of the premaxilla seems to be absent in *B. arabicus*, but the area is covered with matrix and a bone fragment.

Structures on ventral surface: The labial ridge is broken away from the triturating surface of the premaxilla in *Bothremys arabicus*, but its preserved morphology is consistent with *B. maghrebiana* and *B. cooki*. There is a considerable difference, however, in the shape of the central depression formed medial to the lingual ridge (fig. 151). This concavity is relatively narrow in *B. cooki* and *B. maghrebiana* and much wider in *B. arabicus*. The width in *B. arabicus* is similar to what would be reconstructed for *Chedighaii hutchisoni*, but not for *C. barberi*. The concavity is distinctly formed with sharp margins. In *B. cooki* and *B. maghrebiana* the concavity lies on half of the premaxilla. As preserved in *B. arabicus*, the concavity lies on more than half of the premaxilla, but an unknown amount is missing anteriorly and it could be the same in all three.

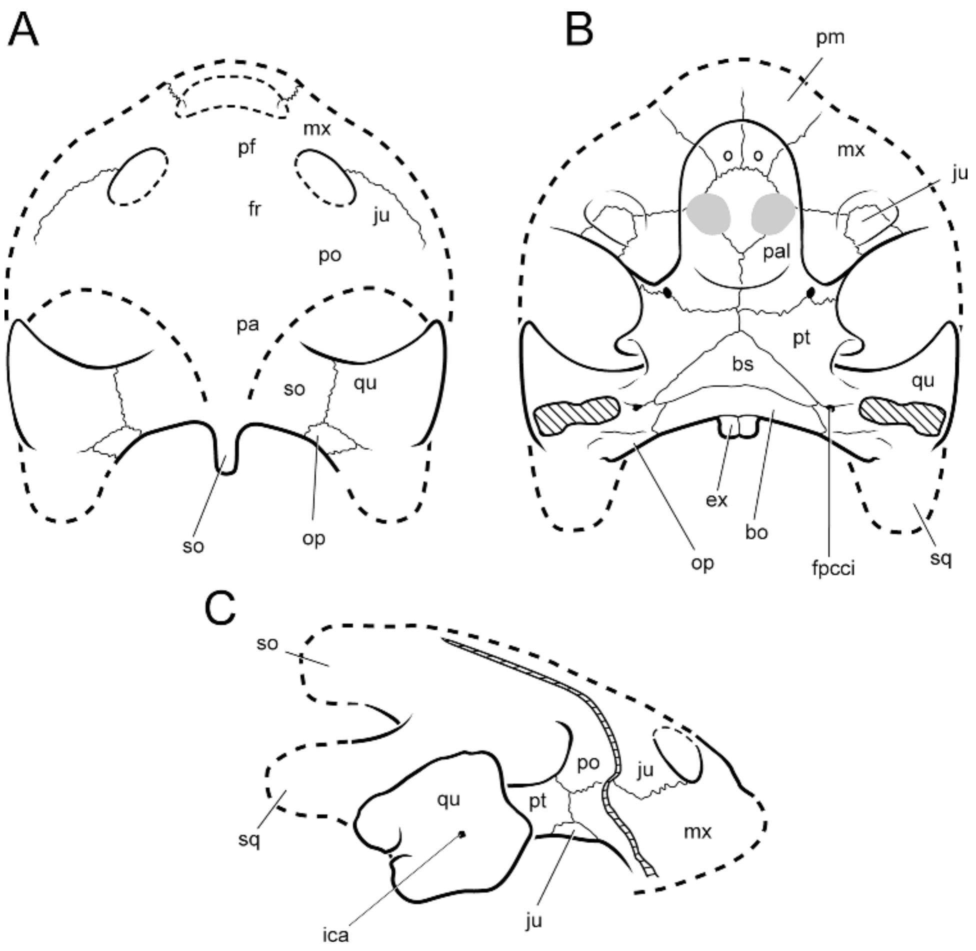

Fig. 150. *Bothremys arabicus* Zalmout, Mustafa, and Wilson, 2005. YUP-HUS 100 holotype. Partially restored skull. **A**, dorsal; **B**, ventral; **C**, lateral. [R. Rogge, del.]

The left premaxilla has a distinct foramen praepalatinum near its posterior edge close to but not in the premaxilla-vomer suture, much as in *B. maghrebiana*.

MAXILLA (figs. 150–153)

Preservation: Both maxillae are present in *Bothremys arabicus* but are damaged to a varying extent. The right one is missing everything from just below the orbit dorsally. The left one has the ventral orbital margin preserved. None of the posterolateral edges is preserved.

Contacts of vertical plate: The maxilla in *Bothremys arabicus* contacts the prefrontal anterodorsally, the premaxilla anteromedially, and the jugal posterodorsally.

Structures of vertical plate: The left maxilla in *Bothremys arabicus* has a low dorsal process with a portion of the prefrontal suture. The process is low, as in *B. cooki* and *B. maghrebiana*. The maxilla in *B. arabicus* forms the lateral wall of the apertura narium externa, which slopes medially as it goes dorsally to enclose an oval opening, as in the other *Bothremys* species. A margin of matrix continues the maxilla edge of the apertura to form a dorsal margin, but there is no evidence of bone here, and it seems to have been formed during creative preparation. The width between orbit and apertura seems similar to that in *B. maghrebiana* and less than in *B. cooki*.

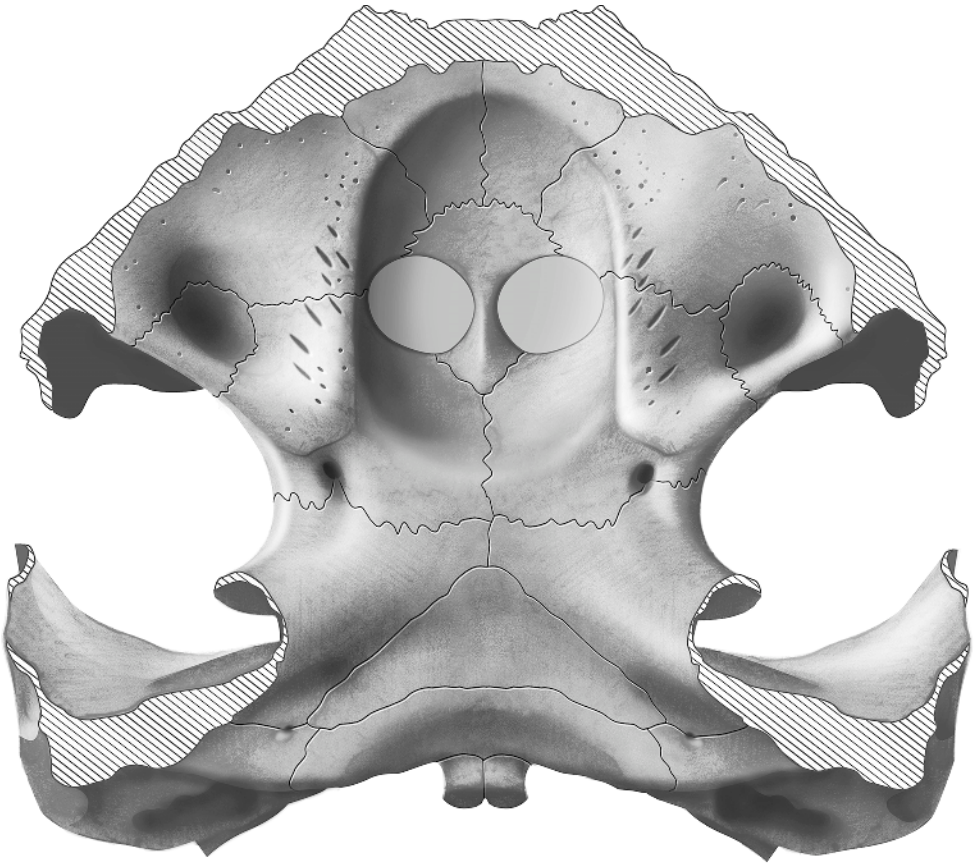

Fig. 151. *Bothremys arabicus* Zalmout, Mustafa, and Wilson, 2005. YUP-HUS 100 holotype. Partially restored ventral view. [F. Ippolito, del.]

In lateral view the maxilla in *B. arabicus* is not as deep as in other *Bothremys* species, but the entire ventral edge is broken, and the maxilla could very well have been the same. The jugal suture is jagged but roughly horizontal until it reaches the edge of the bone, where it rises dorsally. This is similar to both *B. cooki* and *B. maghrebiana* despite the larger jugal exposure in *B. arabicus*. The angle of the maxilla to the midline seems a little greater in *B. arabicus* than in *B. maghrebiana* and *B. cooki*, but similar to that in *B. kellyi*. The skull may have been relatively wider and shorter snouted.

Contacts of horizontal plate: The ventral surface of the horizontal plate of the maxilla in *Bothremys arabicus* forms much of the triturating surfaces, and the bone contacts are with the premaxilla anteromedially, the vomer medially, the palatine posteromedially, and the jugal posteriorly. The maxilla forms the lateral part of the central concavity where it has a short suture with the wide vomer. In *B. cooki* this suture is much longer, but in *B. maghrebiana* it is slightly shorter.

Structures of horizontal plate: The apertura narium interna in *Bothremys arabicus* is bounded anterolaterally by the maxilla, medially by the vomer, and posteriorly by the palatines. The apertura is wider than in most of the other Bothremydini except *Chedighaii hutchisoni*, which is about the same size.

The labial ridge of the maxilla is broken ventrally in *B. arabicus*, but the preserved margin is consistent with the shape seen in *B. cooki* and *B. maghrebiana*, which is more acute than the blunt edge of *Zolhafah* and *B. kellyi*. The labial ridge of *B.*

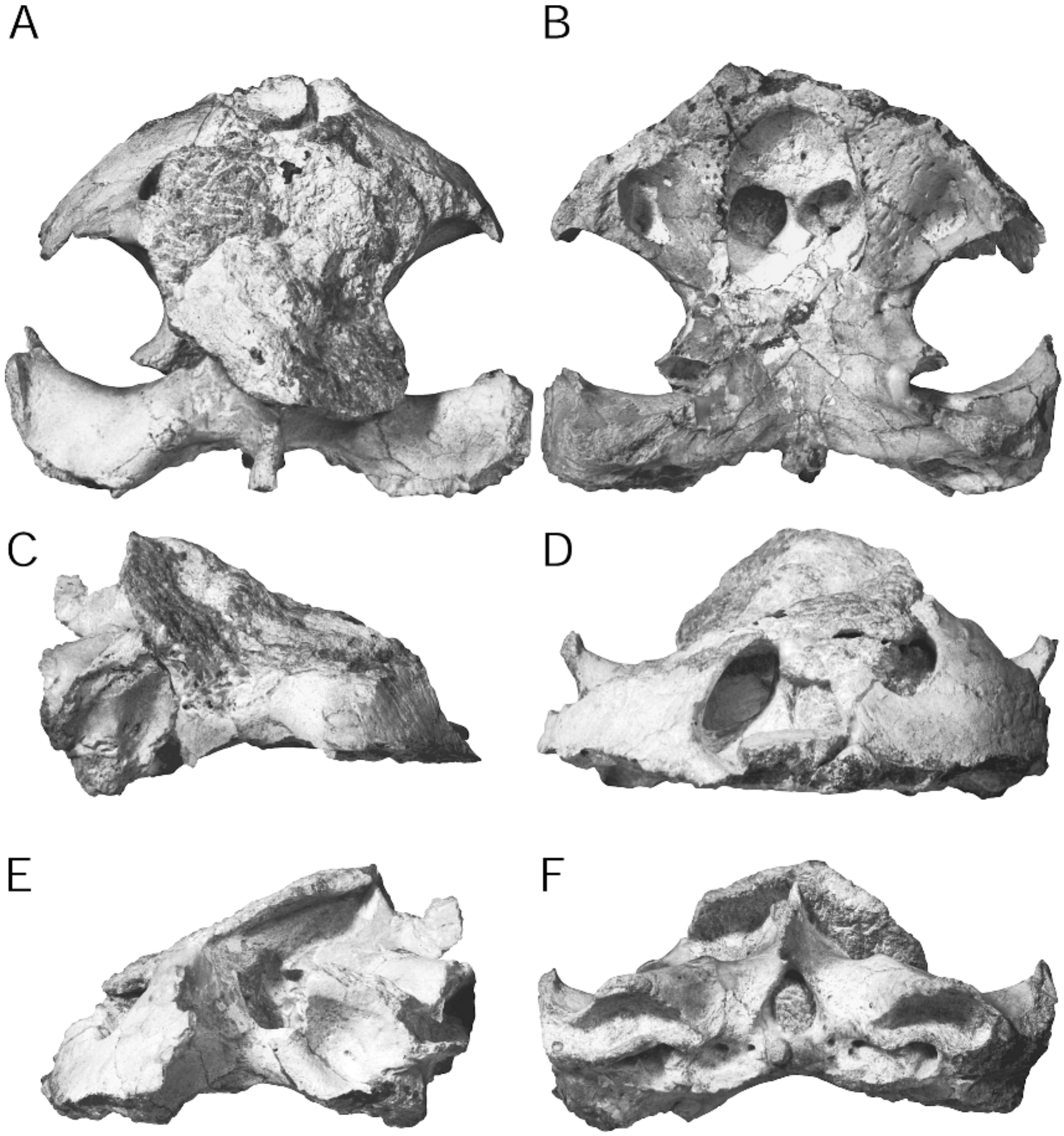

Fig. 152. *Bothremys arabicus* Zalmout, Mustafa, and Wilson, 2005. YUP-HUS 100 holotype. **A**, dorsal; **B**, ventral; **C**, right lateral; **D**, anterior; **E**, left lateral; **F**, posterior. [E. Heck and C. Blik, del.]

arabicus (fig. 151) could not have been as blunt as in *Zolhafah* or *B. kellyi*. The more medial surface of the maxilla is curved to form the slope for the pit, which is mostly formed by the jugal in *B. arabicus*. In contrast to *B. maghrebiana*, the maxilla of *B. arabicus* does not contact the palatine posterior to the pit. It agrees with *B. kellyi* and *B. cooki* in reaching the edge of the fossa temporalis.

Vomer (figs. 150–153)

Preservation: The vomer in *Bothremys arabicus* is completely visible in ventral view with clear sutures, but dorsally it is visible only anteriorly and the sutures are obscured. There is some damage dorsally and slight damage ventrally.

Contacts: The vomer in *Bothremys arabicus* is broad anteriorly where it contacts the premaxilla and maxilla. It is much wider than

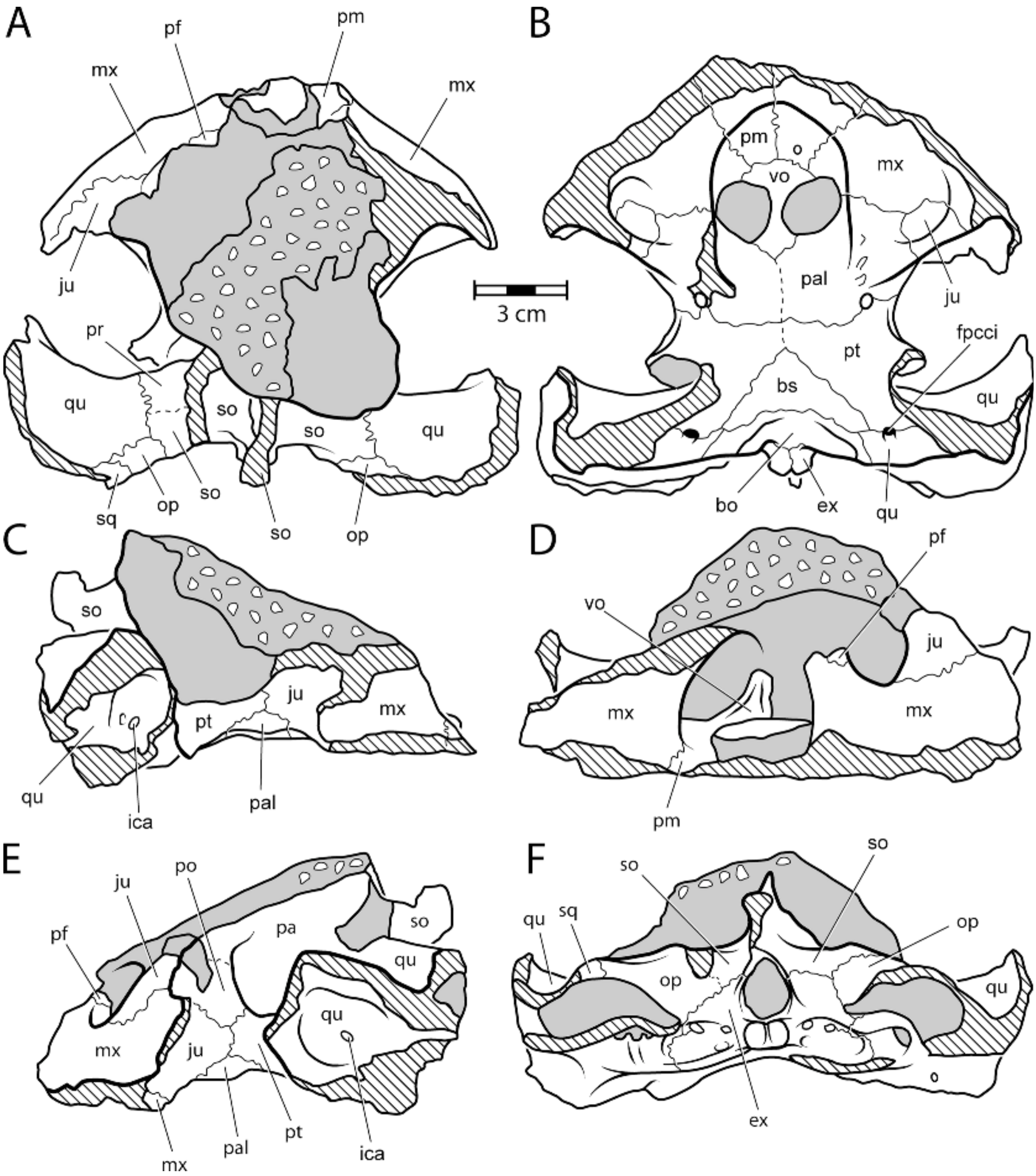

Fig. 153. *Bothremys arabicus* Zalmout, Mustafa, and Wilson, 2005. YUP-HUS 100 holotype. **A**, dorsal; **B**, ventral; **C**, right lateral; **D**, anterior; **E**, left lateral; **F**, posterior. Gray pattern with inclusions indicates mixture of matrix and bone fragments. [D. Marques, del.]

in *B. cooki* and *B. maghrebiana*. This part of the vomer is relatively short in *B. maghrebiana* and *B. arabicus* and much shorter than in *B. cooki*.

Structures: The central column of the vomer is similar in *Bothremys arabicus*, *B. maghrebiana*, and *B. cooki* and it separates the two choanal openings. The posterior swelling of the vomer contacts the two palatines and is similar in size and shape in *B. maghrebiana*, *B. cooki*, and *B. arabicus*. The dorsal surface of the vomer in *B. arabicus* rises sharply and probably helps to form what is likely a very low foramen interorbitale as in *B. maghrebi-*

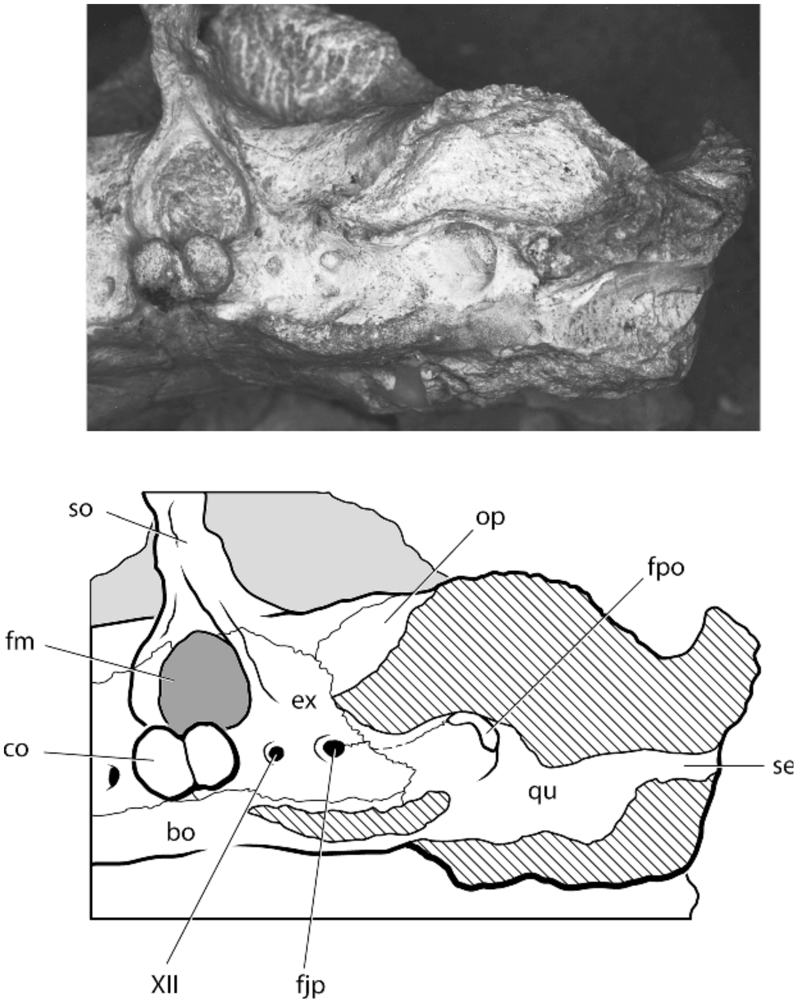

Fig. 154. *Bothremys arabicus* Zalmout, Mustafa, and Wilson, 2005. YUP-HUS 100 holotype. Posterior oblique view. [A. Venjara and E.S. Gaffney, del.]

ana and *B. cooki*. There is some indication of a median trough.

PALATINE (figs. 150–153)

Preservation: Both palatines are preserved nearly complete with nearly all of their sutures clear except on the midline.

Contacts: The palatine contacts the maxilla anteriorly, the jugal anterolaterally, the pterygoid posteriorly, and the other palatine medially. The triturating surface is borne on the palatine posteriorly which has a low ridge, the lingual ridge, running along its medial margin. The palatine contacts in the fossa temporalis are visible on both sides and show no dorsal process, only their exposure beneath the jugal-pterygoid contact.

Structures: The palatine forms the posterior part of the apertura narium interna and the choanal groove. This is wider in *Bothremys arabicus* than in *B. cooki*, but similar to *B. maghrebiana*, which is narrow anteriorly and widens posteriorly. In *B. cooki* the entire central concavity is narrow with nearly parallel sides. In *B. arabicus* the sides are nearly parallel but the whole concavity is wide. Posteriorly the palatine forms nearly all of the foramen palatinum posterius, with only a narrow process of the pterygoid entering it. No part of the dorsal surface of the palatine is visible.

QUADRATE (figs. 150–154)

Preservation: Both quadrates in *Bothremys arabicus* are present but damaged, particularly around the margins of the cavum tympani. Sutures, however, are clear.

Contacts on lateral surface: None preserved, except for a small fragment of squamosal on the left posterior margin.

Structures on lateral surface: The cavum tympani as preserved in *Bothremys arabicus* shows the circular canal for the stapes and the sulcus eustachii; there is no sign of a fossa precolumellaris. The left cavum is better preserved than the right one, and neither has any sign of an antrum postoticum. Comparison with the other *Bothremys* species and *Chedighaii*, all of which have a small antrum, strongly suggests that even the small amount of quadrate preserved in *B. arabicus* would have some indentation for an antrum if one were present. Nonetheless, I have coded it as missing in the dataset.

On the right side there is a small pit just behind the stapedial canal, too far posterior to be a fossa precolumellaris or any part of an antrum postoticum. There is no sign of one on the left.

Contacts on dorsal and anterior surfaces: In *Bothremys arabicus*, the right quadrate has clear sutures with the prootic anteromedially, the supraoccipital medially, and the opisthotic posteromedially. The left quadrate has sutures obscured by poor preservation, but the supraoccipital and opisthotic are visible and a narrow remnant of the squamosal can be seen posteromedially.

Structures on dorsal and anterior surfaces: The foramen stapedio-temporale in *Bothremys arabicus* is visible on the left side in its usual position in the Bothremydini, on the anterior face and close to the foramen nervi trigemini. The poorly preserved foramen nervi trigemini seems to be formed ventrally by the quadrate and probably by the pterygoid. The dorsal surface of the quadrate is rounded and smooth, with no dorsal ridge as in *B. kellyi*. The anterior surface of the otic chamber in *B. arabicus* has a moderately developed overhang, not to the extent seen in *B. kellyi* however.

Contacts on ventral surface: The quadrate in *Bothremys arabicus* contacts the pterygoid anteromedially, the basisphenoid in a narrow contact medially, and the basioccipital posteromedially.

Structures on ventral surface: The condylus mandibularis is broken off on both sides of *Bothremys arabicus*. Its position was just anterior to the condylus occipitalis. There is no fossa pterygoidea. The foramen posterius canalis carotici interni is formed by the pterygoid anteriorly and the quadrate posteriorly, as in *B. maghrebiana*, *B. cooki*, and *Chedighaii*, but in contrast to *B. kellyi*, which has the basisphenoid also enter it.

Contacts on posterior surface: On the occipital surface of the quadrate (fig. 154) in *Bothremys arabicus*, the contacts with the squamosal and opisthotic are largely obscured by the overpreparation and destruction of the quadrate and opisthotic behind the otic chambers, forming paired concavities that are entirely artifacts. The contacts that remain are with the exoccipital medially, the basioccipital ventromedially, and the opisthotic dorsomedially.

Structures on posterior surface: The quadrate in *Bothremys arabicus* forms the lateral and ventral margins of the fenestra postotica, as in other bothremydids. There is a wide area of bone between the fenestra postotica and the more medial foramen jugulare posterius (fig. 154). On the right side the fenestra postotica is oval-shaped with a more ventral and a more dorsomedial enlargement. An opisthotic suture is visible going medially from the fenestra to the exoccipital. On the left side the fenestra postotica is more horizontal and is subdivided into three enlargements, with the central one being largest. The subdivision may be an artifact of preservation as the left side is less well preserved than the right one. Nonetheless, the quadrate-opisthotic suture is also preserved here. Medially the quadrate contacts the exoccipital and more ventrally the basioccipital. The foramen chorda tympani inferior is present at least on the right side.

PTERYGOID (figs. 150–153)

Preservation: Both pterygoids in *Bothremys arabicus* are present and largely complete, lacking some lateral edges and distal margins of the processus trochlearis pterygoidei.

Contacts on ventral surface: The pterygoid meets the palatine anteriorly, the other pterygoid anteromedially, the basisphenoid posteromedially, and the quadrate posterolaterally. The median pterygoid-pterygoid contact is short in *Bothremys arabicus* as it is in *B. cooki* (AMNH 29444) and *B. maghrebiana*. Similarly the angled basisphenoid contact is long in all three.

Structures on ventral surface: The processus trochlearis pterygoidei in *Bothremys arabicus* is very similar to that in the other species of *Bothremys*. The foramen posterius canalis carotici interni is formed anteriorly by the pterygoid and posteriorly by the quadrate, as in *B. cooki* (AMNH 29444) and *B. maghrebiana*, but not in *B. kellyi*, which also has the basisphenoid in the margin. There is no fossa pterygoidea in *B. arabicus*.

Contacts on dorsal surface: The contacts around the base of the processus trochlearis pterygoidei in *B. arabicus* are with the palatine anteroventrally, the jugal anterolaterally, the postorbital dorsolaterally, and a very narrow one with the parietal dorsally.

Structures on dorsal surface: A small part of the medial surface of the sulcus palatinopterygoideus and the processus inferior parietalis is exposed on the left side in *Bothremys arabicus*, but the bone is broken and poorly preserved. There is no sign of sutures or the foramen nervi trigemini.

SUPRAOCCIPITAL (figs. 150, 153, 154)

Preservation: The ventral part of the supraoccipital in *Bothremys arabicus* is preserved, but much of the crista supraoccipitalis is gone. The lateral process of the supraoccipital is intact on the right side, but it is broken and restored with resin on the left side. The anterior contact with the parietal is mostly restored with resin.

Contacts: The supraoccipital contact with the parietal is obscured by matrix and damage. On the otic chamber the supraoccipital contacts the prootic anterolaterally, the quadrate in a wide contact laterally, the opisthotic posterolaterally, and the exoccipital posteroventrally.

Structures: The supraoccipital in *B. arabicus* forms the dorsal margin of the foramen magnum, which is very similar to that in other species of *Bothremys*. The crista supraoccipitalis is broken, but, as preserved, it is thick and has a blunt ventral margin relative to that in *B. maghrebiana*.

EXOCCIPITAL (figs. 150, 153, 154)

Preservation: Both exoccipitals are preserved and have clear sutures.

Contacts: The exoccipital in *Bothremys arabicus* contacts the supraoccipital dorsally, the opisthotic dorsolaterally, the quadrate ventrolaterally, and the basioccipital ventrally, as in the other species of *Bothremys* and *Chedighaii*.

Structures: The condylus occipitalis in *Bothremys arabicus* is entirely formed by the exoccipitals, as in other Bothremydini. The foramina nervi hypoglossi are two in number: a larger more dorsal one and a smaller ventral one. The foramen jugulare posterius is entirely formed by the exoccipital, with a horizontal suture showing exoccipital meeting exoccipital lateral to the foramen. The size of the foramen jugulare posterius is significantly smaller than in *B. cooki* (AMNH 29444) and about the same as in *B. maghrebiana* and *B. kellyi*. On the right side just below the foramen jugulare posterius is a foramenlike indentation, the result of a preparation artifact. The lower part of the exoccipital in *B. arabicus* is developed into a distinct concavity, similar to those in *B. kellyi* and *Chedighaii hutchisoni*.

BASIOCCIPITAL (figs. 150–153)

Preservation: The basioccipital in *Bothremys arabicus* is preserved with clear sutures, but its surface is chewed up a bit.

Contacts: As in *Bothremys maghrebiana*.

Structures: The basioccipital in *B. arabicus* does not enter the base of the condylus occipitalis or any part of it. There is a shallow concavity on the midline, as in *B. maghrebiana* and *B. kellyi*. As in the other Bothremydini, there is no distinct tuberculum basioccipitale, just a low, horizontal ridge near the basioccipital-exoccipital suture.

PROOTIC (figs. 150, 153)

Preservation: Both prootics in *Bothremys arabicus* are present and probably complete, but the left one is slightly damaged medially and both are obscured by matrix.

Contacts: The prootic contacts the quadrate laterally and the supraoccipital posterodorsally in *Bothremys arabicus*. The other contacts are covered by matrix or are damaged (left side).

Structures: The left prootic in *Bothremys arabicus* shows the foramen stapedio-temporale lying just medial to the quadrate at the ventral end of the prootic-quadrate suture. The foramen is filled with matrix and partially damaged, but it is clearly on the anterior surface of the otic chamber. The area of the foramen nervi trigemini is close, but it is too poorly preserved for a more precise determination.

OPISTHOTIC (figs. 150, 153, 154)

Preservation: Both opisthotics are present in *Bothremys arabicus* with clear sutures, and they were probably complete originally, but much of their posterior surfaces have been removed by overpreparation.

Contacts: The squamosal contact in *Bothremys arabicus* is preserved only in a small section on the left side.

Structures: Although it is badly damaged, it is likely that *Bothremys arabicus* had the horizontal shelf seen in *Chedighaii* and *B. kellyi*. The foramen postotica in *B. arabicus* is formed by the opisthotic and quadrate, as in other turtles, and it is more horizontal than in other Bothremydini.

BASISPHENOID (figs. 150–153)

Preservation: The basisphenoid in *Bothremys arabicus* is complete with clear sutures; only the ventral surface is visible.

Contacts: As in *Bothremys maghrebiana*, with very narrow quadrate contacts.

Structures: *Bothremys arabicus* has an unusually wide, triangular basisphenoid among the Bothremydini. There are no concavities or depressions.

Chedighaii hutchisoni

Known from a single skull, this is one of the two species of Bothremydina without pits on the triturating surface, with both species being united in the genus *Chedighaii*. This skull is in a difficult matrix, but some of the internal areas have been made visible. *Chedighaii* is the sister group to *Bothremys*.

PREFRONTAL (figs. 155, 158)

Preservation: Both prefrontals in KUVP 14765 are present, nearly complete, visible on both surfaces, and with clear sutures.

Contacts: As in other bothremydids, the prefrontal of *Chedighaii hutchisoni* contacts the frontal posteriorly, the other prefrontal medially, and the maxilla anteroventrolaterally. The process to the maxilla extends ventrally to approach, but not meet, the palatine. There is a prefrontal-palatine contact in *Bothremys cooki*, but *B. maghrebiana* is similar to *C. hutchisoni*. On the ventral surface the frontals extend anteriorly beneath the prefrontals, as in most other Pelomedusoides.

Structures: In *Chedighaii hutchisoni* the prefrontal is relatively flat on its dorsal surface, similar to *Bothremys*. The prefrontal forms a shallow midline projection along the dorsal margin of the apertura narium externa in *C. hutchisoni*, similar to that in *Bothremys*, but not as extensive as in *Araiochelys*. The entire anterior edge is a natural edge with no sign of contact with a premaxillary process. The interorbital distance, relative to the rest of the skull, is less in *C. hutchisoni* than in *Bothremys* and *Araiochelys*. It is similar to the other Bothremydini.

FRONTAL (figs. 155, 158)

Preservation: Both frontals are preserved completely in KUVP 14765, but the posterior part of their ventral surfaces is obscured by matrix. The sutures are clear.

Contacts: As in other bothremydids, the frontal in *Chedighaii hutchisoni* contacts the prefrontal anteriorly, the postorbital posterolaterally, the parietal posteriorly, and the other frontal medially.

Structures: The dorsal shape of the frontal in *Chedighaii hutchisoni* is similar to that in *Bothremys*, although there is slightly more exposure in the orbital margin. The frontal shape does not vary much among the Bothremydini.

On the ventral surface the frontal of *Chedighaii hutchisoni* has an unusually large, parasagittal ridge forming the lateral margin of the sulcus olfactorius beginning anteriorly at the anterior margin of the frontal and extending ventrally to a greater extent than in any other Bothremydini. This paired ridge

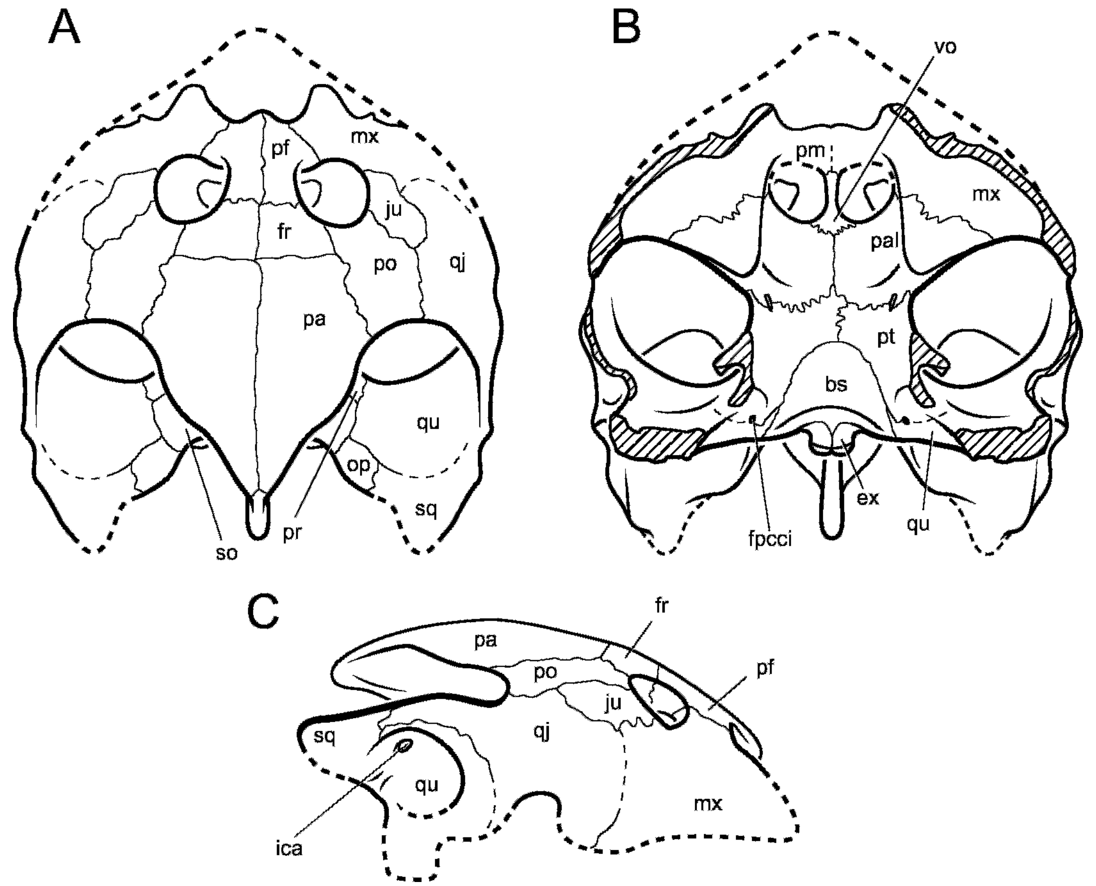

Fig. 155. *Chedighaii hutchisoni*, n. gen. et sp. KUVP 14765 holotype. Partially restored views of skull. **A**, dorsal; **B**, ventral; **C**, lateral. [F. Ippolito, del.]

converges toward the one on the other side ventrally. As preserved, the sulcus olfactorius ridge nearly contacts the vomer, but the skull had clearly been dorsoventrally compressed.

PARIETAL (figs. 155, 158)

Preservation: Both parietals are present in KUVP 14765 and seem to be nearly complete. However, they have been crushed dorsoventrally, particularly on the temporal roof, and most of the ventral surface is obscured by matrix. One area of parietal is exposed in the left fossa temporalis. Sutures are clear on the dorsal surface.

Contacts of dorsal plate: The parietal of *Chedighaii hutchisoni* contacts the frontal anteriorly and the postorbital anterolaterally. Because the temporal emargination is greater in *C. hutchisoni* than in *Bothremys* and *Araiochelys*, the postorbital contact is shorter than in these taxa. The length is slightly shorter in *C. hutchisoni* than in *Foxemys* and *Polysternon*. There is a ventral process, not part of the processus inferior parietalis, that contacts the pterygoid (see below).

Structures of dorsal plate: The degree of temporal emargination in *Chedighaii hutchisoni*, as indicated above by the postorbital suture length, is slightly greater than in other Bothremydini, which do not vary a great deal among themselves. No Bothremydini, including *C. hutchisoni*, has temporal emargination to the extent seen in the Kurmademydini or Cearachelyini. The parietal of *Chedighaii hutchisoni* has a ventral process lateral to the sulcus palatinopterygoideus that forms part of the septum orbitotemporale and reaches the pterygoid at the base of

Fig. 156. *Chedighaii hutchisoni*, n. gen. et sp. KUVP 14765 holotype. Partially restored ventral view. [F. Ippolito, del.]

the processus trochlearis pterygoidei. This process also occurs in *Bothremys*, *Phosphatochelys*, and *Kurmademys*.

Contacts and structures of processus inferior parietalis: The processus is completely obscured by matrix.

JUGAL (figs. 155, 158)

Preservation: Both jugals are preserved in KUVP 14765, but their contacts are not clear due to breakage and cracking. The dorsal and anteroventral contacts are clear on both sides, and the left side shows some of the ventral contact. By using sutures on the internal as well as external surfaces, most of the jugal limits can be determined.

Contacts of lateral plate: The jugal in *Chedighaii hutchisoni* contacts the maxilla ventrally, the (presumed) quadratojugal posteriorly, and the postorbital dorsomedially, as in other Bothremydini in which the cheek is known. The jugal contacts in KUVP 14765 are not entirely clear, but by using internal as well as external surfaces and transferring morphology from side to side, most of the contacts can be determined. The dorsomedial jugal-postorbital contact is visible on both sides as well as the anterior portion of the jugal-maxilla contact. The posteroventral limits of the jugal, however, are unclear except for a short portion on the left side with what is interpreted as the quadratojugal. This portion and the jugal-maxilla suture near the end of the jugal on the right side allow a reasonable interpretation of the limits of the jugal. The jugal in KUVP 14765 does not reach the quadrate nor does it reach the cheek margin. A broad postorbital-quadratojugal contact limits the jugal posteriorly.

Structures of the lateral plate: The jugal in *Chedighaii hutchisoni* forms the posteroventral part of the orbital margin. The jugal extends anteriorly along the orbital margin more than in *Bothremys* and the other Bothremydini.

Contacts of medial process: In the orbital floor, the jugal in *Chedighaii hutchisoni* is exposed laterally and posteriorly, but its precise contacts are obscured by breakage, cracking, and some matrix. As in other bothremydids, the jugal contacts the maxilla anterolaterally and probably the palatine medially.

The septum orbitotemporale of *Chedighaii hutchisoni* is not entirely clear on its anterior surface, but its posterior surface is largely visible. The jugal contacts the postorbital dorsomedially, the palatine ventromedially, the pterygoid posteriorly, and the maxilla ventrally, all as in other Bothremydini. There is no exposure of the jugal on the triturating surfaces as in the pitted Bothremydini.

Structures of medial process: The fossa orbitalis of *Chedighaii hutchisoni* has a large posterior enlargement, formed at least in part by the jugal. This posterior concavity in the fossa orbitalis can also be seen in *Bothremys*, *Araiochelys*, and to some extent in *Foxemys*. *C. hutchisoni*, however, has a relatively larger development of this concavity than in these other forms. The jugal forms the lateral wall of this concavity.

QUADRATOJUGAL (figs. 155, 158)

Preservation: The quadratojugal of KUVP 14765 is not clearly defined by sutures on either side, although much of both bones, particularly the right one, is probably present. Most of the dorsal portions of both quadratojugals are present, with quadrate and postorbital sutures visible, but the ventral margins are all broken edges without a clear maxilla suture. It is possible that a quadrate-maxilla suture was present (see Quadrate). Most of the quadratojugal surface is broken by cracks, and there is some displacement due to dorsoventral crushing.

Contacts: The quadratojugal of *Chedighaii hutchisoni* contacts the postorbital dorsomedially, the jugal anteromedially, and the quadrate posteroventrally. On the right side, a short suture on the cheek is probably between the quadratojugal posterodorsally and the maxilla anteroventrally. Unfortunately, this suture is lost in both directions in broken bone and thus its identification is not certain. The better preserved right quadratojugal clearly shows the posteroventral quadrate suture, but the skull is missing too much ventrally to confirm that a quadrate-maxilla contact was present. Given the amount preserved and the orientation of the suture where it is lost, however, a quadrate-maxilla contact seems unlikely. The quadratojugal in *C. hutchisoni* does extend ventrally more than the one in *Rosasia* and *Bothremys maghrebiana*. Posteriorly the quadratojugal reaches the squamosal, as in the other Bothremydini.

Structures: The quadratojugal in *Chedighaii hutchisoni* forms the lateral edge of the temporal emargination, which is slightly more extensive than in *Bothremys maghrebiana*, *Araiochelys*, *Foxemys*, and *Polysternon*.

SQUAMOSAL (figs. 155, 158)

Preservation: The dorsal parts of both squamosals in KUVP 14765 are present but lack their posterior margins and have been distorted by dorsoventral crushing. The ventral surfaces are broken edges. The few sutures visible are not clear.

Contacts: The squamosal in *Chedighaii hutchisoni* contacts the quadratojugal anterodorsally and the quadrate anteriorly, but this latter contact is unclear. On the occipital surface some of the opisthotic contact is preserved on both sides.

Structures: Both squamosals in *Chedighaii hutchisoni* are very flat as preserved, but this seems to be due to crushing.

POSTORBITAL (figs. 155, 158)

Preservation: Both postorbitals in KUVP 14765 are present with nearly complete lateral plates. The sutures are determinable but not entirely clear. The bone surface is cracked and some of the bone is displaced by dorsoventral crushing. The ventral end of the medial process is visible on the left side with clear sutures.

Contacts of lateral plate: The postorbital of *Chedighaii hutchisoni* contacts the frontal anteromedially, the jugal anterolaterally, the parietal posteromedially, and the quadratojugal posterolaterally.

Structures of lateral plate: The postorbital in *Chedighaii hutchisoni* is a long bone that extends from the orbital margin anteriorly to the temporal margin posteriorly, as in *Bothremys*, *Araiochelys*, *Foxemys*, and *Polysternon* (it is incomplete in the other Bothremydini). Nonetheless, the postorbital is slightly shorter in *C. hutchisoni* than in these other taxa, because the temporal emargination is slightly more extensive.

Contacts of medial process: Although some of the postorbital can be seen in the septum orbitotemporale, its contacts are not determinable due to matrix and cracking. On the posterior surface of the septum orbitotemporale, the postorbital contacts the jugal ventrally, the pterygoid posteroventrally, and a narrow ventral process of the parietal posteriorly (see Parietal).

Structures of the medial process: Due to the ventral parietal process, the postorbital in *Chedighaii hutchisoni* does not form part of the lateral margin of the sulcus palatinopterygoideus as in other Bothremydini.

PREMAXILLA (figs. 155, 158)

Preservation: In KUVP 14765 only small fragments of the posteromedial part of each premaxilla are preserved as flat plates attached to the anterior margin of the vomer.

MAXILLA (figs. 155–158)

Preservation: The dorsomedial parts of both maxillae in KUVP 14765 are present, along with much of the right triturating surface, but none of the margin, neither the labial ridge or cheek, is preserved. Most of the sutures are discernable, except for the posterior one.

Contacts of vertical plate: Both premaxillae are mostly absent, and the anterior margins of the maxillae are broken edges. The preserved contacts of the maxilla in *Chedighaii hutchisoni* are the prefrontal anterodorsally, the jugal posterodorsally, and, probably, the quadratojugal posteriorly. It is unlikely that a quadrate contact was present (see Quadratojugal). Posteriorly, the maxilla is either missing or badly cracked, obscuring any sutures. The lower margins of quadrate and maxilla are missing on both sides. One short length of suture on the right side is visible posteriorly; it is probably the quadratojugal contact.

Structures of vertical plate: The maxilla forms the ventral margin of the orbit, which in *Chedighaii hutchisoni* forms a low wall lateral to the fossa orbitalis. The dorsal process of the maxilla is much thinner in *C. hutchisoni* than in *Bothremys*. The apertura narium externa in *C. hutchisoni* is much narrower than in *Zolhafah* but is also narrower than in *Bothremys*. It is similar in relative width to *Polysternon* and *Foxemys*.

Contacts of horizontal plate: The preserved contacts of the maxilla in *Chedighaii hutchisoni* are with the palatine posteromedially and the jugal posterodorsally. There is no vomer contact as preserved, but both maxillae and vomer have broken edges here.

Structures of horizontal plate: As in the other Bothremydini, the triturating surface in *Chedighaii hutchisoni* is formed by the maxilla anteriorly and the palatine posteriorly. The surface is a large, flat, triangular area, similar in size to the other Bothremydini (fig. 156). It differs strongly from *Bothremys*, *Araiochelys*, *Zolhafah*, and *Rosasia* in lacking any depression or pit, agreeing with *C. barberi*. The labial ridge is completely missing on the left side and only a small, damaged section is present on the right. It is preserved as a shallow, blunt edge, less acute than in *Foxemys* but similar to *Bothremys*. Because the labial ridge and premaxillae are missing, the original anterior extent of the triturating surface in KUVP 14765 cannot be determined. As preserved, the medial extent of the maxilla in KUVP 14765 is not as great as in other Bothremydini. As a result, the choanal grooves and apertura narium interna are larger in *C. hutchisoni* than in the other Bothremydini. The triturating surface in *C. hutchisoni* is broadly curved, concave downward, very similar to *Foxemys*.

In the floor of the fossa orbitalis, the maxilla forms the lateral part, with the

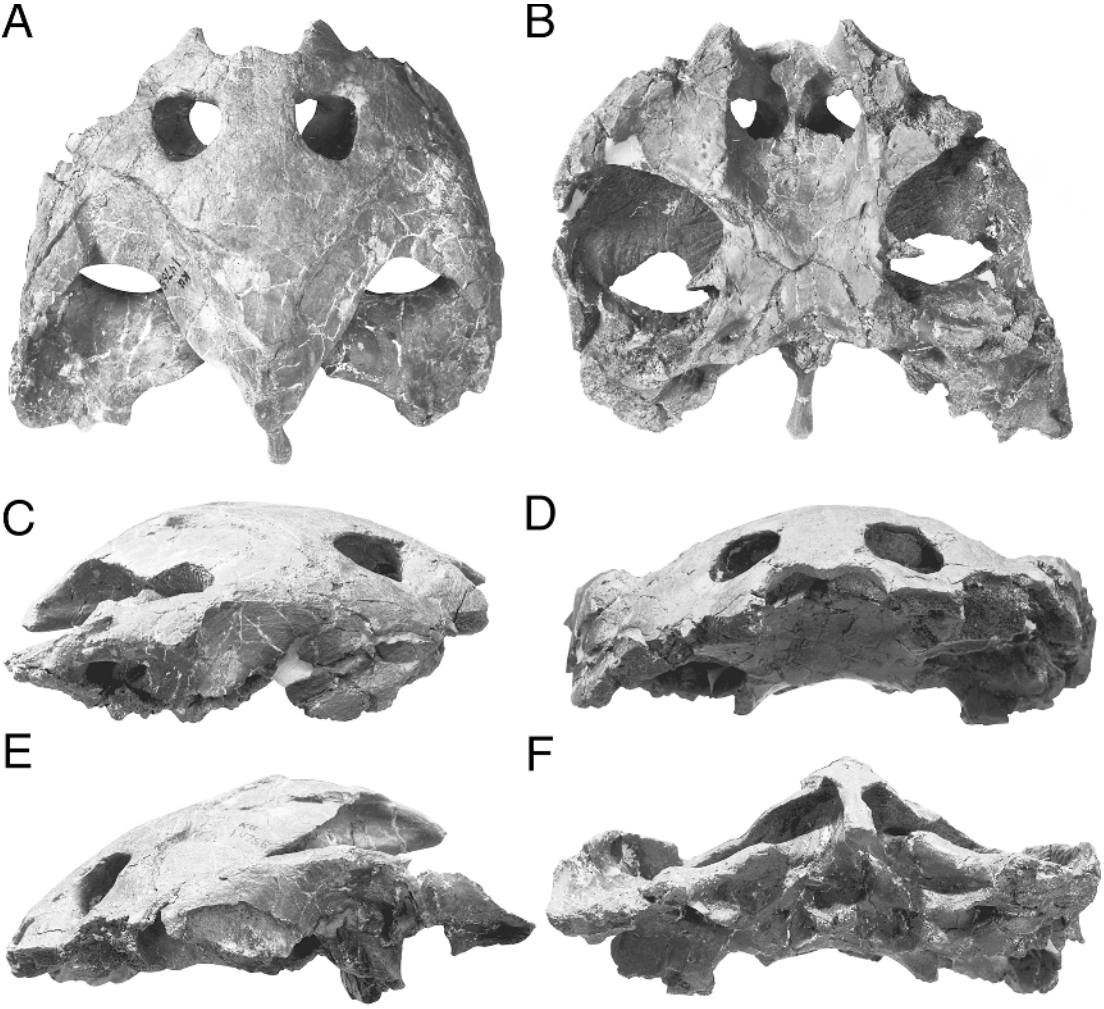

Fig. 157. *Chedighaii hutchisoni*, n. gen. et sp. KUVP 14765 holotype. **A**, dorsal; **B**, ventral; **C**, right lateral; **D**, anterior; **E**, left lateral; **F**, posterior. [F. Ippolito, del.]

prefrontal anterior and the palatine posterior. As preserved the maxilla (on each side) has a small exposure on the foramen orbitonasale such that the prefrontal and palatine do not contact. There is a small foramen in the maxilla, possibly the foramen alveolare superius.

VOMER (figs. 155–158)

Preservation: The vomer in KUVP 14765 is nearly complete, with clear sutures undistorted and visible on its dorsal and ventral surfaces.

Contacts: The vomer in *Chedighaii hutchisoni* contacts the premaxillae anteriorly and the palatines posteriorly. Although nearly all of the premaxillae and the medial edges of the maxillae are missing, enough of the vomer and premaxillae are present to show that, as preserved, the maxillae do not contact the vomer, in contrast to all other Bothremydini (including *Zolhafah*; see Vomer). However, the anterolateral margins of the vomer are broken edges, and missing expansions could have contacted the maxillae.

Structures: The vomer in *Chedighaii hutchisoni* is the typical bar expanded at both ends. The anterior expansion as preserved is much less than in *Bothremys*, *Foxemys*, or

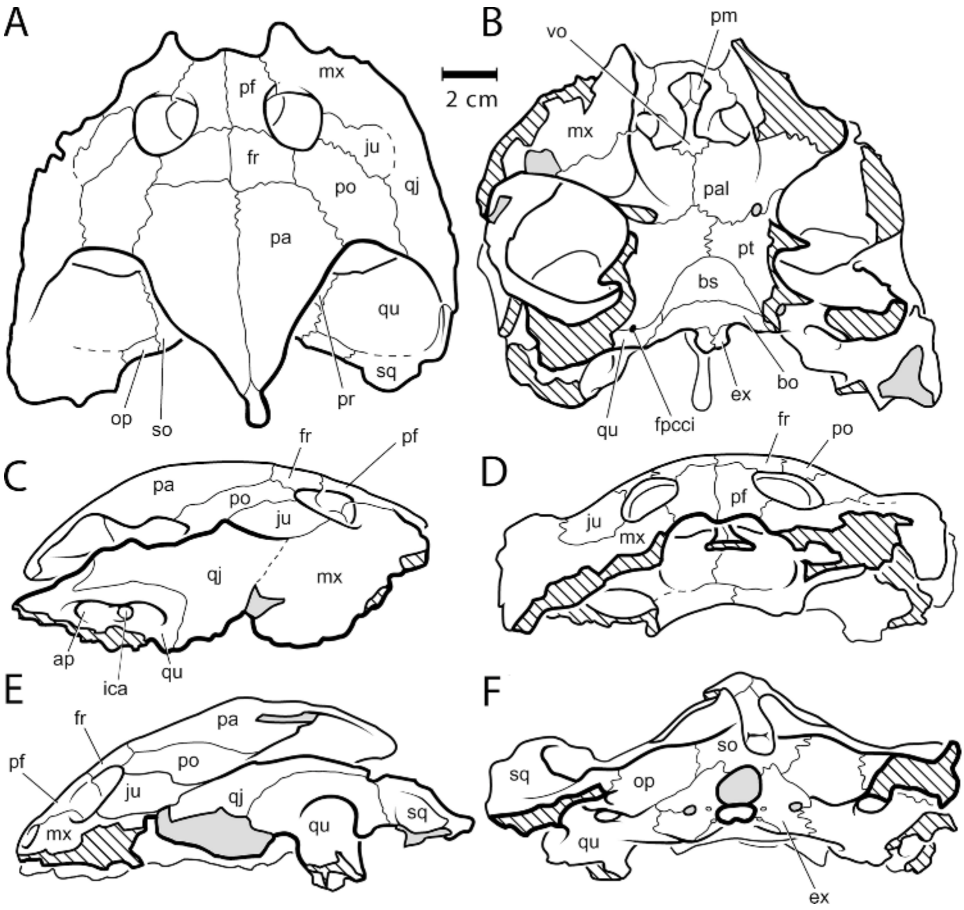

Fig. 158. *Chedighaii hutchisoni*, n. gen. et sp. KUVP 14765 holotype. **A**, dorsal; **B**, ventral; **C**, right lateral; **D**, anterior; **E**, left lateral; **F**, posterior. [F. Ippolito, del.]

Rosasia. It is possible that its more lateral expansions are broken off. The vomer is also in one plane, not stepped as in *Rosasia*. On its dorsal surface is a median groove, as in most of the other vomers that have this area visible. The vomer is not preserved in *C. barberi*.

PALATINE (figs. 155–158)

Preservation: Most of both palatines in KUVP 14765 are complete, but the left one is broken anteriorly, and both have cracking and some crushing. Most of the sutures are clear.

Contacts: The palatine in *Chedighaii hutchisoni* contacts the vomer anteromedially, the maxilla anterolaterally, the pterygoid posteriorly, and the other palatine medially. On the dorsal surface, a parietal contact cannot be determined.

Structures on dorsal surface: The dorsal surface of the palatine in KUVP 14765 is mostly obscured by matrix. In the floor of the fossa orbitalis the palatine forms the posteromedial part of the floor. The fossa is relatively large in *Chedighaii hutchisoni* (see Jugal) and has a large posterior concavity formed at least by palatine, jugal, and postorbital.

Structures on ventral surface: The palatine of *Chedighaii hutchisoni*, as in other Bothremydini, forms the posteromedial part of the large, triangular triturating surface (fig. 156). The palatine part of the surface is relatively flat, with a low but acute ridge along the posterolateral margin of the triturating surface. Along the anterior edge of the ridge is a shallow trough, mostly formed on the palatine. The ridge is continuous medially with the lingual ridge, a low ridge marking the medial edge of the triturating surface.

The palatine forms most of the large choanal trough extending posteriorly from the fossa nasalis. The apertura narium interna, formed posteriorly by the palatines, is relatively large in *Chedighaii hutchisoni*, as is the choanal trough. In *Bothremys*, *Araiochelys*, and particularly *Rosasia*, the apertura and choanal trough are much narrower. The foramen palatinum posterius is best seen on the left side, and it is formed mostly by the palatine, with the pterygoid forming the posterior margin.

QUADRATE (figs. 155, 158, 159)

Preservation: Most of both quadrates are preserved in KUVP 14765; the ventral parts are missing and other areas are obscured by crushing and breakage. The right processus articularis is gone and the left one is damaged on the articular surface. The cavum tympani on the left side is missing its anteroventral margin, and the cavum on the right side lacks its entire ventral margin as well as the antrum postoticum and incisura columellae auris. Some crushing has distorted the cavum tympani on the right side but it retains the antrum and incisura. The dorsal surfaces of both quadrates have breaks and are slightly crushed. Sutures are difficult to make out, but most of the contacts are determinable.

Lateral surface contacts: The anterior and anterodorsal margins of the quadrate in *Chedighaii hutchisoni* are curved, contacting the quadratojugal in the typical C-shaped suture. Although the more ventral parts of both bones are gone, there is no indication of the anterior quadrate process seen in *Bothremys*, *Araiochelys*, and *Rosasia*. The maxilla could still reach the quadrate, however, as it does in *Azabbaremys*. Posterodorsally the quadrate contacts the squamosal, but only short sections of the suture are preserved on each side.

Lateral surface structures: The quadrate in *Chedighaii hutchisoni* is not exposed on the temporal emargination due to the squamosal-quadratojugal contact. Only the dorsal part of the cavum tympani is preserved on either side, and the presence of a lateral shelf ventrally, as in *Araiochelys* and *Bothremys*, cannot be determined. The incisura columellae auris, preserved on the right side only, is the typical bothremydid foramen, widely separated by bone from the sulcus eustachii. There is enough cavum tympani present to show that a fossa precolumellaris is absent. The antrum postoticum is present on both sides but variably crushed and damaged. However, it seems to have been comparable in size to that in *Bothremys maghrebiana* and *Araiochelys*. The antrum postoticum in *Chedighaii hutchisoni* faces more anteriorly, as in *B. maghrebiana*, rather than more laterally, as in *Araiochelys*. The sulcus eustachii is incomplete on both sides, but the preserved morphology agrees with *B. maghrebiana*.

Dorsal and anterior surface contacts: The dorsal and anterior contacts of the otic chamber portion of the quadrate in *Chedighaii hutchisoni* are with the prootic anteromedially, the supraoccipital medially, the opisthotic posteromedially, and the squamosal posteriorly, as in all other Bothremydini except *Zolhafah* (see *Zolhafah*, Supraoccipital).

Dorsal and anterior surface structures: The dorsal and lateral margins of the foramen stapedio-temporale can be seen in KUVP 14765 on the left side. As in other Bothremydidae (except *Kurmademys*), the foramen is on the anterior face of the otic chamber and not visible in dorsal view. The foramen stapedio-temporale is placed medially, as in *Bothremys*, *Zolhafah*, and *Rosasia*. The foramen nervi trigemini is damaged in KUVP 14765, but the foramen stapedio-temporale does not seem to be as close to it as it is in *Bothremys*.

Contacts on ventral surface: Ventrally the quadrate in *Chedighaii hutchisoni* meets the pterygoid anteromedially. Some of both bones are broken on both sides so that the quadrate ramus of the pterygoid is incomplete, but it seems to be very similar to that in *Bothremys maghrebiana*. Medially the quadrate reaches the basisphenoid in a very

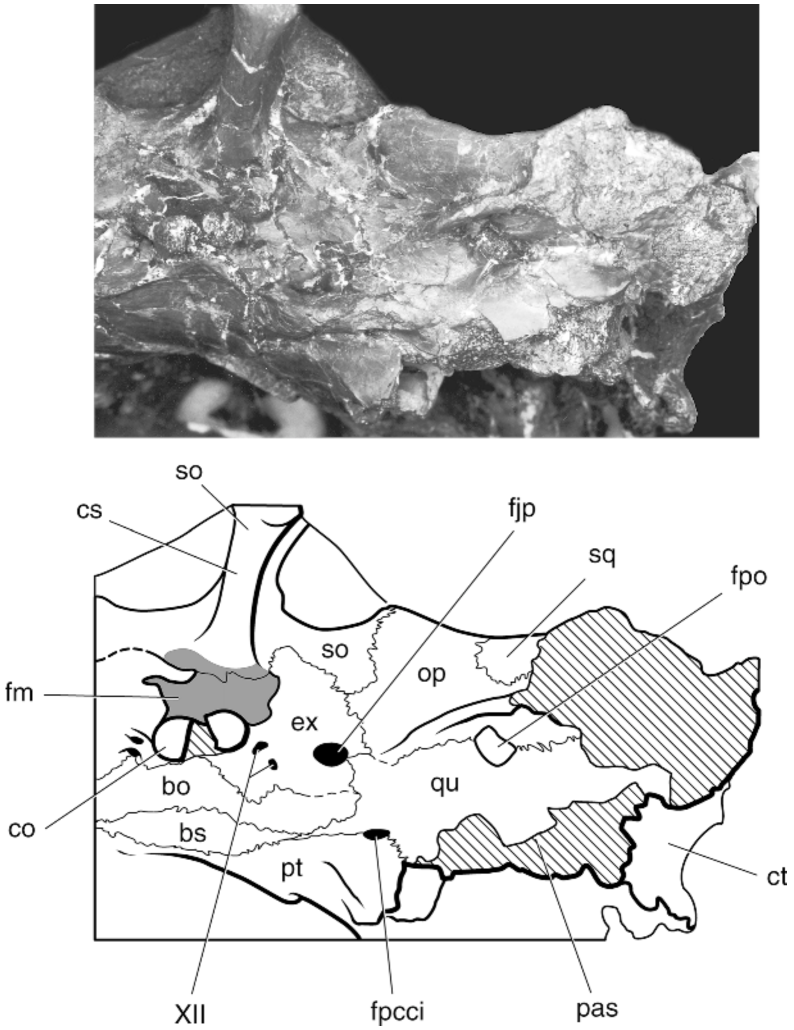

Fig. 159. *Chedighaii hutchisoni*, n. gen. et sp. KUVP 14765 holotype. Posterior oblique view of skull. [A. Venjara and E.S. Gaffney, del.]

narrow contact, as in *Bothremys maghrebiana* and *Zolhafah* but in contrast to the wider contact in *Foxemys*. Posteromedially the quadrate contacts the basioccipital, as in *Bothremys*.

Structures on the ventral surface: There is no fossa pterygoidea in *Chedighaii hutchisoni*, although some of the area is damaged. The processus articularis is completely missing on the right side of KUVP 14765, and the left one is damaged and lacks the condylus mandibularis. The condylus mandibularis is on about the same plane as the condylus occipitalis in *C. hutchisoni*, as it is in *Bothremys maghrebiana*, *Rosasia*, and *Zolhafah*. The condylus mandibularis is more posterior in these forms than in *Araiochelys*, *Foxemys*, and *Polysternon*.

The foramen posterius canalis carotici interni in KUVP 14765 is clearly preserved on the right side but it is present, although damaged, on the left. The foramen is formed anteriorly by the pterygoid and posteriorly by the quadrate and it lies lateral to the basisphenoid at about the level of the basisphenoid-basioccipital suture. The formation and position of the foramen posterius canalis carotici interni are the same in *Chedighaii hutchisoni* and in *Bothremys maghrebiana*.

The quadrate in *Chedighaii hutchisoni* forms the lateral part of the low tuberculum basioccipitale along with the basioccipital more medially.

Contacts on the posterior surface: The quadrate in *Chedighaii hutchisoni* contacts the squamosal dorsolaterally (sutures mostly unclear and damaged), the opisthotic dorsomedially, the exoccipital medially, and the basioccipital ventromedially.

Structures on the posterior surface: The fenestra postotica in *Chedighaii hutchisoni* (fig. 159) is completely enclosed by bone and is oval in shape, not distinctly partitioned into two parts (e.g., *Bothremys maghrebiana* and *Araiochelys*). More posterolaterally on the quadrate and opisthotic there is a low ridge that probably reflects the stapedial artery and lateral head vein position. On the posterior surface of the left processus articularis is a foramen and groove that seems to be the foramen chorda tympani inferius.

PTERYGOID (figs. 155–159)

Preservation: Most of both pterygoids in KUVP 14765 are present, but the quadrate processes and the ventral parts of each processus trochlearis pterygoidei are broken off. Few of the dorsal sutures are visible, but the ventral and anterolateral ones are clear. There is some cracking and displacement.

Contacts on ventral surface: As in other bothremydids, the pterygoid contacts in *Chedighaii hutchisoni* are with the palatine anteriorly, the basisphenoid posteromedially, the quadrate posterolaterally, and the other pterygoid anteromedially. The pterygoid midline contact is shorter than in *Polysternon* but much longer than in *Araiochelys* and *Bothremys maghrebiana*.

Structures on ventral surface: The processus trochlearis pterygoidei in *Chedighaii hutchisoni* is nearly at right angles to the midline, as in *Foxemys*, and in contrast to *Bothremys*, *Rosasia*, *Zolhafah*, and *Araiochelys*. There is no fossa pterygoidea but the right pterygoid has a low ridge and change in surface plane, just anterior to the foramen posterius canalis carotici interni, which probably represents the attachment area of the M. pterygoideus. The foramen posterius canalis carotici interni is formed mostly by the quadrate (see Quadrate), with its anterior margin formed by the pterygoid. The foramen palatinum posterius is mostly formed by the palatine (see Palatine), but the pterygoid forms a small part of its posterior margin.

Contacts on dorsal surface: At the base of the processus trochlearis pterygoidei in *Chedighaii hutchisoni* the pterygoid contacts the jugal anterolaterally, the palatine anteroventrally, the postorbital dorsolaterally, and the parietal dorsally. The parietal contact is unusual (see Parietal) but the others are common in bothremydids. The contacts of the crista pterygoidea are obscured by matrix and some breakage, but the prootic contact is visible.

Structures on dorsal surface: Nearly all of the dorsal surface of the pterygoid in *Chedighaii hutchisoni* is obscured by matrix, although some of the foramen nervi trigemini margin is visible on the left side.

SUPRAOCCIPITAL (figs. 155, 158, 159)

Preservation: The supraoccipital in KUVP 14765 is complete, but dorsoventral crushing has caused breaks between the crista supraoccipitalis base and the lateral projections, and the crista is pushed down into the foramen magnum (ouch). Anterolateral sutures are determinable, but the foramen magnum sutures are obscured by breakage.

Contacts: As in other bothremydids, the supraoccipital of *Chedighaii hutchisoni* contacts the parietal dorsally and anteriorly, the prootic anterolaterally, the quadrate laterally, the opisthotic posterolaterally, and the exoccipital posteroventrally.

Structures: The crista supraoccipitalis is complete in *Chedighaii hutchisoni* and extends posteriorly to the level of the squamosal limits as preserved. The crista of *C. hutchisoni* is thickened along its ventral edge, as in other bothremydids, but it is also thickened along its dorsal edge. The crista of *C. hutchisoni* is a thick, heavy plate in comparison to those in other Bothremydini, perhaps due to its much larger size.

The median plate of the supraoccipital underlies the two parietals along the midline.

This contact is obscured by matrix anteriorly, but its posterior limits show differences with other bothremydids. In most turtles the supraoccipital is a vertical plate that underlies the median contact of the parietals so that only the parietals form the temporal roof. In *Chedighaii hutchisoni* the supraoccipital sends horizontal processes laterally that underlie the parietals for a short distance at the posterior end of the temporal roof. This condition has not been seen in other bothremydids. On the dorsal surface the parietals meet almost to the end of their length except for a short space where the supraoccipital is exposed between them.

EXOCCIPITAL (figs. 155, 158, 159)

Preservation: Both exoccipitals are present in KUVP 14765, but they have extensive cracking that obscures some sutures and features.

Contacts: As in other bothremydids, the exoccipital of *Chedighaii hutchisoni* contacts the supraoccipital dorsally, the opisthotic laterally, the quadrate ventrolaterally, and the basioccipital ventrally.

Structures: The foramen magnum in KUVP 14765 is deformed by the ventral displacement of the supraoccipital, but otherwise it seems to be as in other bothremydids. The condylus occipitalis is formed entirely by the exoccipitals, including the neck. A small spur of basioccipital lies on the ventral surface along the exoccipital suture. As preserved, the exoccipitals in the condylus are slightly disarticulated and displaced relative to each other. The foramen jugulare posterius in *Chedighaii hutchisoni* is completely closed by bone. The left one is closed by a broad lateral meeting of dorsal and ventral processes of the exoccipital, but the right one is closed by a thin process of quadrate.

Two foramina nervi hypoglossi lie near the base of the condylus occipitalis, ventrolateral to the foramen magnum. The two on the right are formed entirely in the exoccipital, but the left two have the more lateral foramen partly formed by the basioccipital.

BASIOCCIPITAL (figs. 155, 158, 159)

Preservation: The basioccipital in KUVP 14765 is complete with clear sutures, but it is cracked and slightly distorted.

Contacts: The basioccipital in *Chedighaii hutchisoni* has the usual bothremydid contacts: basisphenoid anteriorly, quadrate laterally, and exoccipitals dorsally.

Structures: The basioccipital in *Chedighaii hutchisoni* makes up most of the tuberculum basioccipitale, with the quadrate only forming a small part laterally. A shallow, median concavity lies between the tuberculae and is formed almost entirely by the basioccipital. The basioccipital in *C. hutchisoni* has a small, acute process extending posteriorly into the base of the condylus occipitalis.

PROOTIC (figs. 155, 158)

Preservation: Both prootics are preserved in KUVP 14765, but the sutures are poorly preserved and covered by matrix medially.

Contacts: The prootic in *Chedighaii hutchisoni* contacts the supraoccipital posteromedially (seen on both sides), the pterygoid ventrally (seen only on the left), and the quadrate laterally (seen on both sides). There is no opisthotic contact due to the supraoccipital-quadrate contact. The presumed contact with the parietal is covered by matrix.

Structures: The foramen nervi trigemini is mostly covered by matrix in KUVP 14765. The foramen stapedio-temporale is visible on the left side and is relatively small (possibly reduced in size by postmortem distortion), with its medial limits being obscured by matrix. The foramen is placed well onto the anterior surface of the otic chamber and even faces ventrally to a slight extent. It is not visible in dorsal view.

OPISTHOTIC (figs. 155, 158, 159)

Preservation: Both opisthotics are preserved in KUVP 14765, but they are damaged by cracking and crushing with some displacement. Most of the sutures can be made out, particularly on the right side.

Contacts: As in other bothremydids, the opisthotic in *Chedighaii hutchisoni* contacts the supraoccipital anteromedially, the quadrate anterolaterally, the squamosal posterolaterally, and the exoccipital posteromedially. There is no prootic contact.

Structures: The opisthotic in *Chedighaii hutchisoni* forms the dorsal part of the fenestra postotica (see Quadrate). Just above the fenestra is a prominent, horizontal shelf

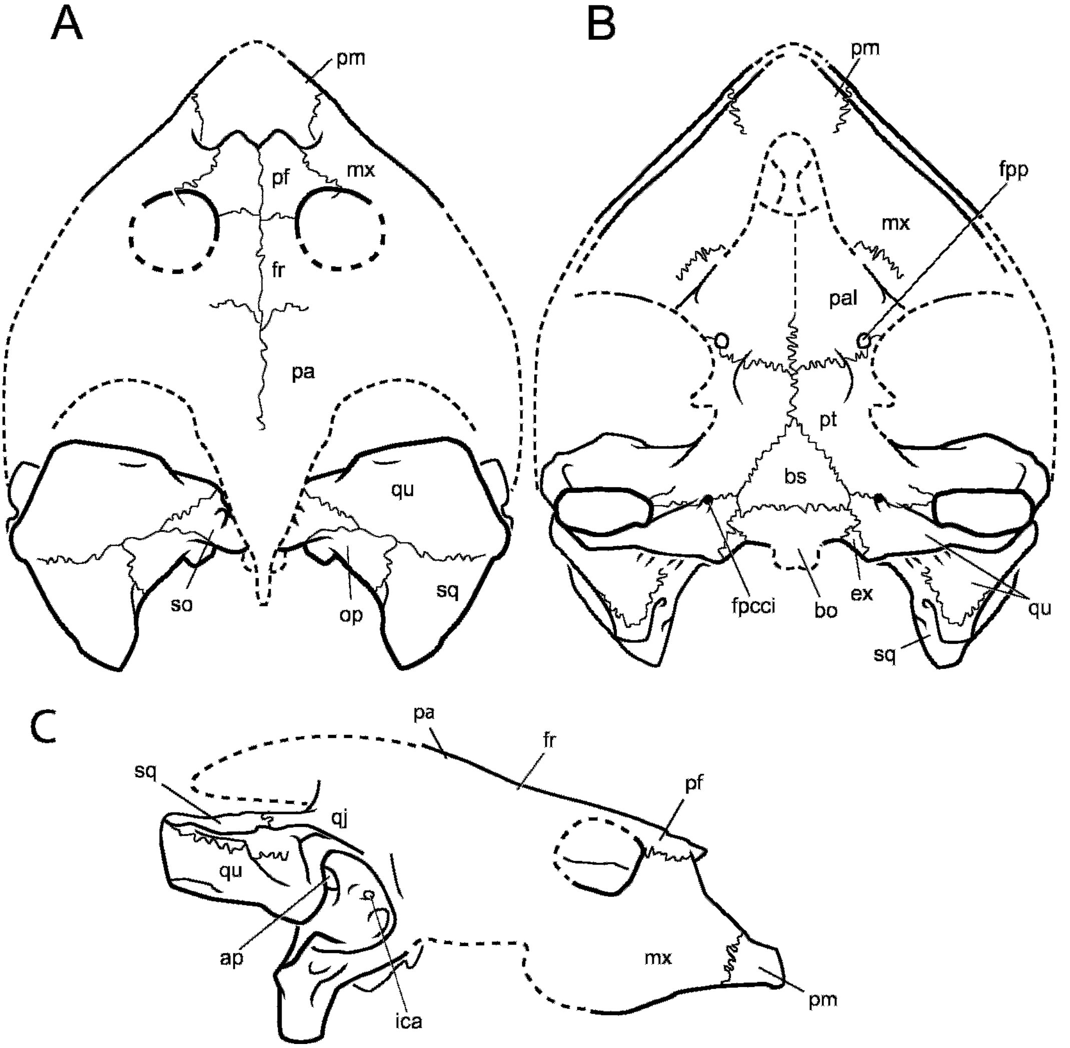

Fig. 160. *Chedighaii barberi*, n. gen. Partially restored views of skull based on ALAB PV 2001.2. **A**, dorsal; **B**, ventral; **C**, lateral. [F. Ippolito, del.]

running along most of the opisthotic length. Other bothremydids have a ridge here, but *C. hutchisoni* is unusual in that the ridge is extended in length posteriorly and reduced in thickness. The relative distance between the fenestra postotica and the foramen jugulare posterius seems to be greater in *C. hutchisoni* than in *Bothremys*, *Araiochelys*, or *Zolhafah*.

BASISPHENOID (figs. 155–158)

Preservation: The basisphenoid is present in KUVP 14765, clearly defined with clear sutures, but it has cracks causing slight displacement. Only the ventral surface is visible.

Contacts on ventral surface: As in other bothremydids, the basisphenoid of *Chedighaii hutchisoni* contacts the pterygoids anterolaterally, the basioccipital posteriorly, and the quadrate posterolaterally. The quadrate contact is very narrow, as in *Bothremys* but in contrast to *Foxemys* and *Polysternon*.

Structures on ventral surface: The basisphenoid has a slight posterior depression

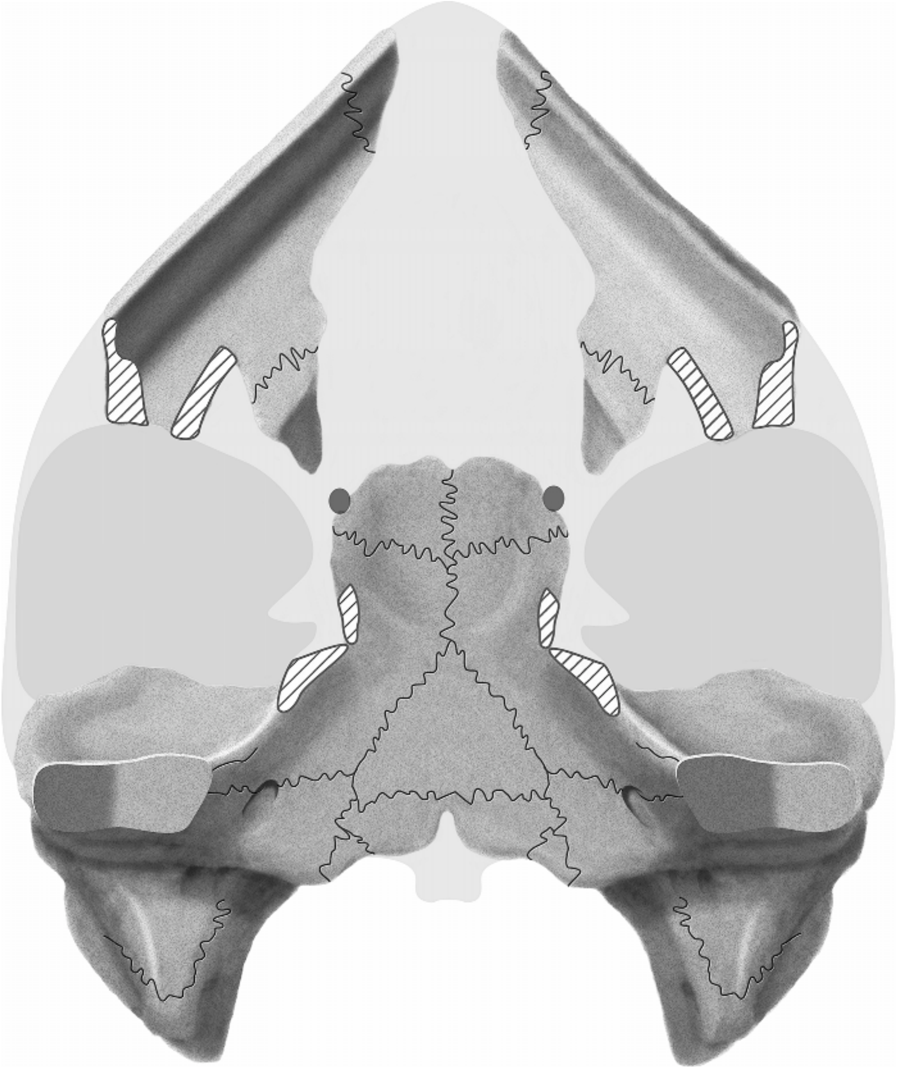

Fig. 161. *Chedighaii barberi*, n. gen. Partially restored ventral view based on ALAB PV 2001.2. [J. Dowis, del.]

continuing from the basioccipital. The basisphenoid in *Chedighaii hutchisoni* has the usual triangular shape, but its anterior edge is broadly curved, not meeting in a point as in *Bothremys* and *Araiochelys*. The basisphenoids in *Zolhafah* and *Rosasia* are also blunt, as in *Polysternon* and *Foxemys*.

Contacts and structures on dorsal surface: The dorsal surface is not visible in KUVP 14765.

Chedighaii barberi

Two partial skulls and a skull endocast are the basis for the skull descriptions for this taxon. The species type specimen is a shell (Schmidt, 1940). The two skulls have shell material associated with them that is the basis for the identification. However, considering the conservative nature of other bothremydid shells, it is possible that more than one species have similar shells and that the cranial material here identified as *C. barberi* represents more than one species. Furthermore, the skulls are not complete enough to be sure that there are not some differences that have been missed due to nonpreservation. Nonetheless, the two skulls agree in all the preserved areas. Another consideration is the wide geographic spread (fig. 18) of shells attributable to *Chedighaii*, consistent with more than one species. See Note Added in Proof.

The endocast (figs. 166, 167) is identified as *C. barberi* because it agrees closely with the two partial skulls. The endocast is not just the cavum cranii but almost the entire (negative) skull, including the fossa orbitalis and fossa nasalis. The fact that it lacks pits (although subtle) was missed by the original describer (Gaffney, 1977a; hey, it was a long time ago). The endocast shows some interesting information about the skull (see below), and a mold of the endocast allows direct comparisons to be made with the other skull specimens.

In the collections of the North Carolina State Museum is a series of otic chambers from the Campanian Tar Heel Formation of North Carolina (Gaffney and Schneider, ms.). These chambers are indistinguishable from the *Chedighaii barberi* ear regions available from the Selma Formation skulls but are too incomplete to be identified with certainty as *C. barberi*. The quadrate of one of these is figured here (fig. 286D).

One of the partial skulls, FMNH PR247, was described by Gaffney and Zangerl (1968), and the endocast, YPM PU 12951, was described by Gaffney (1977a).

PREFRONTAL (figs. 160, 165)

Preservation: Portions of both prefrontals are present in ALAB PV 2001.2, with the left prefrontal being the most complete among the three specimens. This bone has the prefrontal descending process, the anterior margin, and part of the orbital rim preserved. The right prefrontal has only the horizontal area next to the midline. Both prefrontals preserve the ventral surface. In FMNH PR 247 portions of the horizontal plates of both prefrontals are present, but the margins are eroded. In the endocast, there are small fragments of both prefrontals anteriorly, and part of the ventral surface is on the endocast.

Contacts: The visible contacts in all three *Chedighaii barberi* specimens show the prefrontal meeting the other prefrontal medially, the maxilla anteroventrolaterally, and the frontal posteriorly. The maxillary contact does not form a dorsal extension as in *Bothremys cooki* and *B. maghrebiana*. The palatine is not well preserved, so possible contacts or a close approximation of palatine and prefrontal as in *C. hutchisoni* is not determinable.

Stuctures: The dorsal plate of the prefrontal in *Chedighaii barberi* is very similar to that in *C. hutchisoni*. There is a midline projection that is nearly identical in extent and shape, and the shape of the apertura narium externa margin is the same. The dorsal margin of the orbital rim is not preserved in any specimen except the endocast, and this shows that the interorbital distance in *C. barberi* is relatively narrow, as in *C. hutchisoni* but in contrast to the wider distance in *Bothremys*.

FRONTAL (figs. 160, 165)

Preservation: Parts of both frontals are preserved in FMNH PR 247 and ALAB PV 2001.2, but neither has the lateral, orbital margin region preserved. The endocast has the ventral surface of both frontals visible.

Contacts: The frontal in *Chedighaii barberi* contacts the other frontal medially, the prefrontal anteriorly, the parietal posteriorly, and the postorbital (visible only in the endocast) posterolaterally, all as in other Bothremydini.

Structures: The orbital margin is seen only in the endocast, which shows that *Chedighaii barberi* has the orbits facing dorsally, as in *Bothremys* and *C. hutchisoni*, as well as relatively small orbital openings, also in these taxa. The sulcus olfactorius is relatively narrow, as in *C. hutchisoni* and *Bothremys*.

PARIETAL (figs. 160, 165)

Preservation: The medial parts of both parietals are present in ALAB PV 2001.2 and FMNH PR 247; part of the ventral surface is in YPM PU 12951.

Contacts of dorsal plate: The parietal in *Chedighaii barberi* contacts the frontal anteriorly, the other parietal medially, and the supraoccipital posteroventrally. The lateral contact with the postorbital is visible in the endocast.

Structures of dorsal plate: The limits of the temporal roof are not preserved in any of the *Chedighaii barberi* specimens. In the endocast, the parietal has a ventral process forming part of the posterior wall of the fossa orbitalis, lateral to the sulcus palatinopterygoideus, as in other Bothremydini.

Contacts of processus inferior parietalis: Only the dorsal part of the processus is preserved in FMNH PR 247 and ALAB PV 2001.2; no ventral contacts are preserved. In YPM PU 12951 most of the processus is preserved on both sides, but the ventral contacts are missing.

Structures of processus inferior parietalis: The foramen interorbitale of *Chedighaii barberi* is preserved only in the endocast, and it is very similar to that in *C. hutchisoni*. The foramen nervi trigemini is not preserved.

JUGAL (figs. 160, 165, 167)

Preservation: The jugal is preserved only on the right side of ALAB PV 2001.2 and in the endocast as an imprint. The portion preserved in ALAB PV 2001.2 is a thin layer of the medial process that lies posterior to the maxilla and forms the anterior wall of the temporal chamber. The endocast portion is the region of the jugal forming part of the fossa orbitalis.

Contacts of lateral plate: Not preserved.

Structures of lateral plate: Not preserved.

Contacts of medial process: In the floor of the fossa orbitalis, the jugal contacts the maxilla anteromedially and the palatine medially. In the septum orbitotemporale, the jugal contacts the postorbital dorsomedially. The portion of the medial process preserved in ALAB PV 2001.2 contacts the maxilla only.

Structures of medial process: The endocast and the partial skull, ALAB PV 2001.2, show that *Chedighaii barberi* did not have the jugal forming part of a pit on the triturating surfaces as in *Bothremys*. This is clear from ALAB PV 2001.2 alone, because it is the posterior part of the triturating surface on the maxilla that is actually preserved (figs. 164, 165). In YPM PU 12951 (figs. 166, 167) it is less obvious, but the jugal and maxilla form a deep rim below the orbital margin, as in *C. hutchisoni*, which is very different from the absent rim of *Bothremys cooki*. The pit itself would not be seen in the endocast, but the floor of the fossa orbitalis is clearly very similar in *C. hutchisoni* and *C. barberi* and distinct from the floor in *Bothremys*.

The pitted bothremydids all have at least some of the jugal significantly altered from the primitive condition to form part of the pit. Enough of the jugal (and maxilla) is preserved in *C. barberi* to show that a pit was absent and that the jugal has no exposure on the triturating surface. The jugal in *C. barberi* is exposed in the anterior wall of the fossa temporalis, as in *C. hutchisoni*.

QUADRATOJUGAL

Preservation: No fragment remains of the poor quadratojugal in any of the three *Chedighaii barberi* specimens.

SQUAMOSAL (figs. 160, 165)

Preservation: Most of both squamosals are present in ALAB PV 2001.2, but only a fragment remains in FMNH PR 247. The anterodorsal margin is missing on both sides of ALAB PV 2001.2. The endocast has nothing of this bone.

Contacts: The squamosal in *Chedighaii barberi* contacts the quadrate anteriorly and anteromedially and the opisthotic medially. The anterodorsal margin is missing; a quadratojugal contact cannot be determined.

Structures: The squamosal in *Chedighaii barberi* has the posterior triangular projection typical of the Bothremydini, with a ventral ridge and thin, dorsolateral shelf continuing the line of the temporal emargination. The antrum postoticum is a narrow canal, as in *Bothremys* and *C. hutchisoni*.

POSTORBITAL (fig. 167)

Preservation: The only postorbital information for *Chedighaii barberi* is on the endocast which shows the exposure of the bone in the posterior wall of the fossa orbitalis.

Contacts and structures of lateral plate: Not preserved.

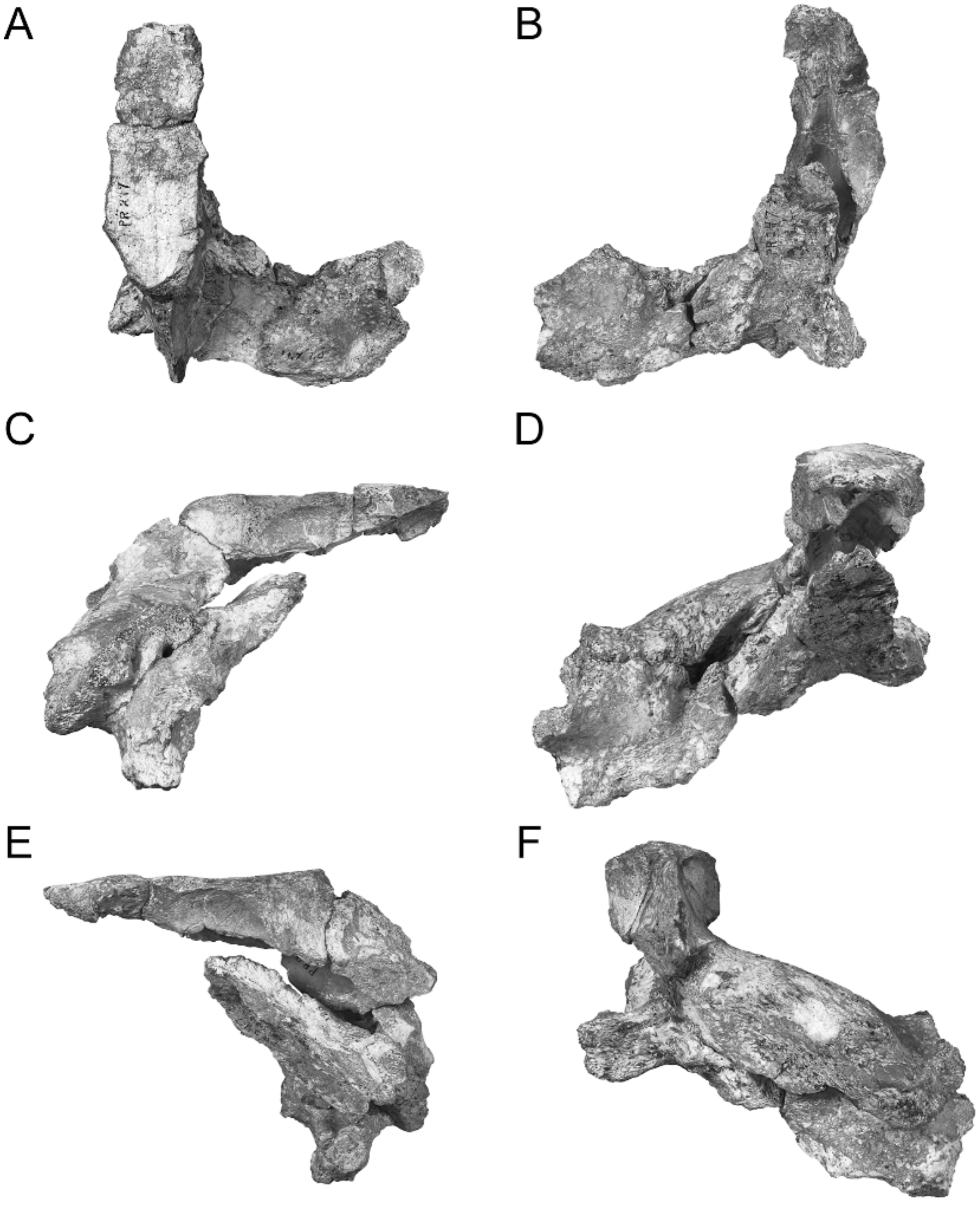

Fig. 162. *Chedighaii barberi*, (identified in proof as *Bothremys* sp.) FMNH PR 247. **A**, dorsal; **B**, ventral; **C**, right lateral; **D**, anterior; **E**, left lateral; **F**, posterior. See also Gaffney and Zangerl (1968) for other figures. [E. Ullo, del.]

Contacts of medial process: In the endocast the fossa orbitalis shows the postorbital contacting the frontal anteromedially, the parietal posteromedially, the jugal ventrolaterally, and the palatine ventrally.

Structures of medial process: Only the endocast provides information on this area,

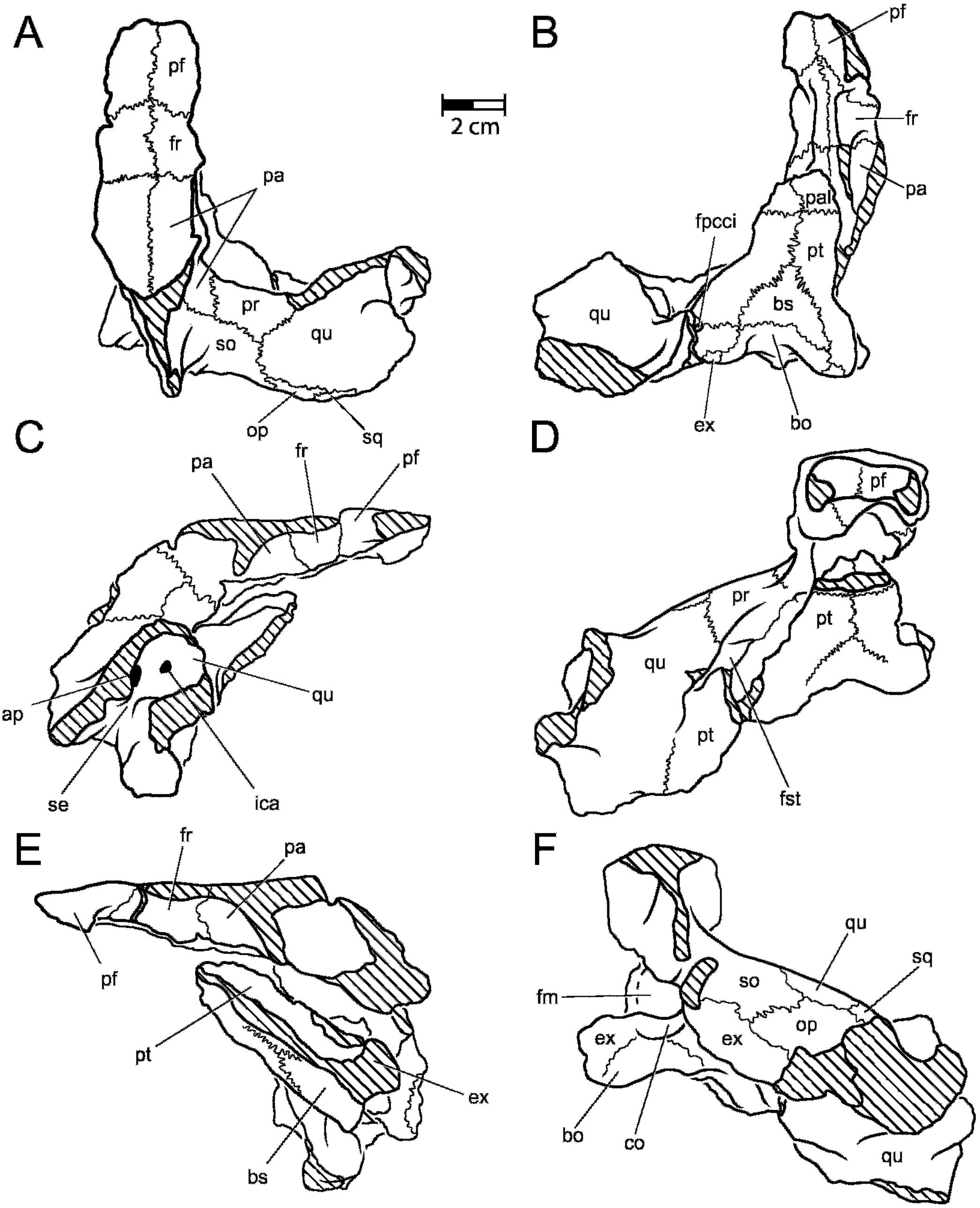

Fig. 163. *Chedighaii barberi* (identified in proof as *Bothremys* sp.). FMNH PR 247. **A**, dorsal; **B**, ventral; **C**, right lateral; **D**, anterior; **E**, left lateral; **F**, posterior. [E. Ullo, del.]

and it shows the fossa orbitalis, that is, the anterior wall of the septum orbitotemporale. The fossa orbitalis of *Chedighaii barberi* has a large posterior/posteroventral chamber formed primarily by the postorbital, jugal, parietal, and palatine. This chamber is particularly apparent in the endocast when the anterior position of the orbital margin is compared with the rest of the fossa. This posteroventral chamber in *C. barberi* is very similar to the one in *C. hutchisoni*, but the chamber is present in nearly all bothremydids.

PREMAXILLA (figs. 160, 161, 165, 167)

Preservation: The left premaxilla, lacking its more medial portion, and a small part of the right oneare preserved in ALAB PV 2001.2. The endocast shows the dorsal surface of the premaxilla.

Contacts: The premaxilla contacts the maxilla posteriorly and the other premaxilla medially. A possible vomer contact is not preserved.

Structures on dorsal surface: The endocast shows a relatively large premaxilla forming the floor of a wide fossa nasalis. The fossa is also wide in *Chedighaii hutchisoni*, although its floor and the premaxillae are missing. The fossa in *Bothremys* seems to be relatively narrower. The foramen praepalatinum lies within the premaxilla. It seems unlikely that a dorsal process, as in *Araiochelys* and *Bothremys*, was present in *C. barberi*. The endocast shows a relatively flat floor anteriorly, although the actual margin of the apertura narium externa is not present.

The ventral margin of the apertura narium externa is preserved laterally in ALAB PV 2001.2, and it shows a protuberant premaxilla, distinct from *Bothremys* and other Bothremydini. The midline portion is missing, so its complete outline is unknown, but it clearly had an apertura that faced more dorsally than in the other Bothremydini. Unfortunately, the ventral part of the apertura is missing in *Chedighaii hutchisoni*.

Structures on ventral surface: The labial ridge in *Chedighaii barberi* is straight, in contrast to the pinched or curved one in other Bothremydini. The premaxilla edge continues the shape and line of the maxilla edge. The ridge is acute along the margin; its surface is curved convex laterally and flat medially. None of the medial plate is preserved.

MAXILLA (figs. 160, 161, 165, 167)

Preservation: Nearly all of the vertical plate is preserved on the left side of ALAB PV 2001.2 and much of it on the right. The endocast preserves the maxillary surface inside the fossa nasalis and fossa orbitalis.

Contacts of vertical plate: The right and left maxillae of ALAB PV 2001.2 show the anterior contact with the premaxilla. The left maxilla has the anterodorsal contact with the prefrontal. The prefrontal extends ventrally along the dorsal process of the maxilla, as in *Chedighaii hutchisoni*, and probably comes close to a palatine contact. The palatine is present on the left side of ALAB PV 2001.2, but it is broken in the area of possible prefrontal contact. The position of the jugal contact on the lateral surface of the maxilla is indeterminate. The possible contact of the maxilla with the quadrate and quadratojugal is also indeterminate.

Structures of vertical plate: The orbital margin is not preserved in ALAB PV 2001.2 or FMNH PR 247, but in ALAB PV 2001.2 much of the rim is present. This agrees with the endocast in showing that there was a high rim above the floor of the fossa orbitalis. The deep maxilla seen in *Chedighaii barberi* also occurs in *C. hutchisoni* and *Bothremys*. The maxilla forms the dorsolateral edge of the apertura narium externa (see also Premaxilla, Prefrontal). In *C. barberi* the apertura is strongly inclined so that it faces anterodorsally, probably as in *C. hutchisoni* but in contrast to other Bothremydini, which are not as strongly inclined. The fossa nasalis in *C. barberi* is relatively wide, as in *C. hutchisoni* and *Bothremys*. It leads into the choanal passages, seen in the endocast and in fragments in ALAB PV 2001.2.

Contacts of horizontal plate: The maxilla contacts the premaxilla anteriorly, but the medial plate here is missing. The posteromedial maxilla-palatine contact is preserved in part on the left side of ALAB PV 2001.2, as is the jugal contact posterolaterally (see Jugal). In the endocast, the floor of the fossa orbitalis shows the dorsal surface contacts: palatine posteromedially and the jugal posterolaterally.

Structures of horizontal plate: The triturating surface in *Chedighaii barberi* is preserved only to a limited extent. Anteriorly it is missing, but the posterior part can be determined accurately using the two maxillae preserved in ALAB PV 2001.2. The labial ridge on the maxilla is as described for the premaxilla: relatively thin, acute margin, outer surface convex laterally, inner surface flat. The labial ridge in ventral view is straight, in contrast to *Bothremys* and other Bothremydini. Although curved, only *Araiochelys*, in addition to *C. barberi*, has a fairly thin labial ridge. It is possible, of course, that *C. hutchisoni* also has a narrow labial ridge, but this area is not known in that species. In lateral view, the labial ridge of *C. barberi* is slightly curved, concave ventrally. This is also unique among Bothremydini.

The triturating surface of *Chedighaii barberi* is only preserved in a short section on the left side of ALAB PV 2001.2. Nonetheless, there is enough preserved to determine that pits are absent and that it is much narrower than in *C. hutchisoni.* The part of maxilla preserved in ALAB PV 2001.2 shows a broad curve from the sloped internal surface of the labial ridge to the horizontal medial plate of the maxilla. In the pitted bothremydids this area is clearly marked by the concavity for the pit. The jugal in ALAB PV 2001.2 is not exposed in the triturating surface, and less of the palatine is exposed. The broad curved surface of the triturating surface in ALAB PV 2001.2 is narrower than in *C. hutchisoni*, and the angle of inclination of the labial ridge is somewhat more acute in *C. barberi*, presumably correlated with the narrower surface. The anterior median concavity is not preserved in *C. barberi*, but the medial edge of the triturating surface allows a certain amount of restoration to be controlled. It seems unlikely that in *C. barberi* there would be room for a wide anterior median concavity as seen in *C. hutchisoni.* A more likely size would be that seen in *Bothremys cooki* and *Araiochelys*.

VOMER

Preservation: Not preserved.

PALATINE (figs. 160, 161, 165, 167)

Preservation: Part of the palatine just medial to the maxilla is present on the left side of ALAB PV 2001.2. The right maxilla in ALAB PV 2001.2 also has a small piece of palatine in this area. The endocast shows most of the dorsal surface of the palatine, but its anteromedial part is missing. Part of both palatines remains just anterior to the pterygoid in FMNH PR 247.

Contacts: The palatine contacts the maxilla anterolaterally, the other palatine medially, the pterygoid posteriorly, and the parietal dorsally in the anterior surface of the septum orbitotemporale. A possible vomer contact is indeterminate. The floor of the fossa orbitalis shows the palatine contacting the jugal anterolaterally, the maxilla anteriorly, and the postorbital dorsally.

Structures on dorsal surface: The palatine forms the posterior floor and much of the posterior wall of the fossa orbitalis, as in *Chedighaii hutchisoni.* The fossa orbitalis in *C. barberi* has the posteroventral enlargement seen in *C. hutchisoni*, *Bothremys*, *Araiochelys*, and *Rosasia.* The endocast shows this structure particularly well.

Structures on ventral surface: The palatine section preserved in ALAB PV 2001.2 lies just medial to the maxilla and forms the medial edge of the triturating surface. There is a narrow ledge above the triturating surface that curves medially to form the choanal wall. There is no real lingual ridge in either *Chedighaii* species; the edge just turns dorsally at its margin. The angle of the medial edge of the triturating surface seems to preclude a wide anterior median concavity (see Maxilla) in *C. barberi*; instead, a narrow one, as in *Araiochelys* and *Bothremys cooki*, seems more likely. The apertura narium interna is also probably much narrower in *C. barberi* than in *C. hutchisoni*, but the posterior entry of the choanal passage seems about the same width.

QUADRATE (figs. 160, 163, 165, 286D)

Preservation: Most of both quadrates are present in ALAB PV 2001.2, but they lack the contacts with cheek elements and are broken around the anterior margin of the cavum tympani. In FMNH PR 247 most of the right quadrate is present, but it also lacks sutural contacts around the cavum tympani margins. The endocast has no quadrate information. A number of otic chambers probably belonging to *Chedighaii barberi* are in the North Carolina State Museum and are being described by Gaffney and Schneider (ms). One of these chambers, NCSM 12766, is figured here (fig. 286D).

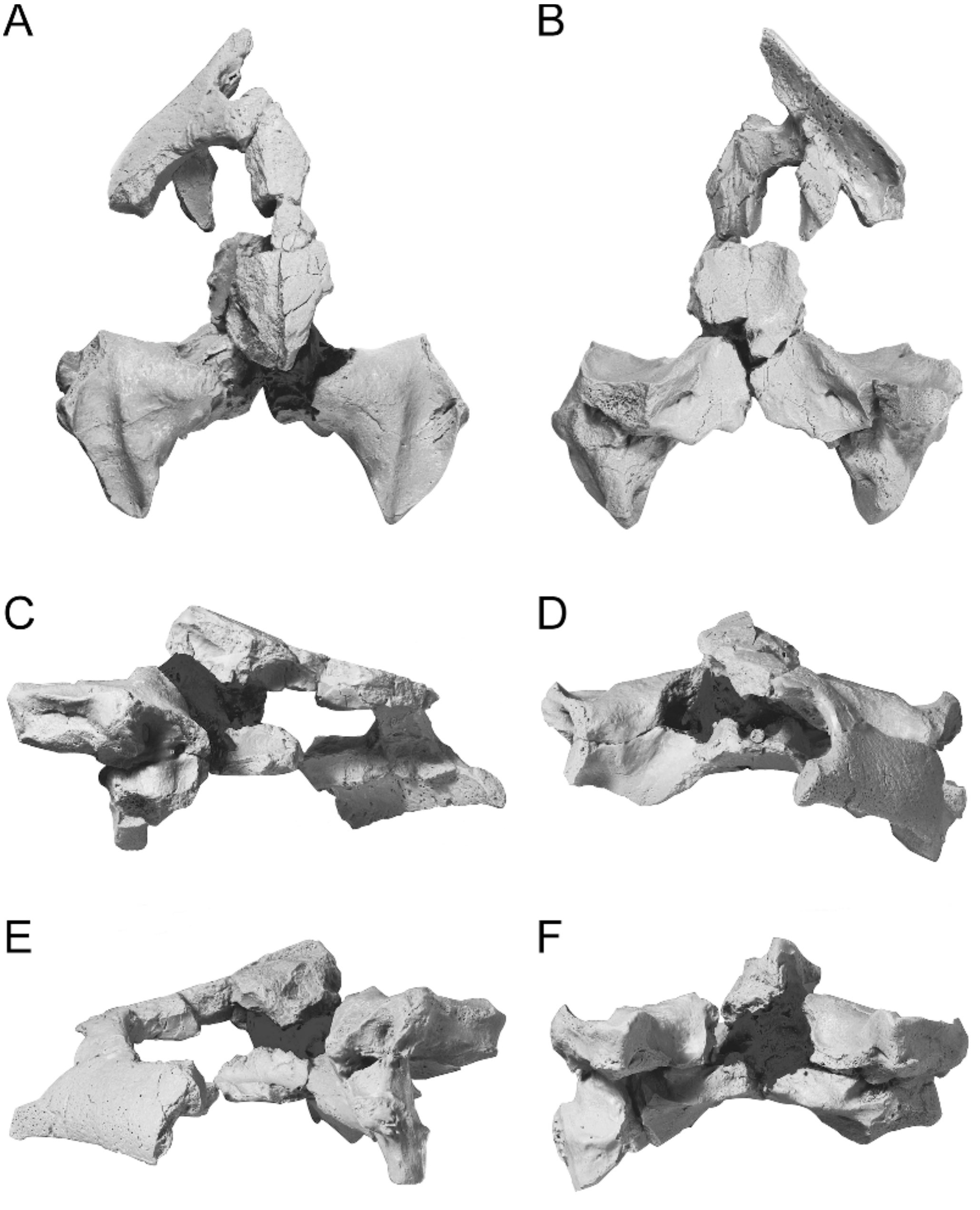

Fig. 164. *Chedighaii barberi* (Schmidt, 1940). ALAB PV 2001.2. **A**, dorsal; **B**, ventral; **C**, right lateral; **D**, anterior; **E**, left lateral; **F**, posterior. [J. Dowis, del.]

Contacts on lateral surface: The only lateral contacts preserved are with the squamosal, which the quadrate contacts posterodorsally.

Structures on lateral surface: The cavum tympani can be determined using both ALAB PV 2001.2 and FMNH PR 247, although FMNH PR 247 is the most

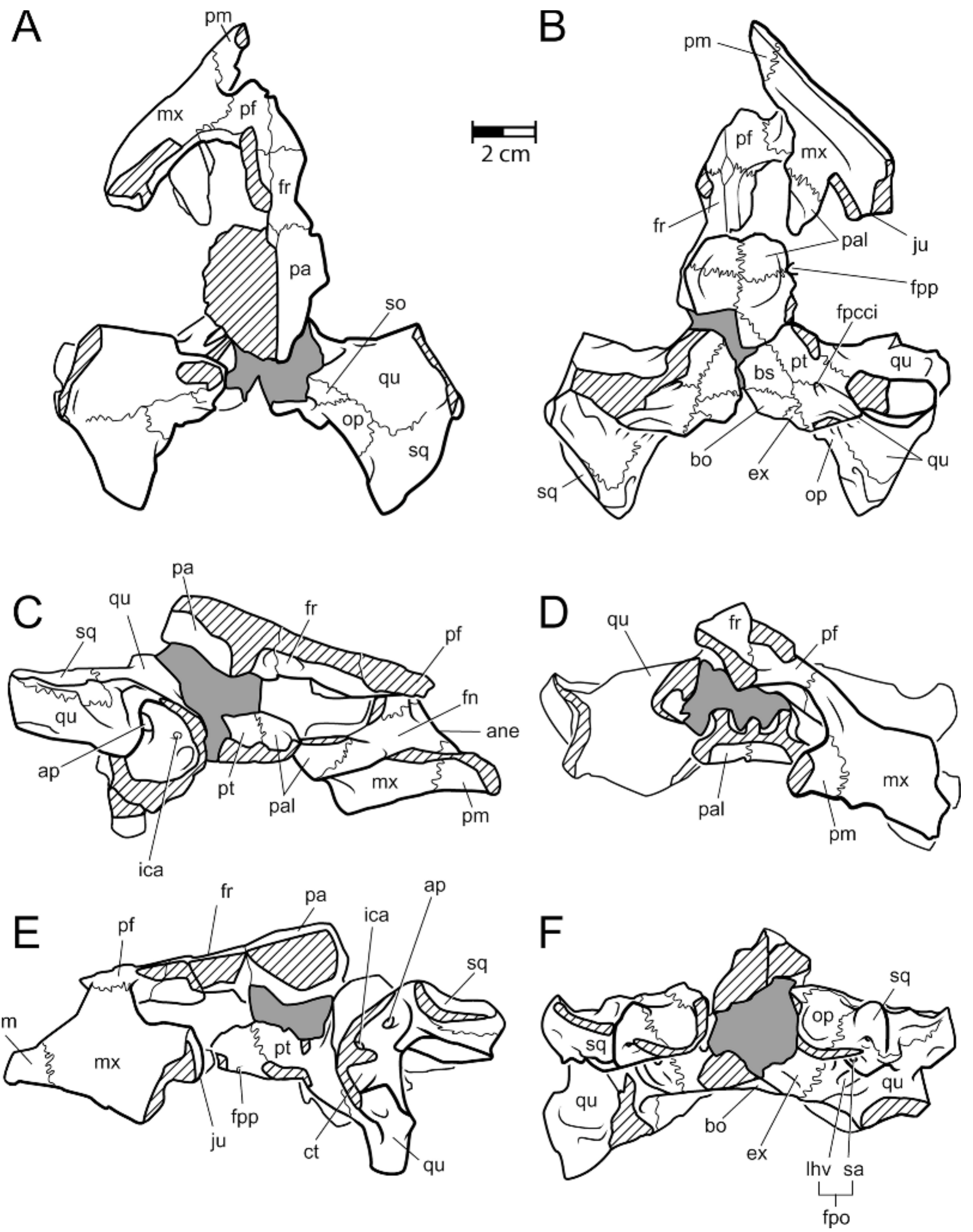

Fig. 165. *Chedighaii barberi* (Schmidt, 1940). ALAB PV 2001.2. **A**, dorsal; **B**, ventral; **C**, right lateral; **D**, anterior; **E**, left lateral; **F**, posterior. [J. Dowis, del.]

complete. The cavum in *Chedighaii barberi* is similar to that in *C. hutchisoni*: fossa precolumellaris absent, incisura columellae auris fully enclosed by bone and widely separated from the sulcus eustachii, antrum postoticum relatively small and tube-like, and shelf below cavum tympani present. The antrum in *C. barberi*,

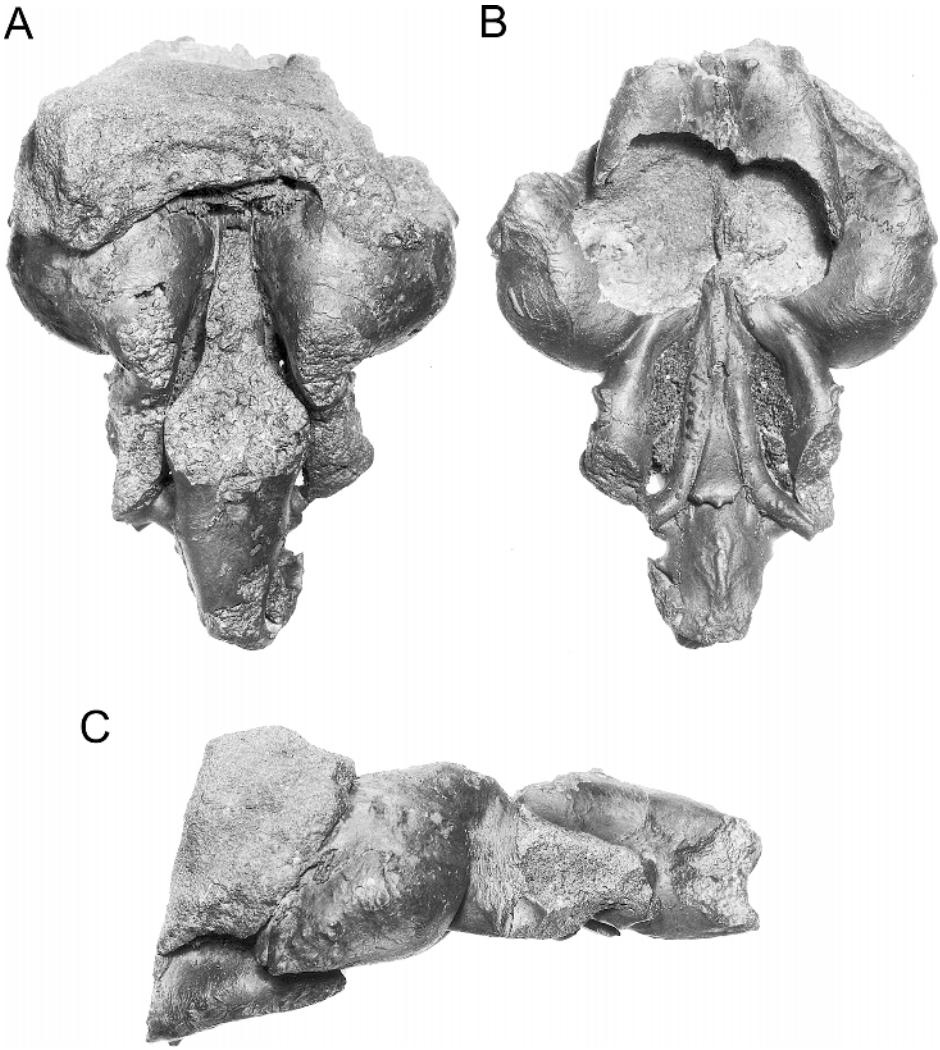

Fig. 166. *Chedighaii* sp. YPM PU 12951. Natural endocast of skull. **A**, dorsal; **B**, ventral; **C**, left lateral. From Gaffney (1977a). [C. Tarka, del.]

however, is smaller than that in *C. hutchisoni*.

Contacts on dorsal and anterior surfaces: As in *Chedighaii hutchisoni* and other Bothremydini, the quadrate in *C. barberi* contacts the prootic anteromedially, the opisthotic posteromedially, the supraoccipital medially, and the squamosal posterolaterally.

Structures on dorsal and anterior surfaces: The foramen stapedio-temporale in *C. barberi* is best seen in FMNH PR 247 and is well anterior on the otic chamber, near the foramen nervi trigemini.

Contacts on ventral surface: The quadrate contacts the pterygoid anteromedially, the basisphenoid medially, and the basioccipital posteromedially.

Structures on ventral surface: There is no fossa pterygoidea in *Chedighaii barberi* or *C. hutchisoni*, however, the bone surface is slightly depressed (so am I) around the foramen posterius canalis carotici interni in both species. The foramen posterius canalis

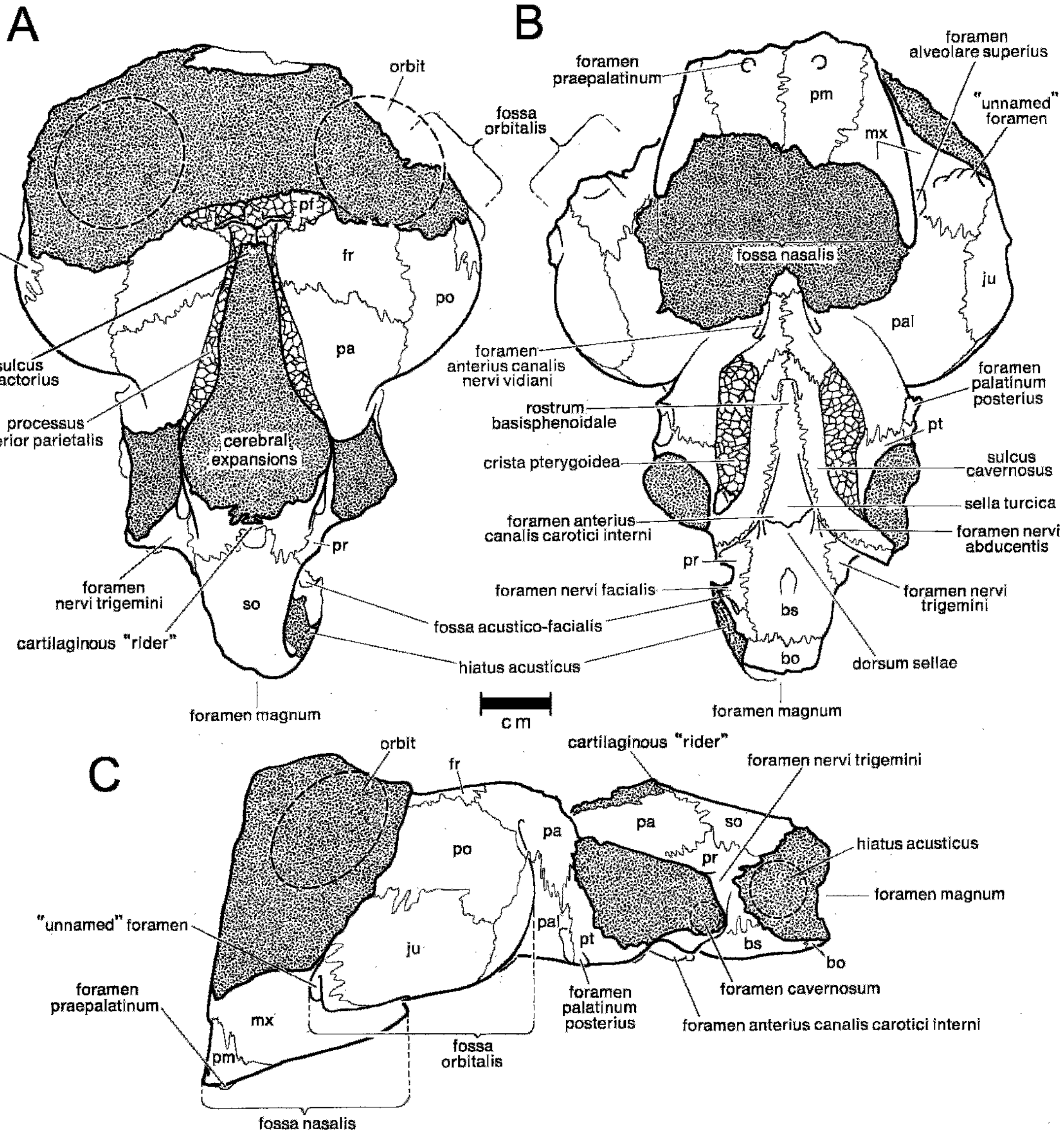

Fig. 167. *Chedighaii* sp. YPM PU 12951. Natural endocast of skull. Irregular stipple is broken matrix, and the reticulate pattern shows areas retaining bone (from Gaffney,1977a). **A**, dorsal; **B**, ventral; **C**, left lateral. [L. Meeker, del.]

carotici interni is formed by the pterygoid anteriorly and the quadrate posteriorly, as in *C. hutchisoni*, *B. cooki*, *B. maghrebiana*, *Araiochelys*, and *B. arabicus*. The condylus mandibularis in *C. barberi* is slightly anterior to the condylus occipitalis, whereas in *C. hutchisoni* it is even with the condylus occipitalis.

Contacts on posterior surface: The quadrate contacts the squamosal dorsolaterally, the opisthotic dorsomedially, the exoccipital medially, and the basioccipital ventromedially.

Structures on the posterior surface: The occipital surface of the skull in ALAB PV 2001.2 and FMNH PR 247 is not well preserved, so all the features cannot be seen clearly. The fenestra postotica is completely separated into two foramina (right side of ALAB PV 2001.2): a smaller, dorsomedial one for the stapedial artery, and a larger, ventrolateral one for the infamous lateral head vein. These divisions are only low ridges in *Chedighaii hutchisoni.*

PTERYGOID (figs. 160, 161, 163, 165, 167)

Preservation: All three specimens of *Chedighaii barberi* have some part of the pterygoid preserved, but none is even partially complete. The two sides of ALAB PV 2001.2 have the best pterygoids, with both lacking the processus trochlearis pterygoidei, the lateral margins, and the thin bone near the foramen nervi trigemini. The posterior and medial part of the right pterygoid remains in FMNH PR 247, but the bone surface is eroded. The endocast shows the medial dorsal surface of the pterygoid and some of the sulcus palatinopterygoideus floor.

Contacts on ventral surface: The pterygoid contacts the palatine anteriorly (only a few fragments of bone in ALAB PV 2001.2 and a small part of the palatine in FMNH PR 247), the quadrate posterolaterally, the other pterygoid medially, and the basisphenoid posteromedially. The basisphenoid contact is straight in *Chedighaii barberi* and curved in *C. hutchisoni.*

Structures on ventral surface: The processus trochlearis pterygoidei and associated flange are missing. The fossa pterygoidea is absent, but there is a shallow depression around the foramen posterius canalis carotici interni, which is formed between the pterygoid and quadrate. The foramen palatinum posterius medial margin that is formed by the pterygoid is present on both sides of ALAB PV 2001.2. It is in about the same position as in *Chedighaii hutchisoni.*

Contacts on dorsal surface: Although much of the dorsal surface of the pterygoid is visible, the crista pterygoidea is broken off close to its base in both ALAB PV 2001.2 and FMNH PR 247 and it is obscured by matrix in YPM PU 12951.

Structures on dorsal surface: A portion of the damaged foramen nervi trigemini is preserved on the left side of ALAB PV 2001.2 and shows that the pterygoid entered the foramen. Part of the sulcus and canalis cavernosus is adjacent.

SUPRAOCCIPITAL (figs. 160, 163, 167)

Preservation: The anterior part of the supraoccipital, lacking all but the base of the crista supraoccipitalis, is present in FMNH PR 247. A small section of the cavum cranii in YPM PU 12951 shows a supraoccipital imprint. A small part of the anteroventral edge and the lateral processes are preserved in ALAB PV 2001.2.

Contacts: The supraoccipital contacts the parietals anterodorsally, the prootic anterolaterally, the quadrate laterally (this is incorrectly identified as opisthotic in Gaffney and Zangerl, 1968: fig. 18), and the exoccipitals posteroventrally.

Structures: The base of the crista supraoccipitalis is preserved and it agrees with that in *Chedighaii hutchisoni.*

EXOCCIPITAL (figs. 160, 163, 165)

Preservation: Most of the right exoccipital is present in FMNH PR 247, but it is eroded and not well preserved so that sutures and foramina are unclear. The better preserved ALAB PV 2001.2 has some of both exoccipitals present, but the condylus occipitalis and most of the dorsal portions are broken away.

Contacts: The exoccipital in *Chedighaii barberi* contacts the supraoccipital dorsally, the opisthotic laterally, the quadrate ventrolaterally, and the basioccipital ventrally.

Structures: The shape of the foramen magnum in *Chedighaii barberi* cannot be determined, although one was almost certainly present. The only part of the condylus occipitalis preserved is in FMNH PR 247, and it does not show sutures; most of the bone surface is eroded away. The foramen nervi hypoglossi are present, but their position relative to sutures is unclear. The foramen jugulare posterius is also not well preserved. The fenestra postotica is widely separated by bone from the foramen jugulare posterius, and the lateral margin of the foramen jugulare posterius is largely present, showing that it was closed.

BASIOCCIPITAL (figs. 160, 163, 165)

Preservation: Most of the basioccipital is present in ALAB PV 2001.2 and FMNH PR 247, but it is damaged and the condylus occipitalis is missing or badly preserved.

Contacts: The basioccipital in *Chedighaii barberi* contacts the basisphenoid anteriorly, the quadrate laterally, and the exoccipital posterodorsally, as in the other Bothremydini.

Structures: Whether the basioccipital in *Chedighaii barberi* contributes to the condylus occipitalis cannot be determined. Distinct but shallow tubercula basioccipitale are present in *C. barberi*, and they are very similar in shape and position to those in *C. hutchisoni*. There is a shallow median concavity in *C. barberi* that is also the same as in *C. hutchisoni*.

PROOTIC (figs. 160, 163)

Preservation: The best prootic is on the right side of FMNH PR 247, with only small portions of the prootic remaining in ALAB PV 2001.2.

Contacts: The prootic in *Chedighaii barberi* contacts the parietal dorsomedially, the quadrate laterally, and the supraoccipital posterodorsally. The dorsal opisthotic contact is prevented by the broad quadrate-supraoccipital contact, as in most Bothremydini. The ventral pterygoid contact is likely but not preserved.

Structures: Very little of the internal features of the prootic are visible, although the path of the foramen nervi facialis can be seen on the left side of ALAB PV 2001.2. The position of the foramen nervi trigemini can be made out in both ALAB PV 2001.2 and FMNH PR 247, but its margins are gone.

OPISTHOTIC (figs. 160, 163, 165)

Preservation: Both opisthotics are present in ALAB PV 2001.2, missing their posterior edges and thinner occipital processes. The same is true of FMNH PR 247, but it also suffers from erosion disease.

Contacts: The opisthotic in *Chedighaii barberi* contacts the supraoccipital anteromedially, the quadrate anterolaterally, the squamosal posterolaterally, and the exoccipital posteromedially.

Structures: The fenestra postotica in *Chedighaii barberi* (see Quadrate) is subdivided into two foramina; its medial limits are formed by the opisthotic. The foramen jugulare posterius (see Exoccipital) is enclosed by bone and widely separated from the fenestra postotica.

BASISPHENOID (figs. 160, 163, 165, 167)

Preservation: All three skulls of *Chedighaii barberi* preserve the basisphenoid. Dorsal and ventral surfaces are in ALAB PV 2001.2, but it is missing its posterodorsal part and has breakage dorsally. All of the bone is present in FMNH PR 247, but the bone surface is eroded. The endocast shows nearly all of the dorsal surface in high fidelity (see also Gaffney, 1977a: fig. 3).

Contacts on ventral surface: The basisphenoid in *Chedighaii barberi* contacts the pterygoid anterolaterally, the basioccipital in a straight suture posteriorly, and the quadrate in a very narrow suture posterolaterally.

Structures on ventral surface: The ventral surface in *Chedighaii barberi* is flat, as in *C. hutchisoni*.

Contacts on dorsal surface: The basisphenoid in *Chedighaii barberi* contacts the pterygoid anterolaterally, the prootic laterally (seen in endocast), and the basioccipital posteriorly.

Structures on dorsal surface: The rostrum basisphenoidale in *Chedighaii barberi* (Gaffney, 1977a: fig. 3) is an elongate rod, seen in all three specimens, that is similar in length and width to that in *Podocnemis* (Gaffney, 1979a: fig. 54) rather than to the rostrum in *Pelusios* (fig. 24), which is wider and shorter. The sella turcica is elongate and deep, also as in *Podocnemis* and in contrast to *Pelusios*. The dorsum sellae in *C. barberi* overhangs the sella turcica to a greater extent than usually seen in *Pelusios* or *Podocnemis*. The foramen anterius canalis carotici interni lie at the corners of the sella turcica as usual. The processus clinoideus is absent; the canalis nervi abducentis is a shallow groove. This condition also occurs in *Bothremys cooki* and *B. maghrebiana*.

TRIBE TAPHROSPHYINI

SUBTRIBE TAPHROSPHYINA

Taphrosphys sulcatus

This, the first described bothremydid (Leidy, 1856, as *Platemys sulcatus*), is still known only from three incomplete skulls, as well as from a great deal of partial shell

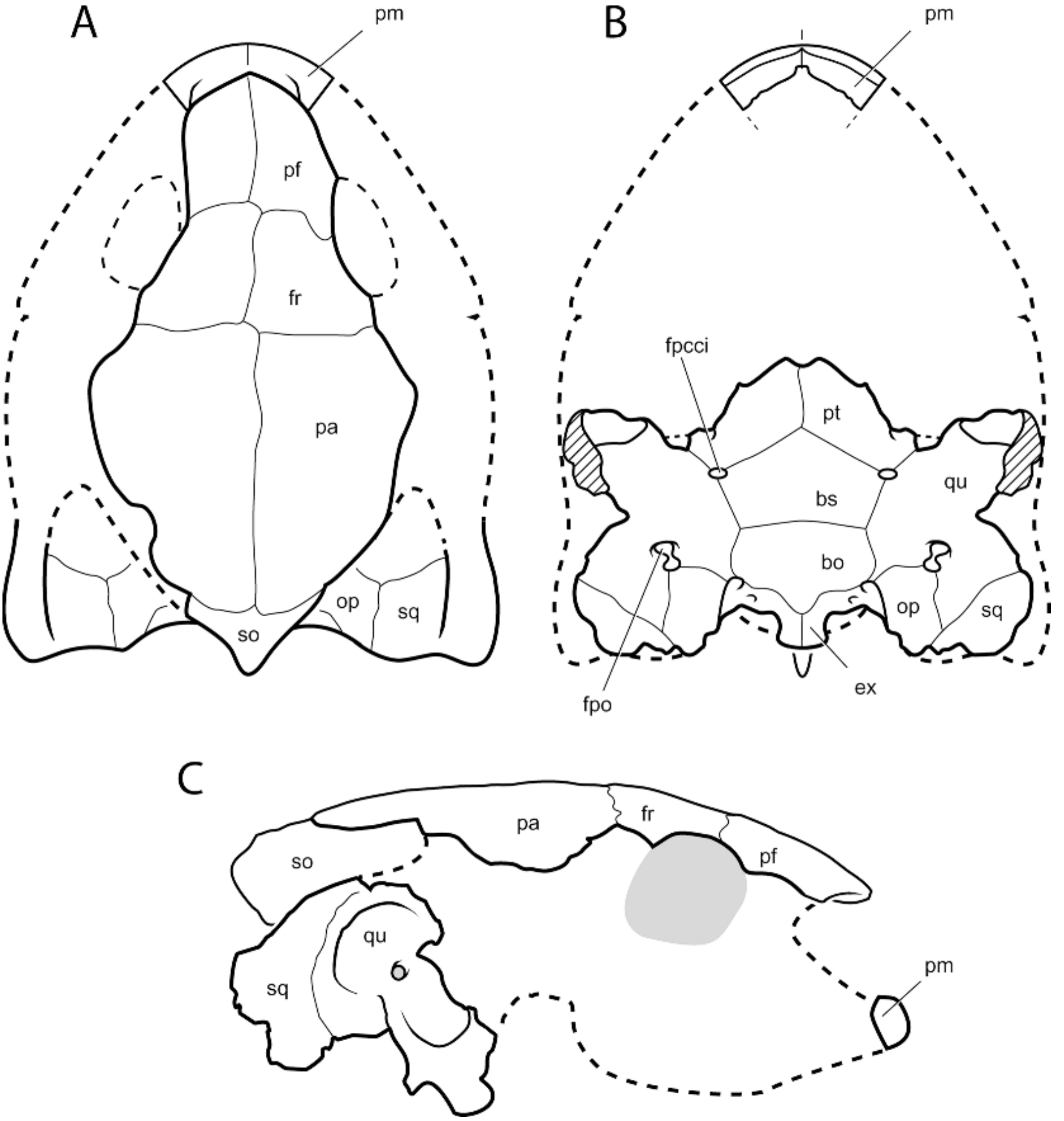

Fig. 168. *Taphrosphys sulcatus* (Leidy, 1856). Composite restored views of skull based on ANSP 15544, NJSM 11362, and YPM PU 18707. **A**, dorsal; **B**, ventral; **C**, lateral. [F. Ippolito, del.]

material. One of three species making up the genus, *Taphrosphys sulcatus*, is weakly supported as the sister taxon to *T. ippolitoi. Taphrosphys* itself is the sister group to *Rhothonemys, Phosphatochelys*, and *Ummulisani*.

Taphrosphys ippolitoi has the most complete cranial material of the three species. The three species of *Taphrosphys* are described in three separate sections, but only one species has the primary description and comparisons, depending on which species has the best preserved bone being described. The reader will therefore need to look at all three sections even if only one species is of interest. The particular species that has the best bone

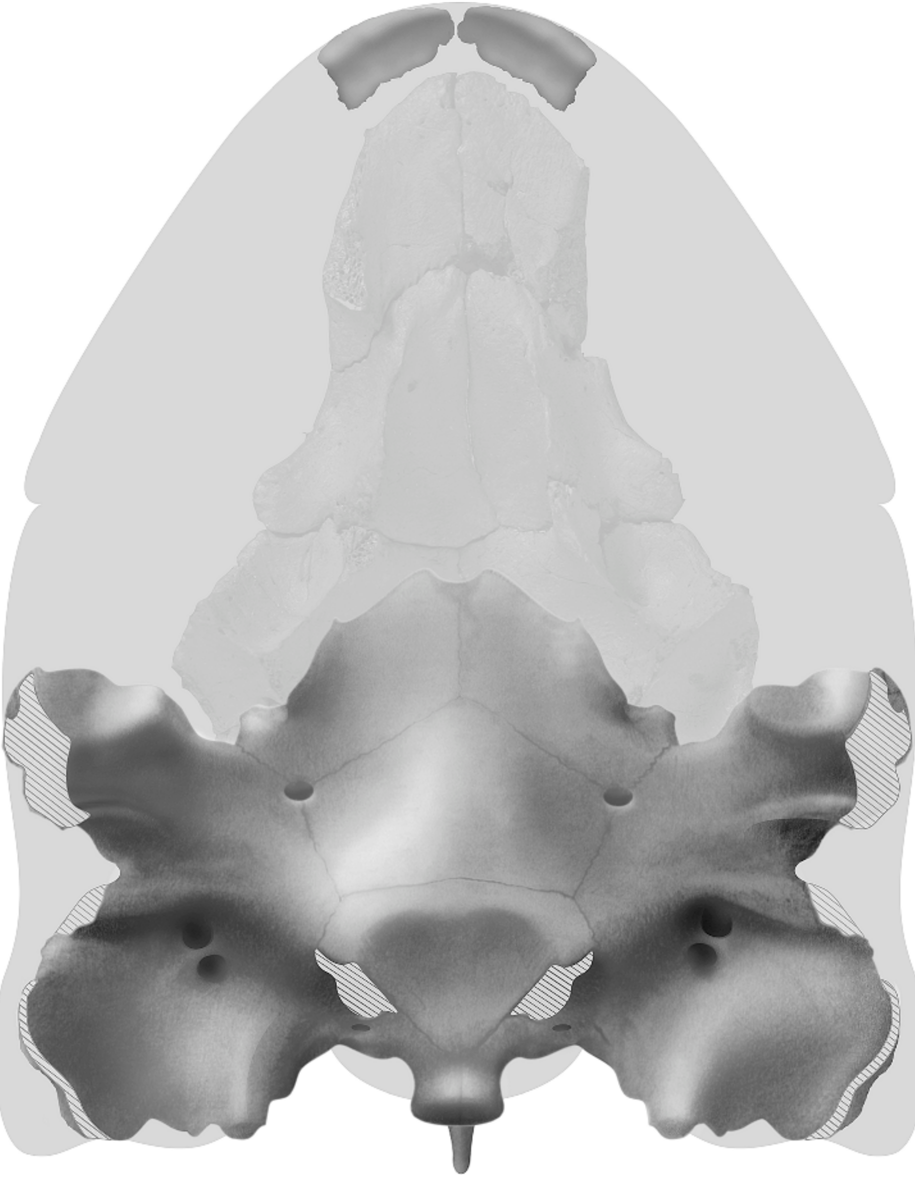

Fig. 169. *Taphrosphys sulcatus* (Leidy, 1856). Partially restored ventral view of skull based primarily on NJSM 11362 with additions from YPM PU 18707 and ANSP 11362. Ventral view of skull roof of ANSP 15544 in light gray. [F. Ippolito, del.]

description for that particular element is always indicated in all three species descriptions.

PREFRONTAL (figs. 168, 170)

Preservation: Both prefrontals are present in ANSP 15544 and are undistorted. However, the ventral process on both sides is broken off.

Contacts: In ANSP 15544 the prefrontal only contacts the parietal posteriorly and the other prefrontal medially, as the maxilla is missing. As in the other two *Taphrosphys* species, the frontal underlies the prefrontal ventrally, forming a V-shaped suture with the apex on the median suture line.

Structures: The prefrontal dorsal plate in *Taphrosphys sulcatus* is very similar to that in *T. congolensis* and *Azabbaremys*. It is smooth and lacks the swelling seen in *T. ippolitoi*. As in *T. ippolitoi* and *T. congolensis* the prefrontal in *T. sulcatus* is relatively thick, particularly along the midline, in contrast to most other bothremydids (e.g., *Galianemys*).

The ventral surface of the prefrontal is visible in *Taphrosphys sulcatus*. It is very similar to that area in *T. congolensis*. The ventral process of the prefrontal and the anterior orbital margin are missing in both prefrontals in ANSP 15544. However, the right prefrontal has the dorsal orbital margin preserved as in *T. congolensis*.

FRONTAL (figs. 168, 170)

Preservation: Both frontals are nearly complete in ANSP 15544 and are visible dorsally and ventrally with clear sutures.

Contacts: The frontal in *Taphrosphys sulcatus*, as preserved in ANSP 15544, only contacts the prefrontal anteriorly and the parietal posteriorly. However, on both sides the frontals and parietals show that a postorbital was present and contacted the posterolateral edge of the frontal. This contact, however, is much shorter in *T. sulcatus* and *T. congolensis* than in *Azabbaremys*.

Structures: The frontal forms most of the dorsal orbital margin in *Taphrosphys sulcatus*, as in *T. ippolitoi* and most other bothremydids. When the orbit of *T. sulcatus* is restored on the basis of the curvature seen in ANSP 15544, the size is consistent with what could be restored for *T. ippolitoi* and *T. congolensis* based on different combinations of preserved elements. However, there is no one skull of *Taphrosphys* that has the orbit completely preserved, and the size and shape could vary among the three species.

PARIETAL (figs. 168, 170, 172, 173)

Preservation: Both parietals in ANSP 15544, the best skull roof for *Taphrosphys sulcatus*, are present and complete with no distortions except for the lateralmost margins, which are missing, and nearly all of the processus inferior parietalis, which is also gone on both sides. A partial skull, YPM PU 18707, has part of the left parietal preserved but it is much less complete than ANSP 15544. Another more complete skull, NJSM 11362, has both parietals present. These are complete dorsally and have good contacts with the supraoccipital, but they also lack most of the processus inferior parietalis on both sides.

Contacts of dorsal plate: In *Taphrosphys sulcatus* only the anterior contact with the frontal and the posteroventral contact with the supraoccipital are preserved.

Structures of dorsal plate: The posterior edge of the parietal in *Taphrosphys sulcatus* that forms the edge of the temporal emargination is preserved in both ANSP 15544 and NJSM 11362, but it is more complete in the latter. The degree of emargination in *T. sulcatus* is consistent with *T. ippolitoi* and is very similar to that in *T. congolensis*. The emargination limits are not determinable in *T. sulcatus*, as they are in *T. congolensis*. However, the emargination seems to be slightly wider in *T. congolensis* than in *T. sulcatus* because the parietal dorsal plate is slightly wider in *T. sulcatus* than in *T. congolensis*. The parietal margin of the temporal emargination in *T. sulcatus* appears to be straight or slightly convex laterally. The parietal on the midline extends posteriorly to the supraoccipital, being exposed in dorsal view as a small triangular or oblong shape.

Contacts of processus inferior parietalis: In *Taphrosphys sulcatus*, NJSM 11362 has enough of the foramen nervi trigemini on the pterygoid and prootic preserved to show that the parietal contacted those bones on either side of the foramen and made up its anterodorsal margin. The processus inferior parietalis also contacted the crista pterygoidea, as seen in NJSM 11362 and YPM PU 18707.

Structures of processus inferior parietalis: In *Taphrosphys sulcatus* only the very dorsal portion of this wall can be seen in ANSP 15544 and NJSM 11362. It is nearly identical to that in *T. congolensis*.

JUGAL

Preservation: Among the specimens identifiable as *Taphrosphys sulcatus*, there is no jugal. Due to the absence of the other palatal elements, maxilla, palatine, as well as

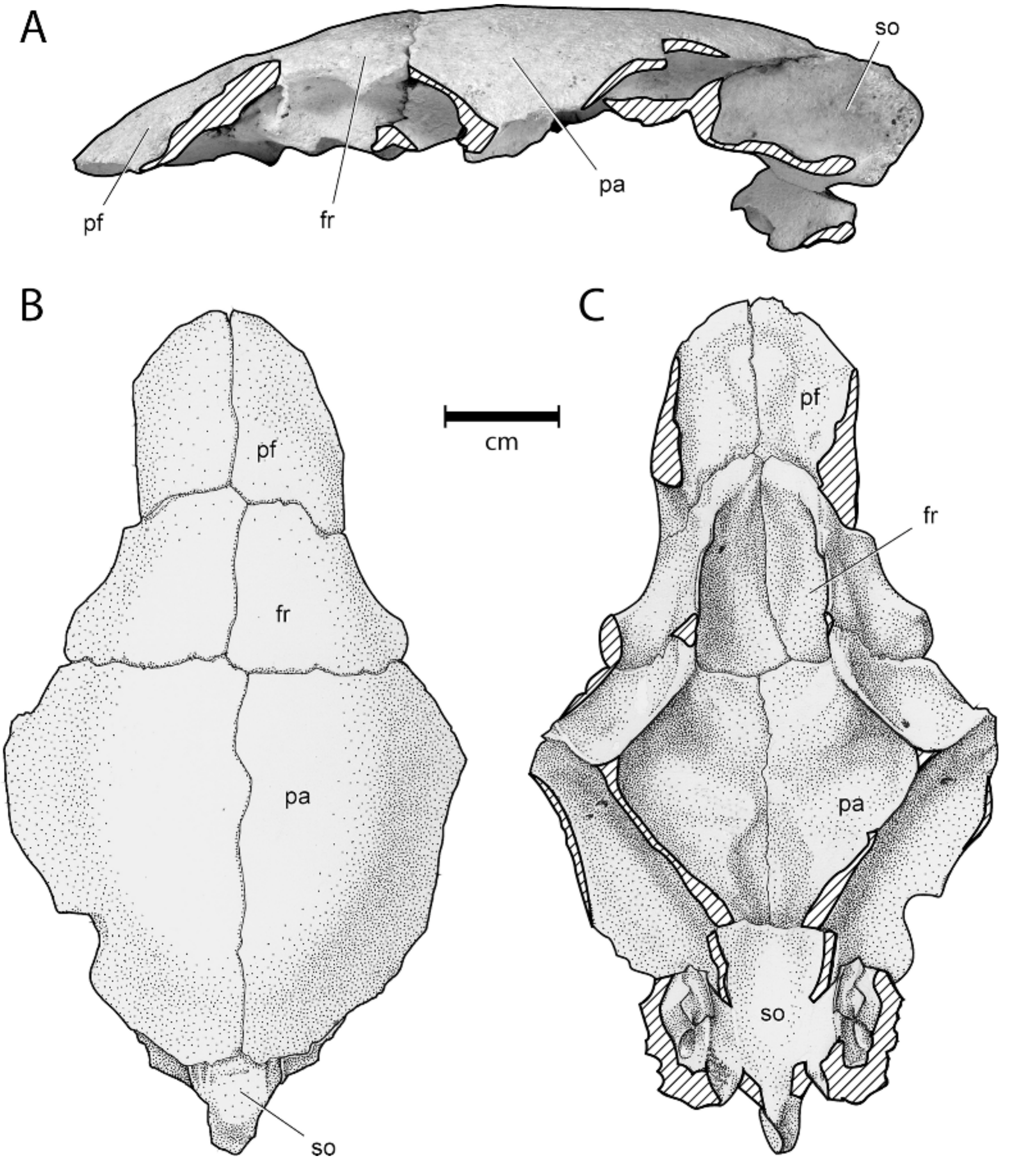

Fig. 170. *Taphrosphys sulcatus* (Leidy, 1856). ANSP 15544 skull roof. **A**, left lateral; **B**, dorsal; **C**, ventral (parts B and C modified from Gaffney, 1979a). [F. Ippolito and J. Emry, del.]

cheek elements, it is not possible to find an adjacent bone articulating with the jugal.

QUADRATOJUGAL

Preservation: The element is absent in all available specimens of *Taphrosphys sulcatus*.

SQUAMOSAL (figs. 168, 169, 176, 177)

Preservation: The nearly complete right squamosal is present in NJSM 11362. It lacks its anteriormost margin and a small section of the posterior margin. ANSP 15544 has a right squamosal that is complete except for its ventral margin and its anteriormost edge.

Contacts: The squamosal has the same contacts on all three *Taphrosphys* species: it lies on the quadrate, contacting it anteriorly and anteromedially, and it contacts the opisthotic medially and the quadratojugal anterodorsally.

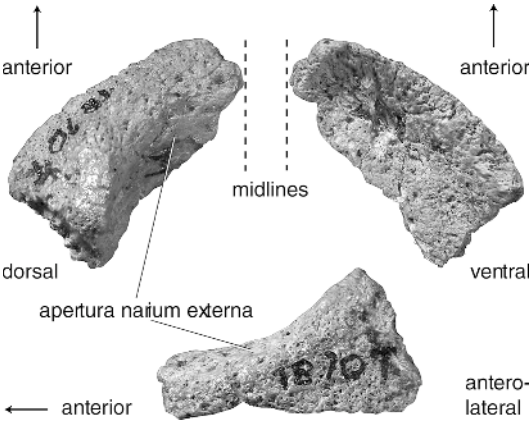

Fig. 171. *Taphrosphys sulcatus* (Leidy, 1856). YPM PU 18707, left premaxilla in three views. [F. Ippolito, del.]

Structures: The antrum postoticum in *Taphrosphys sulcatus* is particularly visible in ANSP 15544, which includes a disarticulated right quadrate and right squamosal (fig. 176). The antrum itself is described under Quadrate, but its posterior cap is formed by the squamosal and can be seen in this specimen. In most turtles the antrum postoticum is a large cavity surrounded by relatively thin walls. In many bothremydids the antrum is small or absent. In *Taphrosphys* it is much smaller than in pelomedusids and smaller than in *Galianemys*, but it is still distinct. The removable right squamosal of ANSP 15544 shows that even though the antrum is reduced almost to a canal, it still significantly affects the formation of the squamosal and forms a smooth, hemispherical pocket that surrounds the tubelike extension of the quadrate.

The squamosal of *Taphrosphys sulcatus*, seen in NJSM 11362 (fig. 177), has a distinct ventral flange developed to about the same extent as in *T. congolensis*, both of which are smaller than in *T. ippolitoi*. Although the posterior margins of all the *T. sulcatus* squamosals are broken, they are very thin, and a posterior extension of the sort seen in *Labrostochelys* was not present.

POSTORBITAL

Preservation: Although one was almost certainly present, there is no postorbital in any available specimen of *Taphrosphys sulcatus*.

Contacts and structures: The only information on the postorbital in *Taphrosphys sulcatus* relates to the sutured edges on the frontals and parietals in ANSP 15544. These are consistent with a postorbital that is the same size and shape as the ones in *T. congolensis* and *T. ippolitoi*.

PREMAXILLA (figs. 168, 169, 171)

Preservation: The available material of *Taphrosphys sulcatus* lacks all the bones of the palate except for a single premaxilla, the left one, in YPM PU 18707. This element lacks its posterior plate.

Contacts and structures: The premaxilla in YPM PU 18707 is very similar to the better preserved premaxilla in the other *Taphrosphys* species, except that the labial ridge is deeper in *T. congolensis* than in *T. sulcatus* and *T. ippolitoi*. See *T. ippolitoi* description for more information on the *Taphrosphys* premaxilla.

MAXILLA

Preservation: Although one was almost certainly present, there is no maxilla in any of the available *Taphrosphys sulcatus*.

VOMER

Preservation: The vomer is missing.

PALATINE

Preservation: Although one was almost certainly present, it is not preserved in the available specimens of *Taphrosphys sulcatus*.

QUADRATE (figs. 168, 169, 172, 173, 176, 177)

Preservation: Partial left and right disarticulated quadrates of *Taphrosphys sulcatus* are present in ANSP 15544, and a nearly complete right quadrate is in NJSM 11362.

Contacts on lateral surface: All three *Taphrosphys sulcatus* quadrates completely lack the anterior part of the bone, and the only suture visible in lateral view is the posterior one with the squamosal, which is the same as in the other two *Taphrosphys* species.

Structures on lateral surface: The cavum tympani in *Taphrosphys* is distinctly oval or kidney bean-shaped, not circular as in *Azabbaremys* and *Phosphatochelys*. *T. sulcatus* shows this shape, as do the other two *Taphrosphys* species. In *T. sulcatus* the cavum is slightly deeper than in *T. congolensis*,

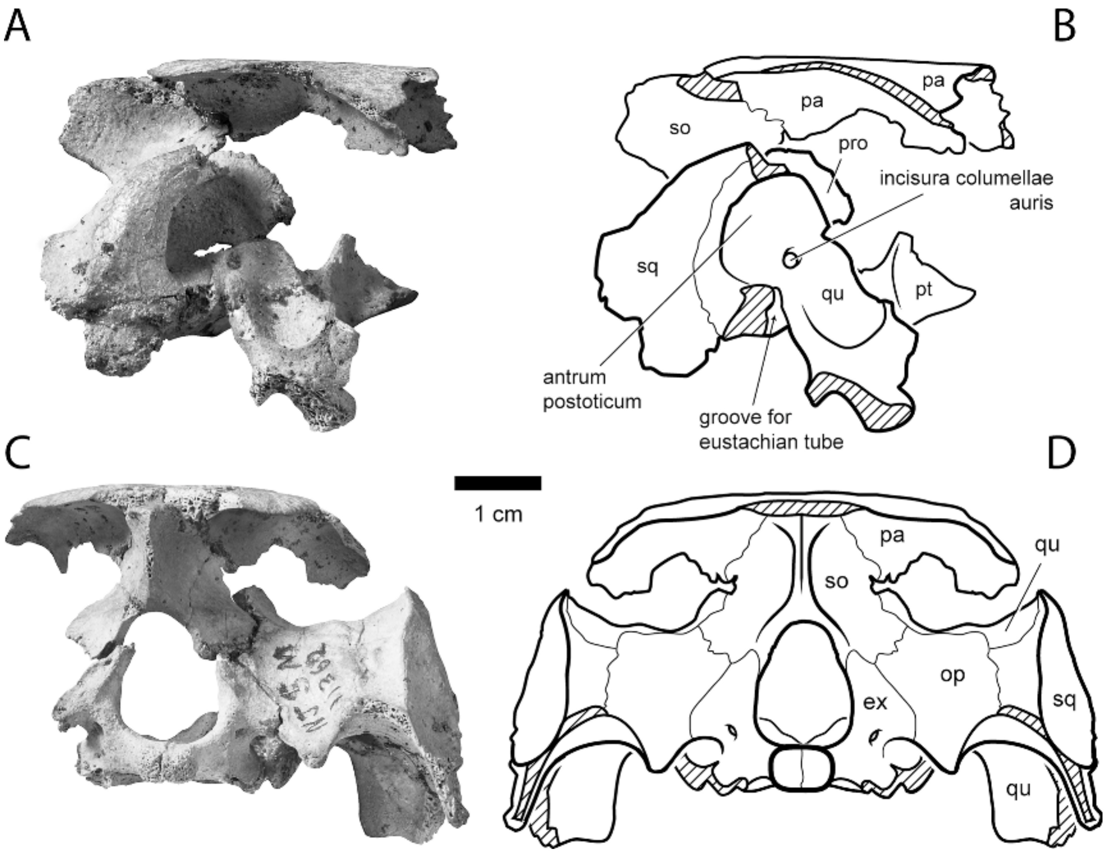

Fig. 172. *Taphrosphys sulcatus* (Leidy, 1856). NJSM 11362, incomplete posterior part of skull. **A**, **B**, right lateral view; **C**, posterior; **D**, posterior partially restored. [F. Ippolito, del.]

particularly the anteroventral part of the concavity. The incisura columellae auris in all *Taphrosphys* and in all Taphrosphyini is a round canal well separated by bone from the eustachian tube groove. In *T. sulcatus* there is a barely discernable groove from the incisura to the eustachian groove; a similar groove is in *T. congolensis*. However, in *T. ippolitoi* the groove is well defined by two parallel ridges, similar to the condition in *Galianemys*.

The antrum postoticum in *Taphrosphys sulcatus* is smaller than in pelomedusids and is similar in size to that in *Phosphatochelys*. The antrum in *T. ippolitoi* is slightly smaller than in *T. sulcatus*; the *T. congolensis* quadrates are crushed down to the level of the antrum so that neither is visible. In *T. sulcatus* the antrum postoticum is close to the lateral edge of the quadrate, as in *Phosphatochelys*, but in *T. ippolitoi* the antrum is placed more deeply in the cavum tympani, presumably because the cavum is deeper.

Although the anterior part of the cavum tympani is missing in all *Taphrosphys sulcatus* specimens, and the upper part of the cavum is crushed in *T. congolensis*, comparison can still be made with *T. ippolitoi*. In the former two species the cavum is about as deep as in *Phosphatochelys* and *Galianemys*, but in *T. ippolitoi* the cavum tympani is about double the depth. This affects the entire area of the cavum so that there is a large dorsal overhang and a large shelf ventrally.

The eustachian tube in bothremydids (except for *Foxemys*, *Cearachelys*, and *Polysternon*) is separated by a solid bony wall from the stapes. A notch, the sulcus eustachii, carries the tube into the cavum tympani medial to the tympanic membrane. This notch is formed by the quadrate, and in *Taphrosphys sulcatus* and *T. congolensis* it

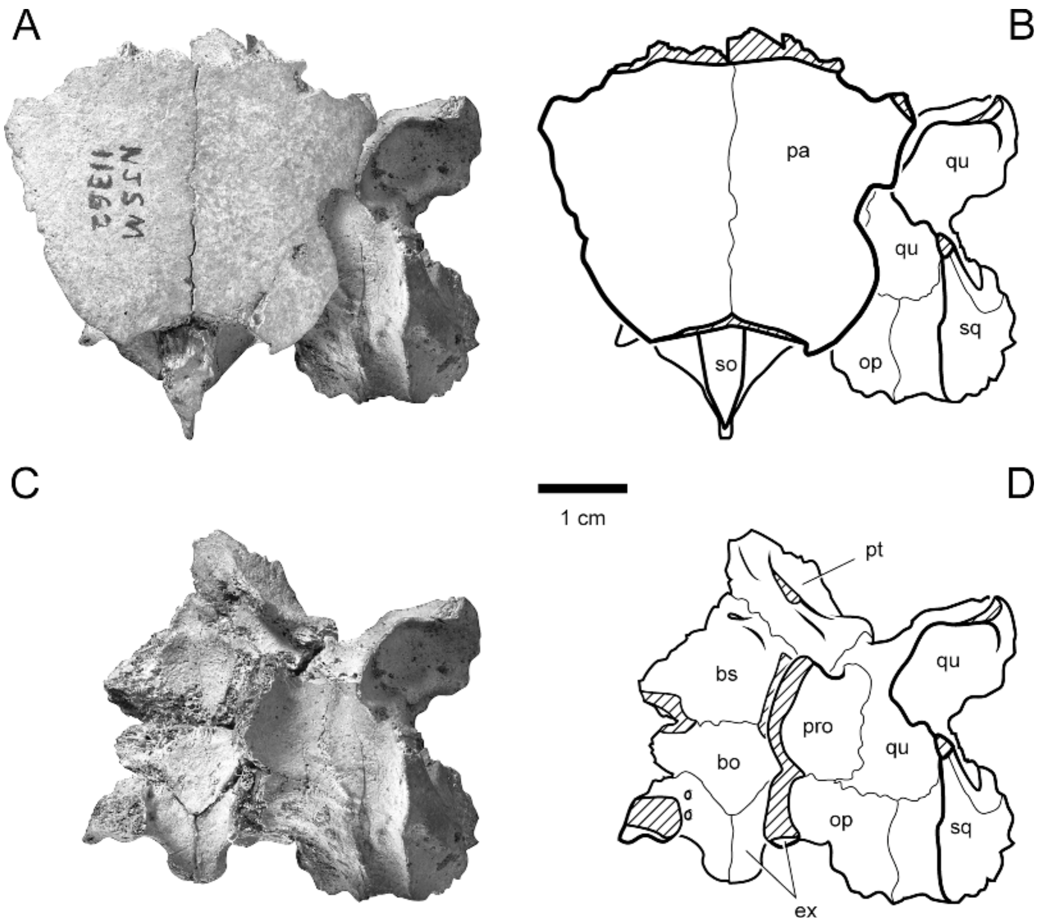

Fig. 173. *Taphrosphys sulcatus* (Leidy, 1856). NJSM 11362, incomplete posterior part of skull. **A**, **B**, dorsal view with parietals and supraoccipital articulated; **C**, **D**, dorsal view with skull roof removed to show otic chamber and internal surface of braincase. [F. Ippolito, del.]

opens directly ventral to the incisura columellae auris. In *T. ippolitoi* the notch opens posteroventrally at an angle to the incisura. The eustachian tube notch in *T. sulcatus* and *T. congolensis* is more open, but in *Taphrosphys ippolitoi* there is a flange of quadrate projecting posterodorsally from the lower edge of the notch that partially closes the notch.

Contacts on dorsal and anterior surfaces: The dorsal contacts of the quadrates are the same in all three *Taphrosphys* species and in the Taphrosphyini: prootic anteromedially, opisthotic posteromedially, and squamosal posterolaterally. There is no quadrate-supraoccipital contact.

Contacts on ventral surface: The quadrate in all three *Taphrosphys* species contacts the opisthotic posteromedially, the squamosal posterolaterally, the pterygoid anteromedially, the basisphenoid medially, and the basioccipital posteromedially. In *T. ippolitoi* and *T. congolensis* there is a posteromedial contact with the exoccipital just behind the basioccipital. In *T. sulcatus*, ANSP 15544, this part of the quadrate is broken off, but an exoccipital contact was likely based on the articulated basioccipital and exoccipitals of YPM PU 18707, which show a contact area for the quadrate on the exoccipital.

Structures on ventral surface: The quadrate structures in ventral view are also very similar in the three *Taphrosphys* species. The foramen posterius canalis carotici interni is formed at the junction of the quadrate, basisphenoid, and pterygoid. The foramen is

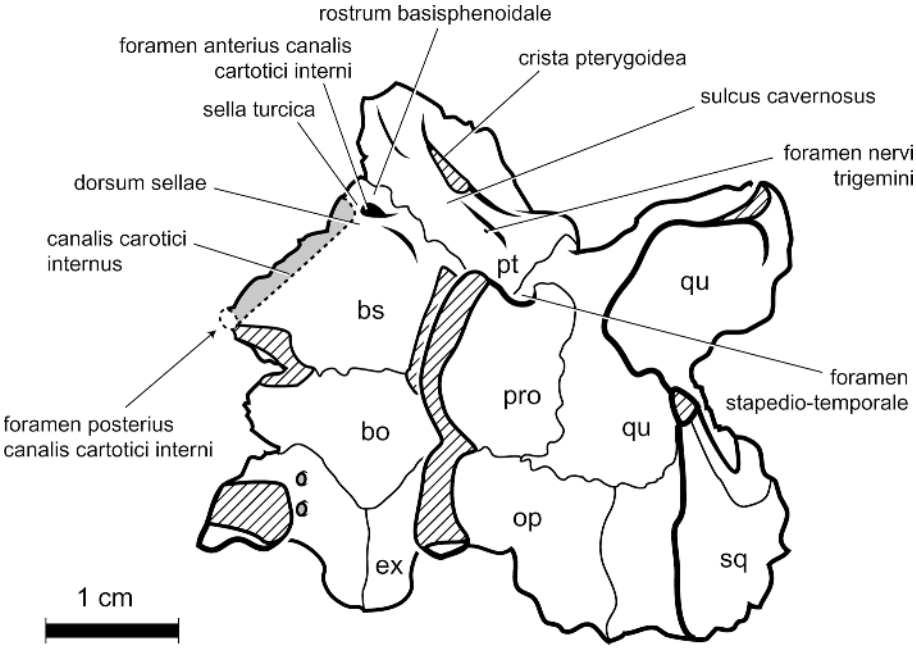

Fig. 174. *Taphrosphys sulcatus* (Leidy, 1856). NJSM 11362, incomplete posterior part of skull with skull roof removed (see previous figure for photograph). [F. Ippolito, del.]

clear in *T. ippolitoi* (fig. 277D) and *T. sulcatus*, but the margins are eroded in *T. congolensis*. Nonetheless, small edges of the foramen are visible and the canalis caroticus internus can be followed to this point. There is no pterygoideus muscle attachment scar (as seen in some other bothremydids like *Arenila*) in any of the three *Taphrosphys* species. The condylus mandibularis is positioned well anterior to the condylus occipitalis.

Structures on posterior surface: The fenestra postotica (fig. 177) is intact and uncrushed on the right side of NJSM 11362 in *Taphrosphys sulcatus*, on the right side of AMNH 30042 in *T. ippolitoi*, and on the left side of *T. congolensis*. In *T. sulcatus* and *T. congolensis* the fenestra is figure eight-shaped, an oval pinched in the center to separate the more dorsal stapedial artery from the more ventral lateral head vein. In the right side of *T. congolensis*, broken bone fragments separate the two parts into foramina, but this seems to be due to partial crushing. In *T. ippolitoi*, however, the fenestra is subdivided by bone that appears to be uncrushed and in its original condition. The quadrate in *Taphrosphys* as in other turtles forms the ventral part of the fenestra postotica, with the opisthotic forming the dorsal part. In *T. ippolitoi* the quadrate forms the process dividing it into two foramina.

In the three species of *Taphrosphys* there is a variably developed ridge on the posterior surface of the processus articularis of the quadrate. This ridge extends from the ventral part of the processus dorsomedially to the base of the processus and may have formed a concavity for the depressor mandibulae attachment. The ridge is larger and more massive in *T. ippolitoi* but it is well developed in *T. sulcatus*, although incompletely preserved. Both have a shallow, ventrally facing trough formed by the ridge. In *T. congolensis* the ridge is much less prominent, possibly exaggerated by crushing of this part of the processus articularis. A similar ridge and trough is present in *Labrostochelys*; a rudimentary one is in *Phosphatochelys* and *Azabbaremys*.

PTERYGOID (figs. 168, 169, 172, 174, 177)

Preservation: The right pterygoid in *Taphrosphys sulcatus* is preserved in NJSM

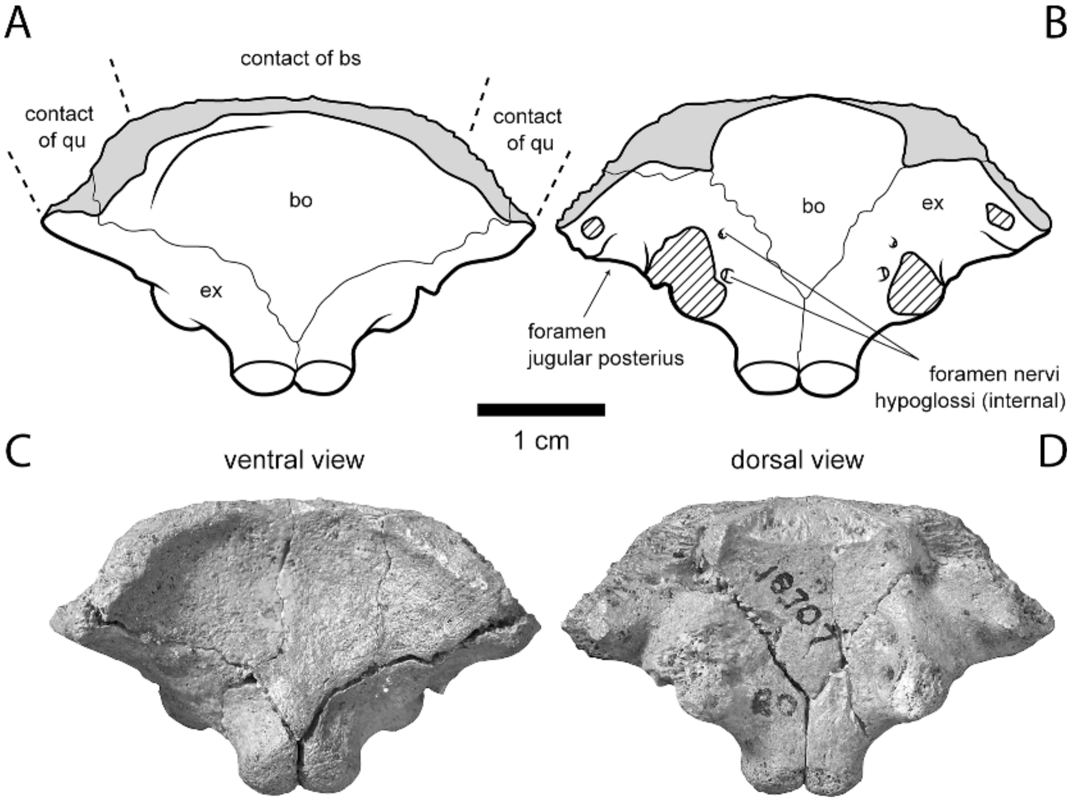

Fig. 175. *Taphrosphys sulcatus* (Leidy, 1856). YPM PU 18707, basioccipital and both exoccipitals. **A**, ventral; **B**, dorsal; **C**, ventral; **D**, dorsal. [F. Ippolito, del.]

11362 and in YPM PU 18707. Both are uncrushed and free of matrix on all sides, but they lack the processus trochlearis pterygoidei.

Contacts on ventral surface: See *Taphrosphys ippolitoi* for description.

Structures on ventral surface: See *Taphrosphys ippolitoi* for description.

Contacts on dorsal surface: The areas of the anterior contacts of the processus trochlearis pterygoidei, the sulcus palatinopterygoideus, and the posterior wall of the fossa nasalis are either absent or badly damaged in all three *Taphrosphys* species. The parietal contacts the crista pterygoidea anteriorly. More posteriorly there is a quadrate contact behind the foramen nervi trigemini on the dorsal surface.

Structures on the dorsal surface: The area of the processus trochlearis pterygoidei and sulcus palatinopterygoideus in *Taphrosphys* is either missing (*T. sulcatus*) or badly damaged (*T. congolensis* and *T. ippolitoi*), but enough of the parietal is preserved to show that the septum orbitotemporale was absent, as in *Azabbaremys* and *Phosphatochelys*.

The disarticulated pterygoids (YPM PU 18707 and NJSM 11362) of *Taphrosphys sulcatus* allow description of the internal aspects of the dorsal pterygoid surface (fig. 174), some of which is also visible in *T. congolensis*. There is a prominent crista pterygoidea articulating with the processus inferior parietalis. This wall is relatively narrow, as in *Azabbaremys* and *Phosphatochelys*, not extending to the anterior portion of the pterygoid or involving the palatine. Lateral to the crista pterygoidea, near the palatine contact, is a small foramen, the foramen nervi vidiani, as in most other Pelomedusoides. Medial to the crista pterygoidea is the sulcus cavernosus, and medial to that, in the suture between pterygoid and basisphenoid, is the canalis caroticus internus

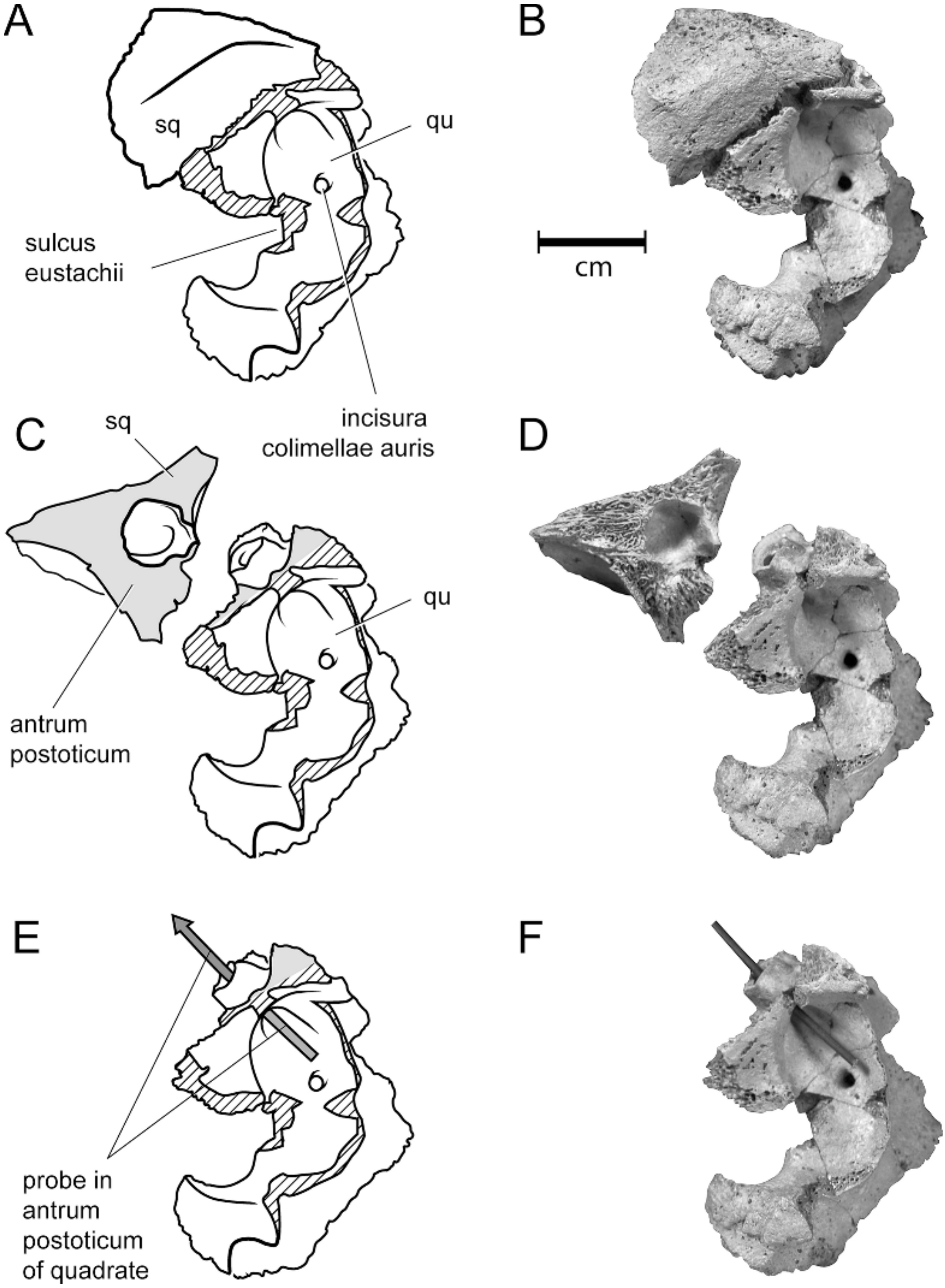

Fig. 176. *Taphrosphys sulcatus* (Leidy, 1856). ANSP 15544, right quadrate and squamosal, in different stages of disarticulation to show the formation of the antrum postoticum. Lateral view with anterior to the right in all figures. **A**, **B**, squamosal and quadrate articulated; **C**, **D**, squamosal pulled off quadrate and rotated to show anteroventral surface of squamosal; **E**, **F**, quadrate alone with probe extending through antrum postoticum. [F. Ippolito, del.]

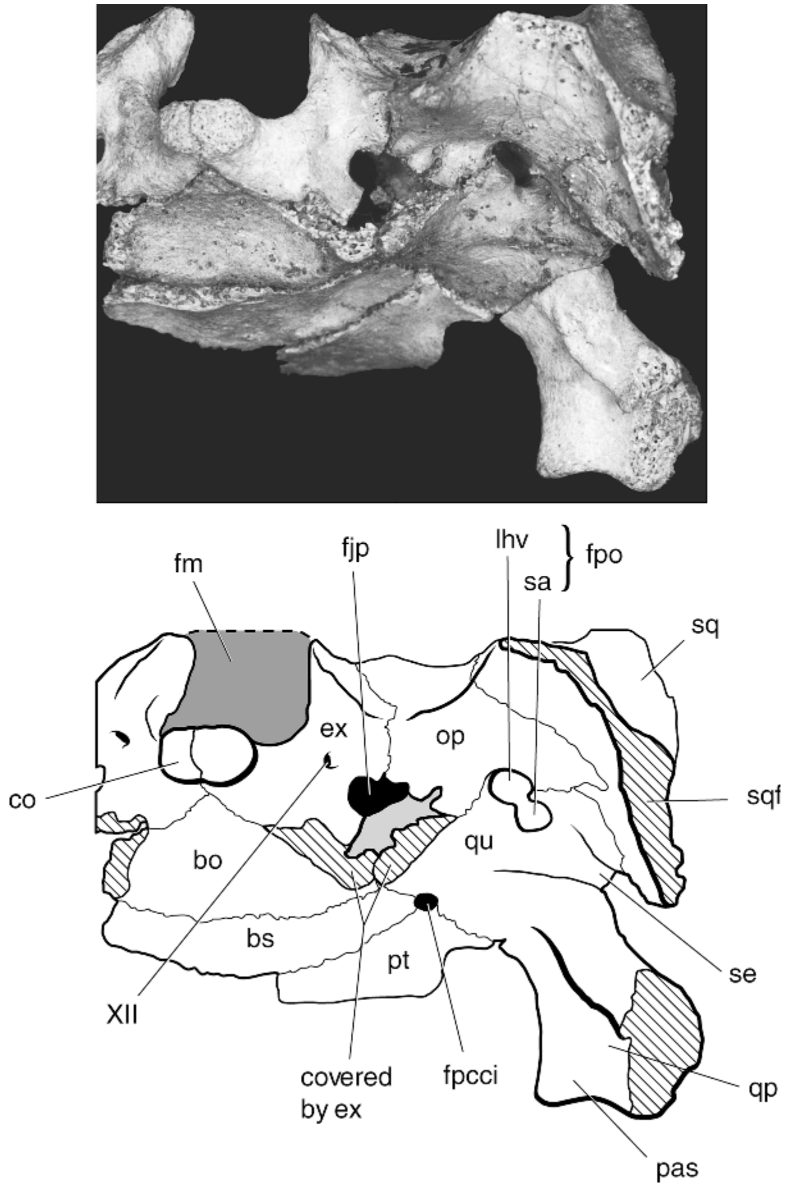

Fig. 177. *Taphrosphys sulcatus* (Leidy, 1856). NJSM 11362. Posterior oblique view of skull. [E.S. Gaffney and A. Venjara, del.]

leading to the foramen posterius canalis carotici interni.

In *Phosphatochelys*, four bones make up the foramen nervi trigemini: parietal, prootic, pterygoid, and quadrate. In *Taphrosphys congolensis* at least the prootic and pterygoid enter the margin (preserved only on the right side) with possibly the quadrate, with the parietal being uncertain. In *T. sulcatus* the pterygoid clearly makes up the ventral margin and the quadrate probably enters it, but the prootic and parietal contributions are not determinable. Although the foramen stapedio-temporale is very close to the foramen nervi trigemini in *Taphrosphys*, its exact margins are ambiguous, except in *T. ippolitoi*, AMNH 30500. In this specimen, the foramen nervi trigemini and foramen stapedio-temporale are joined by the same outer rim formed by the parietal, prootic, pterygoid, and quadrate. This is quite different from the situation in *Phosphatochelys* and *Labrostochelys* in which the two foramina are very close but not actually fused. A thin sheet of prootic separates the two foramina, but it lies posterior to the outer rim.

SUPRAOCCIPITAL (figs. 168, 170, 172)

Preservation: A complete supraoccipital in *Taphrosphys sulcatus* is preserved in NJSM 11362 and a nearly complete one is in ANSP 15544.

Contacts: All three *Taphrosphys* species have these contacts: parietals dorsally, prootic anterolaterally, opisthotic laterally, and exoccipital posteroventrally. There is no quadrate contact.

Structures: The crista supraoccipitalis is short in *Taphrosphys sulcatus*, as in *Azabbaremys* and *Phosphatochelys*. Although in *T. congolensis* the margin is broken, it is thin and unlikely to be more extensive than in *T. sulcatus*. In *T. ippolitoi* its length is indeterminate.

EXOCCIPITAL (figs. 168, 172, 175, 177)

Preservation: Both exoccipitals in *Taphrosphys sulcatus* are preserved in NJSM 11362 and are prepared on all surfaces and completely visible. However, both have a small portion of the ventrolateral process broken. YPM PU 18707 has both exoccipitals, which are complete and visible ventrally but lack the dorsal processes.

Contacts: The contacts are the same in all three *Taphrosphys* species: supraoccipital dorsally, opisthotic laterally, quadrate ventrolaterally, basioccipital ventrally, and the other exoccipital ventromedially.

Structures: In all three *Taphrosphys* species the exoccipitals meet on the midline to form the condylus occipitalis and its neck in ventral view. Dorsally, the contact extends farther anteriorly to exclude the basioccipital from the floor of the foramen magnum. This is similar to the *Azabbaremys* condition, but *Phosphatochelys* has the basioccipital separating the exoccipitals to a slightly greater degree.

All three species of *Taphrosphys* have two pairs of the foramen nervi hypoglossi that penetrate the exoccipital (figs. 175, 177), with the more medial foramen being slightly larger than the more lateral one. The foramen jugulare posterius is completely enclosed, formed medially by the exoccipital and laterally by the opisthotic in all three species. The more lateral foramen nervi hypoglossi actually opens in the medial wall of the foramen jugulare posterius in all three *Taphrosphys* species, as it does in *Phosphatochelys*.

BASIOCCIPITAL (figs. 168, 169, 175)

Preservation: The complete basioccipital in *Taphrosphys sulcatus* is present in YPM PU 18707 and NJSM 11362; both are visible dorsally and ventrally. In NJSM 11362 the posterolateral margins are eroded, but they are complete in YPM PU 18707.

Contacts: The contacts are the same in all three *Taphrosphys* species: basisphenoid anteriorly, quadrate laterally, and exoccipitals posteriorly.

Structures: The condylus occipitalis is discussed under Exoccipital. All three *Taphrosphys* species have a shallow median concavity that parallels the basisphenoid suture. It is developed to about the same extent in *Taphrosphys* as it is in *Phosphatochelys*. It is not as flat as in *Azabbaremys*. The basioccipital of *Taphrosphys* also resembles *Phosphatochelys* in having a curved anterior margin rather than the straighter margin seen in *Azabbaremys*.

The tuberculum basioccipitale in *Taphrosphys ippolitoi* is more distinct than in *Azabbaremys*, *Phosphatochelys*, or the other two *Taphrosphys* species. In *T. ippolitoi* the tuberculum, formed by basioccipital and exoccipital, extends posterolaterally to form a distinct shelf ventral to the foramen jugulare posterius. This is not developed in *T. sulcatus* or *T. congolensis*.

PROOTIC (fig. 174)

Preservation: In *Taphrosphys sulcatus* the right and left disarticulated and complete prootics are preserved in YPM PU 18707. The nearly complete right prootic is in NJSM 11362.

Contacts: In all three *Taphrosphys* species there are the following contacts: parietal medially, quadrate laterally, supraoccipital posterodorsally, pterygoid ventrally, and opisthotic posteriorly.

Structures: In *Taphrosphys sulcatus*, *T. congolensis*, and *T. ippolitoi* the prootic forms the lateral and dorsal part of the anterior-facing foramen stapedio-temporale. The more medial limits and the separation between the foramen stapedio-temporale from the foramen nervi trigemini, also roofed by the prootic, are not clear in *T. sulcatus* and *T. congolensis*. In *T. ippolitoi* these two foramina are fused into a common opening, in contrast to *Phosphatochelys* and *Labrostochelys*. The *Taphrosphys sulcatus* specimens show the internal features of the prootic, but they do not differ from other Pelomedusoides.

OPISTHOTIC (figs. 168, 172, 174, 177)

Preservation: In *Taphrosphys sulcatus* a nearly complete right opisthotic is present in NJSM 11362 and a nearly complete right opisthotic is present in YPM PU 18707.

Contacts: In all three *Taphrosphys* species the contacts are: supraoccipital anteromedially, prootic anteriorly, quadrate anterolaterally and ventrally, squamosal posterolaterally, and exoccipital posteromedially.

Structures: The dorsal surface is the same in all three *Taphrosphys* species and differs from *Phosphatochelys* and *Azabbaremys* only in having a more extended posterior process at the end of the opisthotic.

On the ventral surface the opisthotic forms the roof of the fenestra postotica and the lateral wall of the foramen jugulare posterius. In all three *Taphrosphys* species the foramen jugulare posterius is closed by a process of the opisthotic contacting the dorsal and ventral margins formed by the exoccipital. The fenestra postotica in *T. sulcatus* and *T. congolensis* are figure eight-shaped openings with the dorsal half for the stapedial artery and the lateral head vein in the ventral half. The opisthotic forms most of the dorsal half and the quadrate the ventral half. In *T. ippolitoi* the fenestra postotica is divided by bone into two foramina, with the process being formed equally by opisthotic and quadrate, although there is cracking in this area and the quadrate alone may form the process.

BASISPHENOID (figs. 168, 169, 174)

Preservation: There is a nearly complete basisphenoid for *Taphrosphys sulcatus* showing both dorsal and ventral surfaces in NJSM 11362.

Contacts: In all three *Taphrosphys* species the basisphenoid contacts are: pterygoid anterolaterally, quadrate laterally, and basioccipital posteriorly. The prootic should contact the basisphenoid laterally on its dorsal surface, and in *T. congolensis* crushed bone from the prootic does lie on the basisphenoid, but not in its original condition. In NJSM 11362 the ventromedial edge of the prootic has been lost, and no basisphenoid contact is present.

Structures: In ventral view the basisphenoid is very similar in all three *Taphrosphys* species. The basisphenoid is five-sided in all three species, in contrast to the more triangular shape of *Phosphatochelys*, *Azabbaremys*, and *Labrostochelys* and to the V-shaped outline of *Arenila*. The dorsal surface is visible in all three *Taphrosphys* species. Beginning anteriorly on the basisphenoid, the anteriormost feature is the rostrum basisphenoidale, the ossification of the anterior portion of the trabeculae. In *T. congolensis* the rostrum is a laterally compressed process with a dorsal midline ridge, rather than being a cylinder commonly seen in other Pelomedusoides like *Pelusios* (fig. 24). In *T. ippolitoi* and *T. sulcatus* the midline area of the basisphenoid is flat, with no indication of an elongated or ridged rostrum basisphenoidale, a condition unusual for turtles. Directly posterior to the rostrum in *T. congolensis* is a well-defined oval depression, the sella turcica. Its floor is below the base of the rostrum basisphenoidale; there are deep lateral ridges and a high posterior dorsum sellae completely defining the deep sella turcica. This condition is more pronounced than in most turtles. In *T. sulcatus* and *T. ippolitoi* the sella turcica is a barely defined feature; there is only a low pair of anteromedial ridges along the basisphenoid-pterygoid suture, and a very low, nearly absent, dorsum sellae. Such a low and undefined sella turcica is unusual for turtles. The dorsum sellae of *T. congolensis* is high and nearly vertical. In *T. sulcatus* and *T. ippolitoi* it is a low, barely defined swelling. At the dorsolateral margin of the dorsum sellae in *T. congolensis* is the paired, relatively large, processus clinoideus, unusually well developed for a pelomedusoid. There is no sign of a processus clinoideus in *T. sulcatus*; however, some erosion has taken place here on both sides, and a pair could easily have been present, although not as large as in *T. congolensis*. In *T. ippolitoi* the processus is low on both sides. The foramen anterius canalis carotici interni in *T. congolensis* is closer to the midline than that foramen in *T. sulcatus* and *T. ippolitoi*. The foramen is also angled to face anteromedially in *T. congolensis* due to the narrow sella turcica, while in *T. sulcatus* and *T. ippolitoi* the foramen anterius canalis carotici interni faces anteriorly and is not contained in a narrow sella turcica.

Taphrosphys ippolitoi

This species of *Taphrosphys* is represented by a nearly complete skull (AMNH 30042) and a partial skull (AMNH 30500) that shows internal features of the braincase. Together, they make this species the most completely known of the genus.

PREFRONTAL (figs. 178, 181, 183)

Preservation: Both prefrontals of *Taphrosphys ippolitoi* are present in AMNH 30042 and AMNH 30500. In AMNH 30042 they are pushed ventrally away from their original position, almost completely collapsing the fossa nasalis. Their ventral surfaces cannot be seen. Sutural contacts are clear in both skulls. There is some distortion posterolaterally in AMNH 30500, and the ventral edges are broken in AMNH 30500.

Contacts: As in other bothremydids, the prefrontal in *Taphrosphys ippolitoi* contacts the other prefrontal medially, the frontal posteriorly, and the maxilla ventrolaterally. In AMNH 30042 both prefrontals are in roughly life position, but they have been separated from their original contacts.

Structures: The dorsal plate of the prefrontal in *Taphrosphys ippolitoi* has the typical morphology seen in other Taphrosphyini, such as *Azabbaremys*. In *T. ippolitoi* the anterior margin of the prefrontal, which forms the dorsal edge of the apertura narium externa, is more protuberant than in *T. sulcatus*, *T. congolensis*, or *Azabbaremys*. The prefrontal in all three *Taphrosphys* species is thick on the midline, as in *Azabbaremys* and in contrast to *Galianemys*. In *T. ippolitoi*, however, the bone thickens anteriorly so that the anterior projection has a swelling visible in dorsal view, being thickest on the midline. This is absent in *T. sulcatus* and *T. congolensis*, as well as in other bothremydids. The ventral surface of most of the prefrontal is visible in AMNH 30042 and shows the roof of the relatively large fossa nasalis characteristic of *T. ippolitoi*. The fossa is smaller in *T. sulcatus* and *T. congolensis*. The prefrontal in *Taphrosphys ippolitoi* forms the anterodorsal margin of the orbit, as in other *Taphrosphys* species.

FRONTAL (figs. 178, 181, 183)

Preservation: Both frontals of *Taphrosphys ippolitoi* are present in both specimens and are undistorted. There is some breakage posterolaterally. Although the frontals are in good shape in AMNH 30042, the palatines have been crushed dorsally and obscure the posteroventral morphology of the sulcus olfactorius of the frontals, but this is visible in AMNH 30500.

Contacts: The frontal in *Taphrosphys ippolitoi* has these common bothremydid contacts: frontal on midline, prefrontal anteriorly, and parietal posteriorly. AMNH 30500 lacks postorbitals. The usual postorbital contact posterolaterally is obscured in AMNH 30042 due to breakage of both frontal and parietal and the apparent absence of the postorbital due to breakage. Although the space between the jugal and parietal seems to require a postorbital in the orbital margin, whether it contacted the frontal is unclear. There is a postorbital-frontal contact in *T. congolensis* and *T. sulcatus*.

Structures: The frontal forms most of the dorsal orbital margin in *Taphrosphys ippolitoi*, as in *T. sulcatus*. The margin is slightly eroded on both sides, and the shape of the orbit is not completely determinable. However, it is consistent with the orbital edge preserved in *T. sulcatus*. In *Azabbaremys* the frontal forms much less of the margin than in *Taphrosphys*.

The ventral surface of the frontal in *Taphrosphys ippolitoi* shows a well-defined sulcus olfactorius formed by a deep parasagittal ridge that increases in height poste-

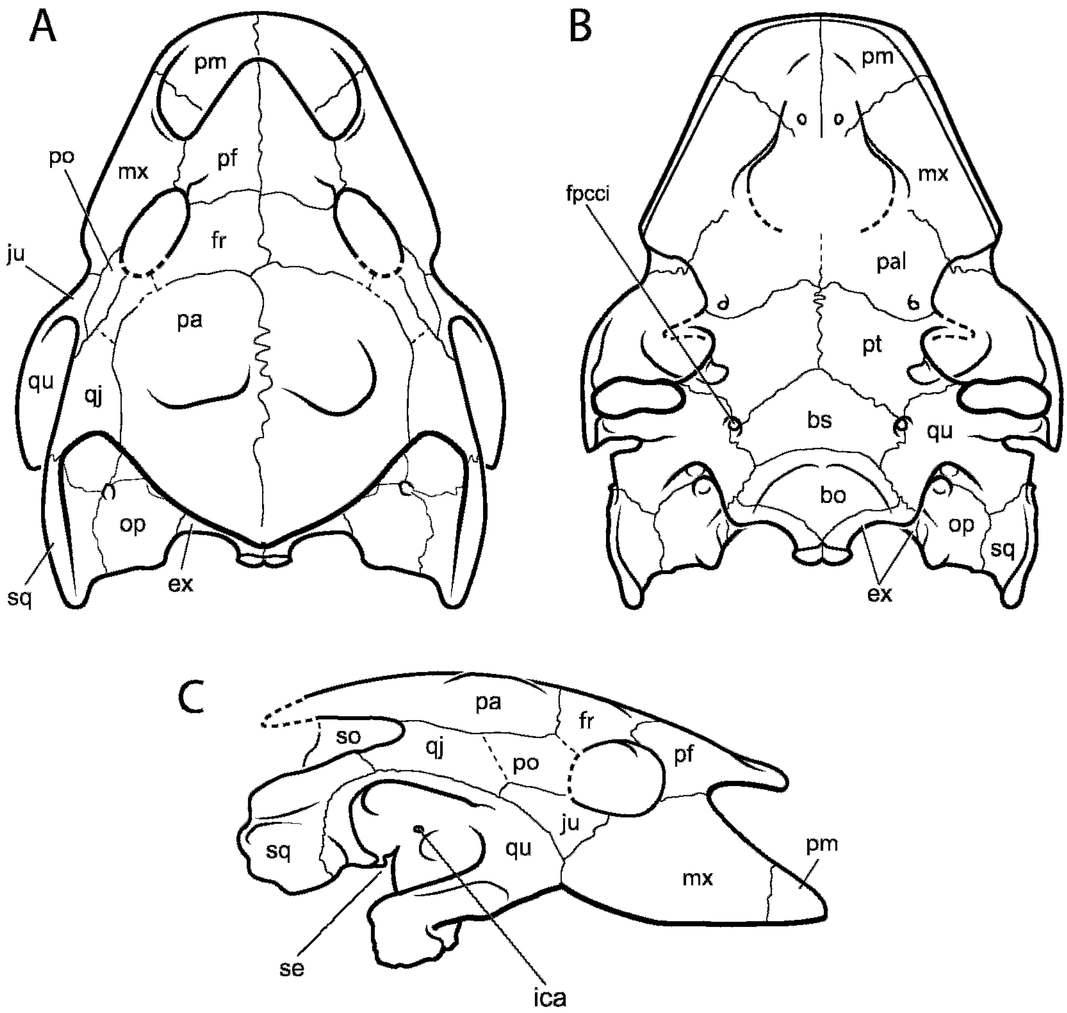

Fig. 178. *Taphrosphys ippolitoi*, n. sp. Partially restored views of skull based on AMNH 30042 holotype with additions from AMNH 30500. **A**, dorsal; **B**, ventral; **C**, lateral. For more detailed view of area around foramen posterius canalis carotici interni, see figure 277D. [F. Ippolito, del.]

riorly to merge with the processus inferior parietalis. The sulcus olfactorius ridge in *T. ippolitoi* is somewhat deeper than that in *Azabbaremys* and much deeper than that in *Galianemys*. The ridge in *T. ippolitoi* is also deeper than that in *T. sulcatus*. The frontal is unknown in *T. congolensis*.

PARIETAL (figs. 178, 181, 183)

Preservation: Both parietals are present in AMNH 30042 but both are damaged by breakage, particularly distally. Both also show some dislocation. Significant distortion seems to be absent, the sutures are clear, and only the dorsal surface is visible. In AMNH 30500 both parietals are nearly complete and visible dorsally and ventrally.

Contacts of dorsal plate: In the available material of *Taphrosphys ippolitoi*, the parietal in AMNH 30042 contacts the frontal anteriorly, the other parietal medially, and the supraoccipital posteromedially and ventrally, all as in other bothremydids. As preserved, the right parietal is overlapped by the right jugal anterolaterally, and the left parietal is near the left jugal. However, we have concluded that this is a result of crushing and considerable loss of height of

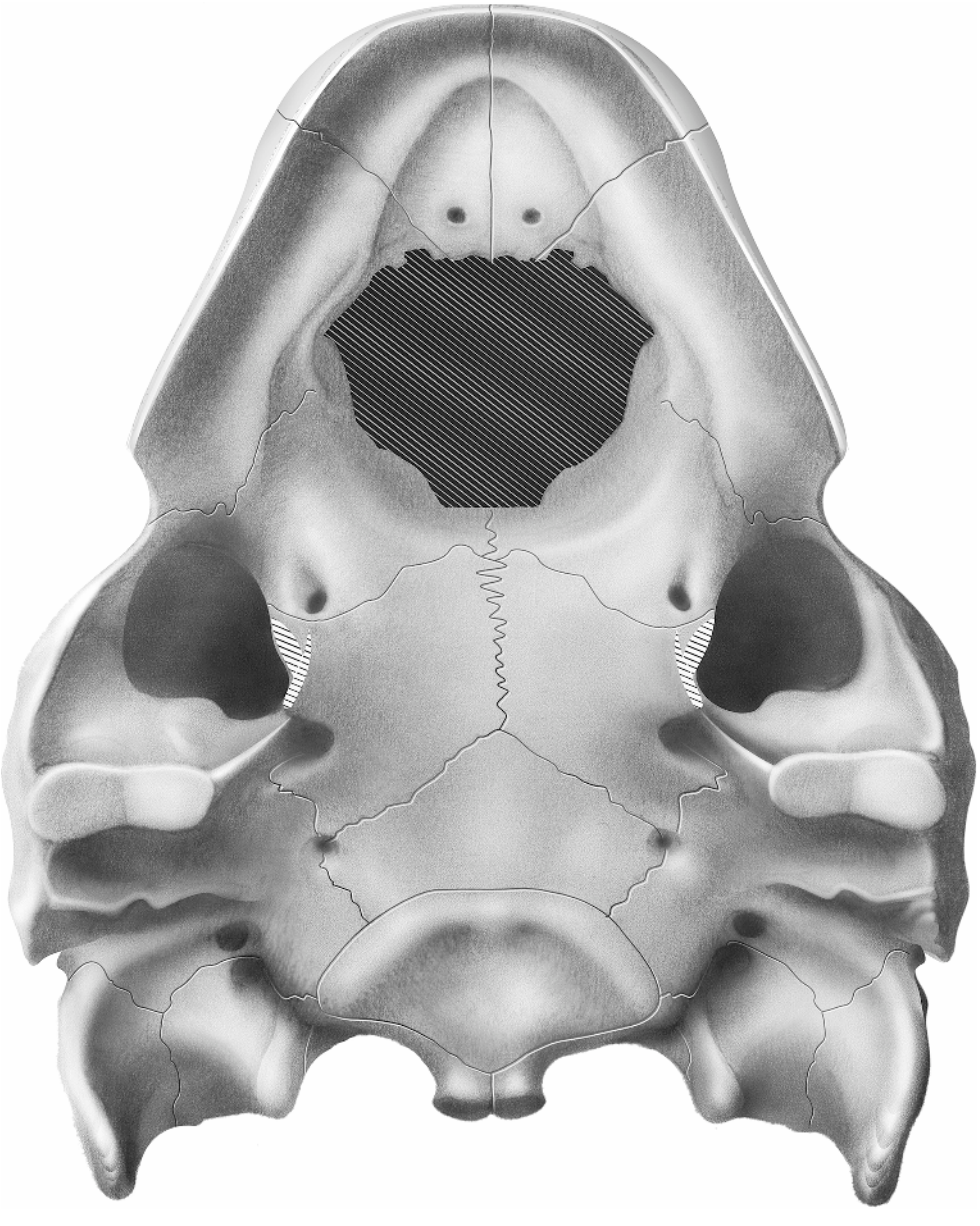

Fig. 179. *Taphrosphys ippolitoi*, n. sp. Partially restored ventral view based on AMNH 30042 holotype and AMNH 30500. [F. Ippolito, del.]

the skull. Conservative restoration (fig. 178) strongly supports the interpretation that another bone was anterolateral to the parietal, presumably the postorbital. The parietal in *Taphrosphys ippolitoi* contacts the thin quadratojugal laterally, as in *T. congolensis*.

Structures of dorsal plate: The dorsal plate of the parietal in *Taphrosphys ippolitoi* has a shape that is very similar to that in *T. congolensis* and *T. sulcatus*. A very small section of the parietal-supraoccipital suture remains at the posterior edge of the skull roof in AMNH 30042.

The surface of the parietal, frontal, and prefrontal of *Taphrosphys ippolitoi* in AMNH 30042 has a roughly corrugated texture, in contrast to the very smooth surface in *T. sulcatus* and *T. congolensis*. In AMNH 30500 the surface is slightly rugose, but not corrugated as in AMNH 30042. Scale sulci are not visible in any of the *Taphrosphys* skulls.

Contacts of processus inferior parietalis: In *Taphrosphys ippolitoi*, AMNH 30500 has most of the processus inferior parietalis preserved. There is no palatine contact, but the usual, wide pterygoid contact extends posteriorly to the foramen nervi trigemini where the prootic contacts the parietal posteroventrally. Posteriorly the supraoccipital contacts the parietal.

Structures of processus inferior parietalis: The processus inferior parietalis in *Taphrosphys ippolitoi* is wider than in *Azabbaremys* and *Phosphatochelys*. It forms the anterodorsal margin of the foramen nervi trigemini, which is nearly combined with the foramen stapedio-temporale. The combined foramina form the common margin of an oval opening, with a narrow sheet separating the two foramina, well posterior to the common margin.

JUGAL (figs. 178, 181)

Preservation: In *Taphrosphys ippolitoi* both jugals are present in AMNH 30042, and both are in roughly their original position. However, they have been slightly disarticulated and disturbed. The left one seems to be more complete and may not be missing anything but some edges. The right jugal is smaller and seems to have more broken edges and probably lacks larger areas. AMNH 30500 lacks jugals.

Contacts of lateral plate: In *Taphrosphys ippolitoi* the left jugal in AMNH 30042 is in articulation with the maxilla anteroventrally in a suture that extends from the lower margin of the orbit to the maxilla-quadrate contact. On the right side in AMNH 30042, the jugal is displaced medially but the sutural surface is clear on the maxilla. Posteroventrally, the jugal contacts the quadrate, but it is displaced on the left side with some matrix in the jugal-quadrate suture. On the right side the jugal is more displaced and missing its posteroventral edge so that the jugal-quadrate suture is actually a narrow space.

Structures of lateral plate: Posterodorsally the right jugal in *Taphrosphys ippolitoi*, AMNH 30042, contacts the parietal margin as preserved, but this is interpreted as due to postmortem crushing in which the postorbital and quadratojugal are either covered or missing. In the reconstruction the jugal only contacts the postorbital and quadratojugal along its dorsal margin. Unfortunately, neither the postorbital or quadratojugal is clearly preserved in the region of their contacts with the jugal. A postorbital-jugal contact is very likely because what seems to be that contact is preserved at least in part on both jugals. The jugal-quadratojugal contact, however, is more speculative because this area is not preserved in either skull. The jugal of *Taphrosphys ippolitoi* enters the posteroventral margin of the orbit, and this is preserved on both sides in AMNH 30042. As in *T. congolensis*, the quadrate-maxilla contact prevents a jugal exposure on the cheek.

Contacts and structures of medial process: A portion of the medial jugal process in *Taphrosphys ippolitoi* is present on both sides of AMNH 30042, but displacement and breakage prevent a detailed description.

QUADRATOJUGAL (figs. 178, 181, 183)

Preservation: In AMNH 30042 the quadratojugal is completely missing on the left side, and only its narrow posterior extension is present on the right. In AMNH 30500, most of both quadratojugals are present.

Contacts and structures: The quadratojugal in *Taphrosphys ippolitoi* contacts the quadrate ventrally in a wide suture and the squamosal posteriorly in a very narrow suture. It contacts the parietal medially and the jugal anteroventrally. The anterodorsal suture is very likely present but not clearly preserved.

The quadratojugal forms part of the anterolateral edge of the temporal emargination. The quadratojugal in *T. ippolitoi* agrees with that in *T. congolensis*.

SQUAMOSAL (figs. 178, 183, 184, 286E)

Preservation: In *Taphrosphys ippolitoi* both squamosals are present in both skulls and they are nearly complete. In AMNH 30042 the left one is damaged dorsally and lacks the parasagittal ridge. Both lack part of the posterior margin. In AMNH 30500 the left one is broken dorsally.

Contacts: As in *Taphrosphys sulcatus*.

Structures: The antrum postoticum in *Taphrosphys ippolitoi* is preserved completely and prepared on the right side of AMNH 30042 and of AMNH 30500. It is similar in size and shape to that in *T. sulcatus*, but the lateral wall formed of quadrate plus squamosal is thicker in *T. ippolitoi* than it is in *T. sulcatus*. The ventral flange of the squamosal in *Taphrosphys ippolitoi* is deeper than in both *T. sulcatus* and *T. congolensis*. Its ventral margin is also curved medially in *T. ippolitoi*, rather than straight, as in *T. sulcatus* and *T. congolensis*. Although the posterior margin of the squamosal is slightly thicker than in the other two species, it does not extend posteriorly to a greater degree.

POSTORBITAL (fig. 178)

Preservation: Although one was almost certainly present in *Taphrosphys ippolitoi*, few of the fragments in the area of the postorbital can be clearly identified as such and none has clear contacts.

Structures and contacts: In *Taphrosphys ippolitoi* both the jugal and parietal on the left side and to some extent on the right side of AMNH 30042 preserve contacts that are best interpreted as postorbital sutures. The reconstruction hypothesizes a postorbital very similar to that in *T. congolensis* with a narrow frontal contact, a long orbital margin exposure, and a long jugal contact. AMNH 30500 preserves what are probably the postorbital contact on the anterolateral margin of both parietals and the posterior contact with both quadratojugals, so the contacts and shape of the postorbital can be determined. There is no sign of a medial process of the postorbital in *Taphrosphys ippolitoi*; the medial process of the postorbital seems to be absent in the other *Taphrosphys* species.

PREMAXILLA (figs. 178, 179, 181)

Preservation: Both premaxillae are present in AMNH 30042: the left one is complete, and the right one lacks a small portion of the posterior plate. Premaxillae are missing in AMNH 30500.

Contacts: In *Taphrosphys ippolitoi* the midline contact is completely preserved for the full length of the element, and there is a presumed contact edge for the vomer, which is missing. Posterolaterally the premaxilla contacts the maxilla in a suture that is comparable in height to that in *T. congolensis* (the contact in *T. sulcatus* is not completely preserved).

Structures on dorsal surface: The premaxilla forms the floor of the apertura narium externa, which can be entirely reconstructed in *Taphrosphys ippolitoi* and partially in the other two *Taphrosphys* species. The apertura in *T. ippolitoi* is significantly wider than in the other two species, withmuch of the width being formed by a broader premaxilla. The floor of the fossa nasalis is also broader and deeper in *T. ippolitoi* than in the other two species.

Structures on ventral surface: In ventral view the premaxilla of *Taphrosphys ippolitoi* forms the medial portion of the triturating surface. Due to its greater width, it forms more of this surface in *T. ippolitoi* than in the other *Taphrosphys* species. The labial ridge in *T. ippolitoi* is similar to that in *T. sulcatus*, both of which are shallower than in *T. congolensis*. The anterior part of the triturating surface in *T. ippolitoi* is wider than in the other two species. The medial edge of the triturating surface is a very low ridge separating the nutrient-rich surface from the smooth medial area. This medial area is a shallow concavity; the comparable area is missing in *T. congolensis* and *T. sulcatus*. Near the posterior edge is the foramen praepalatinum, completely formed by the premaxilla in *T. ippolitoi*.

MAXILLA (figs. 178, 179, 181)

Preservation: Both maxillae are preserved and are nearly complete and uncrushed in AMNH 30042, although they are slightly displaced from their original positions. Maxillae are missing in AMNH 30500.

Contacts of vertical plate: The maxilla of *Taphrosphys ippolitoi* contacts the premaxilla anteriorly and the prefrontal anterodorsally. Posterodorsally there is a clear contact with the jugal that seems to exclude any contact with the postorbital. Posteriorly, below the jugal contact there seems to be

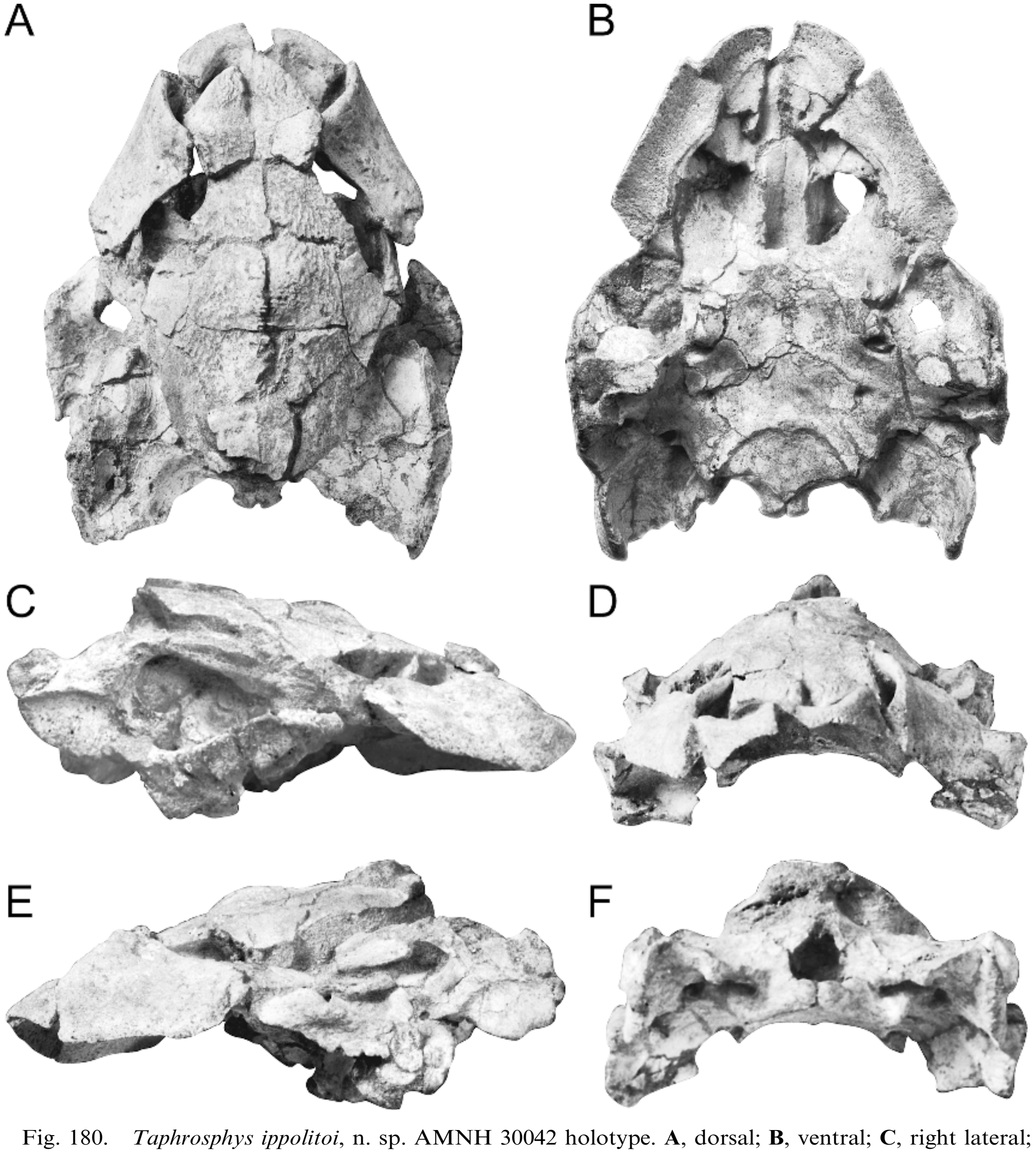

Fig. 180. *Taphrosphys ippolitoi*, n. sp. AMNH 30042 holotype. **A**, dorsal; **B**, ventral; **C**, right lateral; **D**, anterior; **E**, left lateral; **F**, posterior. [F. Ippolito, del.]

a quadrate contact, although it is not present on either side as preserved. On the left side there is obvious displacement, but the maxilla and quadrate are very close nonetheless. In the restoration it is difficult to bring the surrounding elements into position without a strong maxilla-quadrate contact. There is no quadratojugal contact.

Structures of the vertical plate: The apertura narium externa lateral margins are slightly flared laterally in *Taphrosphys ippolitoi*, in contrast to *T. congolensis* in which they lie in the plane of the rest of the maxilla. The entire anterior half of the maxilla in *T. ippolitoi* is expanded laterally so that the snout is flared, in contrast to the more acute

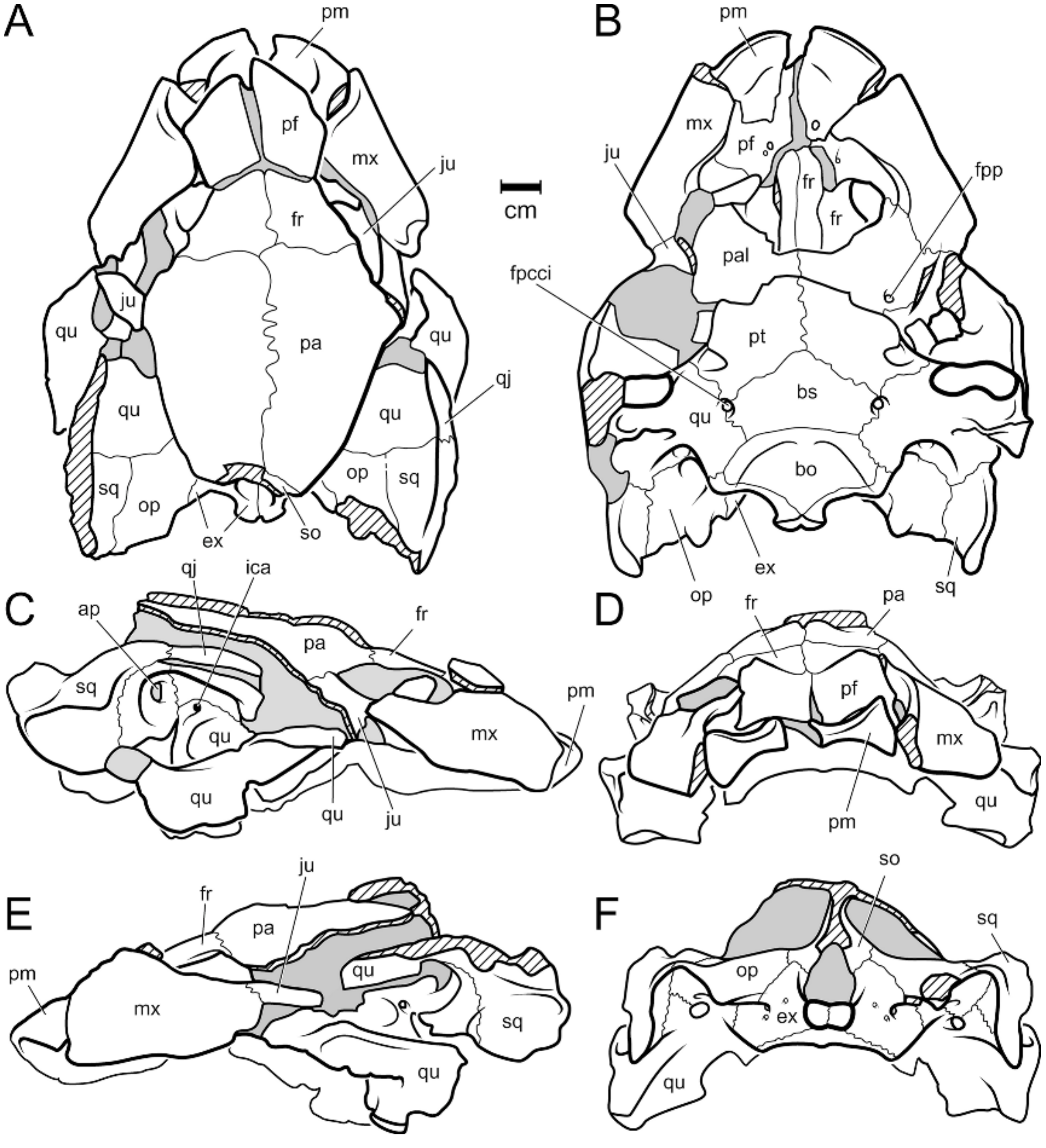

Fig. 181. *Taphrosphys ippolitoi*, n. sp. AMNH 30042 holotype. **A**, dorsal; **B**, ventral; **C**, right lateral; **D**, anterior; **E**, left lateral; **F**, posterior. [F. Ippolito, del.]

snout of *T. congolensis* and, presumably, *T. sulcatus*. In *T. sulcatus* the small premaxilla suggests a narrower snout, more like *T. congolensis* than *T. ippolitoi*.

Contact of horizontal plate: Very little of the dorsal surface of the fossa orbitalis is visible in *Taphrosphys ippolitoi*, so the elements making up the floor of the fossa orbitalis are not determinable. See *T. congolensis* for other contacts.

Structures of horizontal plate: The triturating surface of the maxilla in *Taphrosphys ippolitoi* has an acute, relatively deep labial ridge with a broadly curved medial surface, similar to that in *Labrostochelys*. This is in contrast to the medial surface meeting the

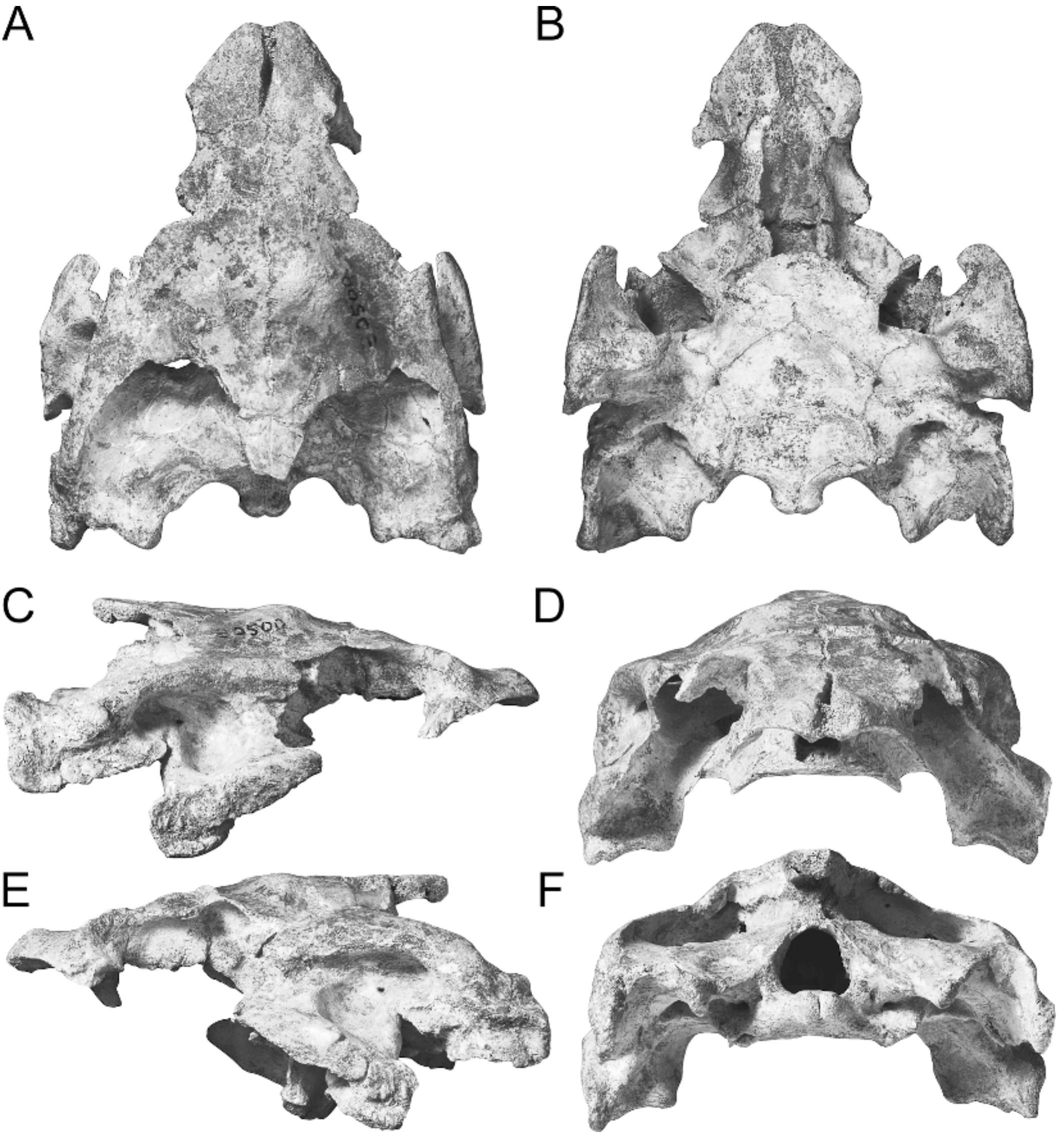

Fig. 182. *Taphrosphys ippolitoi*, n. sp. AMNH 30500. **A**, dorsal; **B**, ventral; **C**, right lateral; **D**, anterior; **E**, left lateral; **F**, posterior. [F. Ippolito, del.]

labial ridge at right angles, as in *Azabbaremys*. The maxillary triturating surfaces of *T. ippolitoi* and *T. congolensis* are very similar, with *T. ippolitoi* being slightly more expanded anteriorly.

VOMER

Preservation: The vomer is missing in both skulls of *Taphrosphys ippolitoi*, but a sutural margin on the posterior edge of the left premaxilla in AMNH 30042 suggests that one was present.

PALATINE (figs. 178, 179, 181)

Preservation: Both palatines are present and nearly complete in AMNH 30042, although both lack their anterior margins. Both are fractured and pushed dorsally above the level of the pterygoids. Palatines are missing in AMNH 30500.

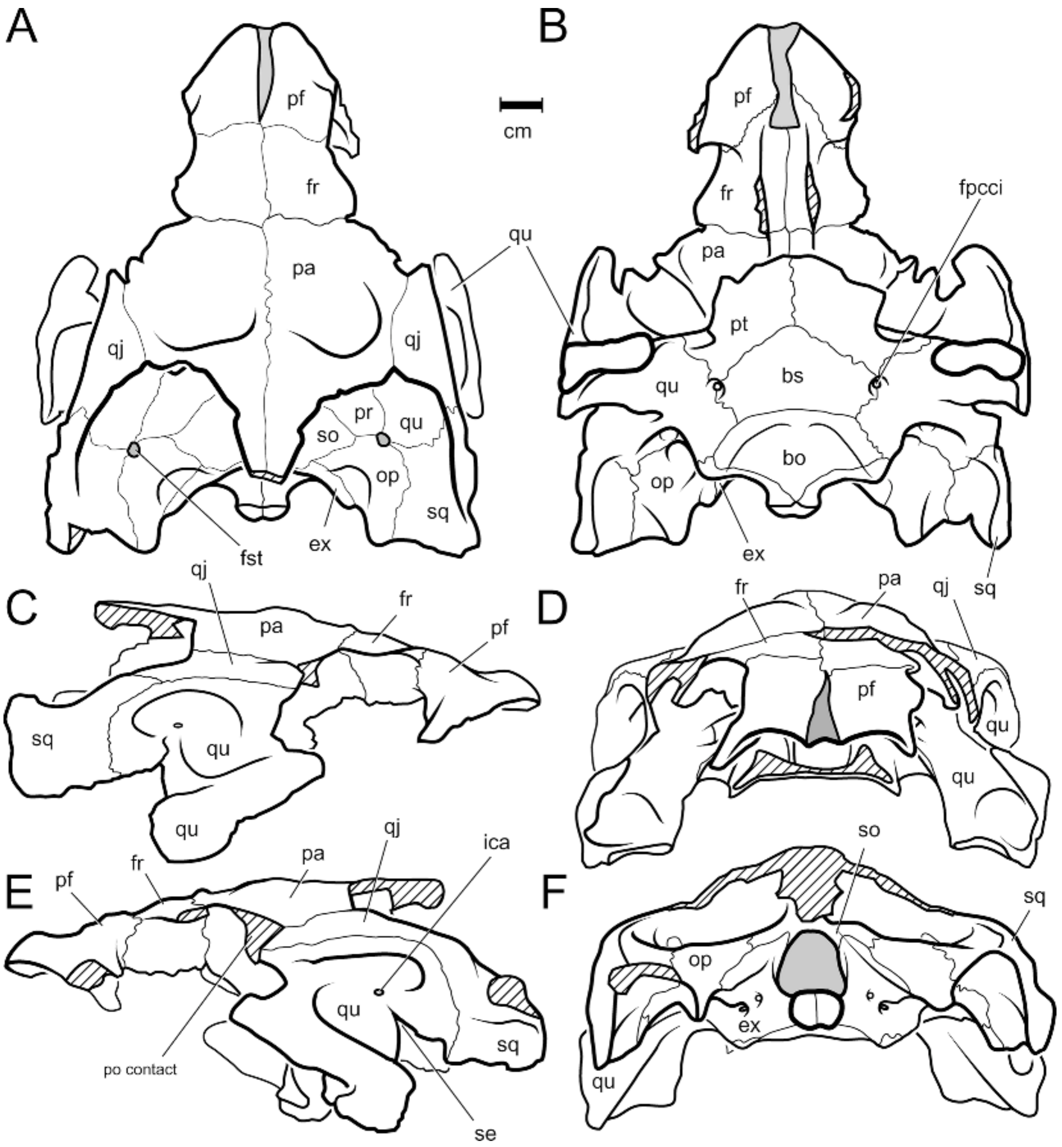

Fig. 183. *Taphrosphys ippolitoi*, n. sp. AMNH 30500. **A**, dorsal; **B**, ventral; **C**, right lateral; **D**, anterior; **E**, left lateral; **F**, posterior. [F. Ippolito, del.]

Contacts: Both *Taphrosphys ippolitoi* and *T. congolensis* specimens show the palatine contacting the maxilla anterolaterally, the other palatine medially, and the pterygoid posteriorly. There is probably a lateral contact with the jugal, but it is either disarticulated (*T. ippolitoi*) or missing (*T. congolensis*). The possible vomer contact is not preserved in either specimen. The dorsal surface contacts are not visible in either *T. ippolitoi* or *T. congolensis*.

Structures: The palatines of *Taphrosphys ippolitoi* and *T. congolensis* are very similar in shape and size. The palatine in both species does not enter onto the triturating surface to a significant extent, in agreement with other Taphrosphyini. Both species also lack the strong dorsal arching of the

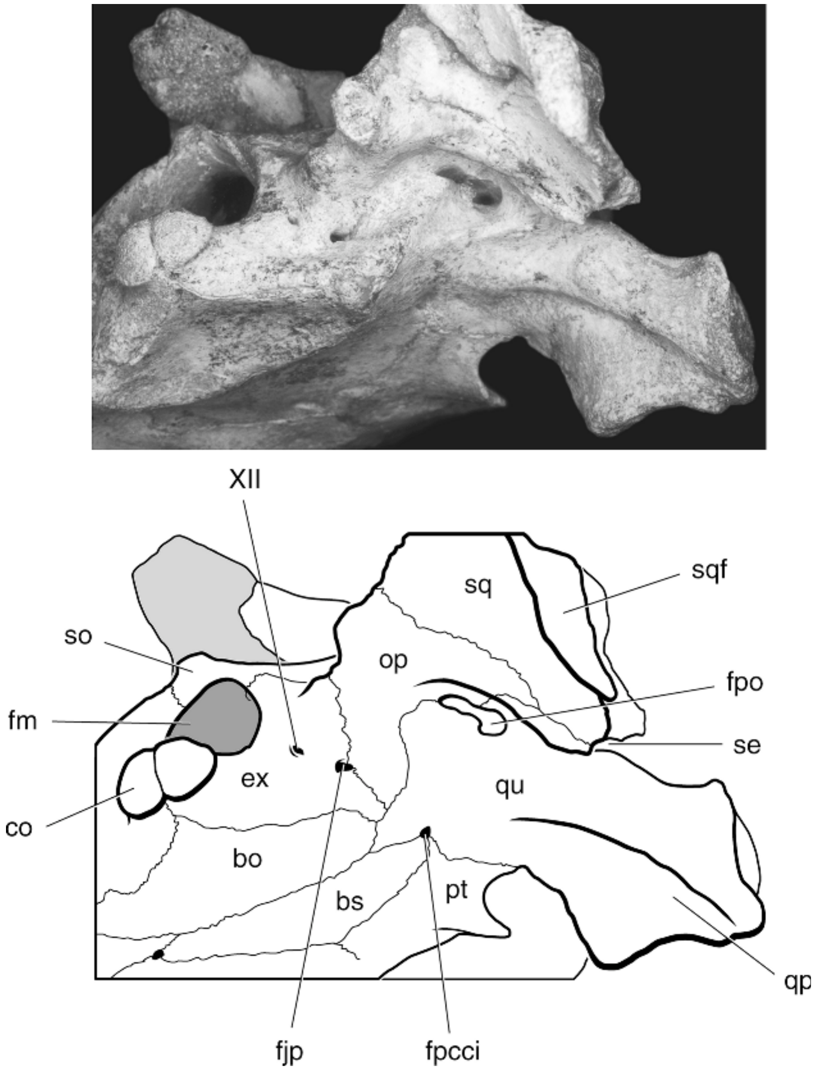

Fig. 184. *Taphrosphys ippolitoi*, n. sp. AMNH 30500. Posterior oblique view of skull. [A. Venjara and E.S. Gaffney, del.]

palatine seen in *Azabbaremys* and *Phosphatochelys*.

QUADRATE (figs. 178, 183, 184, 286E)

Preservation: In AMNH 30042 both quadrates are present and nearly complete although fractured. There is some ventral displacement of the dorsal part, particularly in the left quadrate. Both quadrates lack the anterodorsal sutural edge. In AMNH 30050, both quadrates are uncrushed and complete, except for their anterior margins.

Lateral view contacts and structures: The maxilla-quadrate contact of *Taphrosphys ippolitoi* is described under Maxilla, and the quadrate is described under *T. sulcatus*.

Dorsal view contacts and structures: See *Taphrosphys sulcatus* for description.

Ventral view contacts and structures: See *Taphrosphys sulcatus* for description.

PTERYGOID (figs. 178, 179, 181, 277D)

Preservation: Both pterygoids are present in AMNH 30042, but they are visible only in ventral view. Each pterygoid is also nearly complete except for some fractures and the broken processus trochlearis pterygoidei, which is on each side, although displaced. In AMNH 30500, both pterygoids are present but lack their anterior area and processus trochlearis pterygoidei. The dorsal surface is visible.

Contacts on ventral surface: In all three *Taphrosphys* species these contacts are the same: palatine anteriorly, other pterygoid anteromedially, basisphenoid posteromedially, and quadrate posterolaterally. The pterygoids in *Taphrosphys* are not as completely separated by the basisphenoid as in *Azabbaremys* and *Phosphatochelys*.

Structures on ventral surface: Although at least part of the processus trochlearis pterygoidei is present in *Taphrosphys congolensis* and *T. ippolitoi* (but not *T. sulcatus*), the angle or relative size is not determinable. The quadrate ramus of the pterygoid is preserved in all three *Taphrosphys* species and is very similar to that in *Azabbaremys* and *Phosphatochelys*. There is no depression or attachment scar for the pterygoideus musculature as seen in *Arenila*. The foramen posterius canalis carotici interni is formed equally by the pterygoid, basisphenoid, and quadrate in all three *Taphrosphys* species (fig. 277D). The edges of this foramen are slightly eroded in *T. congolensis* and *T. sulcatus*, but it is well preserved on the left side of AMNH 30042, *T. ippolitoi*. In AMNH 30500, the foramen posterius canalis carotici interni is formed mostly by the basisphenoid and quadrate, with the pterygoid nearly squeezed out. The foramen in AMNH 30042 is at the bottom of a slight depression that angles dorsomedially. There is no evidence that the pterygoid in any *Taphrosphys* species forms part of the foramen palatinum posterius.

Contacts on dorsal surface: See *Taphrosphys sulcatus* for description.

Structures on dorsal surface: See *Taphrosphys sulcatus* for description.

SUPRAOCCIPITAL (figs. 178, 181)

Preservation: In *Taphrosphys ippolitoi* in AMNH 30042, the anterior portion of the supraoccipital is largely covered by matrix, but the right portion is visible. The crista supraoccipitalis is broken at the foramen magnum. In AMNH 30500 the supraoccipital is entirely visible with clear sutures, but it also is missing nearly all of the crista supraoccipitalis.

Contacts and structures: See *Taphrosphys sulcatus* for description.

EXOCCIPITAL (figs. 178, 183, 184)

Preservation: Both exoccipitals are preserved and nearly complete in both skulls of *Taphrosphys ippolitoi.*

Contacts and structures: See *Taphrosphys sulcatus* for description.

BASIOCCIPITAL (figs. 178, 179, 183, 184, 277D)

Preservation: The basioccipital is complete and visible in ventral view in both skulls of *Taphrosphys ippolitoi.*

Contacts and structures: See *Taphrosphys sulcatus* for description.

PROOTIC (fig. 183)

Preservation: Although both prootics are presumed to be present in *Taphrosphys ippolitoi*, they are completely covered in AMNH 30042. In AMNH 30500, both prootics are visible, well preserved, and have clear sutures.

Contacts and structures: See *Taphrosphys sulcatus* for description.

OPISTHOTIC (figs. 178, 183, 184)

Preservation: In *Taphrosphys ippolitoi* in AMNH 30042, both opisthotics are present and nearly complete. The right is missing its posterior margin. Both are fractured on their dorsal surfacebut are in their original positions. Ventrally the right opisthotic is better preserved in the fenestra postotica region. In AMNH 30500 both opisthotics are complete with clear sutures.

Contacts and structures: See *Taphrosphys sulcatus* for description.

BASISPHENOID (figs. 178, 179, 183, 277D)

Preservation: The basisphenoid is complete, in both AMNH 30500 and AMNH 30042 of *Taphrosphys ippolitoi.*

Contacts and structures: See *Taphrosphys sulcatus* for description.

Taphrosphys congolensis

The single skull representing this species is crushed dorsoventrally, but during preparation, some of the skull roofing elements were removed, giving access to the internal basicranium and allowing reconstruction of the

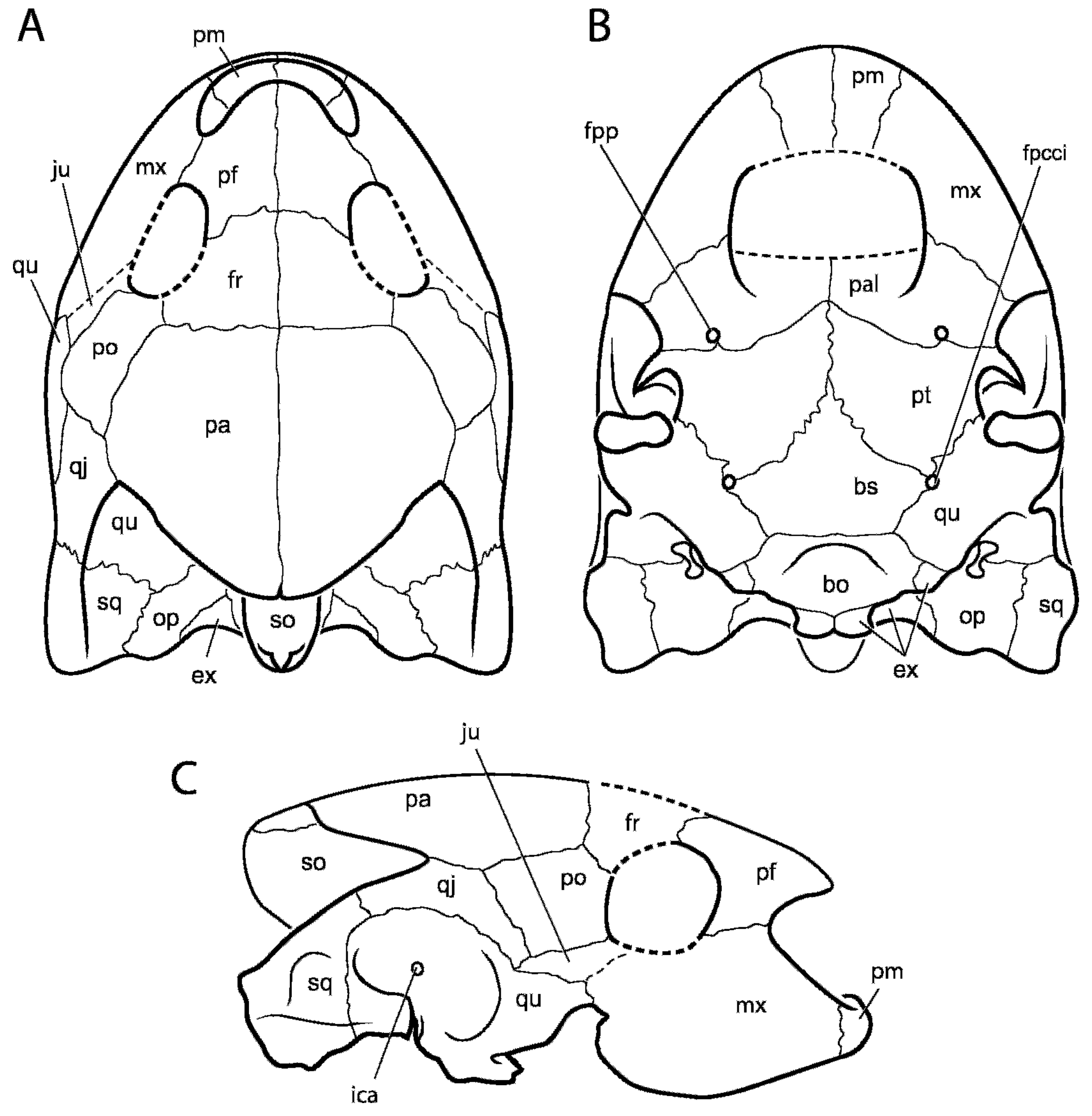

Fig. 185. *Taphrosphys congolensis* (Dollo, 1913). MRAC uncatalogued skull. Partially restored skull. **A**, dorsal; **B**, ventral; **C**, lateral. [F. Ippolito, del.]

skull roof. *Taphrosphys congolensis* is weakly supported as the sister taxon to the other two *Taphrosphys* species. The type of this species is a shell, and this skull was apparently not found associated with a shell of *Taphrosphys congolensis*, it was only found in the same unit.

Prefrontal (figs. 185, 188)

Preservation: Only the left prefrontal in *Taphrosphys congolensis* is preserved, but it seems to be nearly complete. Although it is disarticulated and not in its original position with regard to the neighboring bones, the element itself appears to be uncrushed and not distorted. All of the dorsal and most of the ventral surfaces are visible.

Contacts: The prefrontal of *Taphrosphys congolensis* as preserved lies on the internal surface of the maxilla and partially contacts the parietal posteriorly. These are not its original relations and are due to postmortem disarticulation and disturbance of this element. Sutural surfaces are clear for the usual

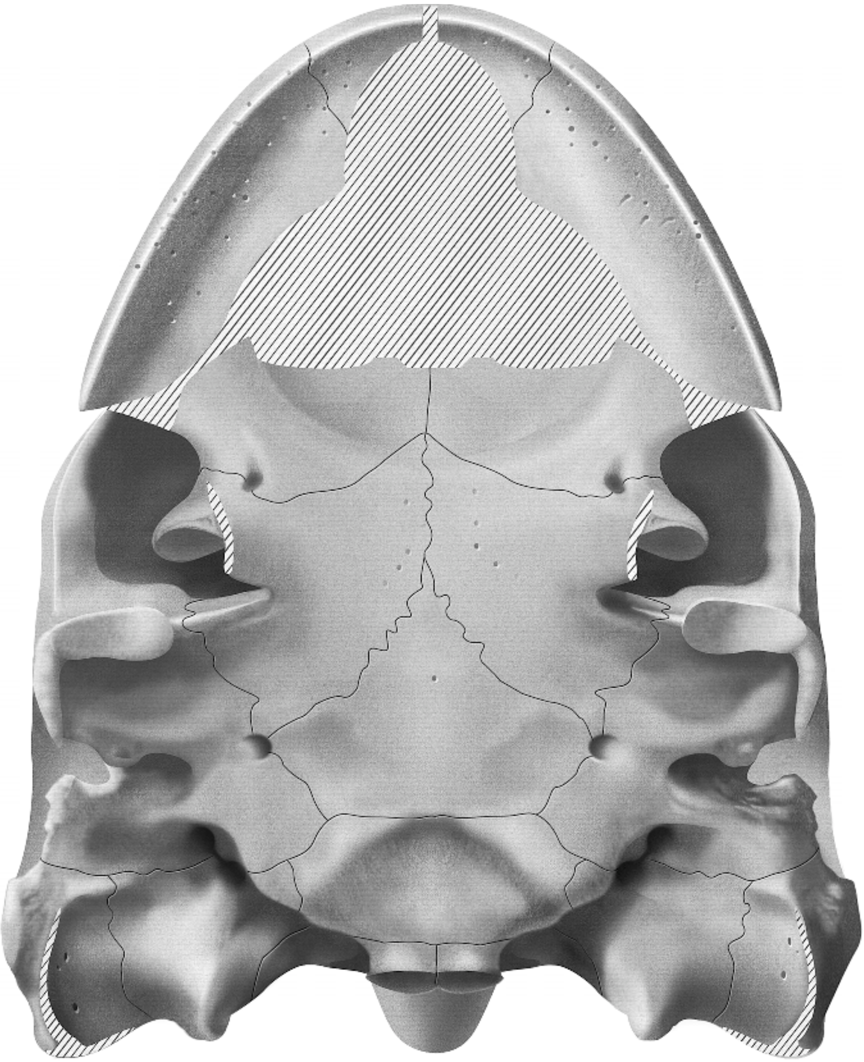

Fig. 186. *Taphrosphys congolensis* (Dollo, 1913). Partially restored ventral view of skull based on MRAC uncatalogued. [F. Ippolito, del.]

bothremydid contacts: prefrontal medially, maxilla ventrolaterally, and frontal posteriorly.

Structures: The prefrontal in *Taphrosphys congolensis* is very similar to that bone in *Azabbaremys, T. ippolitoi*, and *T. sulcatus*, although it is incomplete in the latter. Its surface is smooth and lacks the swelling seen in *T. ippolitoi*. The ventral surface of the prefrontal is largely visible in this specimen and shows the roof of the fossa nasalis, smaller than in *T. ippolitoi* but the same as in *T. sulcatus*. The midline suture is also visible, showing the bone to be much thicker on the midline than more laterally. *Taphrosphys congolensis* has a completely preserved ventral process of the prefrontal. This process forms most of the anterior orbital margin and a portion of the dorsal margin, a degree of orbital exposure also found in *Azabbaremys*.

FRONTAL (fig. 185)

Both frontals are completely missing in *Taphrosphys congolensis*. However, the preservation of the surrounding bones (prefrontal, parietal, and postorbital) gives a good idea of the position and shape of the frontal in *T. congolensis*.

PARIETAL (figs. 185, 188)

Preservation: Both parietals are preserved in *Taphrosphys congolensis* and are complete except for some missing edges laterally. The ventral and dorsal surfaces are visible on the right parietal, which has been removed from the rest of the specimen. The ventral edge and the contact of the processus inferior parietalis on both sides are either broken off (right) or crushed ventrally (left) and not visible.

Contacts of dorsal plate: As preserved, the left parietal of *Taphrosphys congolensis* touches (but does not share a suture with) the left prefrontal. A frontal was originally between these two bones, and the present condition is due to postmortem disarticulation and disturbance. The right and left parietals overlie the respective postorbitals and quadratojugals, a condition that is interpreted as the result of postmortem disarticulation. However, the relative positions of these bones have not changed much from the life position, so that the parietal contacted the postorbital anterolaterally and the quadratojugal posterolaterally, as indicated in the restoration (fig. 185).

The dorsal plate of the right parietal is more complete than the left one. The lateral edges are broken, but they very nearly fit with the associated postorbital and quadratojugal. Restored from these elements, the parietal has an anterolateral postorbital contact and a lateral quadratojugal contact. The postorbital contact is longer than the quadratojugal one. The other two *Taphrosphys* species are not well preserved in this area, but what is preserved in both is consistent with the condition in *Taphrosphys congolensis*.

Structures of the dorsal plate: The dorsal plate of the parietal is nearly complete in *Taphrosphys congolensis*. The emargination extends about halfway anteriorly up the length of the parietal, in contrast to forms like *Azabbaremys* in which it extends for only about one-third the length. More of the otic chamber is also exposed, but the degree of emargination is less than in *Galianemys* and much less than in *Kurmademys*. The edge of the parietal forming the emargination in *T. congolensis* is nearly straight with a small bulge just anterior to the supraoccipital contact.

Contacts of processus inferior parietalis: Although it is clear that most of the parietal contacted the crista pterygoidea in *Taphrosphys congolensis* as in all other turtles, the position of the foramen nervi trigemini and the bones forming it cannot be seen.

Processus inferior parietalis: The dorsal parts of this wall are present on both sides, and the cavum cranii roof forming the cerebral expansions is visible. These are very similar in both *Taphrosphys congolensis* and *T. sulcatus* (indeterminate in *T. ippolitoi*). The processus inferior parietalis in *T. congolensis* and *T. sulcatus* is clearly wider than in *Azabbaremys*, which has an unusually narrow one.

JUGAL (figs. 185, 188)

Preservation: On the left side, a portion of what appears to be the jugal is preserved in *Taphrosphys congolensis*. Adjacent articulating elements (maxilla, quadrate, postorbital, and squamosal) provide some information on the jugal shape and contacts on the cheek. The medial process, however, is largely missing. On the right side a small fragment of what seems to be jugal is present between quadrate and postorbital.

Contacts and structures of lateral plate: In *Taphrosphys congolensis* the jugal shape is based primarily on a reconstruction of the elements around it. There is some degree of guesswork involved in this reconstruction because few of the surrounding elements are themselves in their original positions.

The maxilla-quadrate contact prevents a cheek exposure of the jugal, and the lower edge of the jugal contacts these two bones. The dorsal edge of the jugal contacts the postorbital anteriorly and the quadratojugal posteriorly. Presumably the jugal enters the orbital margin because a postorbital-maxilla contact, which would prevent that, is unlikely. However, none of the fragments possibly identifiable as jugal seems to have a natural edge. As reconstructed, the jugal in *Taphrosphys congolensis* is relatively long anteroposteriorly and short in height, similar to that bone in *T. ippolitoi*. It is possible that the jugal was nearly the same in both species, given the uncertainty of its shape in *T. congolensis*.

QUADRATOJUGAL (figs. 185, 188)

Preservation: Both quadratojugals are present in *Taphrosphys congolensis*. The right one is well preserved and in articulation with the postorbital and quadrate. The left one is fractured but complete and only slightly displaced anteriorly. Both have been pushed ventrally into the upper part of the quadrate. The left quadratojugal is fractured and partially distorted, but the right one appears to be in its original shape.

Contacts: The quadratojugal in *Taphrosphys congolensis* has a long ventral suture with the quadrate and a shorter anterior suture with the postorbital. Dorsomedially there is a short contact, visible on the left side, with the parietal posterior to the postorbital. The quadratojugal in *T. congolensis* and *T. ippolitoi* does not extend ventrally along the anterior margin of the quadrate to reach the cheek margin due to a jugal-quadrate contact. However, there is not a complete dorsal restriction of the quadratojugal as seen in *Phosphatochelys*, which has a postorbital-quadrate contact, absent in *Taphrosphys*. The jugal-quadratojugal contact is not clearly preserved in *T. congolensis*, but there is a sutural margin preserved on the right quadratojugal that is best interpreted as this contact. The reconstruction is consistent with this interpretation (fig. 185). The posteriormost extension of the quadratojugal contacts the squamosal in a narrow suture above the quadrate.

Structures: The quadratojugal in *Taphrosphys congolensis* is curved to cover the lateral part of the skull roof and part of the cheek. The right quadratojugal shows a well-preserved temporal margin just lateral to the parietal contact. The temporal emargination is formed laterally by the quadratojugal and part of the squamosal.

SQUAMOSAL (figs. 185, 188, 189)

Preservation: Both squamosals in *Taphrosphys congolensis* are present, uncrushed, and lack only their posterior margins.

Contacts: As in *Taphrosphys sulcatus*.

Structures: The antrum postoticum on the quadrate in *Taphrosphys congolensis* is crushed on both sides, so the internal structure of the antrum in the squamosal is not visible. The size and shape of the squamosal in *T. congolensis* are very similar in *T. sulcatus*. The ventral flange on the squamosal is nearly complete on the left side and is nearly identical to that in *T. sulcatus*.

POSTORBITAL (figs. 185, 188)

Preservation: Both postorbitals in *Taphrosphys congolensis* are preserved in their entirety, but they have been displaced ventrally from their original positions. Both are in roughly their original relations to other skull roof elements, and the right one is still articulated with the quadratojugal, further aiding in the reconstruction.

Contacts: The postorbital of *Taphrosphys congolensis* contacts the quadratojugal posteriorly and the parietal medially. A short sutural margin anteromedially is interpreted as a frontal contact, and the ventral sutural margin is interpreted as the jugal contact.

Structures: The anterior margin of the postorbital in *Taphrosphys congolensis* forms the posterior margin of the orbit. There is no exposure on the cheek or temporal emargination.

An important feature of most pleurodire postorbitals is the medial process that forms much of the septum orbitotemporale. However, in *Azabbaremys*, *Labrostochelys*, and *Phosphatochelys* this process is absent and the wall is open. In *Taphrosphys congolensis* both postorbitals are dropped ventrally out of their original positions, but both are only fractured and not crushed or deformed. Some of their medial-ventral surface is also visible. Although the matrix has not been entirely removed, there is no sign of a medial process in either postorbital, and the condition is the same as in the other Taphrosphyini.

PREMAXILLA (figs. 185, 186, 188)

Preservation: The left premaxilla is present in *Taphrosphys congolensis*, uncrushed but lacking its posteromedial extension.

Contacts: As in other bothremydids, the premaxilla of *Taphrosphys congolensis* meets the other premaxilla medially on the midline and the maxilla posterolaterally. The vomer and its presumed contact are missing.

Structures: The labial ridge is preserved in all three *Taphrosphys* species. The ridge is relatively shallow in *T. ippolitoi* and *T. sulcatus*, both of which presumably had at least a slight notching or upswing to the

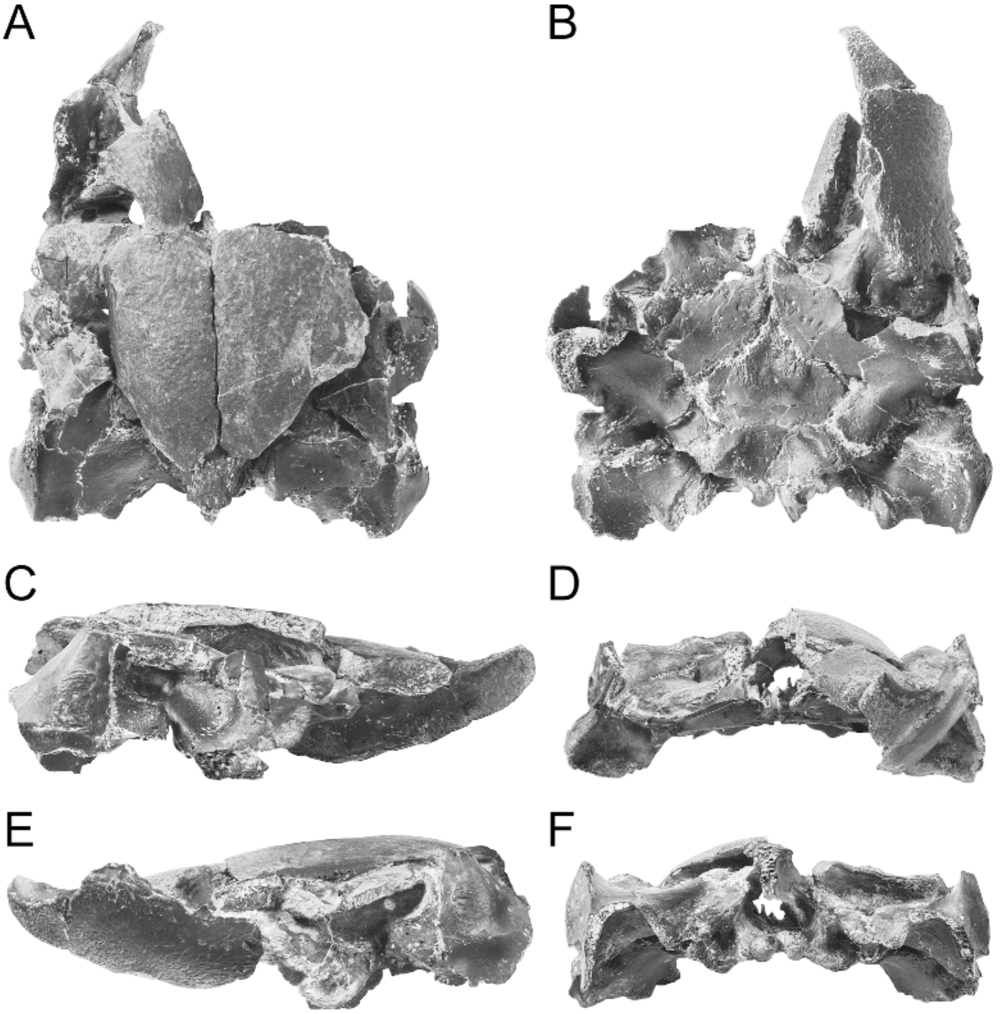

Fig. 187. *Taphrosphys congolensis* (Dollo, 1913). MRAC uncatalogued. **A**, dorsal; **B**, ventral; **C**, right lateral; **D**, anterior; **E**, left lateral; **F**, posterior. [F. Ippolito, del.]

labial ridge in anterior view. In contrast, *T. congolensis* has a deeper and more acute labial ridge that would not form a dorsal curve.

MAXILLA (figs. 185, 186, 188)

Preservation: Only the left maxilla is preserved; it is uncrushed but pushed medially out of its original position. Its dorsal margins are mostly broken.

Contacts of vertical plate: The anteromedial contact with the premaxilla is present and intact. As preserved, despite being pushed medially, there is still a maxilla-quadrate contact posteriorly, and this is interpreted as original. The jugal is not present, but a short part of the jugal suture is interpreted as present. The anterodorsal suture with the prefrontal is partially preserved.

Structures of vertical plate: The vertical plate forms the labial ridge in *Taphrosphys congolensis* and is similar to that in *T. ippolitoi*, but it curves anteromedially rather than flares laterally as in *T. ippolitoi*. The maxilla is missing in *T. sulcatus*.

Contacts of horizontal plate: In both *Taphrosphys ippolitoi* and *T. congolensis* the maxilla has the same contacts: premaxilla anteromedially and palatine posteromedially. In both species the jugal (or a fragment of it)

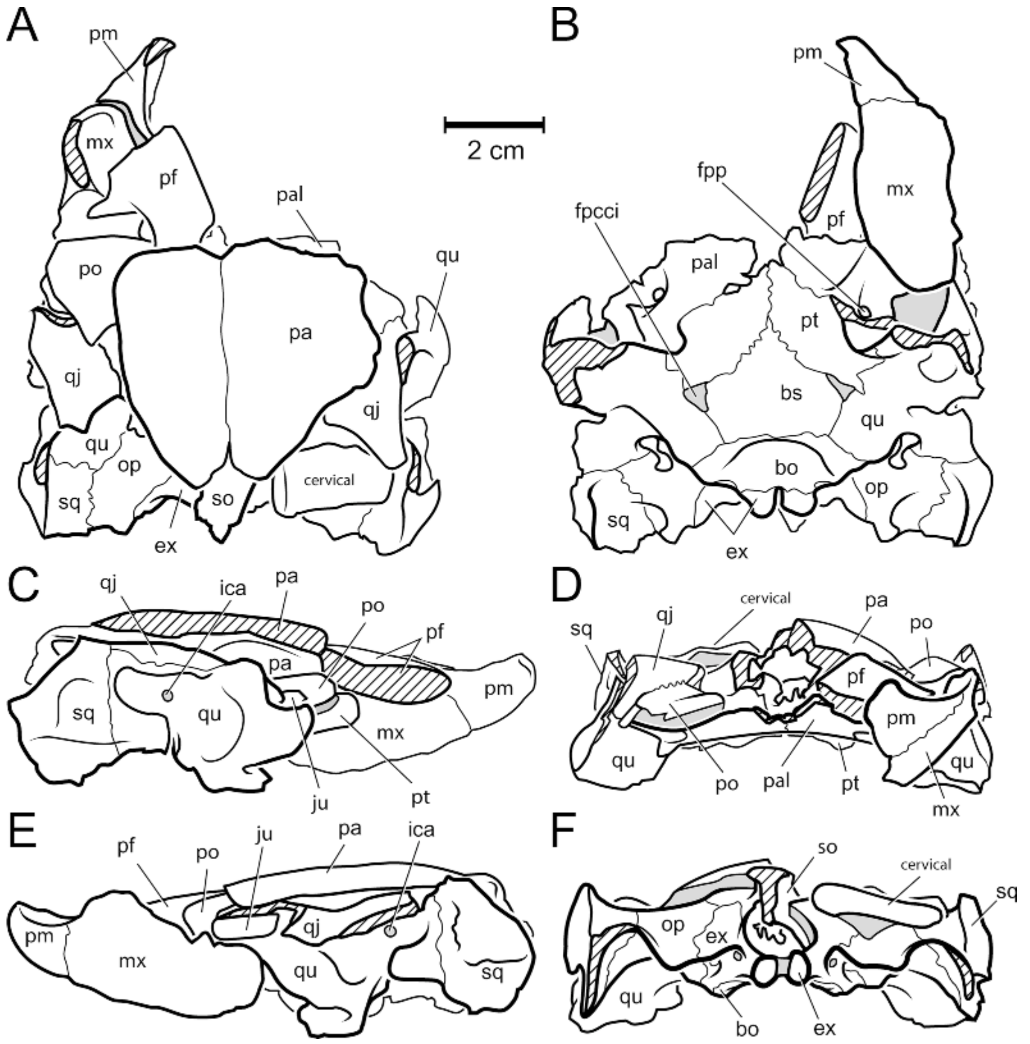

Fig. 188. *Taphrosphys congolensis* (Dollo, 1913). MRAC uncatalogued. **A**, dorsal; **B**, ventral; **C**, right lateral; **D**, anterior; **E**, left lateral; **F**, posterior. [F. Ippolito, del.]

is present but displaced, still indicating the usual pelomedusoid posterolateral contact. Although it is not completely certain, a medially meeting process of the maxilla is unlikely in both *T. congolensis* and *T. ippolitoi*. In *T. congolensis* the medial margin of the maxilla seems to be complete enough to show that a process is absent. In *T. ippolitoi* the maxilla has a medial process, but it stops short of the midline due to the large premaxilla.

Structures of horizontal plate: See *Taphrosphys ippolitoi* for description.

VOMER

Preservation: The vomer is missing in *Taphrosphys congolensis*.

PALATINE (figs. 185, 186, 188)

Preservation: In *Taphrosphys congolensis* the left palatine is nearly complete, lacking its anterior margin, but the right one is missing its anterior half. Both are slightly fractured but in their original positions.

Contacts: See *Taphrosphys ippolitoi* for description.

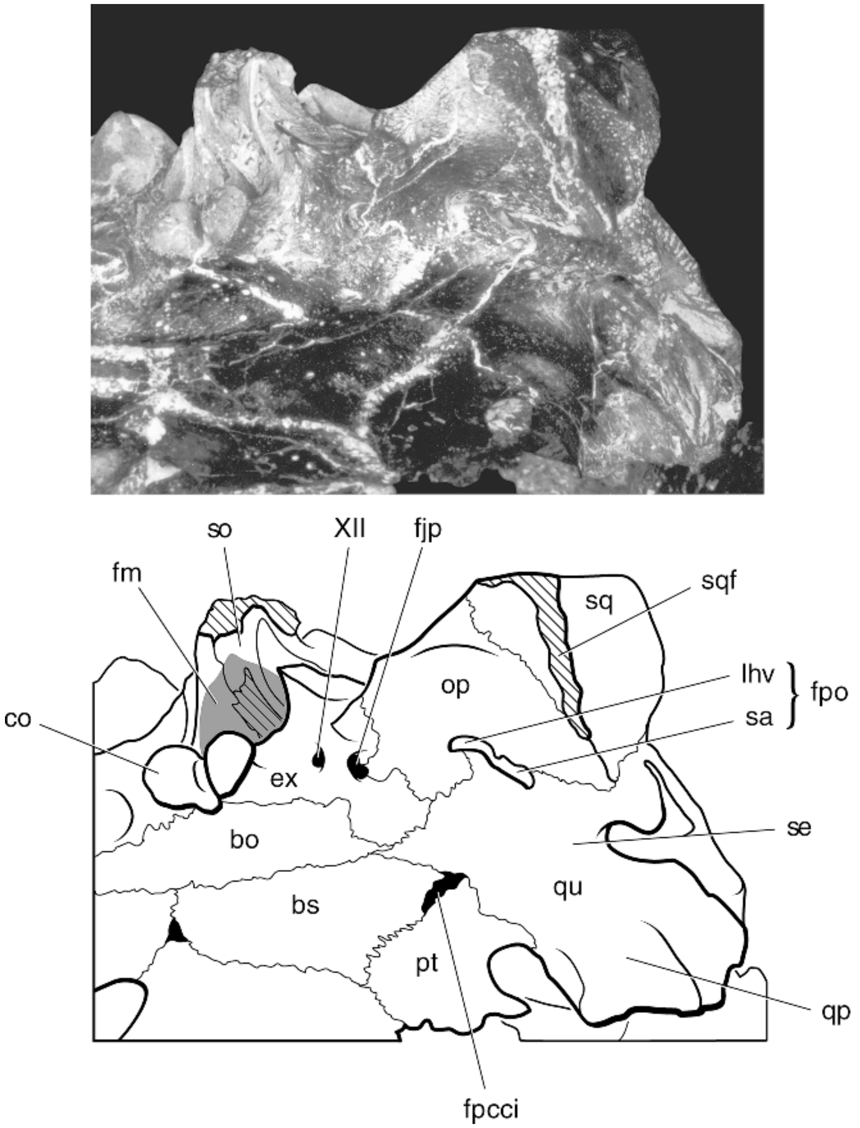

Fig. 189. *Taphrosphys congolensis* (Dollo, 1913). MRAC uncatalogued. Posterior oblique view of skull reversed from left side. [E.S. Gaffney and A. Venjara, del.]

Structures: See *Taphrosphys ippolitoi* for description.

QUADRATE (figs. 185–189)

Preservation: Both quadrates are present in *Taphrosphys congolensis* with the ventral halves relatively well preserved, but both have the dorsal half of the cavum tympani and antrum postoticum crushed. The dorsomedial margins are mostly damaged or covered.

Lateral view contacts and structures: The maxilla-quadrate contact is described under Maxilla, and the quadrate is described under *Taphrosphys sulcatus*.

Dorsal view contacts and structures: See *Taphrosphys sulcatus* for description.

Ventral view contacts and structures: See *Taphrosphys sulcatus* for description.

Pterygoid (figs. 185–189)

Preservation: Both pterygoids in *Taphrosphys congolensis* are preserved in articulation, visible at least in part in dorsal as well as ventral view. The pterygoids are complete except for the processus trochlearis pterygoidei, which is missing in the left pterygoid and broken off but present, not in its original position, on the right side.

Contacts on ventral surface: See *Taphrosphys ippolitoi* for description.

Contacts on dorsal surface: See *Taphrosphys sulcatus* for description.

Structures on dorsal surface: See *Taphrosphys sulcatus* for description.

Supraoccipital (figs. 185, 188, 189)

Preservation: The supraoccipital in *Taphrosphys congolensis* is crushed ventrally into the cavum cranii and is missing some of the edge of the crista supraoccipitalis, but the main body of the bone is relatively undistorted and well preserved although partially displaced from surrounding elements.

Contacts and structures: See *Taphrosphys sulcatus* for description.

Exoccipital (figs. 185, 188, 189)

Preservation: Both exoccipitals in *Taphrosphys congolensis* are preserved and nearly complete although the supraoccipital has been crushed ventrally.

Contacts and structures: See *Taphrosphys sulcatus* for description.

(figs. 185–189)

Preservation: The basioccipital in *Taphrosphys congolensis* is complete and visible in ventral view.

Contacts and structures: See *Taphrosphys sulcatus* for description.

Prootic

Preservation: Both prootics are present in *Taphrosphys congolensis*, but only the right one is visible dorsally and anteriorly. It is partially disarticulated from surrounding elements and pushed ventrally.

Contacts and structures: See *Taphrosphys sulcatus* for description.

Opisthotic (figs. 185, 186, 188, 189)

Preservation: Both opisthotics are present and complete in *Taphrosphys congolensis*.

Contacts of structures: See *Taphrosphys sulcatus* for description.

Basisphenoid (figs. 185, 186, 188)

Preservation: The basisphenoid in *Taphrosphys congolensis* is complete with both dorsal and ventral surfaces visible.

Contacts and structures: See *Taphrosphys sulcatus* for description.

Labrostochelys galkini

This unusual species is known from two skulls, one of which (AMNH 30043) is crushed but still well preserved and is the basis for most of the description and figures. *Labrostochelys* is the sister taxon to the remaining members of the subtribe Taphrosphyina.

Prefrontal (figs. 190, 193)

Preservation: Both prefrontals are present in AMNH 30043 and AMNH 29984, but they are more complete in the former. In both specimens the snout elements are displaced ventrally, and in AMNH 30043 they lie on the vomer. However, significant distortion does not seem to have taken place in either skull.

Contacts: The prefrontal of *Labrostochelys* has the three usual contacts: prefrontal on midline, maxilla anteroventrolaterally, and frontal posteriorly. Because of its great length, the prefrontal and maxilla contacts are longer than in any other pleurodire. It is possible that the prefrontal contacted the premaxilla originally via a small anteroventral process that is now lost.

The ventral process of the prefrontal is preserved on both sides of AMNH 30043. Despite some displacement of both bones, it is clear that although the prefrontal comes close to contacting the palatine as preserved, this was not the original condition. The palatine sutural edges match the maxilla sutural edges and the prefrontal seems to be completely excluded.

Structures: The prefrontal of *Labrostochelys* is extremely long and narrow, longer and narrower than in any other turtle. It begins anteriorly at the apertura narium externa and extends posteriorly to the midpoint of the orbit, as in other Pelomedusoides. What in most other Pelomedusoides is

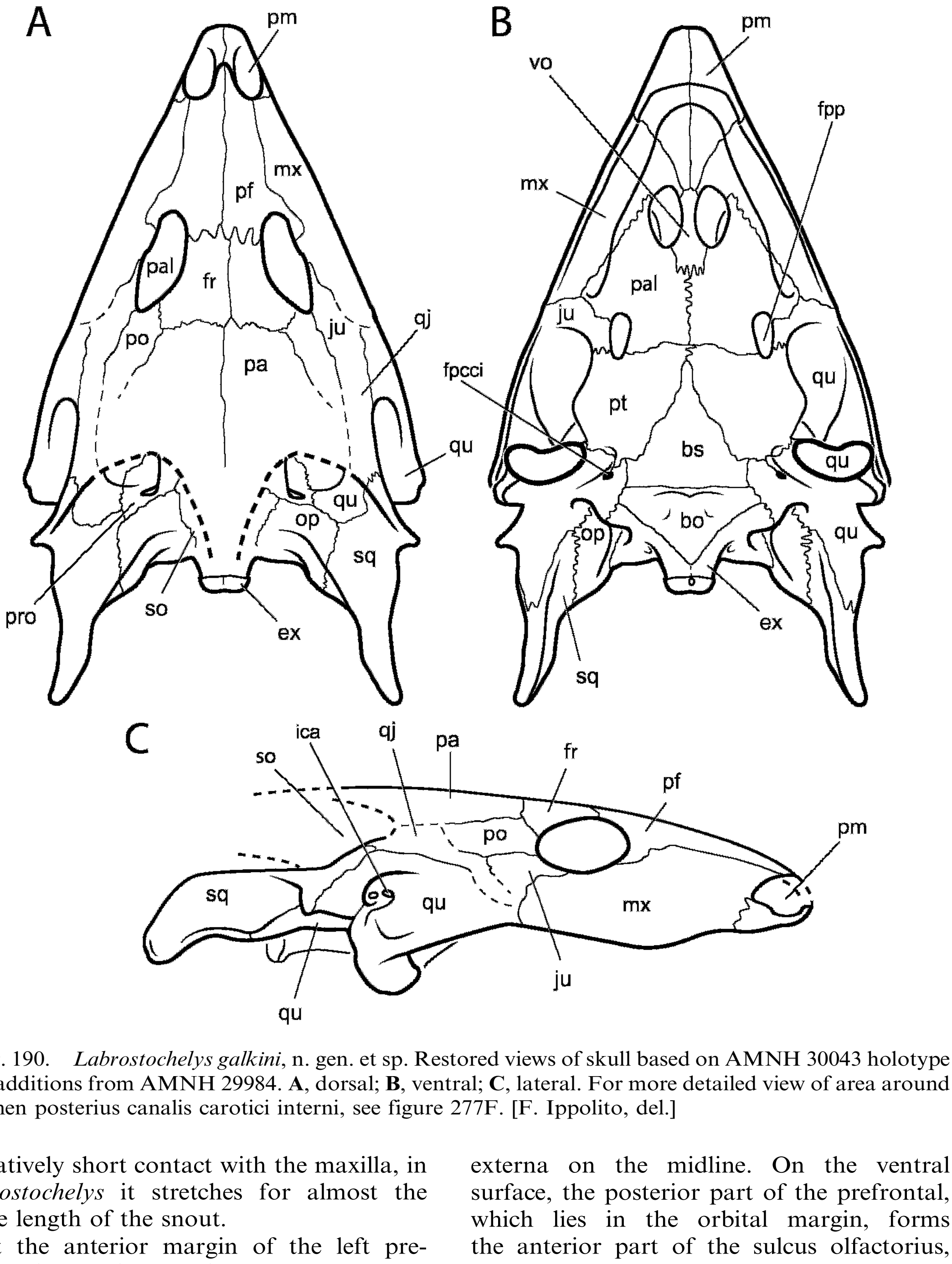

Fig. 190. *Labrostochelys galkini*, n. gen. et sp. Restored views of skull based on AMNH 30043 holotype with additions from AMNH 29984. **A**, dorsal; **B**, ventral; **C**, lateral. For more detailed view of area around foramen posterius canalis carotici interni, see figure 277F. [F. Ippolito, del.]

a relatively short contact with the maxilla, in *Labrostochelys* it stretches for almost the entire length of the snout.

At the anterior margin of the left prefrontal is a thin anterior process, broken anteriorly, that comes close to reaching a rugosity, possibly a suture, on a dorsal process of the premaxilla. It is possible that originally the prefrontal and premaxilla were in contact and divided the apertura narium externa on the midline. On the ventral surface, the posterior part of the prefrontal, which lies in the orbital margin, forms the anterior part of the sulcus olfactorius, much as in other Pelomedusoides such as *Pelusios*.

FRONTAL (figs. 190, 193)

Preservation: Both frontals are preserved in both specimens of *Labrostochelys*.

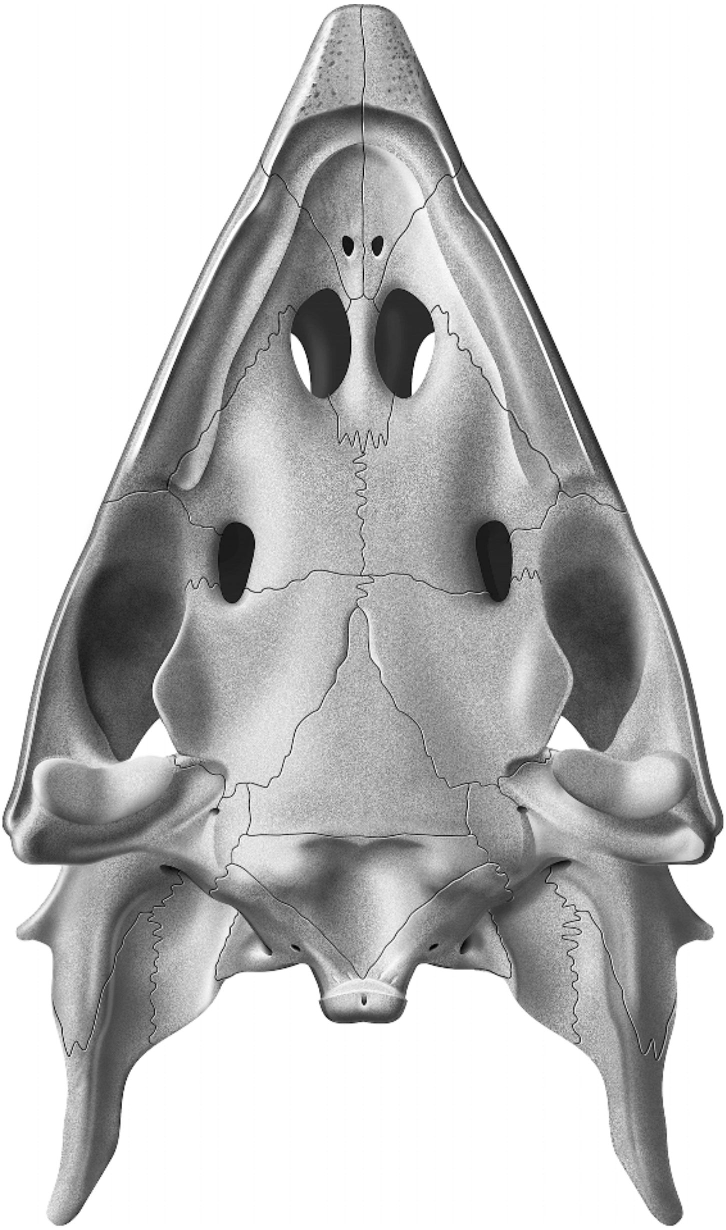

Fig. 191. *Labrostochelys galkini*, n. gen. et sp. Partially restored ventral view of skull based on AMNH 30043 holotype with additions from AMNH 29984. [F. Ippolito, del.]

Contacts: The frontal of *Labrostochelys* has the usual contacts: other frontal on midline, prefrontal anteriorly, postorbital posterolaterally, and parietal posteriorly.

Structures: The frontal is widely exposed in the dorsal orbital margin in *Labrostochelys*, much as in *Taphrosphys* and in contrast to the smaller exposure in *Azabbaremys*. In AMNH 30043 some of the ventral surface of the frontal is visible and shows the sulcus olfactorius to be wide with deep ventral walls.

PARIETAL (figs. 190, 193)

Preservation: The anterior third or so of both parietals is present in AMNH 30043, with AMNH 29984 preserving much more of the temporal area but still missing the posterior parietal margins.

Contacts of dorsal plate: As preserved, the parietal in *Labrostochelys* contacts the frontal anteriorly and the postorbital anterolaterally. Quadratojugal and squamosal contacts are indeterminable.

Structures of dorsal plate: None of the temporal margin is preserved in either skull of *Labrostochelys*. However, natural edges of the quadrate and squamosal on the left side of AMNH 30043 show that the parietal roof was not extensive and probably did not extend posteriorly past the middle of the otic chamber. The skull roof in *Labrostochelys*, although elongate like the rest of the skull, was probably similar in temporal extent to that in *Taphrosphys*.

Contacts of processus inferior parietalis: Much of the ventral process of the parietal is damaged in both skulls, but it can be seen that it has the usual long contact with the pterygoid and a posteroventral contact with the prootic and supraoccipital. A palatine contact at the anterior edge of the processus parietalis inferior is likely but not definite.

Processus inferior parietalis: The parietal forms the anterodorsal edge of the foramen nervi trigemini, along with the prootic and pterygoid. Above the foramen the parietal forms a horizontal ridge that overhangs the foramen nervi trigemini and has a distinct, lateral process anterior to the foramen nervi trigemini. The ridge and process do not appear in any other pelomedusoid.

JUGAL (figs. 190, 193)

Preservation: Both jugals are present in both *Labrostochelys* skulls, somewhat disarticulated but in roughly their original positions.

Contacts: The jugal in *Labrostochelys* contacts the maxilla anteroventrally, the quadratojugal posterodorsally, and the postorbital dorsally. These contacts are highly likely and only slightly disarticulated. As restored, the jugal contacts the quadrate and quadratojugal ventrally and does not enter the cheek margin. This is also likely because of a preserved maxilla-quadrate contact on the right side. The quadratojugal relations, however, are somewhat problematic, as the quadratojugal is preserved only as fragments in AMNH 30043. The quadratojugal probably does not reach the maxilla, but it is possible.

Structures: The jugal in *Labrostochelys* forms the posteroventral margin of the orbit, as in *Taphrosphys ippolitoi*. The medial process of the jugal forms part of the floor of the fossa orbitalis, but none of the septum orbitotemporale, which is absent in *Labrostochelys*.

QUADRATOJUGAL (figs. 190, 193)

Preservation: The quadratojugal is missing in AMNH 29984 and only partially preserved in AMNH 30043. A narrow strip above the quadrate on the right side is quadratojugal, and on the left side a larger piece is present between jugal and quadrate.

Contacts: As restored the quadratojugal of *Labrostochelys* contacts the postorbital anteromedially, the jugal anteroventrally, the squamosal posteriorly, and the quadrate ventrally. A parietal contact is possible but not determinable.

Structures: The quadratojugal forms the posterolateral part of the skull roof emargination. Its medial extent is not determinable. The cheek area is disturbed in both skulls. As restored, the quadratojugal does not enter the cheek emargination, which is virtually absent in *Labrostochelys*.

SQUAMOSAL (figs. 190, 191, 193, 287)

Preservation: Little of the squamosal remains in AMNH 29984, but AMNH 30043 has nearly all of both squamosals.

Contacts: The squamosal of *Labrostochelys* has the usual contacts: quadrate anteriorly, opisthotic medially, and quadratojugal anterodorsally. However, because of its unique shape, the squamosal contact with the quadrate is much longer than in other Taphrosphyini, resulting in a ventral quadrate process lying under the squamosal.

Structures: Instead of the usual cone-shaped squamosal, *Labrostochelys* has a long, narrow squamosal developed into a vertical sheet forming a hornlike process at the back of the skull. This elongate squamosal is also seen in some trionychids, such as *Cycloderma* and *Chitra* (Gaffney, 1979a). The elongation is apparently related to jaw muscle attachments (Schumacher, 1973). The adductor mandibulae attaches on the medial and dorsal surfaces, with the depressor mandibulae attaching on the lateral and ventral surfaces. Interestingly, *Labrostochelys* also has a pocket on the posterior surface of the quadrate, another attachment site for the depressor mandibulae.

The squamosal in *Labrostochelys* forms a small, lateral projection on its lateral surface near the quadrate contact (fig. 287). This is at the anterior margin of a curved ridge that separates the lateral surface from the dorsal surface and would appear to reflect the division of two muscle attachment sites. The antrum postoticum in *Labrostochelys* does not seem to extend into the squamosal in AMNH 30043, but it may in AMNH 29984 (see Quadrate).

POSTORBITAL (figs. 190, 193)

Preservation: The postorbital is present on both sides of AMNH 30043; the left is more complete, but neither includes the posterior limits. The right postorbital of AMNH 29984 is partially preserved.

Contacts: The postorbital of *Labrostochelys* contacts the frontal anterodorsally, the parietal dorsomedially, the jugal anteroventrally, the pterygoid medially, and the quadratojugal posteroventrally. The extent of the posterior contacts is indeterminate.

Structures: The postorbital in *Labrostochelys* forms part of the posterior orbital margin with less exposure than in *Taphrosphys*, *Phosphatochelys*, and *Azabbaremys*. Whether the postorbital extends posteriorly far enough to reach the temporal margin is not determinable, but it seems unlikely based on its preserved shape and similarity to *Taphrosphys*. In contrast to *Phosphatochelys* and *Azabbaremys*, there is a medial process of the postorbital forming at least a partial septum orbitotemporale and entering the sulcus palatinopterygoideus. This is only visible on the right side of AMNH 30043, and it is not well preserved.

PREMAXILLA (figs. 190, 191, 193)

Preservation: Both premaxillae are missing in AMNH 29984, but both are present and well preserved in AMNH 30043.

Contacts: The premaxilla in *Labrostochelys* contacts the maxilla posterolaterally, the premaxilla medially, and the vomer posteromedially. The anterodorsomedial edge of the premaxilla in AMNH 30043 has a short dorsal process that may have contacted an anteroventral process of the prefrontal, producing a divided apertura narium externa. This condition is not found in other Taphrosphyini but is seen in some *Bothremys*.

Structures: The premaxilla forms the ventral margin of the apertura narium externa and floor of the fossa nasalis. The apertura of *Labrostochelys* differs from the other Taphrosphyini in being much smaller and completely, or almost completely, divided on the midline. The uniquely narrow snout of *Labrostochelys* ends anteriorly in premaxillae that come to a blunt point, bearing the apertura narium externa at its end. The foramen praepalatinum on both premaxillae is incomplete, but it seems to have been formed entirely within the premaxilla, close to the midline suture but clearly separated from the vomer.

On the ventral surface, *Labrostochelys* also differs from all other pleurodires in having a premaxilla that bears an elongation anterior to the labial ridge of the triturating surface. This triangular plate bears the floor of the fossa nasalis on its dorsal surface. Ventrally and around its edges are a large number of vascular foramina, indicating that it bore part of the horny beak like the rest of the triturating surface.

The labial ridge is not a distinct ridge, but it forms a line where the flat anterior surface curves sharply dorsally to join the triturating surface proper. The posterior surface of the premaxilla forms a triangular shelf supporting the triturating surface. About midway along the surface, the premaxilla forms a midline concavity that is part of the roof of the mouth and leads into the apertura narium interna. The blunt ridge defining this concavity roughly parallels the labial ridge and may be interpreted as the lingual ridge. Laterally it is continuous with a more defined ridge on the maxilla that is clearly the lingual ridge.

MAXILLA (figs. 190, 191, 193)

Preservation: Both maxillae are present and nearly complete in both specimens.

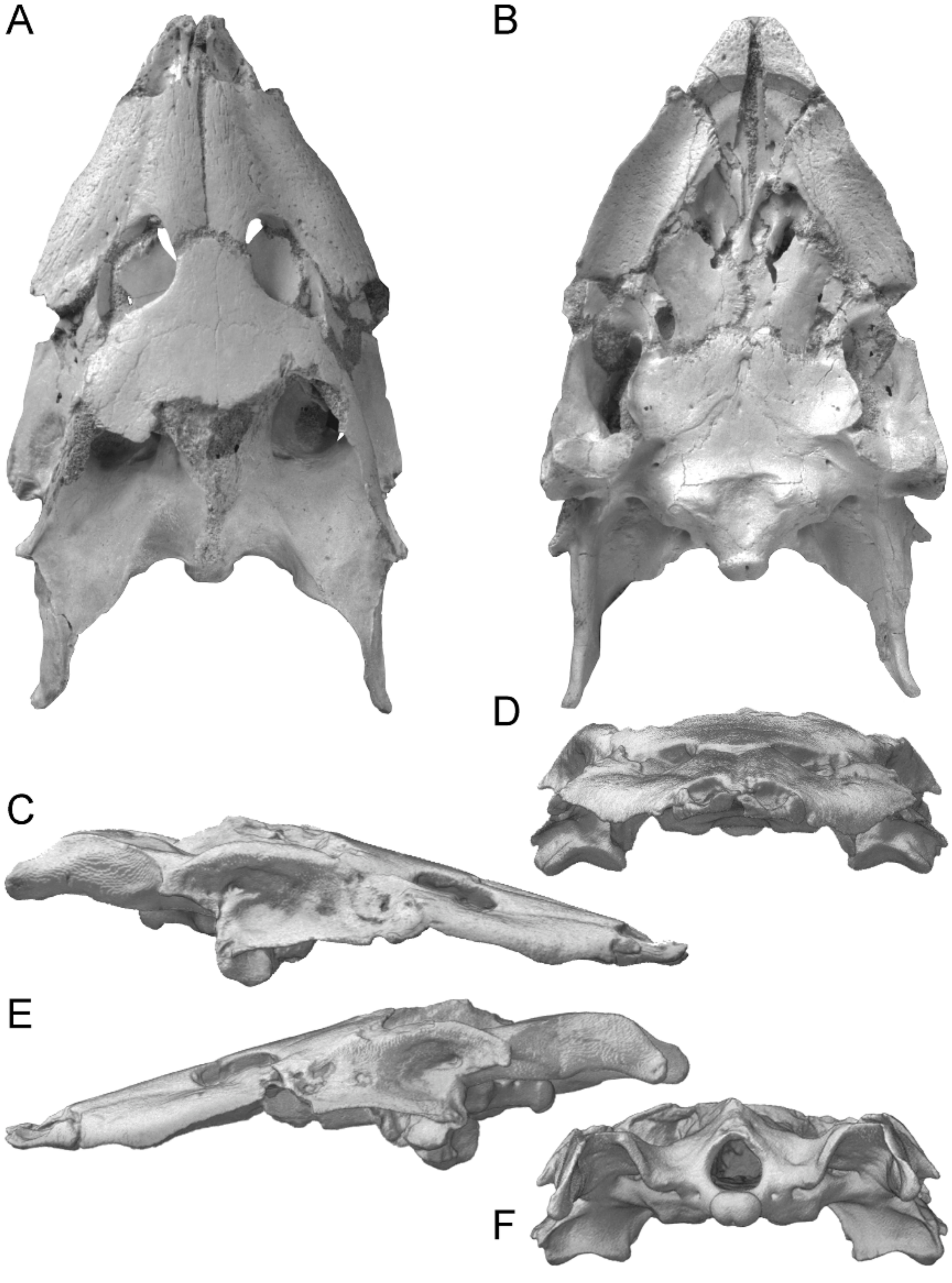

Fig. 192. *Labrostochelys galkini*, n. gen. et sp. AMNH 30043 holotype. **A**, dorsal; **B**, ventral; **C**, right lateral; **D**, anterior; **E**, left lateral; **F**, posterior. Parts D through F are CT scans. CT scans courtesy T. Rowe and the University of Texas Digital Imaging Laboratory. [F. Ippolito, del.]

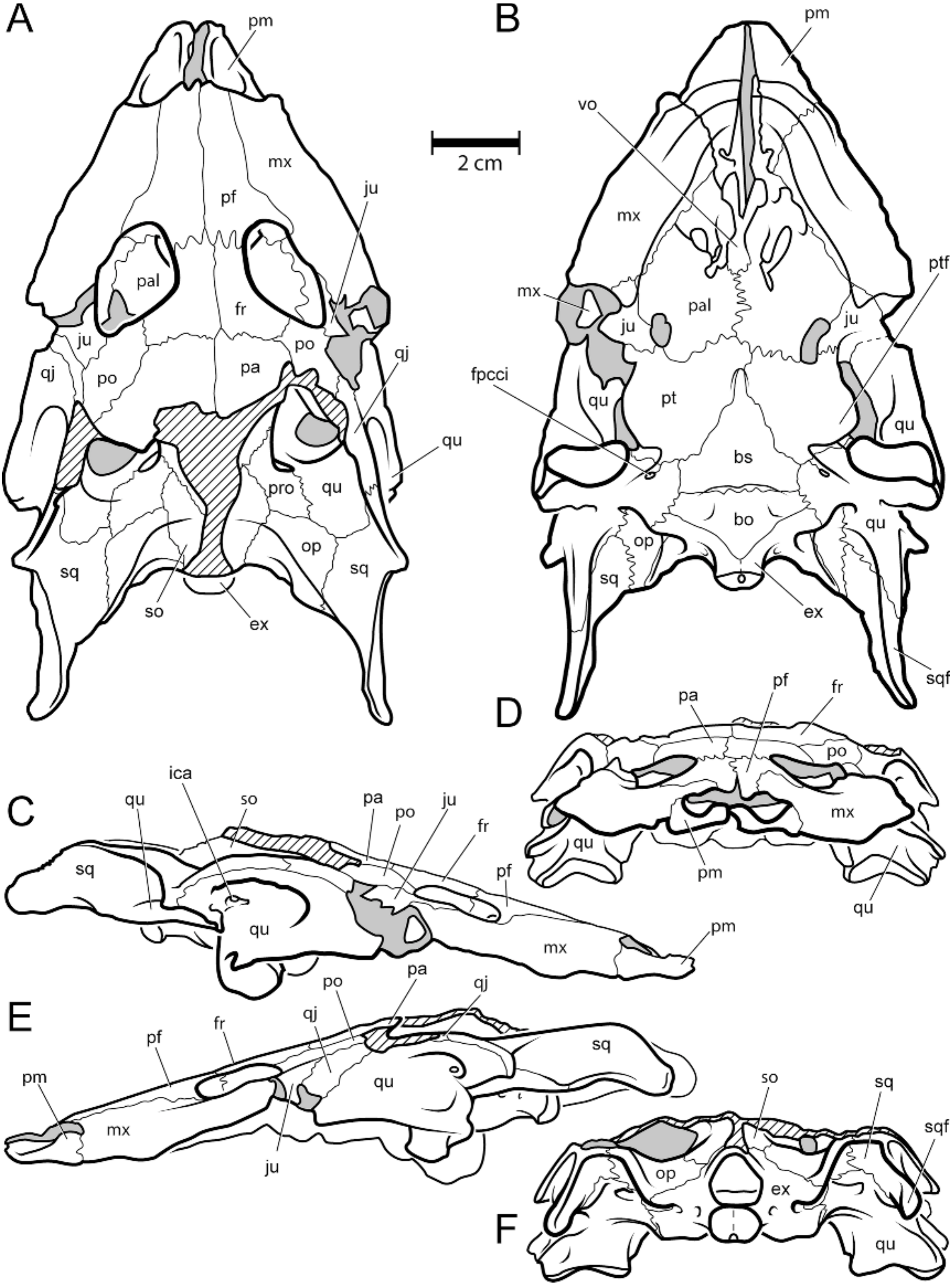

Fig. 193. *Labrostochelys galkini*, n. gen. et sp. AMNH 30043 holotype. **A**, dorsal; **B**, ventral; **C**, right lateral; **D**, anterior; **E**, left lateral; **F**, posterior. [F. Ippolito, del.]

Contacts of vertical plate: In external view, the maxilla of *Labrostochelys* has the usual contacts: premaxilla anteromedially, prefrontal anterodorsally, and jugal posteroventrally, as in *Taphrosphys* and *Azabbaremys*. It is possible that there is a small quadratojugal contact between the jugal and quadrate. The length of the prefrontal-maxilla contact is unique in turtles.

Structures of vertical plate: The dorsal process of the maxilla in *Labrostochelys* lies between the orbit and the apertura narium externa and is relatively distinct in short-snouted forms like *Phosphatochelys*. In *Labrostochelys*, however, the area of the process is extremely lengthened and almost the same height as the posterior part of the bone so that the process is barely recognizable compared with other pleurodires. The maxilla forms the ventral margin of the orbit. Although the area is broken in AMNH 30043 and missing in AMNH 29984, there does not seem to be a cheek emargination, even a low one as in *Taphrosphys*.

Contacts of horizontal plate: The usual contacts are present in *Labrostochelys*: premaxilla anteromedially, palatine posteromedially, and jugal posterolaterally. There is also a short vomer contact just behind the premaxilla anterior to the apertura narium interna. The jugal is slightly displaced on both sides of AMNH 30043 and AMNH 29984, but it seems to have only a short contact without the longer lateral contact usually seen in Pelomedusoides.

In *Labrostochelys* the maxilla sends a small process medially to contact the vomer. Among the other Taphrosphyini, the vomer is unknown in *Taphrosphys* and *Phosphatochelys*, which could have had a contact. There is a contact in *Nigeremys* and *Arenila*, but not in *Azabbaremys*. As in *Taphrosphys*, the palatine does not extend into the area of the triturating surface.

The dorsal surface of the maxilla is visible only to a limited degree in both *Labrostochelys* skulls, but it is clear that the maxilla does not contribute significantly to the floor of the fossa orbitalis. This is similar to the condition in *Taphrosphys* and *Azabbaremys* and in contrast to *Phosphatochelys*.

Structures of horizontal plate: The ventral surface forms the triturating surface, which in *Labrostochelys* is relatively narrow and parallel-sided, similar to that in *Taphrosphys* in width. It is longer than in any Pelomedusoides due to the elongate snout. The labial ridge is deep and thin and curves evenly into the more horizontal part of the surface, in contrast to *Azabbaremys* and *Phosphatochelys*, which have an angled meeting, but very similar to *T. ippolitoi*. In *Taphrosphys* and *Labrostochelys* the maxillary part of the triturating surface is an inverted trough, unlike the morphology in other Pelomedusoides. The lingual ridge in *Labrostochelys* is low but distinct; still, it is slightly higher than in *T. ippolitoi*. The medial edge of the maxilla in *Labrostochelys* forms the apertura narium interna and, despite some breakage, seems to define a smaller apertura than in *Taphrosphys*, *Phosphatochelys*, and *Azabbaremys*.

VOMER (figs. 190, 191, 193)

Preservation: The vomer is present in AMNH 30043, but it is slightly displaced from its sutural contacts and is split anteriorly. Only the ventral surface is visible. The vomer is missing in AMNH 29984.

Contacts: The vomer in *Labrostochelys* contacts the premaxilla anteriorly and the palatines posteriorly, as in all other Pelomedusoides in which it is known. Anterolaterally there is a short maxilla contact (see Maxilla).

Structures: The vomer in *Labrostochelys* is long and narrow, not thick and short as in *Nigeremys* and *Arenila*. There is an expansion at both ends. The vomer does not participate in the foramen praepalatinum. The vomer forms the medial margin of the apertura narium interna, which in *Labrostochelys* is relatively small, smaller than in *Azabbaremys* and *Phosphatochelys*. None of the *Taphrosphys* skulls has well-preserved aperturae, but they seem to be larger than in *Labrostochelys* based on what is preserved.

PALATINE (figs. 190, 191, 193)

Preservation: Both palatines are present in both *Labrostochelys* skulls, but they are better preserved in AMNH 30043.

Contacts: The palatine in *Labrostochelys* has the usual Pelomedusoides contacts: vomer anteromedially, maxilla anterolaterally, palatine medially, and pterygoid posteriorly.

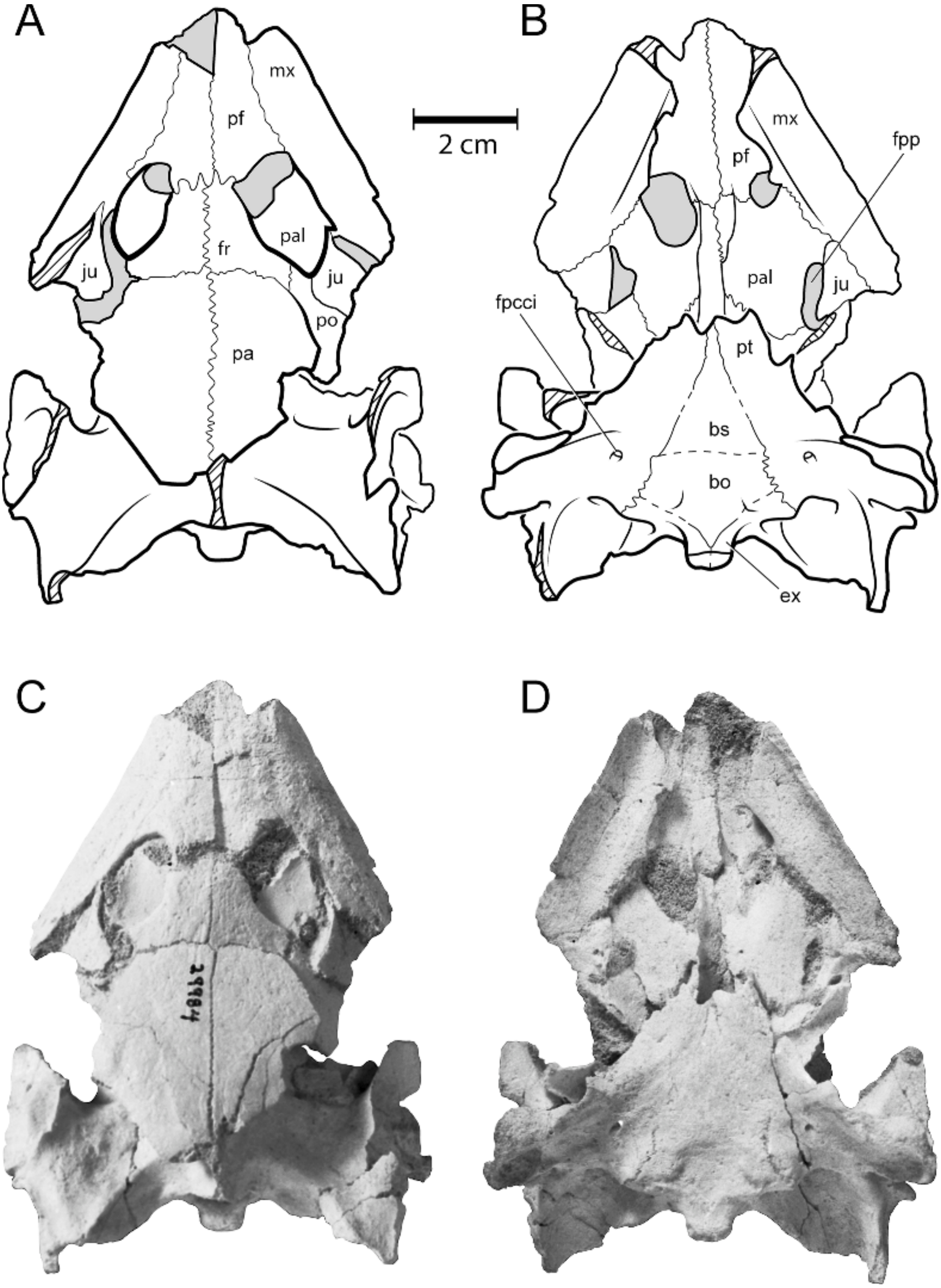

Fig. 194. *Labrostochelys galkini*, n. gen. et sp. AMNH 29984. **A**, dorsal; **B**, ventral; **C**, dorsal; **D**, ventral. [F. Ippolito, del.]

Although both the palatines and jugals are slightly disarticulated and displaced dorsally in both skulls, the usual dorsolateral contact with the jugal is present. A dorsal contact with the parietal is possible but not determinable.

Structures on dorsal surface: The palatine in *Labrostochelys* forms nearly all of the floor of the fossa orbitalis, as in *Taphrosphys* but in contrast to *Phosphatochelys*, which has a much greater maxillary contribution. The foramen orbitonasale is mostly collapsed in both skulls, so it is present but cannot be easily compared with other taxa. The palatine forms the anterolateral edge of the apertura narium interna. This edge is broken so its original position is unknown, but what is preserved shows the apertura to be relatively small (see Maxilla). A dorsal process was probably not present, but the area is collapsed dorsally and not visible. If a process were present, it would probably cause some breakage or displacement through the thin palatine. The sulcus palatinopterygoideus is not well preserved, probably due to the absence of a postorbital wall, allowing dorsoventral crushing and collapse of the area.

Structures on ventral surface: The palatine of *Labrostochelys* is similar to that bone in *Taphrosphys*, broadly curving dorsally into the apertura narium interna, but to a lesser degree than in *Azabbaremys*, *Phosphatochelys*, *Nigeremys*, and *Arenila*. There is no contribution of the palatine to the triturating surface. The foramen palatinum posterius is formed anteriorly by the palatine and posteriorly by the pterygoid. It is larger than in *Phosphatochelys*, *Azabbaremys*, and *Taphrosphys* and roughly similar to those in *Nigeremys* and *Arenila*.

QUADRATE (figs. 190, 191, 193, 195, 277F, 287)

Preservation: Both quadrates in AMNH 30043 are nearly complete. Both in AMNH 29984 are missing the anterior and dorsal areas.

Lateral view contacts: In *Labrostochelys* the quadrate contacts the quadratojugal dorsally and anterodorsally and the squamosal posterodorsally. The squamosal contact (see Squamosal) is unusual in that the quadrate sends a process ventrally beneath much of the squamosal forming the greatly elongated posterior process. There is a maxilla-quadrate contact (see Maxilla); it is short, as in *Taphrosphys congolensis*. It is possible that there is a short jugal contact, as is likely in *T. congolensis* (see Jugal).

Lateral view structures: The cavum tympani of *Labrostochelys* (fig. 287) agrees with other Taphrosphyini in being shallower than in the Pelomedusidae and generally agreeing with the Bothremydini. In *Labrostochelys* the depth of the cavum tympani varies between the two skulls, but in this case AMNH 29984 seems to be better preserved than AMNH 30043. The cavum tympani in AMNH 29984 is deeper than in AMNH 30043, about as deep as in *Taphrosphys*. The two skulls do differ in other features, so this may be individual variation rather than preservation. There is no fossa precolumellaris, and the cavum tympani is smoothly concave except for the antrum postoticum. The cavum tympani in *Labrostochelys* is slightly wider than high, agreeing with *Taphrosphys* (as restored, see *Taphrosphys ippolitoi*) and in contrast to *Azabbaremys* and *Phosphatochelys*, in which it is circular or slightly higher than wide.

As in all other Taphrosphyini, *Labrostochelys* has a closed incisura columellae auris forming a bony canal for the stapes. There is a low groove extending posteroventrally from the incisura columellae auris to a notch on the edge of the quadrate for the eustachian tube, the sulcus eustachii. The sulcus in *Labrostochelys* has a short process extending ventrally (fig. 287), as in *Phosphatochelys*. There is no sign of a dorsal process as seen in *Taphrosphys ippolitoi*.

The antrum postoticum in *Labrostochelys* differs between the two skulls. In AMNH 30043 it is about half the size of that in AMNH 29984. This does not seem to be a preservation or postmortem difference. In AMNH 29984 the antrum is about the size of the antrum in *Phosphatochelys* and *Taphrosphys ippolitoi*. In AMNH 29984 the opening of the antrum is oval, while in *Taphrosphys* and *Phosphatochelys* it is round. The antrum opening faces anterolaterally in both *Labrostochelys* skulls and anteriorly in *Taphrosphys* and *Phosphatochelys*. The antrum postoticum is absent in *Azabbaremys* and *Nigeremys*.

The shelf formed along the ventrolateral margin of the cavum tympani that is un-

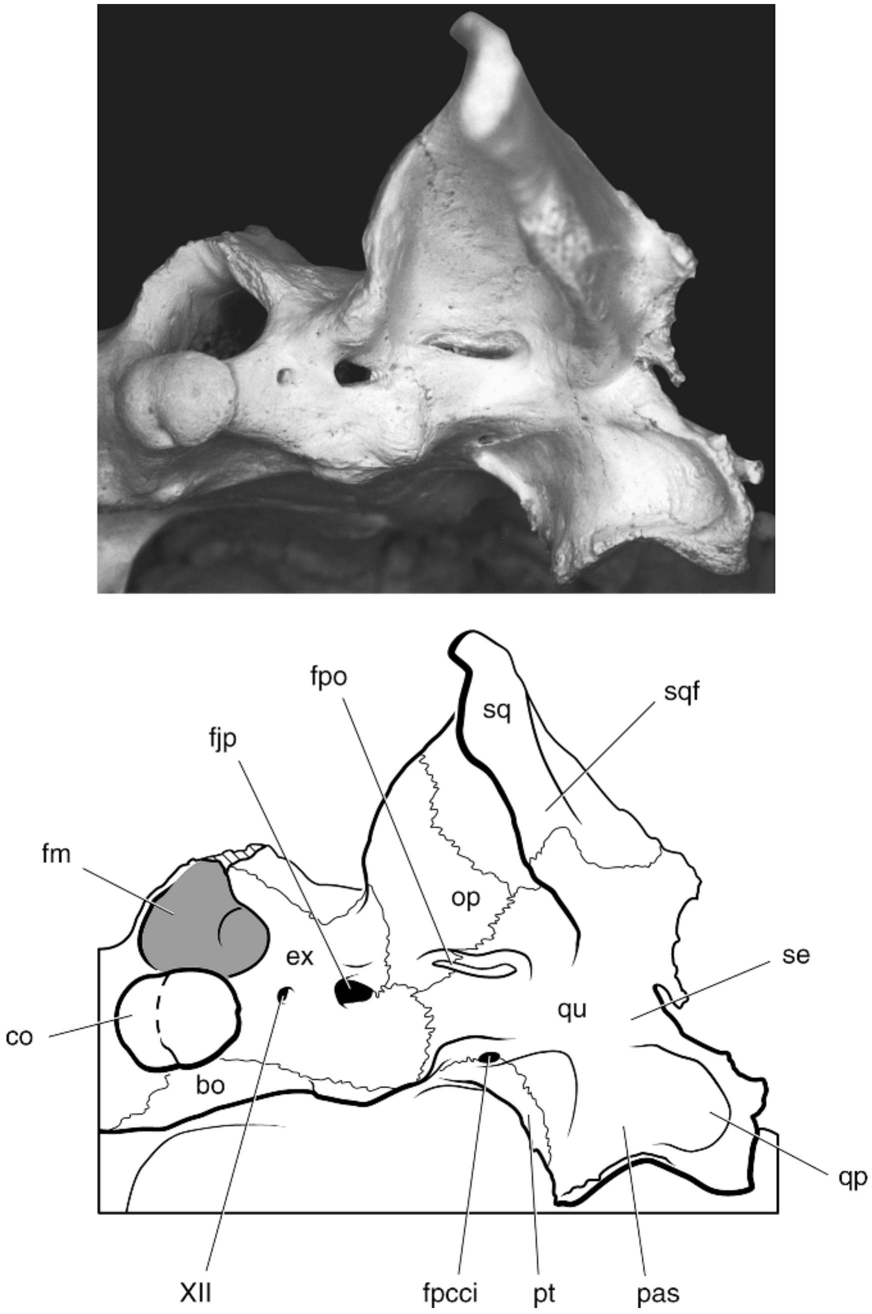

Fig. 195. *Labrostochelys galkini*, n. gen. et sp. AMNH 30043 holotype. Posterior oblique view of skull. [A. Venjara and E.S. Gaffney, del.]

usually large and prominent in *Taphrosphys ippolitoi* is smaller in *Labrostochelys* as it is in *Phosphatochelys*.

Contacts in dorsal view: In *Labrostochelys* the quadrate contacts vary on each side in AMNH 30043. On the right side it contacts the prootic anteromedially, the opisthotic posteromedially, and the squamosal posteriorly. These are the usual contacts in Taphrosphyini. On the left side, the squamosal has an anteromedial extension contacting the prootic, preventing a quadrate-opisthotic contact. This squamosal-prootic contact is unusual, possibly unique in turtles, and is interpreted as an individual variation. In AMNH 29984 the quadrate on the right side shows sutures, but the squamosal sutures are indistinct, so a squamosal-prootic contact cannot be determined.

Dorsal view structures: As in the other Taphrosphyini, the foramen stapedio-temporale in *Labrostochelys* is at the anterior edge of the otic chamber, close to the foramen nervi trigemini.

Ventral view contacts: As in the other Taphrosphyini, the quadrate of *Labrostochelys* contacts the pterygoid anteromedially, the basisphenoid medially, the basioccipital posteromedially, the exoccipital posteromedially (behind the basioccipital), and the squamosal posterolaterally. The basisphenoid and basioccipital contacts in *Labrostochelys* are narrower than in *Taphrosphys*, but similar in extent to *Azabbaremys*. The squamosal-quadrate contact (see Squamosal) is uniquely long in *Labrostochelys* due to the posteriorly extended squamosal and a ventral quadrate process forming its ventral edge.

Ventral view structures: The foramen posterius canalis carotici interni in *Labrostochelys* is formed within the quadrate, but the suture follows it posteriorly from the pterygoid suture, so it may be interpreted as being formed within the pterygoid-quadrate suture (fig. 277F). If interpreted this way it agrees with *Azabbaremys* and *Phosphatochelys* (indeterminate in *Nigeremys*). In *Arenila* it is between the basisphenoid and pterygoid. In *Taphrosphys* it is in the quadrate-pterygoid-basisphenoid suture.

The fenestra postotica in *Labrostochelys* (fig. 195) is formed by the quadrate ventrolaterally and the opisthotic dorsomedially, as in *Azabbaremys*, *Taphrosphys*, and *Phosphatochelys*. The fenestra is elongate horizontally in *Labrostochelys*, rather than being elongate more vertically, as in *Phosphatochelys* and *Azabbaremys*. The stapedial artery portion lies directly lateral (rather than dorsal) to the lateral head vein portion. In *Taphrosphys* the fenestra is usually subdivided by bone, but the portions are more vertical than horizontal, as in *Labrostochelys*.

The foramen chorda tympani inferius is a small hole on the posterior surface of the processus articularis. The posterior surface of the processus articularis in *Labrostochelys* has a posteroventrally opening concavity, similar to one seen in *Taphrosphys ippolitoi* (see *Taphrosphys*). This seems to be an attachment site for the depressor mandibulae (fig. 195). As in *Taphrosphys*, the condylus mandibularis in *Labrostochelys* is far anterior to the condylus occipitalis.

PTERYGOID (figs. 190, 191, 193, 277F)

Preservation: The pterygoids in AMNH 29984 are present but damaged anteriorly and laterally. In AMNH 30043, however, they are just superb! The pterygoid flange, a thin sheet often broken even in recent pleurodire skulls, and almost always damaged in fossils, is complete on both sides of AMNH 30043. The bones articulating anteriorly to the pterygoid have been dislocated and rudely shoved dorsally, but the posterior contacts are still intact.

Contacts on ventral surface: The pterygoid in *Labrostochelys* has the usual Taphrosphyini contacts: palatine anteriorly, pterygoid anteromedially, basisphenoid medially, and quadrate posterolaterally. The pterygoid-pterygoid contact is very short, the same as in *Arenila*, much shorter than in *Taphrosphys*, but shorter than in all the other Taphrosphyini, except for *Arenila*. The anterolateral contact with the jugal is visible in ventral view.

Structures on ventral surface: The processus trochlearis pterygoidei in *Labrostochelys* is very small and oriented posteriorly to an extent that it is not visible in ventral view. In the Taphrosphyini the processus is smaller than in many other pleurodires, but the condition seen in *Labrostochelys* is not even approached in other Pelomedusoides. In some chelids, such as *Chelus* and *Chelodina* (Gaffney, 1979a), the processus is also oriented posteriorly and relatively small, but in none is the processus as small as it is in *Labrostochelys*. The processus trochlearis pterygoidei in *Labrostochelys* parallels the edge of the pterygoid web or flange and trends slightly laterally rather than being completely parasagittal as in some chelids.

The tubelike channel found in *Phosphatochelys* extending anterodorsally from the processus articularis of the quadrate is absent in *Labrostochelys*. This channel is present in *Taphrosphys* and *Azabbaremys*. The pterygoid flange and quadrate ramus in *Labrostochelys* are very close, being similar to Pelomedusidae in this feature. There is no concavity for the pterygoideus muscle attachment, but there is a low ridge on AMNH 30043 extending from the processus articularis medially on the quadrate ramus of the pterygoid that may mark an attachment site edge. The ridge is absent in AMNH 29984. The foramen palatinum posterius in *Labrostochelys* is formed posteriorly by the pterygoid and anteriorly by the palatine (see Palatine).

Contacts on dorsal surface: Some of the dorsal surface of the pterygoid and crista pterygoidea are visible in both *Labrostochelys* skulls, but they are not well preserved and most contacts are unclear. In AMNH 30043, the crista pterygoidea meets the processus inferior parietalis of the parietal in a clear suture seen on both sides. The suture ends anteriorly in matrix, so its entire extent cannot be seen. Posterior to the foramen nervi trigemini the crista meets the prootic and posterolaterally the quadrate, although the entire extent of the latter is unclear. The processus trochlearis pterygoidei has anterior contacts with the jugal anterolaterally and with the postorbital anterodorsally. This area is preserved only on the right side of AMNH 30043 and is not well preserved.

Structures on dorsal surface: Only part of the pterygoid dorsal surface is visible in the two *Labrostochelys* specimens, but some information can be obtained from the CT scans of AMNH 30043.

The processus trochlearis pterygoidei (described above) forms the lateral margin of the sulcus palatinopterygoideus. In *Labrostochelys* this sulcus is not cleanly preserved, but what is preserved differs from other taxa. The sulcus is not preserved in a number of Taphrosphyini, which also makes it hard to interpret *Labrostochelys*. In *Arenila* the septum orbitotemporale and sulcus palatinopterygoideus are preserved and these are similar to the usual bothremydid condition. In *Labrostochelys* the postorbital-pterygoid suture is higher and the bones are much thinner. There is a lateral excavation just above the base of the processus trochlearis pterygoidei that considerably reduced the width and thickness of the septum orbitotemporale in *Labrostochelys* in comparison to *Arenila* and more generalized bothremydids like *Galianemys*. The medial edge of the base of the processus trochlearis pterygoidei is free rather than sutured to the postorbital or parietal. The result is a sulcus palatinopterygoideus that is much wider and more open in *Labrostochelys* than in *Arenila* and more generalized bothremydids. In *Azabbaremys* and *Phosphatochelys* there is no septum orbitotemporale and no lateral definition of the sulcus palatinopterygoideus. *Taphrosphys sulcatus* is not completely preserved in this area; *T. ippolitoi* is also unclear, but could be similar to *Labrostochelys*; and in *T. congolensis* it looks as if the septum is absent, but it is also crushed and unclear. It is possible to interpret the *Labrostochelys* condition as intermediate between the generalized bothremydid condition, like *Arenila*, and the derived condition seen in *Phosphatochelys* and *Azabbaremys*. A medially free pterygoid edge could be a common character for *Labrostochelys*, *Azabbaremys*, and *Phosphatochelys*.

The crista pterygoidea in *Labrostochelys* can be seen in part in both skulls. Although its anterior margin, along with the processus inferior parietalis and whatever contribution the frontal and palatine may make, is not clearly defined, it is apparent that the crista in *Labrostochelys*, as in *Taphrosphys*, is much longer than the very narrow crista of *Azabbaremys* and *Phosphatochelys*. The foramen nervi trigemini in *Labrostochelys* has the usual elements: pterygoid ventrally, parietal anterodorsally, and prootic posterodorsally. The foramen in *Labrostochelys* is nearly circular, while in *Phosphatochelys* and *Azabbaremys* it is oval and more elongated.

SUPRAOCCIPITAL (figs. 190, 193)

Preservation: The supraoccipital is present in both *Labrostochelys* skulls, but all of the posterior portion is gone, as is some of the dorsal area.

Contacts: The supraoccipital in *Labrostochelys* has the usual Taphrosphyini contacts: parietal dorsally, prootic anterolaterally, opisthotic posterolaterally, and exoccipital posteroventrally.

Structures: The most prominent supraoccipital structure, the crista supraoccipitalis, is completely missing in AMNH 30043, and only the base is present in AMNH 29984. The crista is very short in other Taphrosphyini and pleurodires in general.

EXOCCIPITAL (figs. 190, 193, 195, 277F)

Preservation: In *Labrostochelys* both exoccipitals are present and complete in both skulls.

Contacts: As in other Taphrosphyini, contacts in *Labrostochelys* are: supraoccipital dorsally, opisthotic laterally, quadrate ventrolaterally, and basioccipital ventrally.

Structures: The foramen magnum in *Labrostochelys* is as in *Taphrosphys*, being slightly receded anteriorly in comparison to *Phosphatochelys*. The condylus occipitalis is formed entirely from the exoccipitals, and the basioccipital barely enters the neck of the condyle. The foramen nervi hypoglossi consists of a larger, more medial foramen and a smaller one in the medial wall of the foramen jugulare posterius, as in *Phosphatochelys*. This results in only one foramen nervi hypoglossi being visible in direct posterior view. In *Taphrosphys* the more lateral foramen is not placed so far into the foramen jugulare posterius. The foramen jugulare posterius is completely enclosed and widely separated from the fenestra postotica, as in other Taphrosphyini.

BASIOCCIPITAL (figs. 190, 191, 193, 277F)

Preservation: The basioccipital is present and complete in both skulls of *Labrostochelys*. Very little of its dorsal surface is visible except in the CT scans.

Contacts: As in other Taphrosphyini the basioccipital contacts in *Labrostochelys* are: basisphenoid anteriorly, quadrate laterally, and exoccipitals dorsally. The basioccipital-quadrate contact is shorter than in *Taphrosphys* and *Phosphatochelys* but similar to that in *Azabbaremys*. The basioccipital in *Labrostochelys* is more triangular than in the other Taphrosphyini. The straight transverse anterior margin, narrow quadrate contacts, and straight exoccipital contacts diverging from an apex make a uniquely shaped basioccipital.

Structures: The condylus occipitalis in *Labrostochelys* has no basioccipital contribution. The tuberculum basioccipitale is slightly larger in AMNH 29984 than in AMNH 30043, but both are smaller than in *Taphrosphys*. The tuberculum is formed by exoccipital and quadrate to a greater extent than by basioccipital. In *Labrostochelys* the median concavity often seen anterior to the condylus occipitalis is hardly developed. There is a shallow, irregular depression but not the clearly formed, semicircular concavity seen in *Taphrosphys ippolitoi* and *Phosphatochelys*.

PROOTIC (fig. 193)

Preservation: Both prootics are present in both specimens of *Labrostochelys*, but clear contacts are only seen in AMNH 30043.

Contacts: The prootic contacts in *Labrostochelys* are common in other Taphrosphyini: parietal medially, quadrate laterally, supraoccipital posterodorsally, pterygoid ventrally, and opisthotic posteriorly. Additionally, on the left side of AMNH 30043 there is a posterolateral contact with the squamosal (see Squamosal).

Structures: As in other Taphrosphyini, the prootic of *Labrostochelys* forms the dorsal portion of the foramen nervi trigemini along with the parietal and pterygoid. The prootic forms the dorsomedial part of the foramen stapedio-temporale, with the quadrate forming the ventrolateral part. As in other Taphrosphyini, the foramen nervi trigemini is very close to the foramen stapedio-temporale. The foramen stapedio-temporale in *Labrostochelys* opens into a shallow groove, similar to that seen in *Bothremys* (and probably many other Bothremydidae if well enough preserved) leading to the foramen nervi trigemini.

OPISTHOTIC (figs. 190, 193, 195)

Preservation: Both are preserved complete in AMNH 30043, but they lack their posterior edges in AMNH 29984.

Contacts: *Labrostochelys* has the usual Taphrosphyini contacts: supraoccipital anteromedially, prootic anteriorly, squamosal posterolaterally, and exoccipital posteromedially. On the right side of AMNH 30043 the opisthotic has the usual contact with the quadrate anterolaterally. On the left side, however, the squamosal-prootic contact prevents an opisthotic-quadrate contact (see Squamosal). This latter condition is interpreted as an individual variation.

Structures: The opisthotic forms the dorsomedial margin of the fenestra postotica, with the quadrate (see Quadrate) forming the rest. The posterolateral process of the opisthotic (fig. 287) in *Labrostochelys* forms part of a ventrally opening channel at the back of the skull, similar to one seen in *Taphrosphys ippolitoi*. This channel is absent in *Phosphatochelys* and *Azabbaremys*.

BASISPHENOID (figs. 190, 191, 193, 277F)

Preservation: The basisphenoid is complete in both skulls of *Labrostochelys*. Sutures are clearly defined in AMNH 30043, but not in AMNH 29984. The dorsal surface is not visible except in CT scans of AMNH 30043.

Contacts: The basisphenoid of *Labrostochelys* has the usual Taphrosphyini contacts: pterygoids anterolaterally, quadrate laterally, and basioccipital posteriorly. The basisphenoid in *Labrostochelys* is unusually elongate and triangular, quite distinct from the pentagonal shape seen in *Taphrosphys*, the shorter, wider shapes seen in *Azabbaremys* and *Phosphatochelys*, and the V-shape seen in *Arenila* and *Nigeremys*.

Structures: In ventral view, the basisphenoid in *Labrostochelys* is smooth, having no muscle attachment sites, no foramina, no nothing.

Phosphatochelys tedfordi

This species is based on two Eocene specimens, AMNH 30008 (holotype) and MDEt 26, which vary somewhat (table 18) and could be interpreted as separate species. We consider them as the same species and note the differences in the description. *Phosphatochelys* is the sister taxon to *Ummulisani*. The type skull was described by Gaffney and Tong (2003), and some of that description is used here.

PREFRONTAL (figs. 196, 199, 202)

Preservation: Both prefrontals in AMNH 30008 are present and nearly complete with clear sutures. A small amount of the ventral process seems to be broken on both sides. The left prefrontal is completely clear of matrix, but the right one has some matrix posteriorly on its ventral surface. In MDEt 26 the right prefrontal is missing, and the left one lacks its medial edge and is covered by matrix ventrally.

Contacts: The contacts of the prefrontal in *Phosphatochelys* are with the maxilla anterolaterally, the frontal posteromedially, the parietal posterolaterally, and the other prefrontal anteromedially. The parietal-prefrontal contact of *Phosphatochelys* and *Ummulisani* is unusual and in fact unique among pleurodires and cryptodires (Gaffney, 1979a). It is not even approached by any other bothremydid, which generally have large prefrontals. Unlike most Pelomedusoides in which the prefrontals meet on the midline for their entire length, *Phosphatochelys* has a midline length much shorter than its maximum length. The suture with the frontal is strongly convex anteriorly, quite different from the straight suture in *Azabbaremys* and other bothremydids. The median prefrontal contact length is less than the total prefrontal length, as in chelids, *Araripemys*, and euraxemydids. This may be a primitive condition; however, its absence in *Azabbaremys* and other close relatives of *Phosphatochelys* makes this unlikely.

On the ventral surface the prefrontal in *Phosphatochelys* contacts the parietal. The frontal is not exposed on the ventral surface. The ventral process of the prefrontal contacts the dorsal process of the maxilla, as in other Pelomedusoides. This contact area is quite narrow in *Phosphatochelys*, in contrast to the broad contact in *Azabbaremys*. The entire anterior snout area of *Phosphatochelys* is telescoped in comparison to *Azabbaremys*, *Labrostochelys*, and *Taphrosphys*.

Structures: The prefrontal in *Phosphatochelys* agrees with that in *Rhothonemys* and *Ummulisani* in being a relatively large element, larger than in other Taphrosphyini and much larger than in pelomedusids and euraxemydids. The prefrontal in *Phosphatochelys* has a distinct, anterior projection slightly subdividing the apertura narium externa. It is larger than in *Azabbaremys* but smaller than in *Taphrosphys* and *Labrostochelys*.

FRONTAL (figs. 196, 199)

Preservation: Both frontals are present in AMNH 30008. In MDEt 26 the left frontal

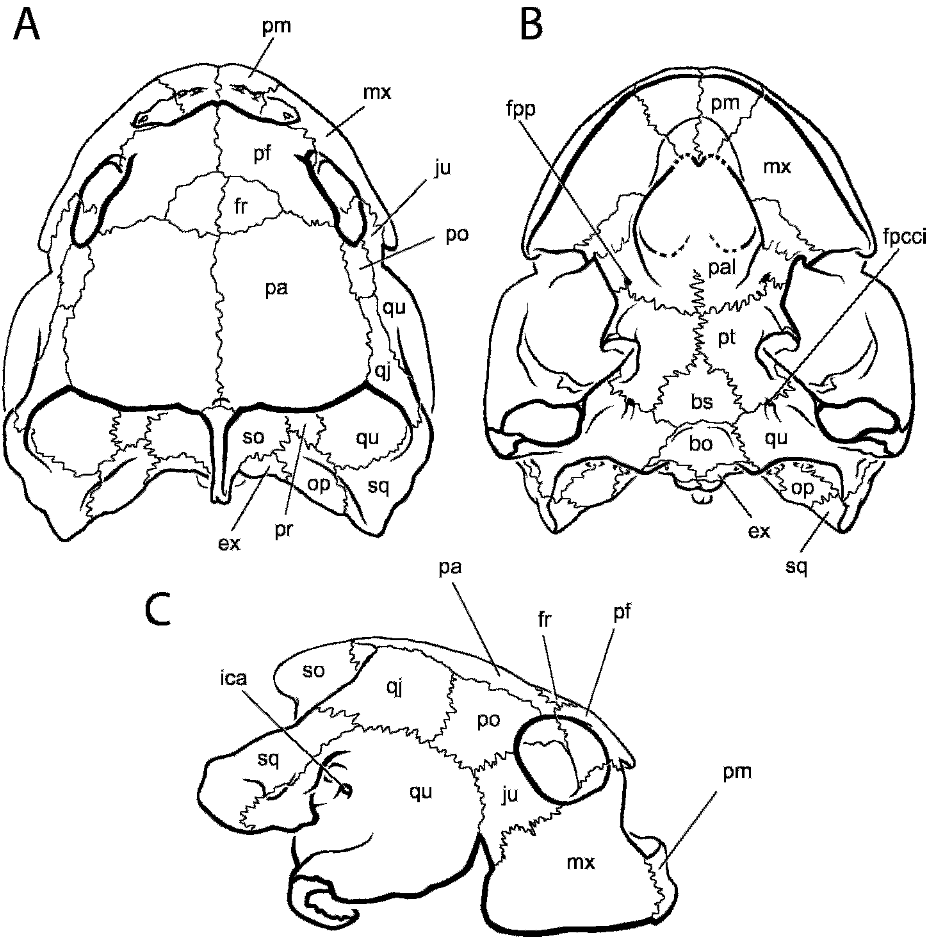

Fig. 196. *Phosphatochelys tedfordi* Gaffney and Tong, 2003. AMNH 30008 holotype. Partially restored views of skull. **A**, dorsal; **B**, ventral; **C**, lateral (from Gaffney and Tong, 2003). [V. Storfer, del.]

is present but lacks its medial margin; the right frontal is missing.

Contacts: On the dorsal surface the frontal in *Phosphatochelys* contacts the prefrontal anterolaterally, the parietal posterolaterally, and the other frontal medially. The frontal is not exposed on the ventral surface, in contrast to all other bothremydids except *Ummulisani.*

Structures: The frontal in *Phosphatochelys* is very unusual for pleurodires, except *Ummulisani.* It is small, widely separated from the orbital margin, and covered ventrally by a sheet of parietal that reaches the prefrontal.

PARIETAL (figs. 196, 199, 202)

Preservation: Both parietals in AMNH 30008 are nearly complete, but some of the ventral surface is damaged or covered by matrix. In MDEt 26, the right parietal has most of the processus inferior parietalis present but largely covered by matrix. The dorsal plate is gone except for a small posteromedial piece. The left parietal has all of the dorsal plate except posterolaterally, where it is broken off. The rest is covered by matrix.

Contacts of dorsal plate: The dorsal plate of the parietal is large, as in *Azabbaremys*, but it is nearly rectangular rather than

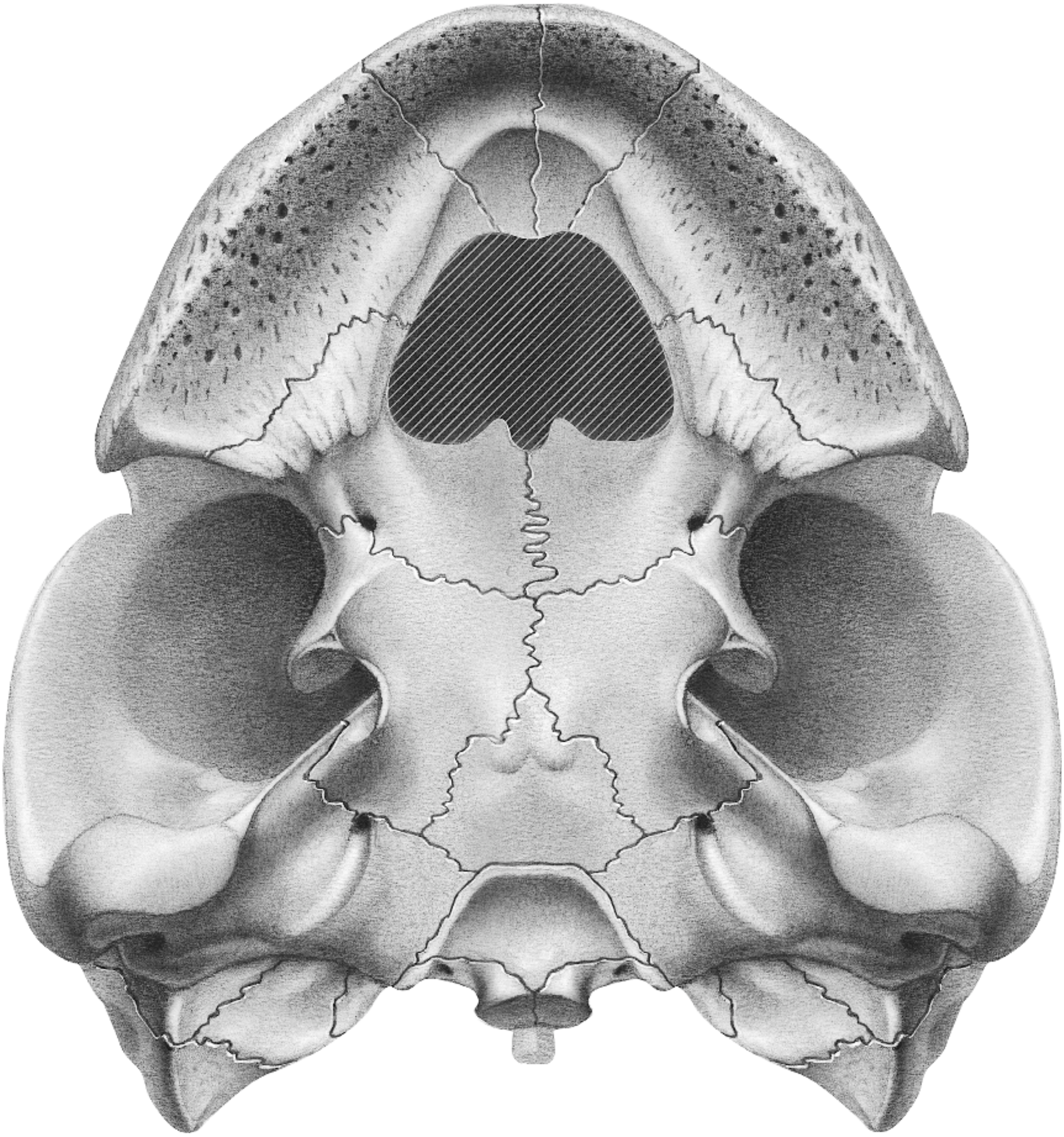

Fig. 197. *Phosphatochelys tedfordi* Gaffney and Tong, 2003. AMNH 30008 holotype. Partially restored ventral view (from Gaffney and Tong, 2003). [F. Ippolito, del.]

being an irregular quadrangle. It contacts the frontal anteromedially and the prefrontal anterolaterally. As mentioned (see Prefrontal), the broad prefrontal contact in *Phosphatochelys* and *Ummulisani* is unique among pleurodires and cryptodires. Also unique among pleurodires is the exposure of the parietal in the margin of the orbit. This condition is not approached by any other pleurodire or cryptodire. Laterally the parietal contacts the postorbital anteriorly and the quadratojugal posteriorly. The quadratojugal-parietal contact only occurs in *Phosphatochelys, Ummulisani*, and *Taphrosphys* among the Bothremydidae. Although it also occurs in the Euraxemydidae and Podocnemididae (including *Hamadachelys*), it seems to be an independent acquisition within the Taphrosphyini.

Structures of dorsal plate: The posterior margin of the parietal along with the quadratojugal form the posterior limits of the posterior temporal emargination. The temporal emargination in *Phosphatochelys* is not different in extent from *Azabbaremys*, but the margin in *Phosphatochelys* is transverse while in *Azabbaremys* it is also straight but trends anterolaterally from the midline. To the extent it is known, this transverse edge is unique in Taphrosphyini, but a number of taxa (*Rosasia*, *Arenila*, *Zolhafah*) are incompletely known in the skull roof. *Taphrosphys* is more emarginate than *Phosphatochelys*. In AMNH 30008 the parietal has a very narrow exposure on the orbital margin (see Postorbital), while in MDEt 26 the postorbital-prefrontal contact prevents this.

Contacts and structures of processus inferior parietalis: The processus inferior parietalis (fig. 202) in *Phosphatochelys*, exposed only on the left side of AMNH 30008, is very narrow, as in *Azabbaremys*, and enters the foramen nervi trigemini, also as in *Azabbaremys*. The processus inferior parietalis contacts the pterygoid ventrally from the foramen interorbitale anteriorly to the foramen nervi trigemini posteriorly. The parietal also sends a process ventrally on the lateral side of the sulcus palatinopterygoideus, which contacts the palatine anteriorly and the pterygoid posteriorly. This process as well as an enclosed sulcus palatinopterygoideus are absent in *Azabbaremys*. As in *Azabbaremys*, the foramen interorbitale of *Phosphatochelys* is relatively small compared with other Pelomedusoides. Posteriorly the parietal contacts the supraoccipital in a nearly vertical suture above the prootic contact.

JUGAL (figs. 196, 199)

Preservation: Both jugals are present in AMNH 30008, but neither is complete. The left one is missing only part of its posterior edge. In MDEt 26 the right jugal is missing. The left one may be lacking part of its posterior edge. Both are mostly covered by matrix on their internal surfaces.

Contacts of lateral plate: The jugal in *Phosphatochelys* contacts the postorbital dorsally and the maxilla ventrally, as in other bothremydids. Because there was probably a narrow cheek emargination, the jugal may have had only a small or no contact with the quadrate (see below). The best preserved cheeks, the right sides of AMNH 30008 and MDEt 26, show no jugal-quadrate contact, but this may be due to breakage.

Structures of lateral plate: The jugal of *Phosphatochelys* is widely exposed in the posteroventral margin of the fossa orbitalis, contacting the postorbital dorsally and the maxilla ventrally, all as in *Azabbaremys*. In both specimens of *Phosphatochelys*, however, there appears to be a free posterior edge along the margin of the left jugal indicating a cheek emargination. The right jugal in AMNH 30008 is damaged posteriorly in this area. On the right side the quadrate and maxilla meet. This may be due to postmortem distortion, and the rest of the skull also supports this interpretation. In MDEt 26 the left jugal has what also appears to be a free edge along its posteroventral margin, just as in the left jugal of AMNH 30008. It seems likely, then, that there was a narrow cheek emargination, as shown in the restored lateral view (fig. 196C) with part of the jugal exposed on the margin of the emargination. Nonetheless, the dorsal placement of the quadratojugal and the close approximation of quadrate and maxilla are similar to *Azabbaremys* and *Taphrosphys*.

Contacts and structures of medial process: The medial process of the jugal is best preserved on the right side of AMNH 30008. It is barely visible in ventral view and does not extend onto the triturating surface. Most of the septum orbitotemporale is absent, as in the other Taphrosphyina, so the jugal has only a ventromedial process that reaches the maxilla and palatine in the orbital floor.

QUADRATOJUGAL (figs. 196, 199)

Preservation: The quadratojugal in AMNH 30008 is present only on the right side; the left one is missing. The quadratojugal is complete except along its anterior margin where some of its edge has been eroded. In MDEt 26 only the left quadratojugal is present and it has broken edges on three sides.

Contacts: The quadratojugal in *Phosphatochelys* contacts the parietal medially, the postorbital anteriorly, the quadrate ventrolaterally, and the squamosal posteroventrally. The area of the postorbital contact is damaged, but the presence of the contact is not in doubt. A quadratojugal-parietal contact also occurs in the podocnemidids, *Erymnochelys* and *Peltocephalus*, but among bothremydids it is known only in *Taphrosphys, Ummulisani*, and *Labrostochelys*. In *Taphrosphys* the quadratojugal is more extensive ventrally, and a jugal-quadrate contact is present.

Structures: In most turtles the quadratojugal is a large C-shaped element lying along the anterior margin of the quadrate on the cheek. This is the case in bothremydids like *Foxemys*, but in the Taphrosphyini (unknown in *Nigeremys* and *Arenila*) the quadratojugal lies well above the main body of the quadrate and there is a jugal-quadrate contact.

SQUAMOSAL (figs. 196, 199, 203, 286C)

Preservation: Both squamosals are present in AMNH 30008; the right one is complete and the left one lacks some of its anterior process. In MDEt 26, parts of both squamosals are present, the left one is nearly complete, but the right one is lacking most of its lateral area.

Contacts: The squamosal in AMNH 30008 is the usual cone-shaped element lying on the posterolateral corner of the quadrate. It contacts the opisthotic medially on the dorsal, medial, and ventral surfaces. A short process of the squamosal contacts the quadratojugal along the lateral edge of the temporal embayment, as in *Azabbaremys*.

Structures: The squamosal in *Phosphatochelys* has a ventral flange or deep ridge, oriented vertically anteroposteriorly (fig. 203, sqf). This also occurs in *Taphrosphys*, *Labrostochelys*, *Ummulisani*, and *Rhothonemys*. On its lateral surface, there is a small ridge or tubercle overlapping outside the sulcus eustachii (fig. 286C) that also occurs in *Taphrosphys* and *Labrostochelys* and in some *Bothremys maghrebiana*.

POSTORBITAL (figs. 196, 199)

Preservation: The postorbital in *Phosphatochelys* is present on both sides of AMNH 30008. The left one is nearly complete; only some of its posterior edge is damaged, but the right postorbital is damaged with its posterior margin missing. The internal surface is visible on the left side, but only partially on the right. In MDEt 26 the postorbital is present on the left side only, in a more posterior, disarticulated fragment that is not definitely in its original position, and in the orbital margin. No medial process is visible.

Contacts of lateral plate: The postorbital of *Phosphatochelys* is a roughly square element, contacting the parietal medially, the quadratojugal posteriorly, the quadrate posteroventrally, and the jugal anteroventrally. The absence of a frontal contact, due to the prefrontal-parietal contact, is unusual and only occurs elsewhere in *Ummulisani*. The short postorbital of *Phosphatochelys* is completely separated from the posterior temporal emargination by the parietal-quadratojugal contact, quite different from the long postorbital of *Azabbaremys* that reaches the temporal emargination. It is possible that a very narrow postorbital-prefrontal contact was present, but as preserved the right side is eroded and the left side is broken at this point. Thus, we have restored the postorbital with no prefrontal contact and a narrow orbital exposure of the parietal. We consider this to be equivocal, however. In MDEt 26, only the left side preserves the postorbital, and here a very small postorbital-prefrontal contact is present, preventing orbital exposure of the parietal.

Contacts of medial process: As in most other Taphrosphyini, *Phosphatochelys* has no jugal-postorbital or palatine-postorbital contact of the medial process. The postorbital-parietal contact is small and there is no pterygoid contact here as well.

Structures of medial process: In most bothremydids the postorbital has a medial process that contacts the jugal and palatine to form the septum orbitotemporale. In the subtribe Taphrosphyina, however, this wall is small or absent. In *Phosphatochelys* the medial surface of the postorbital has a vertical ridge continuous with one from the jugal, which represents the fossa orbitalis margin. A much lower ridge is present in *Azabbaremys*. The postorbital contribution to the floor of the fossa orbitalis is also absent.

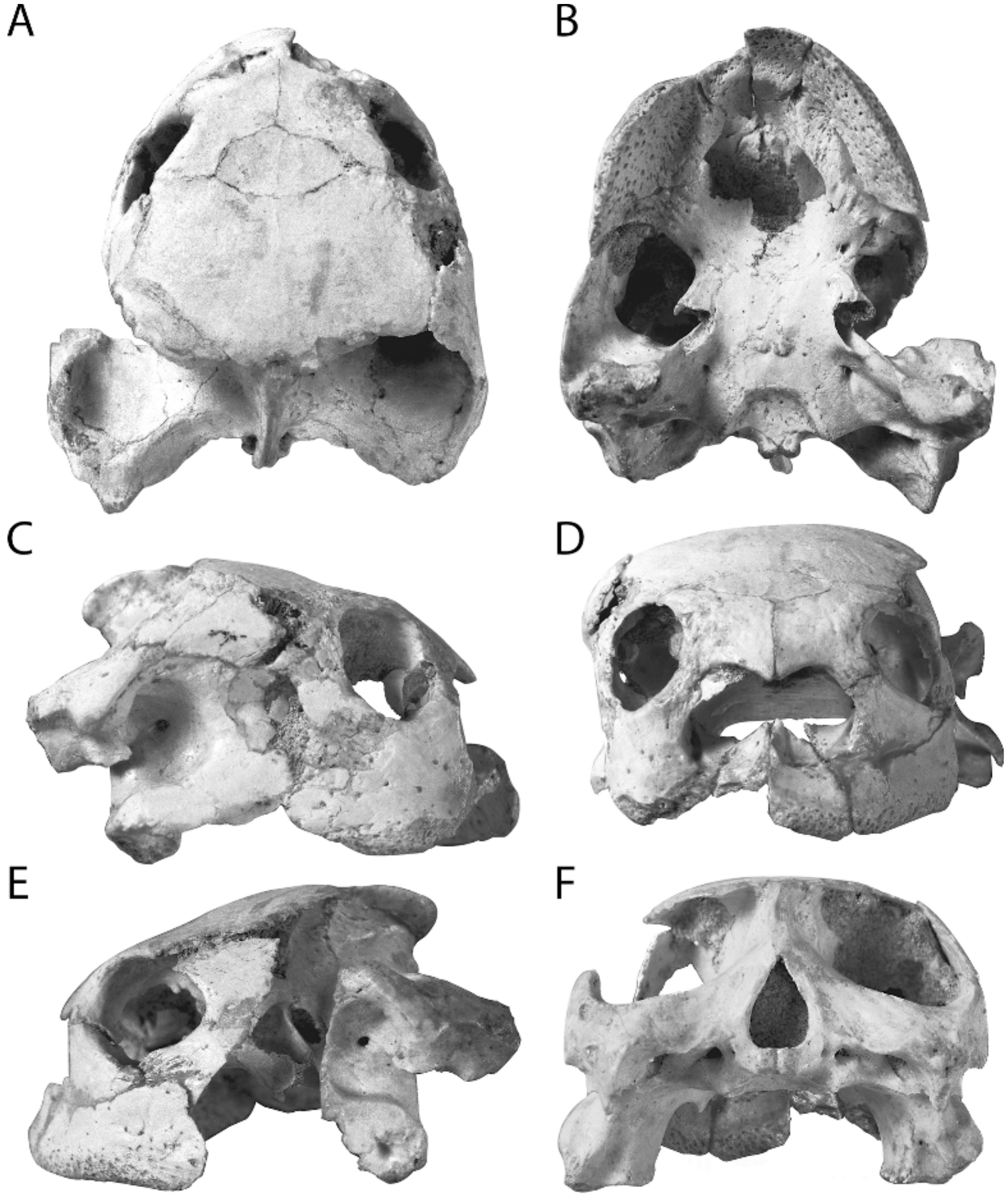

Fig. 198. *Phosphatochelys tedfordi* Gaffney and Tong, 2003. AMNH 30008 holotype. **A**, dorsal; **B**, ventral; **C**, right lateral; **D**, anterior; **E**, left lateral; **F**, posterior. (From Gaffney and Tong, 2003). [B. Degner, del.]

PREMAXILLA (figs. 196, 197, 199)

Preservation: Both premaxillae are present in AMNH 30008, but the right one lacks the labial ridge. In MDEt 26 both premaxillae are also present and nearly complete.

Contacts: The premaxilla in *Phosphatochelys* contacts the maxilla laterally and the other premaxilla medially. The vomer is missing in both skulls.

Structures on dorsal surface: The premaxilla in *Phosphatochelys* forms a deep, acute labial ridge with a median notch, in contrast to the hook seen in *Azabbaremys*. In *Azabbaremys* and many Pelomedusoides the

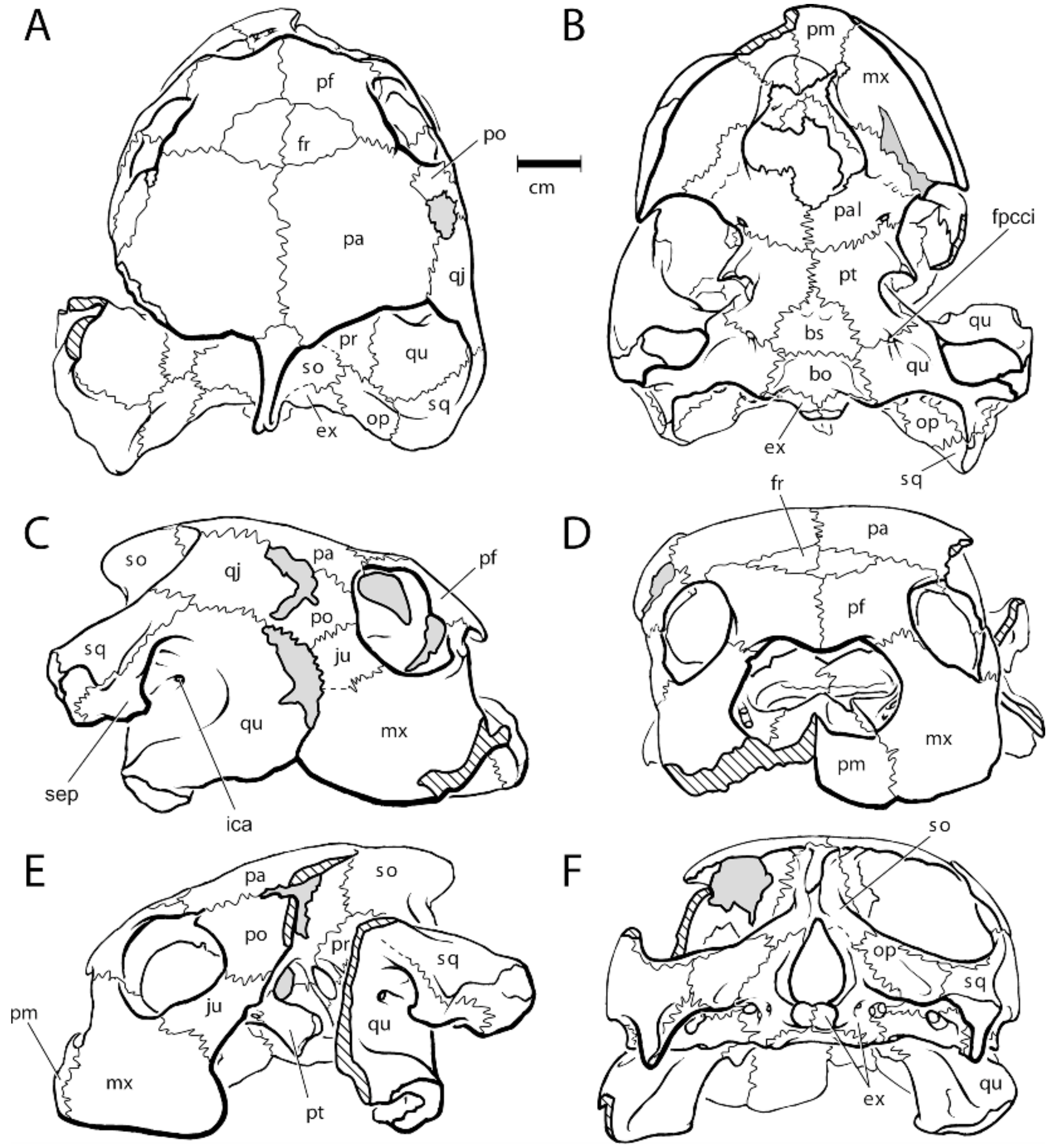

Fig. 199. *Phosphatochelys tedfordi* Gaffney and Tong, 2003. AMNH 30008 holotype. **A**, dorsal; **B**, ventral; **C**, right lateral; **D**, anterior; **E**, left lateral; **F**, posterior. (From Gaffney and Tong, 2003). [V. Storfer, del.]

ventral rim of the apertura narium externa protrudes well anterior to the labial ridge. In *Phosphatochelys*, however, the lower rim of the apertura is distinctly recessed, unlike any other bothremydid, so that the labial ridge is the anteriormost part of the skull. In *Azabbaremys* there is a median ridge with low troughs on either side communicating with the apertura narium externa. In *Phosphatochelys* there is also a median ridge but it is acute, not blunt as in *Azabbaremys*, and there are no troughs. *Phosphatochelys* does have a low concavity on the premaxilla that produces the recessed shape of the lower rim of the apertura. Below the concavity on the anterior face in *Phosphatochelys* there is a distinct pattern of the nutrient foramina, presumably for the horny beak. These occur in a band along the ventral edge of the labial ridge, premaxilla and maxilla, and which is slightly raised above the more dorsal parts of these bones. In *Azabbaremys*, *Taphrosphys*, and other bothremydids, the nutrient foramina are not so prominent on the outer surface of premaxilla and maxilla. The horizontal plate of the premaxilla forms the floor of the fossa nasalis, and in *Phosphatochelys* these form an acute dorsal ridge on the midline that is absent in *Azabbaremys*.

The premaxilla in AMNH 30008 is shorter than the premaxilla in MDEt 26, and it is not as inclined. The median notch is slightly deeper in AMNH 30008 than in MDEt 26. In both specimens there is a distinct sulcus or groove along the ventral edge of the apertura narium externa (fig. 279A). This sulcus is parallel-sided and seems to be a continuation of a sulcus running along the ventrolateral corner of the fossa nasalis (see Maxilla).

Structures on ventral surface: On the ventral surface, the premaxilla in *Phosphatochelys* forms the anterior part of the very high and acute labial ridge, higher than in *Azabbaremys* or any other bothremydid. Also in contrast to *Azabbaremys* and other bothremydids, the horizontal part of the triturating surface in *Phosphatochelys* is very narrow, particularly on the premaxilla, although it is more horizontal in MDEt 26 than in AMNH 30008. The lingual ridge might be identified as the very low, rounded margin separating the triturating surface proper from the median concavity that leads into the apertura narium interna. This concavity is large in *Phosphatochelys*, being wider and more open posteriorly in comparison to *Azabbaremys*.

MAXILLA (figs. 196, 197, 199)

Preservation: Both maxillae are present in AMNH 30008 and both are slightly damaged. The left maxilla is nearly complete but has a horizontal break running through the main body; not much bone seems to be missing however. The right maxilla is missing its anteriormost edge and has a broken area below the orbit. Both have the internal portion preserved. In MDEt 26, both maxillae are preserved; the left one is nearly complete. The right one is missing a small part of its dorsal margin.

Contacts of vertical plate: The maxilla of *Phosphatochelys* contacts the premaxilla anteromedially, the prefrontal anterodorsally in an unusually narrow suture, and the jugal posterodorsally.

Structures of vertical plate: The vertical plate in *Phosphatochelys* is more curved, convex anterolaterally, than the very flat maxilla of *Azabbaremys*, and it has a relatively larger fossa orbitalis and apertura narium externa than in *Azabbaremys*. As preserved, the maxilla contacts the quadrate on the right side. Based on the apparent free edges of the maxilla and jugal on the left side and some distortion on the right side, we have restored *Phosphatochelys* with a narrow cheek emargination. The prefrontal-maxilla contact is best preserved on the left side. It is much narrower than in *Azabbaremys*.

Contacts of horizontal plate: In ventral view, the maxilla contacts the premaxilla anteromedially, the jugal posteriorly, and the palatine posteromedially. In AMNH 3008 the area around the premaxilla-maxilla suture is broken on both sides as the suture approaches the apertura narium interna. The vomer, presumably present, is missing in both specimens. It is possible that the maxilla contacted the vomer, and, if not, it probably came close. The jugal does not extend onto the triturating surface in *Phosphatochelys*. The palatine contact is also farther from the triturating surface than it is in *Azabbaremys*. In the floor of the fossa orbitalis the horizontal plate of the maxilla contacts the palatine posteromedially and the jugal posterolaterally.

Structures of horizontal plate: The medial parts of the maxilla form part of the fossa nasalis anteriorly and the fossa orbitalis posteriorly. The fossa nasalis is relatively large for a bothremydid and does not have the posterolateral pocket seen in *Azabbaremys*. Along the ventrolateral margin of the fossa nasalis is a deep groove beginning as a shallow groove or sulcus (see Premaxilla) on the premaxilla and running posterolaterally to the fossa orbitalis (fig. 279A). This groove has two large foramina in it that open ventrolaterally into the main body of the maxilla. In *Podocnemis* and *Pelusios*, Albrecht (1976) described the canalis infraorbitalis and canalis alveolaris superior system that connect a series of foramina and contain the supramaxillary and superior alveolar arteries. The groove and foramina in *Phosphatochelys* seem to be part of this system. Although we have not seen it developed to this extent in any other Pelomedusoides, other taxa do have foramina in the same place in the fossa nasalis that communicate with the alveolar canals.

The lower border of the orbital margin is relatively high above the floor of the fossa nasalis, resulting in a deep pocket, deeper than seen in *Azabbaremys* and much deeper than seen in *Bothremys*, *Foxemys*, *Podocnemis*, and pelomedusids, but similar in extent to the one in *Rhothonemys*.

The ventral portion of the maxilla bears the triturating surface and forms part of the palate. The labial ridge of *Phosphatochelys* is much deeper than in *Azabbaremys* or other bothremydids. The snout is unusually foreshortened, and the labial ridge is very deep, resulting in a deep, horseshoe-shaped space. The flat portion of the triturating surface width is very small and not distinctly separated from the labial ridge or the lingual edge. The lingual ridge barely exists: it is just the rounded margin for the apertura narium interna. The triturating surface has the usual nutrient foramina but it is smooth, not corrugated as in *Azabbaremys*.

VOMER

Preservation: There is no vomer present in either specimen, but that may be due to postmortem loss.

PALATINE (figs. 196, 197, 199)

Preservation: Both palatines in AMNH 30008 are present but both are missing some of the anterior margin, although the right one seems to be nearly complete. Most of the dorsal surfaces are visible except posteromedially. In MDEt 26, both palatines are complete but visible only in ventral view.

Contacts: The palatine in *Phosphatochelys* contacts the maxilla anterolaterally, the pterygoid posteriorly, and the other palatine medially. In the orbital floor the palatine has a broad anterolateral contact with the maxilla and a broad lateral contact with the jugal. The absence of a septum orbitotemporale is associated with the absence of a postorbital contact.

Structures on dorsal surface: The dorsal surface of the palatine is complex, as it is involved in the fossa orbitalis, the sulcus palatinopterygoideus, and the remnant of the septum orbitotemporale. In *Phosphatochelys*, as in *Azabbaremys* and *Taphrosphys*, the septum orbitotemporale, so prominent in other bothremydids, is mostly absent. In dorsal view the palatine of *Phosphatochelys* is similar to *Azabbaremys* in forming most of the floor of the orbit and in having a broad anterolateral maxilla contact and a broad lateral jugal contact. The surface of the orbital floor is deeply concave, even more than in *Azabbaremys*. In contrast to *Azabbaremys*, *Phosphatochelys* has a narrow but completely enclosed sulcus palatinopterygoideus (figs. 202, 279A). In *Azabbaremys* the lateral wall of the sulcus is gone; in *Phosphatochelys* it is narrow but complete.

Structures on ventral surface: In ventral view the palatine in *Phosphatochelys* is smaller than the unusually large palatine of *Azabbaremys*. The palatine-pterygoid suture is roughly transverse in *Phosphatochelys*, not concave anteriorly as in *Azabbaremys*. The edges of the apertura narium interna in *Phosphatochelys* are best preserved in MDEt 26. They are more circular rather than triangular as in *Azabbaremys*. As in *Azabbaremys*, only a small part of the palatine enters onto the triturating surface. The palatine forms the roof of the choanal opening into the mouth, the apertura narium interna. In *Phosphatochelys*, *Azabbaremys*, and *Nigeremys* this roof is highly arched dorsally, in contrast to the flatter surface of other bothremydids. The foramen palatinum posterius in *Phosphatochelys* is formed almost entirely by the palatine, but it is very close to the pterygoid suture, and a small spur of the pterygoid may enter the foramen. The foramen palatinum posterius of *Phosphatochelys* is in a comparable position to that seen in *Azabbaremys*, but it is much more medial and closer to the apertura narium interna in *Phosphatochelys* than in *Azabbaremys* or other bothremydids.

QUADRATE (figs. 196, 197, 199, 202, 203, 286C)

Preservation: Both quadrates in AMNH 30008 are present and nearly complete. The left one lacks its anterior edge and the right

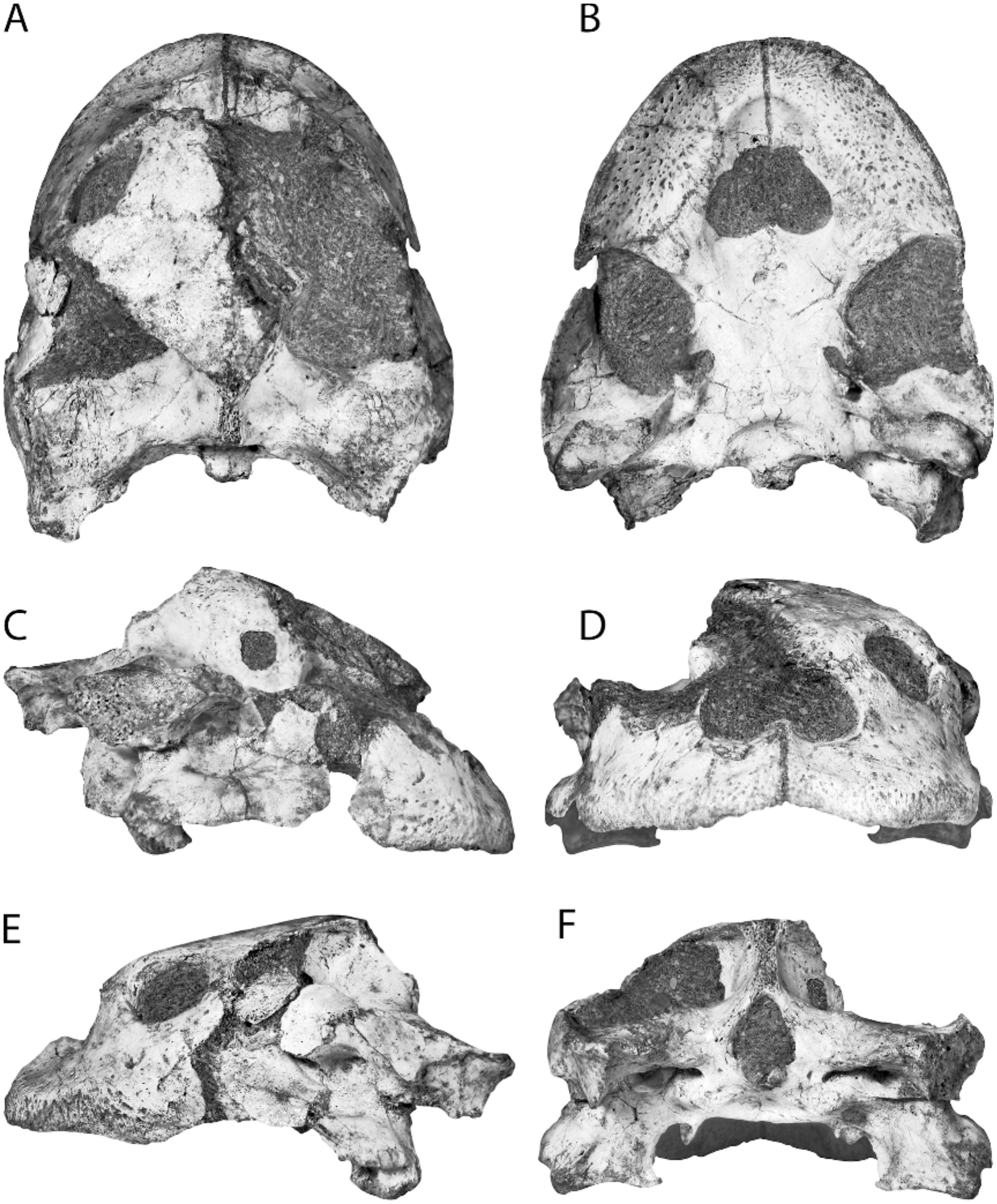

Fig. 200. *Phosphatochelys tedfordi* Gaffney and Tong, 2003. MDEt 26. **A**, dorsal; **B**, ventral; **C**, right lateral; **D**, anterior; **E**, left lateral; **F**, posterior. [C. Blik, del.]

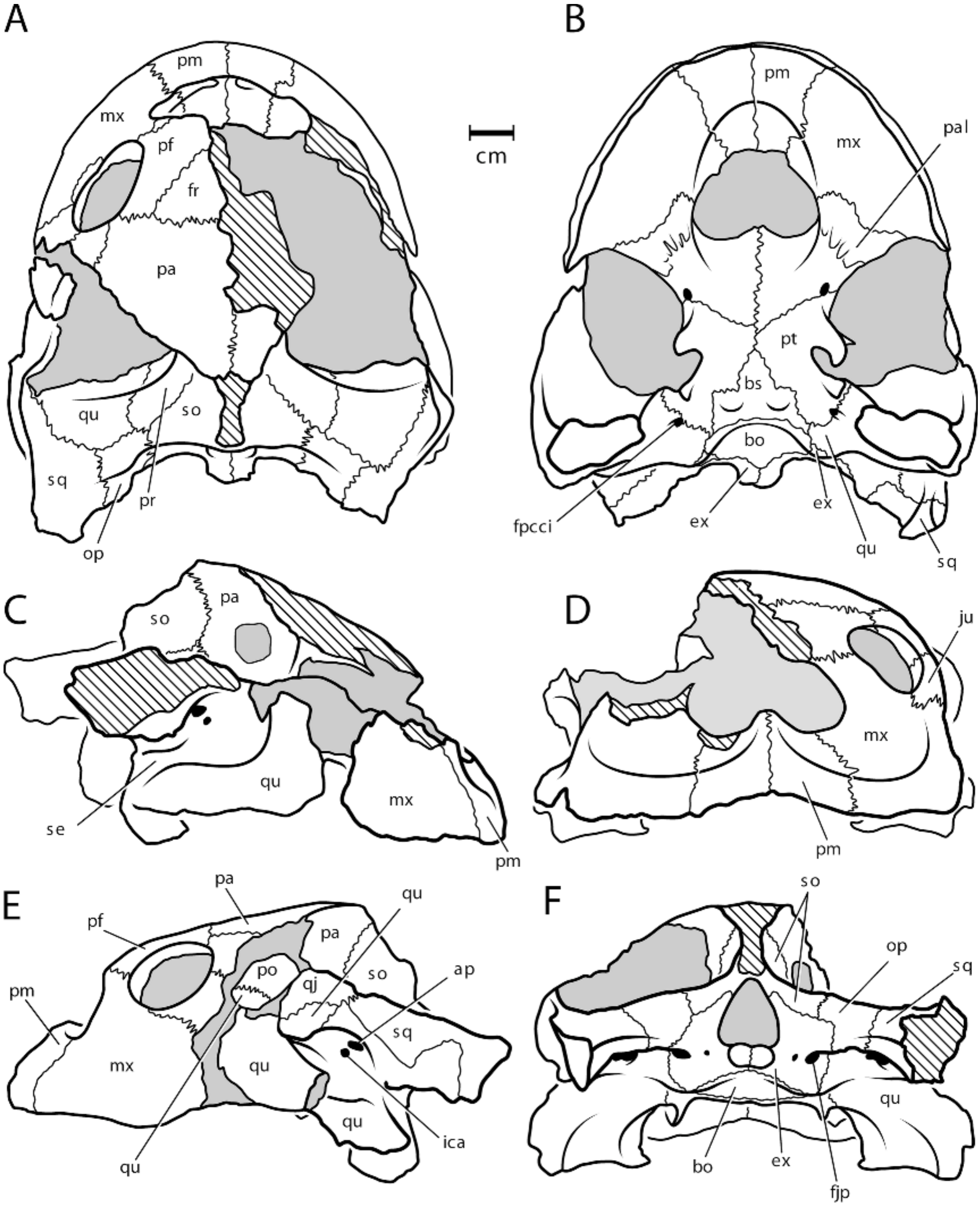

Fig. 201. *Phosphatochelys tedfordi* Gaffney and Tong, 2003. MDEt 26. **A**, dorsal; **B**, ventral; **C**, right lateral; **D**, anterior; **E**, left lateral; **F**, posterior. [C. Blik, del.]

one has some breakage along the jugal-maxilla contact. In MDEt 26, both quadrates are present. The left one seems to be all there, but it is cracked in a number of places with some displacement of the pieces. The right quadrate is less deformed, but it is missing its dorsal margin.

Contacts on lateral surface: In lateral view the quadrate of *Phosphatochelys* contacts the jugal anteriorly, the postorbital anterodorsally, the quadratojugal dorsally, and the squamosal posterodorsally. As preserved, there is a maxilla contact anteroventrally on the right of AMNH 30008, but this is interpreted as a narrow cheek emargination (see Maxilla). Both quadrates in MDEt 26 preserve an anterior margin that looks like a free edge, not a sutural contact.

Structures on lateral surface: The cavum tympani in *Phosphatochelys* (fig. 286C) has a completely enclosed incisura columellae auris, as in *Azabbaremys* and most bothremydids. Also as in *Azabbaremys*, the cavum is hemispherical and lacks a fossa precolumellaris. However, *Phosphatochelys* has a well-developed antrum postoticum, larger than in *Taphrosphys sulcatus*, which is in strong contrast to *Azabbaremys*, which completely lacks an antrum postoticum. At the posterior margin of the cavum tympani in *Phosphatochelys* is a groove for the eustachian tube, as in *Azabbaremys*. In *Azabbaremys* this groove is open, but in *Phosphatochelys* there is a well-developed ventral process or overhang that partially encloses the eustachian tube. As in *Azabbaremys*, there is a shelf along the ventral margin of the cavum tympani. It is very similar in size and shape in both *Phosphatochelys* and *Azabbaremys*.

Contacts on dorsal and anterior surfaces: The quadrate in *Phosphatochelys* contacts the prootic medially, the opisthotic posteromedially, and the squamosal posterolaterally. As in *Azabbaremys* and *Taphrosphys*, there is no quadrate-supraoccipital contact that is seen in other bothremydids. The dorsally directed trough and associated ridge (see Pterygoid) formed by pterygoid and quadrate lie just anterior to these foramina.

Structures on dorsal and anterior surfaces: The quadrate forms the posteroventral margins of the foramen stapedio-temporale and the foramen nervi trigemini, as in other bothremydids. These formaina are verly close to each other in *Phosphatochelys*.

Contacts on ventral surface: In ventral view the quadrate of *Phosphatochelys* contacts the pterygoid anteromedially, the basisphenoid medially, and the basioccipital posteromedially, as in *Azabbaremys* and other bothremydids. As in *Azabbaremys*, there is a narrow contact with the basisphenoid between the broader basioccipital and pterygoid contacts. The quadrate contacts the quadrate ramus of the pterygoid in a suture extending from the basisphenoid along the processus articularis of the quadrate, as in *Azabbaremys* and other pleurodires.

Structures on ventral surface: The foramen posterius canalis carotici interni is formed in the pterygoid-quadrate suture, but more is formed by the quadrate than by the pterygoid. In contrast to *Azabbaremys*, there is no contribution from the basisphenoid. There is a distinct groove on the quadrate leading anteriorly into the foramen posterius canalis carotici interni.

The processus articularis of the quadrate in *Phosphatochelys* is longer than in *Azabbaremys* so that the condylus mandibularis is much farther from the plane of the palate in *Phosphatochelys* than it is in *Azabbaremys*. This is presumably related to the very deep labial ridge in *Phosphatochelys*, although a lower jaw will be needed to demonstrate this. The quadrate and the basioccipital form the tuberculum basioccipitale, which is higher and more prominent than in *Azabbaremys*.

Contacts on posterior surface: In posterior view the quadrate in *Phosphatochelys* contacts the squamosal dorsolaterally, the opisthotic dorsally, the exoccipital medially, and the basioccipital ventromedially (not quite visible in occipital view).

Structures on posterior surface: The quadrate and opisthotic combine to form a fully enclosed fenestra postotica (fig. 203) in *Phosphatochelys*, very similar to that in *Azabbaremys*. In the shelf leading into the fenestra, both dorsally and ventrally, are low spurs suggesting a division of stapedial artery and lateral head vein. However, distinct ridges as seen in *Taphrosphys* are absent. As in *Azabbaremys*, the fenestra postotica of

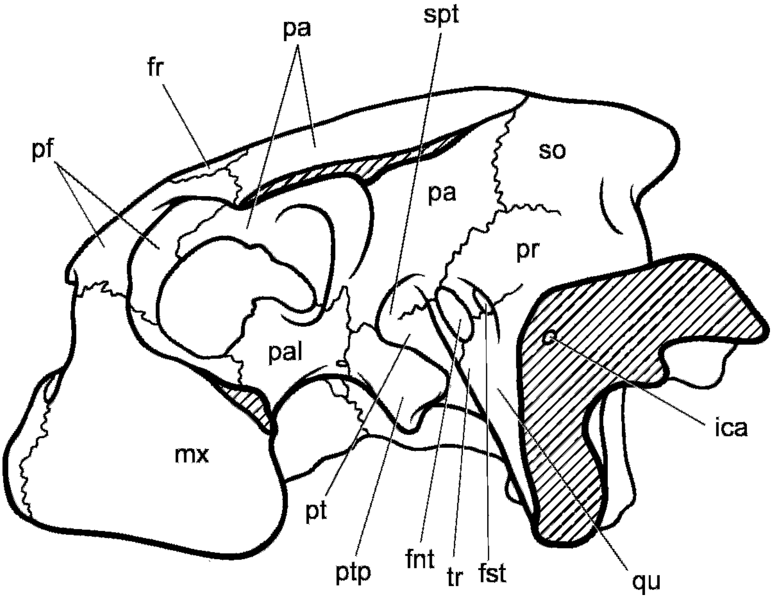

Fig. 202. *Phosphatochelys tedfordi* Gaffney and Tong, 2003. Restored left parasagittal view based on AMNH 30008 holotype. [A. Venjara, del.]

Phosphatochelys is widely separated from the foramen jugulare posterius by a well-developed opisthotic-quadrate contact. In *Phosphatochelys* and *Azabbaremys* the quadrate contacts the exoccipital and basioccipital ventral to the foramen jugulare posterius. On the posterior surface of *Phosphatochelys* is a continuation of the sulcus eustachii from the cavum tympani. This groove is roughly horizontal and is well defined dorsally by a shelf that has a slight ventral ridge resulting in an overhang partially enclosing the groove. Medially the groove flattens out and disappears.

PTERYGOID (figs. 196, 197, 199, 202)

Preservation: Both pterygoids in AMNH 30008 are present and nearly complete. The processus trochlearis pterygoidei is displaced on the right side but intact on the left. Both pterygoids are present and nearly complete in MDEt 26 as well. Only the ventral surfaces are visible due to matrix. On both sides the thin flange below and behind the processus trochlearis pterygoidei is divided into two narrow flanges. However, close examination reveals this to be an artifact of overpreparation; the flange was originally one piece, as in other pleurodires.

Contacts on ventral surface: In ventral view the pterygoid contacts in *Phosphatochelys* are as in other bothremydids: palatine anteriorly, quadrate posterolaterally, basisphenoid posteromedially, the other pterygoid medially. The midline pterygoid contact is slightly longer than in *Azabbaremys*.

Structures on ventral surface: The foramen posterius canalis carotici interni (see Quadrate) lies in the pterygoid-quadrate suture midway between the basisphenoid and lateral edge of the quadrate. Nonetheless, the foramen is in a similar position in *Azabbaremys* despite the fact that the basisphenoid enters the foramen in *Azabbaremys*. The basisphenoid is much wider in *Azabbaremys* than in *Phosphatochelys*, and that may be a factor.

The pterygoideus muscle scar is weakly developed in *Azabbaremys*, but it is absent in *Phosphatochelys*. There is no indication at all of its presence. However, there is a dorsally directed trough formed by pterygoid and quadrate in *Phosphatochelys* that may have held an insertion for the M. pterygoideus (fig. 203, in the area labeled "pt"). This trough has a sharp ridge on the quadrate as its lateral margin and the crista pterygoidea and processus inferior parietalis as its medial limits. It trends posteroventrally from the parietal down to the condylus mandibularis and is open anteriorly. As it reaches the ventral edge of the pterygoid its posterior wall ends, and only the lateral ridge reaches the condylus mandibularis. Thus, in ventral view (fig. 197), the end of the trough lies behind the processus trochlearis pterygoidei just lateral to the thin web of bone behind the processus. This structure, developed to the extent seen in *Phosphatochelys*, and also in *Ummulisani*, is unique among pleurodires. It is possible that this trough contains a division of the M. pterygoideus (Schumacher, 1973), probably either the pars ventrolateralis or possibly the pars ventroposterior (seen in *Podocnemis*).

The processus trochlearis pterygoidei of *Phosphatochelys* is relatively well preserved on both sides. In many pleurodire fossils it is damaged due to the thin bone. In *Azabbaremys* only part of one is preserved, but it is similar to that in *Phosphatochelys*. The processus in both genera extends posteriorly at an angle of roughly 30° from the midline. There is a low ridge along the ventrolateral margin of the processus in *Phosphatochelys*, also as in *Azabbaremys* but absent in pelomedusids. The base of the processus trochlearis pterygoidei contacts the parietal anterodorsally and the palatine anteroventrally. The foramen palatinum posterius (see Palatine) is formed almost entirely by the palatine with a very narrow contribution from the pterygoid.

Contacts on dorsal surface: The pterygoid at the base of the processus trochlearis pterygoidei contacts the parietal anterodorsally and the palatine anterolaterally. The crista pterygoidea is very short in *Phosphatochelys*; the pterygoid contacts the parietal dorsally and the prootic behind the foramen nervi trigemini.

Structures on dorsal surface: The crista pterygoidea in *Phosphatochelys* is completely covered with matrix on the right side and only partially exposed on the left in AMNH 30008. However, the left side does show the anterior margin and the foramen nervi trigemini clearly. The crista pterygoidea in *Phosphatochelys* is narrow in comparison to Bothremydini, but it is not as narrow as in *Azabbaremys*. In *Azabbaremys* both the processus inferior parietalis and the crista pterygoidea are roughly half the width of these walls in *Phosphatochelys*. The posterior edge of the crista pterygoidea forms the anteroventral margin of the foramen nervi trigemini in *Phosphatochelys*, as in *Azabbaremys*. In *Phosphatochelys* in contrast to *Azabbaremys*, there is a high, thin ridge along the anterior margin of the foramen nervi trigemini separating it from the more anterior part of the crista pterygoidea.

SUPRAOCCIPITAL (figs. 196, 199, 203)

Preservation: The supraoccipital in AMNH 30008 is nearly complete and well preserved, with all sides in it being visible. In MDEt 26 the supraoccipital is missing most of the crista supraoccipitalis, but it is otherwise complete.

Contacts: The laterally projecting otic portion of the supraoccipital in *Phosphatochelys* contacts the prootic anterolaterally, the opisthotic laterally, and the exoccipital posterolaterally. It does not contact the quadrate, although in MDEt 26 the opisthotic-prootic contact is much narrower than in AMNH 30008.

Structures: The supraoccipital of *Phosphatochelys* underlies the two parietals on the midline but not to the extent seen in *Azabbaremys*. This is presumably related to the shorter parietals in *Phosphatochelys*, because the supraoccipitals in both *Phosphatochelys* and *Azabbaremys* are quite similar. The crista supraoccipitalis is complete in *Phosphatochelys* and short as in *Azabbaremys*, extending only slightly past the level of the condylus occipitalis. *Phosphatochelys* has a slightly shorter crista than in *Azabbaremys*. The blade of the crista is deeper in *Azabbaremys* than in *Phosphatochelys*, but this seems to be related to the larger foramen magnum of *Phosphatochelys*, being in turn presumably related to its smaller size.

EXOCCIPITAL (figs. 196, 199, 203)

Preservation: Both exoccipitals are preserved in AMNH 30008 and in MDEt 26; they are complete, free of matrix, and have clear sutures.

Contacts: The exoccipital in *Phosphatochelys* contacts the supraoccipital dorsally, the opisthotic laterally, the quadrate ventro-

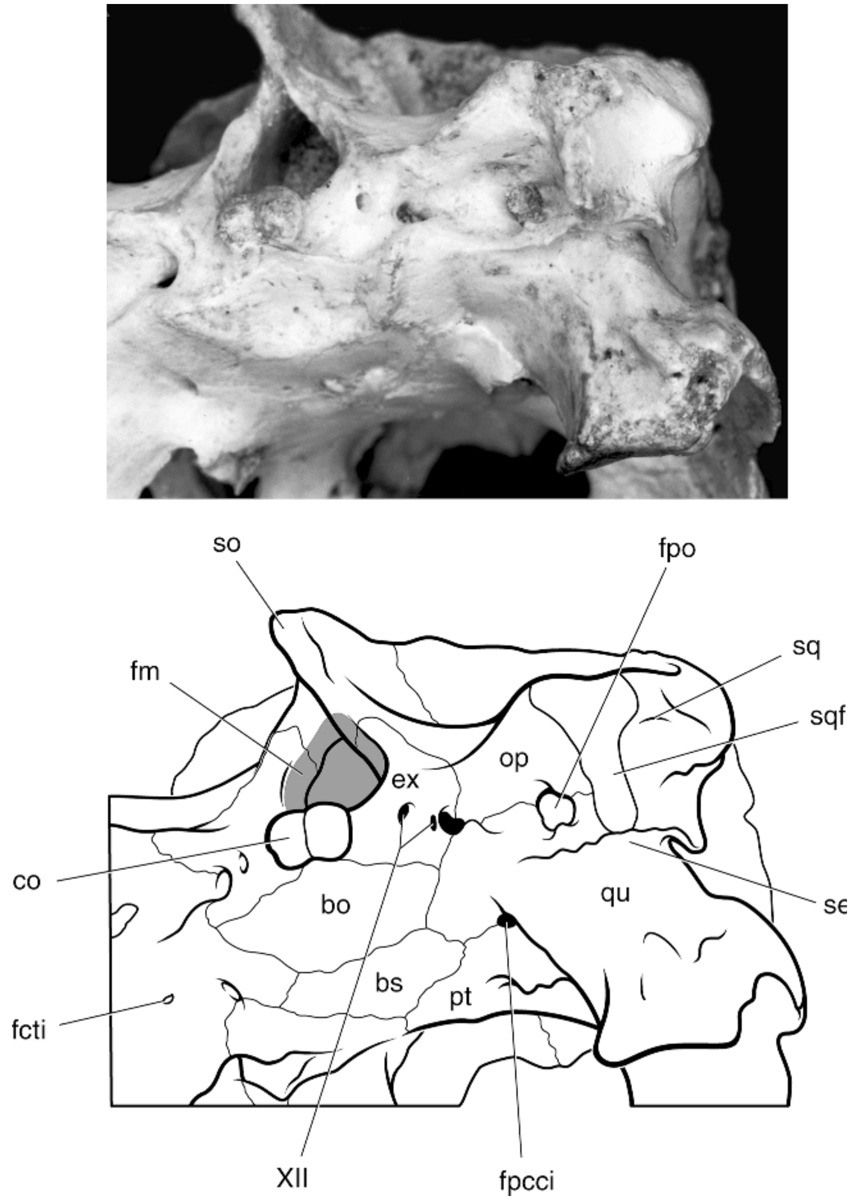

Fig. 203. *Phosphatochelys tedfordi* Gaffney and Tong, 2003. AMNH 30008 holotype. Posterior oblique view of skull. [A. Venjara and E.S. Gaffney, del.]

laterally, and the basioccipital ventrally, as in *Azabbaremys* and other bothremydids.

Structures: The exoccipital in *Phosphatochelys* forms all of the condylus mandibularis, and the basioccipital enters the neck of the condyle and almost reaches the articulation surface, in contrast to the condyle in *Azabbaremys* where the basioccipital is more anterior. The exoccipitals are slightly eroded on the midline or perhaps they were not fully ossified, giving the occipital condyle a bilobed appearance as in BMNH R 16370, the type specimen of *Azabbaremys moragjonesi.* The foramen jugulare posterius is formed mostly by the exoccipital, with between a third and a half being formed by the opisthotic, in contrast to *Azabbaremys* in which only a very narrow process of the opisthotic enters the foramen margin. The foramen jugulare posterius is entirely enclosed by bone, as in *Taphrosphys*, *Arenila*, and *Bothremys* but in contrast to the open condition of *Foxemys* and *Polysternon*.

Between the foramen jugulare posterius and the condylus occipitalis are the two foramina nervi hypoglossi entirely formed by the exoccipital. Their positions differ significantly in *Phosphatochelys* and *Azabbaremys*. In *Phosphatochelys* the more medial foramen lies on the roughly flat posterior surface of the exoccipital and opens posterolaterally and is clearly visible in posterior view. The more lateral foramen lies within the entry to the foramen jugulare posterius and is so far within the margin that it is completely concealed in posterior view on the right side and only barely visible on the left. The more medial foramen nervi hypoglossi in *Phosphatochelys* is larger in diameter than the more lateral one. In *Azabbaremys* both foramina are very close to one another, they are the same size, and neither is close to the foramen jugulare posterius.

BASIOCCIPITAL (figs. 196, 197, 199, 203)

Preservation: The basioccipitals in AMNH 30008 and MDEt 26 are complete and clearly defined.

Contacts: The basioccipital in *Phosphatochelys* contacts the basisphenoid anteriorly, the quadrates laterally, and the exoccipitals posteriorly, as in *Azabbaremys*. *Phosphatochelys* has a broadly curved anterior margin rather than the straight suture seen in *Azabbaremys*. The basisphenoid contact is smaller and the quadrate contact more extensive in *Phosphatochelys*.

Structures: The basioccipital in *Phosphatochelys* makes up the medial half of the very low tuberculum basioccipitale. Between the paired tubercula is a median concavity that is deeper and more clearly defined than in *Azabbaremys*. The concavity in *Phosphatochelys* is almost exactly coincident with the basioccipital.

PROOTIC (figs. 196, 199, 202)

Preservation: Both prootics are present and complete in both skulls. In AMNH 30008 the left one is free of matrix, but the right one is covered anteromedially. Both have clear sutures. In MDEt 26 the prootics appear complete but are covered by matrix anteriorly.

Contacts: The prootic in *Phosphatochelys* contacts the supraoccipital posteromedially, the parietal medially, the pterygoid ventrally (internal to the foramen nervi trigemini), the quadrate laterally, and the opisthotic posterolaterally. The opisthotic contact is broader in AMNH 30008 and narrower in MDEt 26.

Structures: The prootic forms the dorsomedial margin of the foramen nervi trigemini, the parietal forms its anterodorsal margin, the pterygoid forms its anteroventral margin, and the quadrate forms its posteroventral margin. The foramen nervi trigemini is visible and complete on the left side of AMNH 30008 as well as the foramen stapedio-temporale, which lies entirely on the anterior face of the otic chamber and is not visible in dorsal view. This is the same condition in nearly all bothremydids. The quadrate forms the lower half of the foramen stapedio-temporale (see Quadrate). Both foramina are very close to each other.

OPISTHOTIC (figs. 196, 197, 199, 203)

Preservation: Both opisthotics are complete and well preserved with clear sutures in MDEt 26 and AMNH 30008.

Contacts: The opisthotic in *Phosphatochelys* has the usual bothremydid contacts: supraoccipital dorsomedially, prootic anteromedially, quadrate anterolaterally, squamosal posterolaterally, quadrate (again) ventrolaterally, and exoccipital posteromedially.

Structures: The opisthotic forms the roof of the fenestra postotica, with the ventral and greater portion being formed by the quadrate. The fenestra in *Phosphatochelys* is oblong with small ridges distally presumably indicating the positions of the stapedial artery and lateral head vein (see Quadrate). The processus interfenestralis of the opisthotic forms the wall between the fenestra postotica and foramen jugulare posterius, contacting the quadrate ventrally. This wall is quite thick in *Phosphatochelys* as it is in *Azabbaremys* and most Taphrosphyini and Bothremydini.

BASISPHENOID (figs. 196, 197, 199)

Preservation: The basisphenoid is complete and clearly defined in MDEt 26 and AMNH 30008, but its dorsal surface is covered with matrix.

Contacts: The basisphenoid of *Phosphatochelys* is roughly triangular in ventral view. It has a straight posterior contact with the basioccipital, posterolateral contacts with the quadrates, and anterolateral contacts with the pterygoids.

Structures: The basisphenoid in *Phosphatochelys* is about as wide as long, in contrast to the very short and wide basisphenoid in *Azabbaremys*.

Ummulisani rutgersensis

At present, three skulls of this taxon are known, but because two of them were discovered very late in the development of this project, it was only possible to describe in detail and figure one without incurring significant delays. The other two will be described soon (Gaffney and Tong, in prep.). Unfortunately, the figured skull, AMNH 30563, is the least complete of the three; although not ideal, it is complete enough to serve as the type. One of the new skulls, AMNH 30562, is associated with a plastron that we were able to describe and figure (figs. 268, 269), even though the skull is still being prepared. The third skull, AMNH 30569, is nearly complete. Some information from all three skulls is included in the description below.

Ummulisani is the sister taxon to *Phosphatochelys* within the subtribe Taphrosphyina.

PREFRONTAL (figs. 204, 207)

Preservation: Both prefrontals are complete in AMNH 30563 except for a small part of the maxilla contact. The posteromedial edge of the ventral process could have had a palatine contact; if so, this is also missing.

Contacts: There is a long medial contact with the other prefrontal and a very narrow anterolateral contact with the maxilla. The maxilla contact in *Ummulisani* is about the same size and position as in *Phosphatochelys*. It is narrower than in *Taphrosphys* and *Azabbaremys*. The posterior contact in the type specimen of *Ummulisani* is a straight transverse suture with the parietal. In the two other specimens of *Ummulisani*, the small frontals lie in the medial part of this suture. The only other pleurodire or turtle to have a prefrontal-parietal contact is *Phosphatochelys*. *Phosphatochelys* also has small frontals that are separated from the orbital margin by the prefrontal-parietal contact. Many other turtles have small frontals, but none combine that with large prefrontals to produce a prefrontal-parietal contact.

Structures: The prefrontal in *Ummulisani* has the midline projection seen in other Taphrosphyini. It is about the same size and shape as in *Phosphatochelys*.

Ummulisani is unique in having a hornlike process on the anterolateral margin of each prefrontal, developed to about the same extent in all three skulls. This process is cone-shaped and lies at the anterodorsal margin of the orbit. There is nothing similar in any other turtle. *Phosphatochelys* and other Taphrosphyini do not even have swellings or thickened bone in this area. Clearly, these horns were part of the complex rutting rituals in which males bashed what few brains they had out of each other, resulting in their extinction.

The ventral surface is visible in AMNH 30563. The prefrontal forms almost all of the roof of the fossa nasalis and the major part of the sulcus olfactorius.

FRONTAL

The frontal is absent in AMNH 30563, but a small frontal is present in the two other *Ummulisani* specimens, not yet described (Gaffney and Tong, in prep.). The absence of the frontal is presumably individual variation, not of particular systematic significance.

PARIETAL (figs. 204, 207)

Preservation: Both parietals are present in AMNH 30563. The dorsal plate of the right one is complete except on its posterior edge. The left one has a broken lateral and posterior margin. The processus inferior parietalis of both is present but slightly damaged by dorsoventral crushing that has obscured its ventral contacts. The anterior margin of the processus is broken on both sides.

Contacts of dorsal plate: The large parietal of *Ummulisani* contacts the other

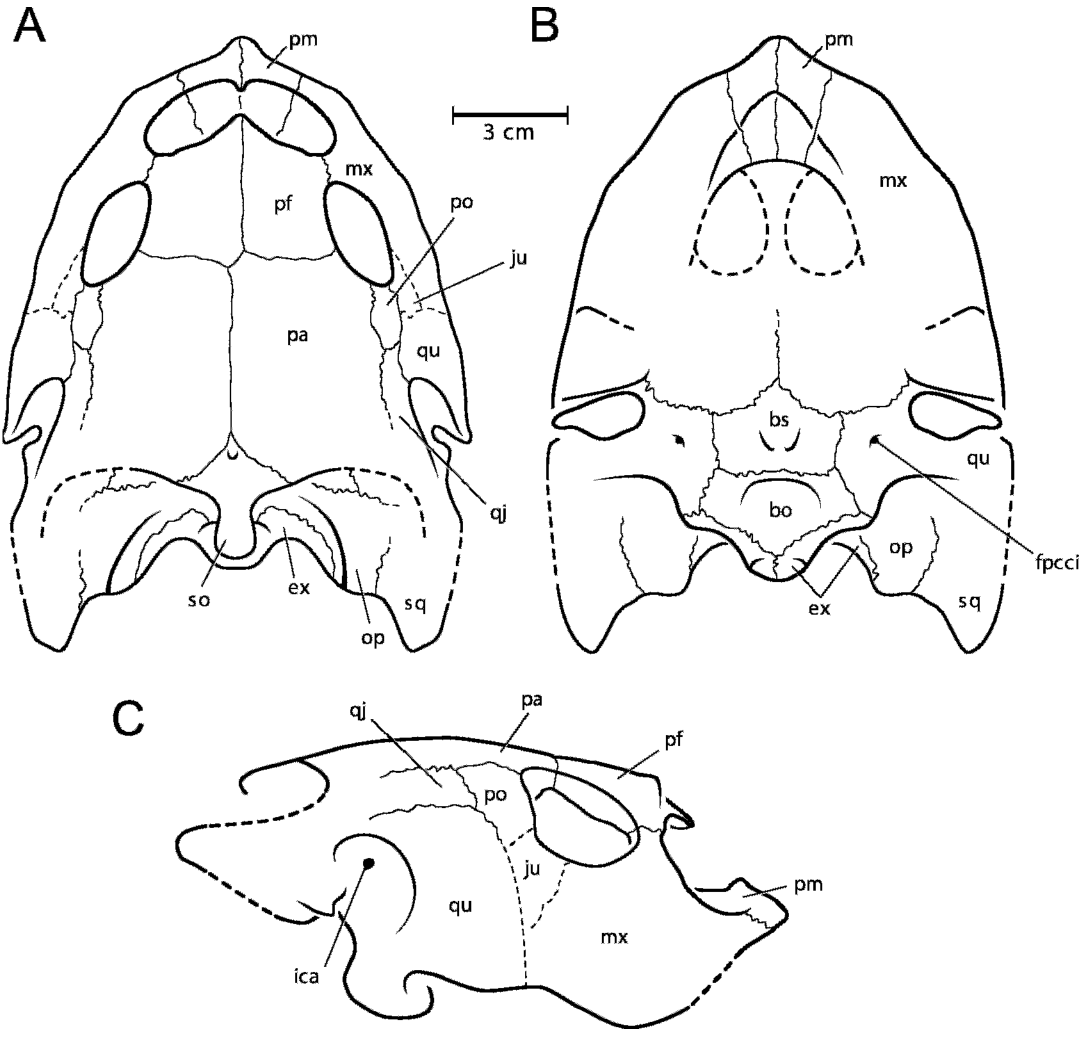

Fig. 204. *Ummulisani rutgersensis*, n. gen. et sp. AMNH 30563 holotype. Partially restored views of skull. **A**, dorsal; **B**, ventral; **C**, lateral. [C. Blik, del.]

parietal medially, the prefrontal anteriorly (see Prefrontal), the postorbital anterolaterally, the quadratojugal posterolaterally, and a small dorsal plate of the supraoccipital posteromedially. Except for the absence of a frontal contact in the type specimen, AMNH 30563, these are similar to ones found in *Phosphatochelys*.

Structures of dorsal plate: The posterior temporal emargination in AMNH 30563 is represented by a broken edge on both sides, but, as preserved, the skull roof is nearly as extensive as in *Phosphatochelys*. The two new skulls show a similarly extensive skull roof. On the ventral surface, *Ummulisani* lacks the septum orbitotemporale and has a transverse ridge instead, marking the posterior limits of the fossa orbitalis. This shows that the fossa orbitalis was expanded, as in *Phosphatochelys*.

Contacts of processus inferior parietalis: The anterior margin of the processus inferior parietalis is mostly a broken edge; only a small part is present on the right side, and the palatines are missing as well. The possible palatine contact, as in *Phosphatochelys*, cannot be determined. The pterygoid contact is much wider in *Ummulisani* than in *Phosphatochelys*. The prootic contact above

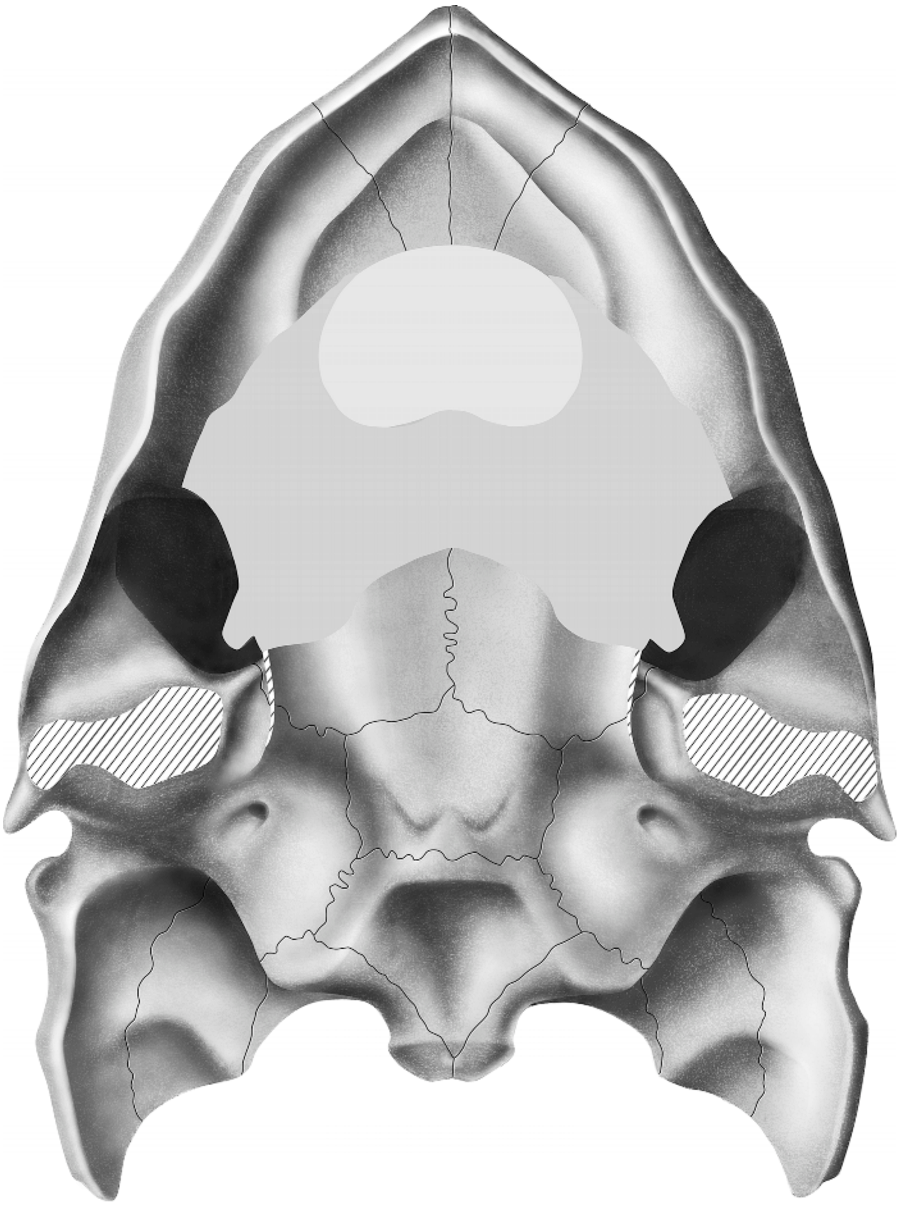

Fig. 205. *Ummulisani rutgersensis*, n. gen. et sp. AMNH 30563 holotype. Partially restored ventral view of skull. [D. Marques, del.]

the foramen nervi trigemini is unclear posteriorly.

Structures of processus inferior parietalis: The foramen interorbitale is too poorly preserved in AMNH 30563 to characterize, but it is possible to say that the remaining portion of the processus inferior parietalis is much wider than in *Phosphatochelys*. In *Phosphatochelys* the parietal has a ventral process that meets the pterygoid lateral to the sulcus palatinopterygoideus. In *Ummulisani*, the pterygoid area defining the sulcus is gone, but a small parietal process is present, although it does not seem to have been long enough to reach the pterygoid when the pterygoid was there.

JUGAL (figs. 204, 207)

Preservation: Only part of the right jugal is probably present in AMNH 30563, and that seems to have been displaced during an earlier bout of preparation. A bone below the orbit has a broken medial process that seems to be identifiable as a jugal, but it overlaps part of the quadrate behind it. The orbital margin and possible sutures, however, suggest that the bone may be the jugal and may only be displaced from its original position. The absence of a medial process and clear sutures preclude any further description.

QUADRATOJUGAL (figs. 204, 207)

Preservation: At least the anterior part of the right quadratojugal is present.

Contacts: The quadratojugal in *Ummulisani* contacts the parietal medially, the postorbital anteriorly, and the quadrate ventrolaterally.

Structures: The quadratojugal in *Ummulisani* is a small element placed well dorsal to the cheek margin. It is rectangular and not C-shaped. In these features it agrees with the quadratojugal in *Phosphatochelys* and *Azabbaremys*.

SQUAMOSAL (figs. 204, 207)

Preservation: The vicissitudes of death have dealt harshly with the squamosals of AMNH 30563. Only a few fragments of the right one remain, and the left one is badly broken and hanging on only by my imagination.

Contacts: The only contact remaining is with the quadrate, somewhat anteromedially.

Structures: The antrum postoticum is absent in *Ummulisani*, and the squamosal has no sign of a remnant canal or space. The left squamosal in *Ummulisani* has enough preserved to show that the ventral flange is large and similar to that structure in *Taphrosphys*, *Rhothonemys*, *Phosphatochelys*, and *Labrostochelys*. The lateral tubercle area is not preserved well enough to determine in AMNH 30563.

POSTORBITAL (figs. 204, 207)

Preservation: Only the right postorbital is present in AMNH 30563.

Contacts of lateral plate: The postorbital in *Ummulisani* contacts the parietal dorsomedially, the quadrate posteroventrally, the quadratojugal posteriorly, and the jugal ventrally. The jugal contact, however, is unclear, as the jugal is not definitely identified. The contacts are as in *Phosphatochelys*.

Structures of lateral plate: The postorbital in *Ummulisani* forms the posterior margin of the orbit and does not enter the temporal margin due to its relatively small size, in comparison to a form like *Azabbaremys*.

Contacts of medial process: The medial process only contacts the parietal medially in *Ummulisani*, as the septum orbitotemporale is nearly absent.

Structures of medial process: As in *Phosphatochelys*, the fossa orbitalis in *Ummulisani* is open posteriorly and the septum orbitotemporale is nearly absent. The postorbital and parietal form a transverse ridge on the ventral surface of the skull roof. This ridge is the remnant of the septum orbitotemporale and forms the posterior margin of the fossa orbitalis. The sulcus palatinopterygoideus is not preserved in AMNH 30563, so its degree of formation is not determinable.

PREMAXILLA (figs. 204–207)

Preservation: Both premaxillae are present and nearly complete in AMNH 30563, but their contacts with the maxillae are broken and filled with glue.

Contacts: The premaxilla in *Ummulisani* contacts the other premaxilla medially and the maxilla posterolaterally. The vomer and the vomer contact are not preserved.

Structures on dorsal surface: The premaxilla forms the floor of the fossa nasalis, which in *Ummulisani* is relatively large. The apertura narium externa is separated from the anterior skull surface only by a low ridge and a slight change in slope in *Ummulisani*, rather than by a sharp change in slope, as in *Phosphatochelys* and other Taphrosphyini. There is a midline ridge or carina that runs from the anterior margin of the premaxilla, the labial ridge, posteriorly through the apertura narium externa and into the fossa nasalis. In *Phosphatochelys*, the ridge is only within the fossa nasalis. In *Ummulisani*, the premaxilla is protuberant on the midline, forming an acute point, rather than the curved snout margin seen in *Phosphatochelys*, *Taphrosphys*, and *Nigeremys*. *Rhothonemys* has a slight protuberance, but not to the extent seen in *Ummulisani*. *Labrostochelys* has an extensive premaxillary process, but it ends in a blunt edge different from that in *Ummulisani*.

The floor of the fossa nasalis is a broad, curved trough separated by the midline carina. There is a groove along the inner margin of the apertura narium externa, like that seen in *Phosphatochelys*. The midline carina has a dorsal process where it intersects the apertura narium externa.

Structures on ventral surface: The labial ridge is inclined in *Ummulisani*, different from the vertical ridge in *Phosphatochelys*. The edge of the ridge is sharp and the bone is much thinner than in *Phosphatochelys*, and the more horizontal triturating surface produces a wider, flat area behind the labial ridge. The midline embayment in *Ummulisani* is wide as in *Phosphatochelys*, but it is much shallower. As on the dorsal surface, the labial ridge forms a pointed anterior protuberance in *Ummulisani* not seen in *Phosphatochelys*.

MAXILLA (figs. 204–207)

Preservation: Most of the right maxilla is present in AMNH 30563, but the ventral margin is missing some of its edges; its medial margin is missing posteriorly. There seems to be a natural edge just behind the premaxilla. The left maxilla only consists of the anterior half of the bone. Its ventral margin is a broken edge. Its medial edge seems to be natural anteriorly, as on the right side. Both maxillae have a posterior broken edge with a very similar shape that is close to where the palatine should be.

Contacts of vertical plate: The maxilla contacts the premaxilla anteriorly, the prefrontal anterodorsally, the jugal posterodorsally, and the quadrate posteroventrally. The jugal contact is only presumed, as the bone is ill defined. The quadrate suture is in a broken area, so its exact position is unclear, but it is not possible that another bone could be there.

Structures of vertical plate: The maxilla forms the ventral part of the orbital margin. There is a sharp rim with a concave pocket below the internal surface, as in *Phosphatochelys* and *Rhothonemys*. Anteriorly the maxilla forms the lateral wall and lateral part of the floor of the fossa nasalis. The orbitonasal bar in *Ummulisani* is narrow, as in *Phosphatochelys*, not wide, as in *Taphrosphys* and other Taphrosphyini.

The maxilla in *Ummulisani* is unusually deep, deeper than other Taphrosphyini except *Phosphatochelys*. Due to the greater snout foreshortening in *Phosphatochelys*, *Ummulisani* has a longer anterior part of the maxilla, as in the other Taphrosphyini. The narrow cheek emargination seen in *Phosphatochelys* is present but poorly preserved in the type skull of *Ummulisani*, but it is clearly present in the other two skulls of *Ummulisani*.

Contacts of horizontal plate: The only contact preserved in AMNH 30563 is anteriorly with the premaxilla, but it is possible that the posteromedial broken edge is close to the palatine contact.

Structures of horizontal plate: The triturating surface in *Ummulisani* is relatively narrow, as in other Taphrosphyini and in contrast to the wide surface of the Bothremydini. The labial ridge in *Ummulisani* is deep, as in *Phosphatochelys*, but it is very thin and curved, in contrast to the thicker, wedge shape in *Phosphatochelys*. The entire triturating surface is curved, as in *Labrostochelys*; it is not a distinct labial ridge meeting a horizontal triturating surface at right angles.

The apertura narium interna is represented by a natural edge of the maxilla that is the anterolateral margin of the apertura. This is similar in position to the apertura in *Phosphatochelys* and *Taphrosphys*. The maxilla forms the lateral part of the floor of the fossa orbitalis. All the other bones are missing, but the maxilla in *Ummulisani* does form more of the floor than does the maxilla in *Azabbaremys*. There is a high, sharp rim to the orbital margin and a ventral pocket formed by the maxilla, as in *Rhothonemys* and *Phosphatochelys*.

VOMER

Preservation: Not preserved in AMNH 30563.

PALATINE

Preservation: Not preserved in AMNH 30563.

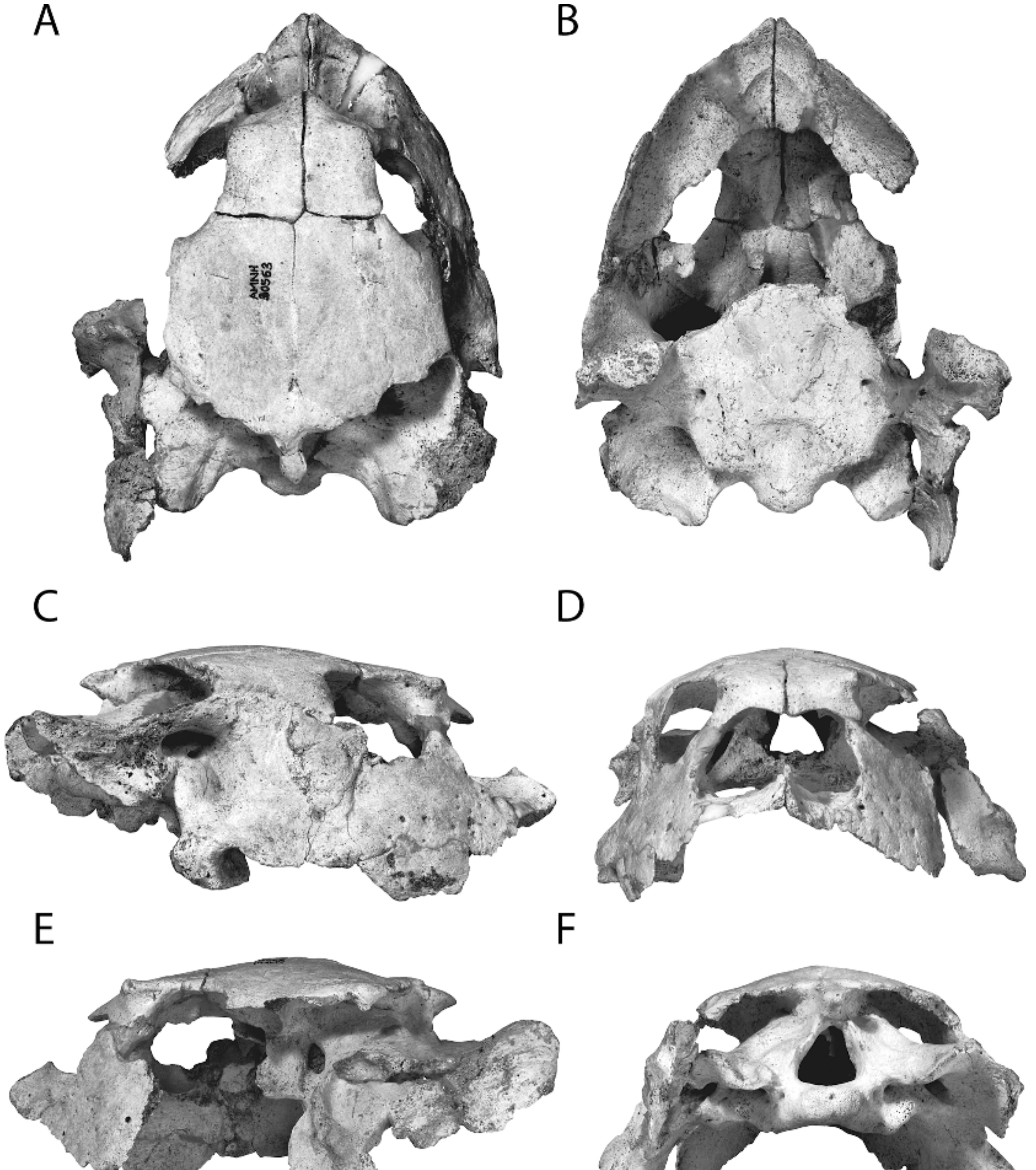

Fig. 206. *Ummulisani rutgersensis*, n. gen. et sp. AMNH 30563 holotype. **A**, dorsal; **B**, ventral; **C**, right lateral; **D**, anterior; **E**, left lateral; **F**, posterior. [C. Blik, del.]

QUADRATE (figs. 204–207)

Preservation: Both quadrates are present in AMNH 30563; the right one is nearly complete except for damage along its anterior margin, and the left is missing its dorsal portions.

Contacts on lateral surface: The quadrate in *Ummulisani* contacts the quadratojugal dorsomedially and the postorbital anteromedially. The anterior margin of the quadrate is not well preserved and the sutures are not entirely clear. However, the quadrate

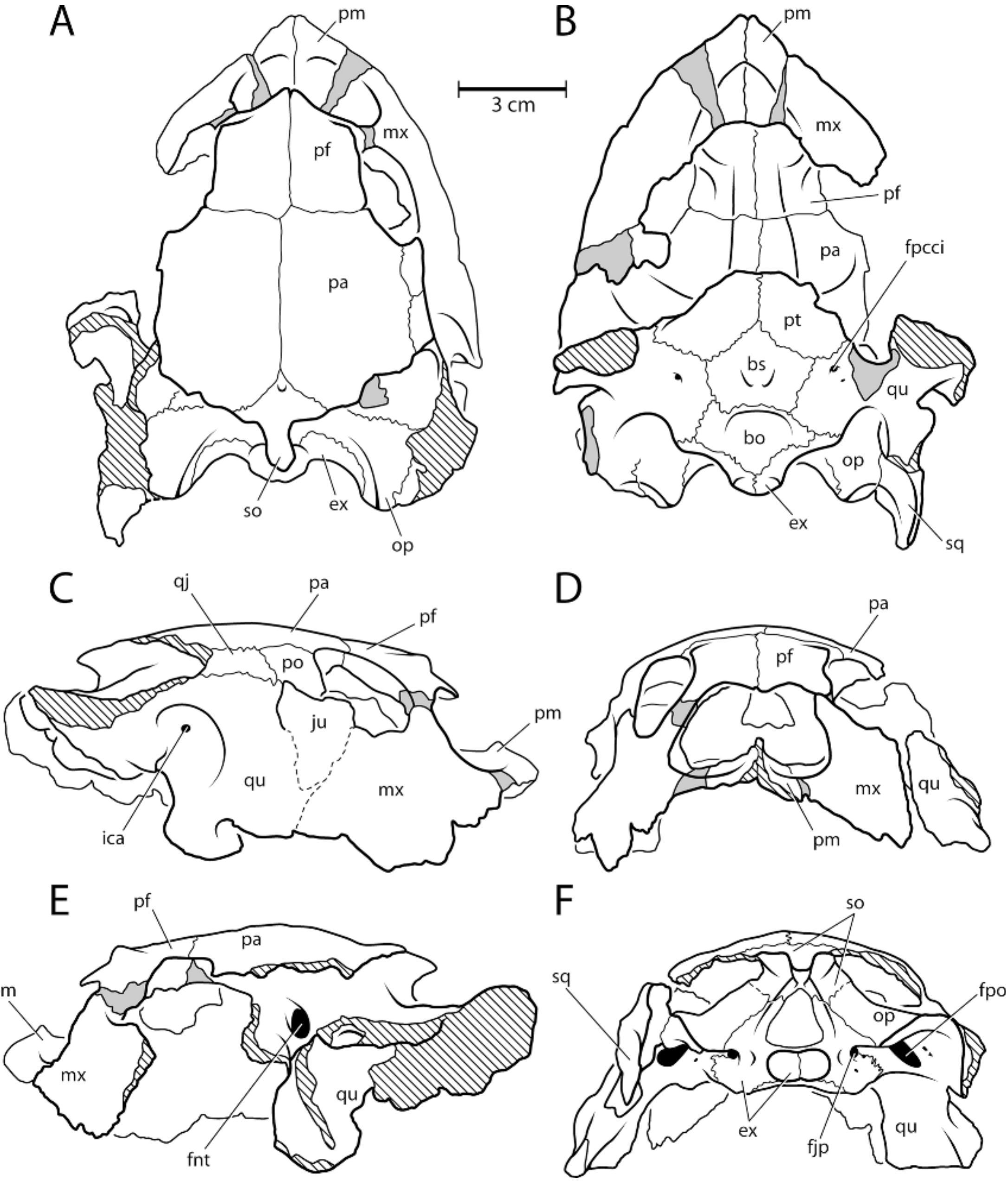

Fig. 207. *Ummulisani rutgersensis*, n. gen. et sp. AMNH 30563 holotype. **A**, dorsal; **B**, ventral; **C**, right lateral; **D**, anterior; **E**, left lateral; **F**, posterior. [C. Blik, del.]

does contact the jugal anterodorsally and the maxilla anteriorly, as in *Phosphatochelys*. The quadrate contacts the squamosal posterodorsally.

Structures: It is not clear whether the quadrate enters the temporal emargination in *Ummulisani* due to damage. The degree of emargination is similar in *Ummulisani* and *Phosphatochelys*, and *Phosphatochelys* has no quadrate exposure along the margin. The lateral surface of the quadrate in *Ummulisani* is expanded anteriorly as in *Phosphatochelys*, forming much of the cheek. Although the cavum tympani is clearly defined, there is a wider, shallow depression paralleling the anterior curved edge of the cavum. This depression extends well onto the cheek.

The cavum tympani in *Ummulisani* is similar to that in *Phosphatochelys*. The incisura columellae auris is the usual canal, with the deepest part of the cavum dorsal and anterior to it. The ventral shelf seen in many bothremydids is present, but not as deep or as well defined as in other taxa, such as *Bothremys*. The antrum postoticum is closed, although the area is a deep concavity posterodorsal to the incisura columellae auris. The sulcus eustachii is a V-shaped notch with a shallow groove extending toward the incisura columellae auris. There is a ventrally directed process on the dorsal edge of the sulcus, as in *Phosphatochelys* and *Labrostochelys*. There is also a broken base for a dorsally directed process on the lower margin of the sulcus eustachii on the right quadrate.

Contacts on dorsal and anterior surface: On the dorsal surface of the otic chamber, the quadrate contacts the prootic anteromedially, the opisthotic posteromedially, and the squamosal posteriorly. There is no supraoccipital contact, agreeing with the other Taphrosphyini.

Structures on dorsal and anterior surface: The foramen stapedio-temporale is only separated from the foramen nervi trigemini by a thin bar. Only a small part of quadrate seems to reach the margin of the foramen stapedio-temporale due to this very medial position. These relations are similar in both *Ummulisani* and *Phosphatochelys*.

Contacts on ventral surface: The quadrate in *Ummulisani* contacts the pterygoid anteromedially, the basisphenoid medially, the basioccipital posteromedially, and the exoccipital posteromedially as well. The basisphenoid contact is wide in *Ummulisani*, as in *Taphrosphys* and in contrast to the narrow contact of other Taphrosphyini.

Structures on ventral surface: There is no fossa pterygoidea in *Ummulisani*, although there is a slight concavity here. The condylus mandibularis is well anterior to the condylus occipitalis and the basisphenoid-basioccipital suture. On the posterior surface of the condylus mandibularis is a shallow depression for the depressor mandibulae, as in *Phosphatochelys*, not a deep depression, as in *Labrostochelys*. The foramen posterius canalis carotici interni is formed completely by the quadrate in *Ummulisani*. *Ummulisani* and *Labrostochelys* are the only pleurodires with the foramen posterius canalis carotici interni entirely formed by the quadrate.

Contacts on posterior surface: The quadrate in *Ummulisani* contacts the squamosal dorsolaterally, the opisthotic dorsomedially, the exoccipital medially, and the basioccipital ventromedially. The exoccipital suture is visible in only a few places.

Structures on posterior surface: The fenestra postotica in *Ummulisani* is fully enclosed by bone, being widely separated from the foramen jugulare posterius. The fenestra postotica is oval, roughly horizontal, with no sign of divisions.

PTERYGOID (figs. 204–207)

Preservation: Both pterygoids are present, but they lack the processus trochlearis pterygoideus and anterior edges. The left one is missing its lateral edge, which is present on the right.

Contacts on ventral surface: The pterygoid in *Ummulisani* contacts the quadrate posterolaterally, the basisphenoid posteromedially, and the other pterygoid medially. The palatine suture may be represented in a small part of the broken anterior edge, indicating that the pterygoid may not have been much longer than preserved.

Structures on ventral surface: There is no deep fossa pterygoidea, only a very shallow, ill-defined depression in the area. The quadrate ramus is slightly more extensive than in *Phosphatochelys*. There is no sign of the foramen palatinum posterius, as all of the anterior edges of the pterygoids are broken. The foramen posterius canalis carotici interni is entirely formed by the quadrate with no pterygoid participation.

Contacts on dorsal surface: The crista pterygoidea of the pterygoid contacts the parietal dorsally and the quadrate posteroventrally below the foramen nervi trigemini. The sutures around the foramen nervi trigemini are not clear, but there seems to be no prootic contact; the parietal enters the margin of the foramen between the pterygoid and prootic.

Structures on dorsal surface: The crista pterygoidea rises posteriorly to just anterior to the foramen nervi trigemini where it drops ventrally, and only a small part enters the foramen margin. The pterygoid bears a low, rounded ridge that is oriented anterodorsally–posteroventrally. It extends from a position anterior to the foramen nervi trigemini ventrally along the quadrate ramus paralleling the quadrate-pterygoid suture. In *Phosphatochelys* this ridge is larger and acute, defining a tubular space anterior to the ridge (see *Phosphatochelys*, Pterygoid).

SUPRAOCCIPITAL (figs. 204, 207)

Preservation: The supraoccipital is present and nearly complete in AMNH 30563. There is some breakage along its right anterolateral margin.

Contacts: The supraoccipital in *Ummulisani* contacts the parietals anteriorly, the exoccipitals posteroventrally, the prootic anterolaterally, and the opisthotic posterolaterally. The sutures, however, are not clear on either side, but there is no quadrate contact, agreeing with other Taphrosphyini.

Structures: The crista supraoccipitalis in *Ummulisani* is a very short, blunt process, with little similarity to the usual flat, vertical plate seen in other turtles. *Phosphatochelys* has a short crista, but it has a clear vertical plate. *Ummulisani* has a low crista with a blunt posterior end that is only slightly raised above the foramen magnum. The supraoccipital in *Ummulisani* has a horizontal contribution to the skull roof that extends anteriorly and laterally more than in other bothremydids. *Taphrosphys* has a wide plate, but not as deep as in *Ummulisani*.

EXOCCIPITAL (figs. 204, 207)

Preservation: Both exoccipitals are present and nearly complete in AMNH 30563.

Contacts: The exoccipital in *Ummulisani* contacts the supraoccipital dorsally, the opisthotic laterally, the quadrate ventrolaterally, and the basioccipital ventrally.

Structures: The foramen magnum in *Ummulisani* is about the same as in other Taphrosphyini. The condylus occipitalis is formed entirely by the exoccipitals. There is very little constriction to form a neck for the condyle. The foramen nervi hypoglossi consist of a larger, more medial foramen and a much smaller, more lateral one, as in other Taphrosphyini. As in *Phosphatochelys*, the more lateral one is very close to the foramen jugulare posterius, although in *Ummulisani* it is not actually within the margin of the foramen jugulare posterius as it is in *Phosphatochelys*. The foramen jugulare posterius is completely closed laterally by the opisthotic-exoccipital contact. The foramen is recessed, with a blunt shelf below, so that it faces more laterally than the foramen does in *Phosphatochelys*.

BASIOCCIPITAL (figs. 204–207)

Preservation: The basioccipital in AMNH 30563 is nearly complete.

Contacts: The basioccipital in *Ummulisani* contacts the basisphenoid anteriorly, the quadrate in a wide suture laterally, and the exoccipital posterolaterally.

Structures: *Ummulisani* has a blunt, low tuberculum basioccipitale formed by the basioccipital and exoccipital that is similar in size and extent to that in *Labrostochelys* and is lower than that in *Phosphatochelys*. There is a shallow concavity on the midline, much the same as in other Taphrosphyini.

PROOTIC (figs. 204, 207)

Preservation: Both prootics in AMNH 30563 are present and nearly complete, but some of the sutures are dim.

Contacts: The prootic in *Ummulisani* contacts the parietal dorsomedially, the quadrate laterally, the supraoccipital posterodorsally, and the opisthotic posteriorly.

Structures: The prootic forms a thin bar separating the foramen nervi trigemini from the foramen stapedio-temporale. In *Ummulisani* the two foramina are not sunk into a common recess, as in *Taphrosphys*, but are still very close, as in *Phosphatochelys*. The prootic forms most of the foramen stapedio-temporale. The foramen stapedio-temporale faces mostly anteriorly and the foramen nervi trigemini faces mostly laterally.

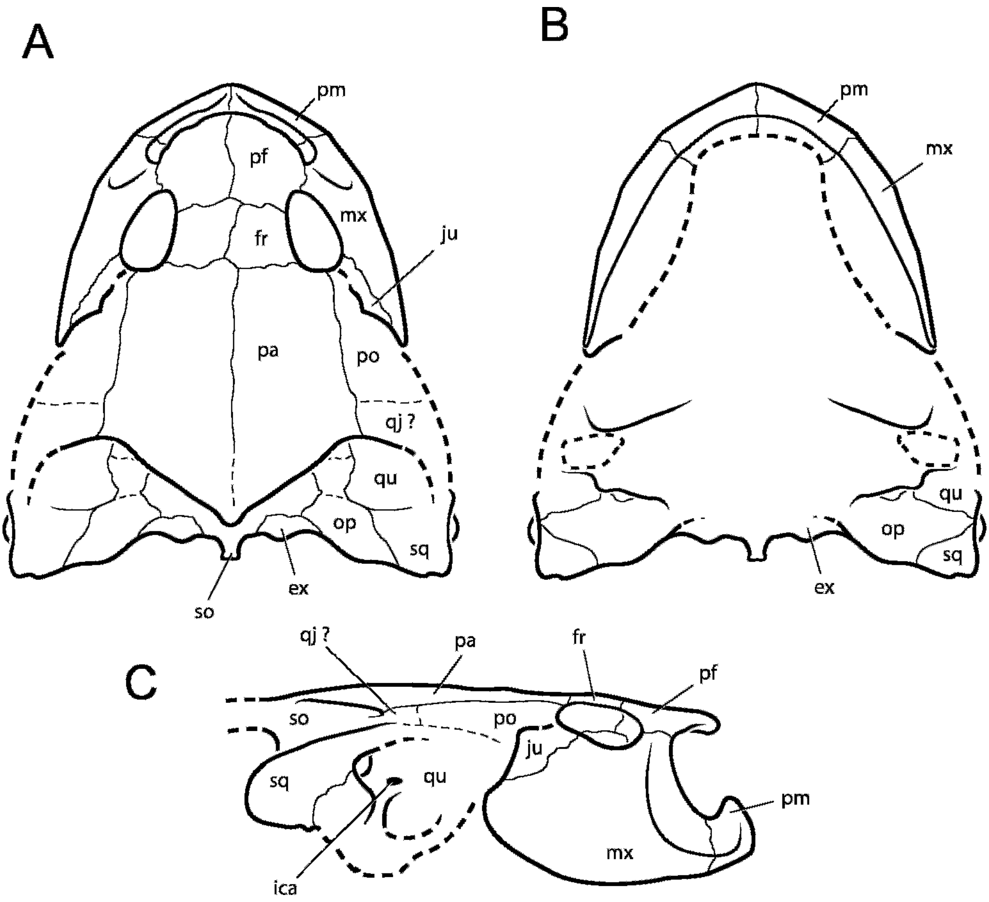

Fig. 208. *Rhothonemys brinkmani*, n. gen. et sp. AMNH 30521 holotype. Partially restored views of skull. [R. Rogge, del.]

OPISTHOTIC (figs. 204–207)

Preservation: Both opisthotics are present in AMNH 30563. The left one is damaged along its posterolateral margin; the right one is also damaged posterolaterally and medially as well, so that some of the sutures are obscured.

Contacts: The opisthotic in *Ummulisani* contacts the supraoccipital anteromedially, the prootic anteriorly, the quadrate anterolaterally, the exoccipital posteromedially, and the squamosal posterolaterally, although much of this latter contact is obscured by breakage.

Structures: The opisthotic enters into the fenestra postotica (see Quadrate) and the foramen jugulare posterius. The opisthotic is part of a posterior flange that, along with the squamosal, forms a ventrally open trough similar to that seen in *Labrostochelys* and *Taphrosphys*, and, to a lesser extent, in *Phosphatochelys*.

BASISPHENOID (figs. 204–207)

Preservation: The basisphenoid in AMNH 30563 is present and complete ventrally. Its dorsal surface has some damage and is partially obscured by matrix.

Contacts on ventral surface: The basisphenoid in *Ummulisani* contacts the pterygoids anterolaterally, the basioccipital posteriorly, and the quadrate in a wide suture laterally.

Structures on ventral surface: The basisphenoid in *Ummulisani* is pentagonal and similar in shape to that in *Taphrosphys*.

However, its anterior margin does have a point on the midline, similar to that in *Phosphatochelys*.

Contacts on dorsal surface: Not determinable.

Structures on dorsal surface: The rostrum basisphenoidale is fused into a single rod anterior to the sella turcica. The sella seems to be wide, not narrow as in *Taphrosphys congolensis*. The dorsum sellae seems to be damaged, but was probably higher than in *T. sulcatus*.

Rhothonemys brinkmani

The single skull representing this species is incomplete, lacking most of the palate and basicranium. *Rhothonemys* is the sister group to *Phosphatochelys* + *Ummulisani*.

PREFRONTAL (figs. 208–211)

Preservation: Both prefrontals are present in AMNH 30521, with both surfaces visible. The left prefrontal lacks its anteromedial edge and the right one has a small broken area ventrally. The right prefrontal is missing some of the ventral margin of its ventral process.

Contacts: The prefrontal in *Rhothonemys* contacts the maxilla anteroventrally, the frontal posteriorly, and the other prefrontal medially. There is no parietal contact, as in *Phosphatochelys*, or a palatine contact, as in *Bothremys* and *Chedighaii*.

Structures: The prefrontal in *Rhothonemys* is relatively large, being larger than the frontal and similar in relative size to the prefrontal in *Phosphatochelys*. The prefrontal in *Rhothonemys* protrudes anteromedially, as in *Phosphatochelys*, producing a blunt point on the midline. In *Rhothonemys* the degree of protrusion is more extensive than in *Phosphatochelys*, also correlated with the larger size of the apertura narium externa. The posterior margin of the prefrontal in *Rhothonemys* is straight, as in *Taphrosphys*, not indented, as in *Phosphatochelys*, due to the very small frontal in that taxon. The prefrontal in *Rhothonemys* forms the anterodorsal margin of the orbit, as in *Taphrosphys*, but does not extend posteriorly to the degree seen in *Phosphatochelys*. The interorbital distance in *Rhothonemys* is much narrower than in *Phosphatochelys* and *Azabbaremys*; it is similar in relative width to *Taphrosphys*.

The ventral process of the prefrontal in *Rhothonemys* separates the very large fossa nasalis from the fossa orbitalis. The process is similar in extent in *Rhothonemys* and *Phosphatochelys* but is thinner than in Pelomedusidae and Cearachelyini. The ventral surface of the prefrontal in *Rhothonemys* forms the roof of the large fossa nasalis and is broadly concave ventrally on each side of the midline (fig. 211A). The shape of this paired depression is more distinct than in *Phosphatochelys*, Pelomedusidae, and Cearachelyini.

FRONTAL (figs. 208–211)

Preservation: Both frontals are present in AMNH 30521, and dorsal and ventral surfaces are visible. The parasagittal ridge delimiting the sulcus olfactorius is broken along its ventral margin in both prefrontals. A small part of the orbital edge is broken posteriorly on both prefrontals, but most of the edge is intact.

Contacts: The frontal in *Rhothonemys* contacts the prefrontal anteriorly, the parietal posteriorly, and the other frontal medially. In most bothremydids the frontal also contacts the postorbital, but in *Rhothonemys* the contact is separated by the parietal exposure in the orbital margin. In *Phosphatochelys* the contact is also lacking, due to the small size of the frontal and the broad prefrontal-parietal contact.

Structures: The frontal in *Rhothonemys* forms the dorsal part of the orbital margin, much as in *Taphrosphys*, and in strong contrast to *Phosphatochelys*, in which the frontal is widely separated from the orbital margin by the parietal-prefrontal contact. The frontal is smaller than the prefrontal in *Rhothonemys*, as it is in *Phosphatochelys*. In *Taphrosphys*, *Azabbaremys*, and *Nigeremys*, it is equal to or larger than the prefrontal. In *Labrostochelys* the prefrontal is very elongate.

The ventral surface of the frontal in *Rhothonemys* (fig. 211A) shows the anteromedial projection, actually broken off on both sides but determinable from the sutural surface on the prefrontal, extending under the prefrontal, as occurs in most bothremydids and many pleurodires. The parasagittal ridge, although incomplete, separating the

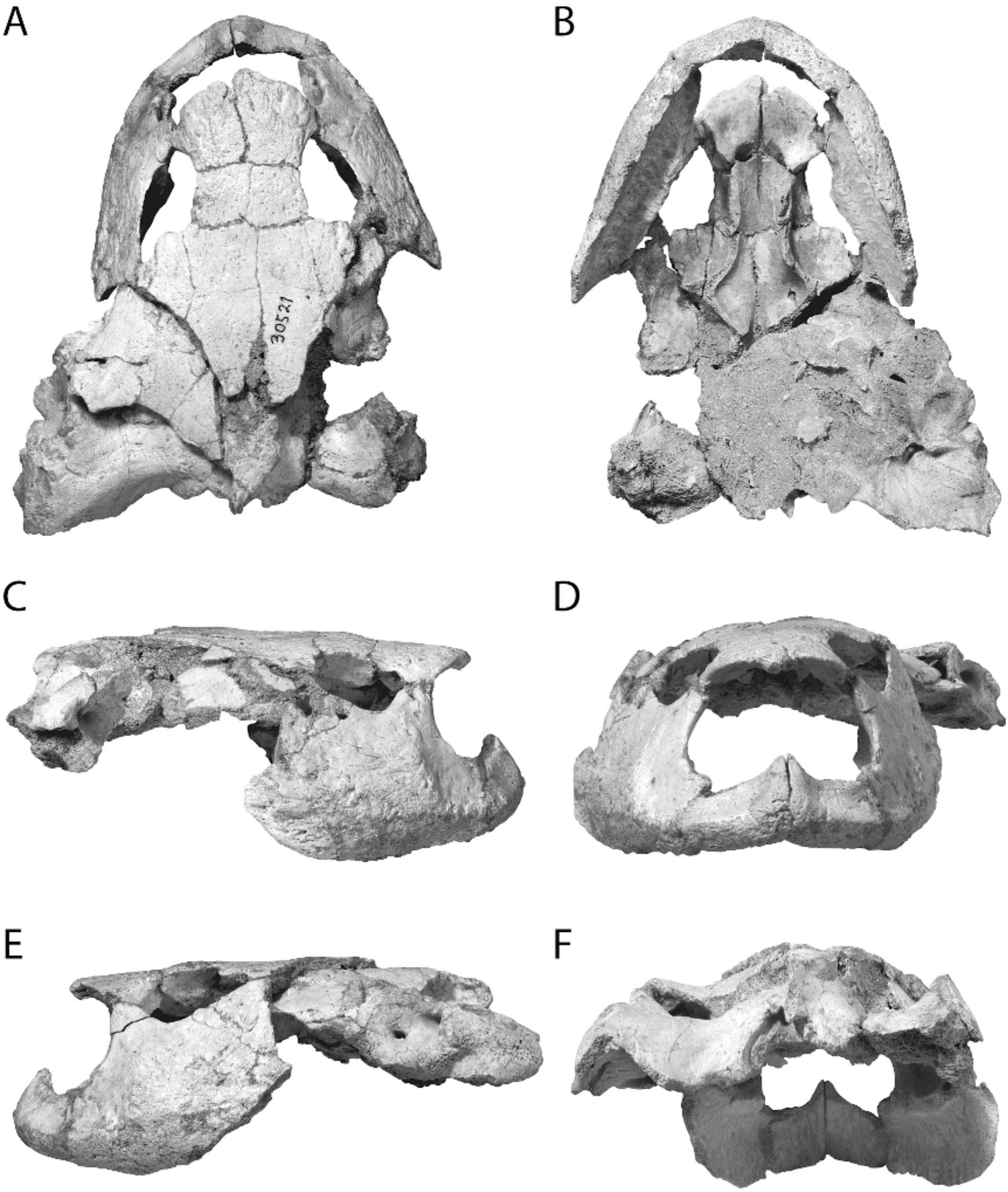

Fig. 209. *Rhothonemys brinkmani*, n. gen. et sp. AMNH 30521 holotype. **A**, dorsal; **B**, ventral; **C**, right lateral; **D**, anterior; **E**, left lateral; **F**, posterior. [C. Blik, del.]

sulcus olfactorius from the fossa nasalis is about the same size as in other bothremydids, such as *Galianemys*. The sulcus in *Phosphatochelys* seems to be formed by the parietal rather than the frontal.

PARIETAL (figs. 208–211)

Preservation: Both parietals are present in AMNH 30521, but they are incomplete ventrally, posteriorly, and laterally. On the left side, the posterior temporal roof margin

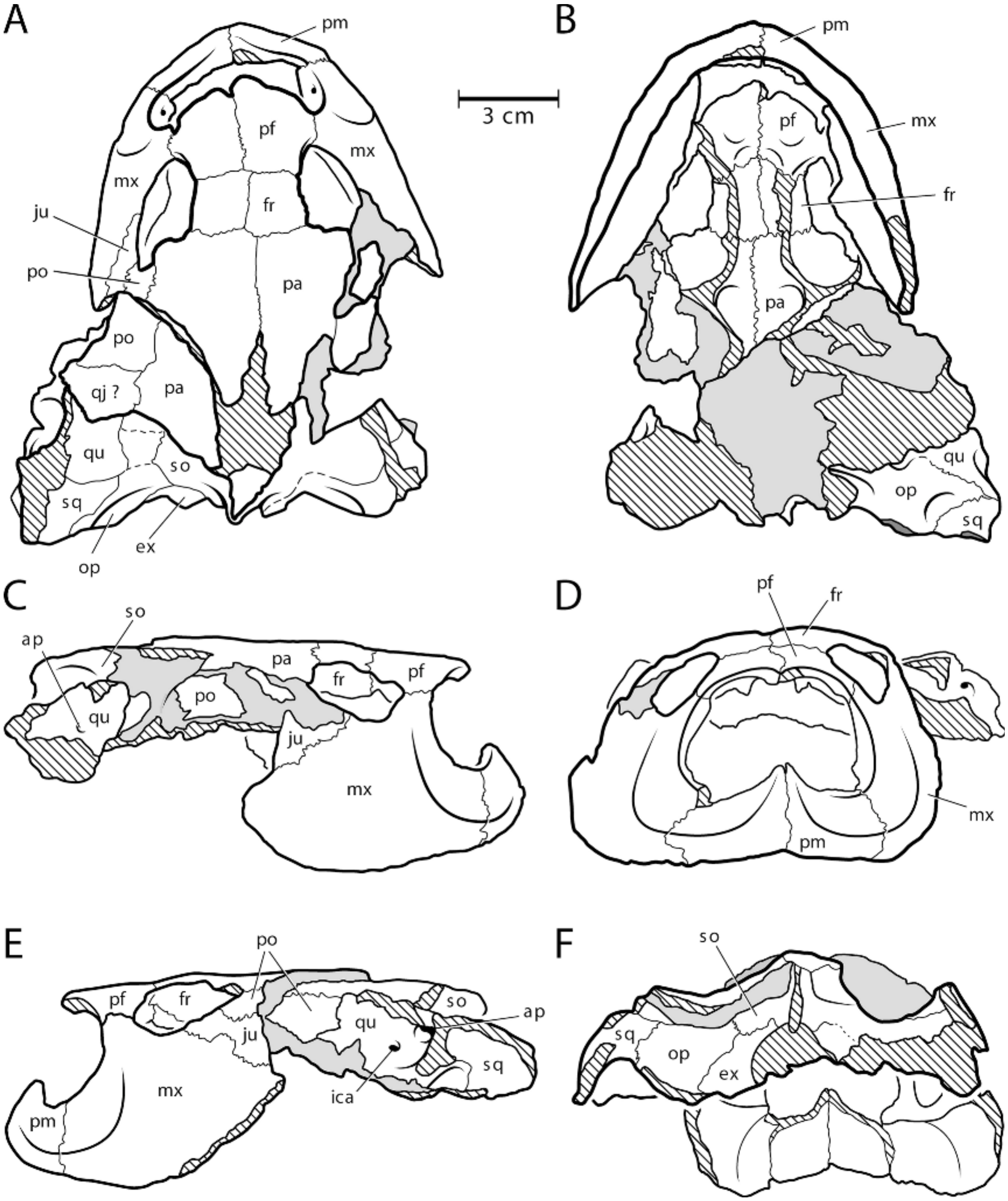

Fig. 210. *Rhothonemys brinkmani*, n. gen. et sp. AMNH 30521 holotype. **A**, dorsal; **B**, ventral; **C**, right lateral; **D**, anterior; **E**, left lateral; **F**, posterior. [C. Blik, del.]

is broken and slightly displaced, but it seems to have its natural edge posteriorly. Ventrally, only the dorsalmost part of the processus inferior parietalis is preserved. None of the actual supraoccipital contact is preserved.

Contacts of dorsal plate: The parietal in *Rhothonemys* contacts the frontal anteriorly, the other parietal medially, and the supraoccipital posteroventrally (displaced and filled with matrix). The postorbital contact is present on the left side and seems to run the length of the parietal. However, the sutures are difficult to discern and a quadratojugal suture cannot be made out, so some of this contact may be the quadratojugal.

Structures of dorsal plate: The edge of the temporal emargination is preserved partially on the left side. Although slightly displaced, the degree of emargination in *Rhothonemys* is similar in extent to that seen in *Phosphatochelys* and *Azabbaremys*, but it is less emarginate than in *Taphrosphys*.

The ventral surface of each parietal is visible in AMNH 30521 (fig. 211), and it has the ridges where the processus inferior parietalis and the fossa orbitalis form walls separating these spaces. Only the dorsal attachment ridges are present; the walls are broken off. The parietal in *Rhothonemys* is relatively farther forward in the skull roof than it is in all other Pelomedusoides except *Phosphatochelys*. This is also expressed in the exposure of the parietal in the orbital margin in *Rhothonemys* and *Phosphatochelys*. The parietal in *Rhothonemys*, *Phosphatochelys*, and *Taphrosphys* forms a pocket in the posterior part of the fossa orbitalis, posterior to the orbital margin and anterior to the septum orbitotemporale ridge (all that remains of this wall). In *Rhothonemys* this pocket (fig. 211) has its walls broken away, but it is very similar to that in *Taphrosphys sulcatus* (fig. 170C) and *T. ippolitoi* (fig. 183B).

Contacts and structures of processus inferior parietalis: The processus inferior parietalis in AMNH 30521 is largely missing, and its ventral contacts and structures cannot be determined.

JUGAL (figs. 208–211)

Preservation: Both jugals are present in AMNH 30521, but neither is complete. The left one is lacking some of its anterodorsal area, where it forms the orbital margin, and some of its medial process appears broken. The right jugal is preserved along its contact with the maxilla, but its posterodorsal area and most of its medial process are missing. The posterior margin of the right jugal is intact, but the left one is a broken surface.

Contacts of lateral plate: The anteroventral contact with the maxilla in *Rhothonemys* runs from the posteroventral orbital margin to the edge of the narrow cheek emargination as in *Phosphatochelys*. The posterior edge of the jugal is exposed on the cheek emargination ventrally, but dorsally its contacts are broken in AMNH 30521. Dorsally, the jugal contacts the postorbital, and although broken, this can be seen on the left side. Posterodorsally, it is likely that the jugal contacts the quadrate and/or the quadratojugal, but this cannot be determined due to crushing and missing bone in this area.

Structures of lateral plate: The fossa orbitalis in *Rhothonemys* forms a large pocket ventral to the orbital margin (fig. 211). This pocket is also found in *Phosphatochelys* and *Taphrosphys* but not, as far as can be seen in the flattened specimens, *Labrostochelys*. In *Rhothonemys* the jugal forms the posterior half of the suborbital pocket; the maxilla forms the anterior half. The jugal in *Rhothonemys* and *Phosphatochelys* is relatively deep dorsoventrally, in contrast to the much shallower jugal in *Taphrosphys* and *Labrostochelys*. The suborbital pocket in *Rhothonemys* is deeper than in *Phosphatochelys*. These pockets are more accurately considered to be one feature, an expanded fossa orbitalis formed by multiple bones (jugal, postorbital, parietal, maxilla), although it is convenient to describe and label the particular areas as separate. In the character descriptions, the fossa orbitalis enlargement is considered one character, character 27.

The posterior margin of the jugal in *Rhothonemys* seems to be a free edge, ending in an acute ridge, not a sutural margin. This is very similar to the jugal in *Phosphatochelys*, which also has a free posterior margin. In *Rhothonemys* the dorsal and posterior elements of this cheek emargination are not known due to crushing and bone loss, but there does not seem to be room for a large quadratojugal or a large cheek emargination. The free edge on the jugal runs dorsally almost to the postorbital contact.

Contacts of medial process: Both jugals in *Rhothonemys* have no preserved contacts medially. The left jugal has a sutural surface on the medial edge of the medial process. This is presumably for the pterygoid and palatine contacts. The medial process does

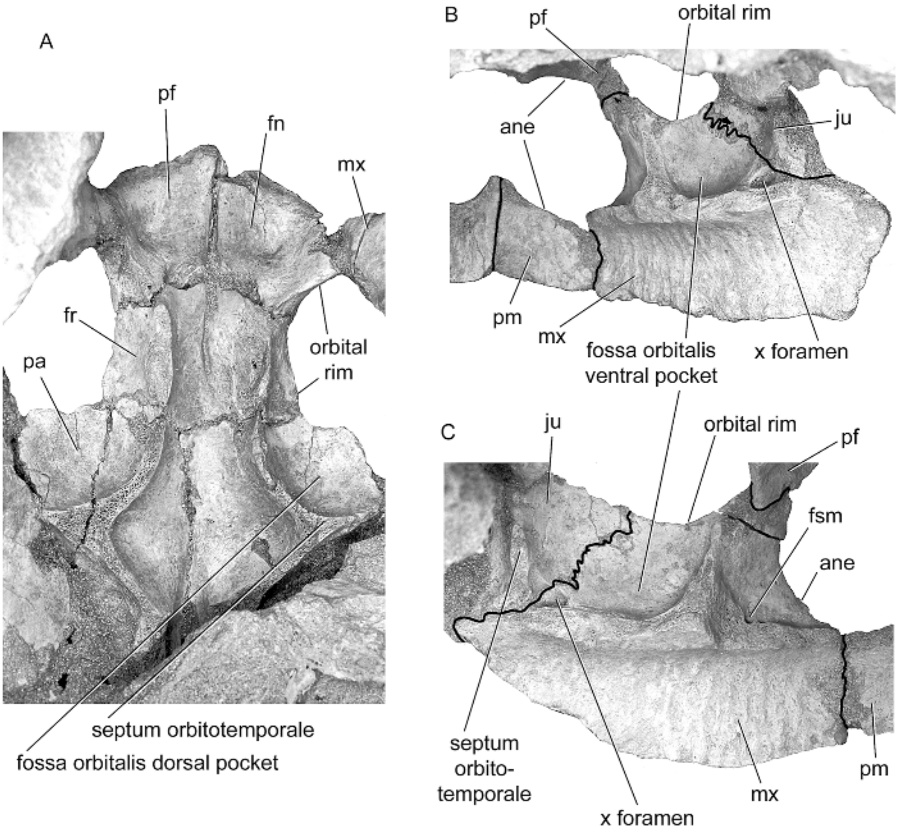

Fig. 211. *Rhothonemys brinkmani*, n. gen. et sp. AMNH 30521 holotype. Internal views of skull showing fossa orbitalis and associated structures. **A**, ventral view of skull roof, anterior to top of page; **B**, anteromedial view of right fossa orbitalis; **C**, medial view of right fossa orbitalis, anterior to right. See text for "x foramen". [E.S. Gaffney, del.]

not really have a horizontal contact with the maxilla as in other Pelomedusoides; only the lateral plate of the jugal does. The lateral plate contacts the postorbital dorsally, but the medial jugal process is present only ventrally, so the postorbital does not participate in the reduced septum orbitotemporale. This condition also occurs in *Phosphatochelys* and *Azabbaremys* (the latter entirely lacks the septum orbitotemporale).

Structures of medial process: The jugal medial process in *Rhothonemys* is well developed ventrally, but incomplete more dorsally, so that the upper half of the septum orbitotemporale is largely absent, in contrast to bothremydids outside the Taphrosphyini. The medial process of the jugal is even smaller in *Phosphatochelys* and *Azabbaremys*. It is present but poorly preserved in *Taphrosphys* and *Labrostochelys*. The fossa orbitalis in *Rhothonemys* has a deep ventral pocket that is defined posteroventrally by the medial jugal process, but posterodorsally it is likely that the fossa is open. Nonetheless, the medial process in *Rhothonemys* is higher and extends farther medially than it does in *Phosphatochelys*.

QUADRATOJUGAL (figs. 208–210)

Preservation: The position and identification of the quadratojugal in AMNH 30521 is problematic. The posterolateral part of the skull roof is mostly missing on the right side and is cracked and poorly preserved on the left. The best guess for the quadratojugal is a plate of bone on the left side lying lateral to the parietal on the posterior margin of the temporal roof. The medial margin is a suture with the parietal; the lateral margin is a broken edge connecting to the quadrate. The anterior margin is a large crack, with no clear sign of a sutural contact. If *Rhothonemys* is similar to *Phosphatochelys*, then this plate of bone is in the same place as the quadratojugal in *Phosphatochelys*. However, if *Rhothonemys* is like *Azabbaremys*, the plate of bone is the posterior continuation of the postorbital and the quadratojugal is a small element, largely lost in the crushed and broken area lateral to the postorbital. However, careful examination of this area does not show any sutural edges either, and there does not seem to be enough bone missing to make up a complete quadratojugal, hence the identifications in figure 210 and the restoration in figure 208. It is still just a guess, though.

Contacts and structures: If this plate of bone is the quadratojugal, it is similar in contacts to those in *Phosphatochelys* and *Taphrosphys*, contacting the parietal medially, the postorbital anteriorly, and the quadrate laterally. The quadratojugal forms the lateral part of the temporal margin.

SQUAMOSAL (figs. 208–210)

Preservation: Most of the left squamosal and a small portion of the right squamosal are present in AMNH 30521. The left squamosal lacks its dorsal and posterior margins. Only the part of the right squamosal immediately posterior to the quadrate is preserved, and this is broken by crushing.

Contacts: The squamosal in *Rhothonemys* contacts the quadrate anteriorly and anteromedially and the opisthotic medially. A possible anterodorsal contact with the quadratojugal is indeterminate due to missing bone.

Structures: The squamosal forms the cone-shaped outer bone for the antrum postoticum. In *Rhothonemys* the antrum is "moderate", similar in size to *Phosphatochelys* and *Taphrosphys*, larger than in *Labrostochelys*, and not absent, as in *Azabbaremys*. The posterior limit of the squamosal is a broken edge on both sides, but it does not seem to be trending into a very elongated shape like that in *Labrostochelys*. There is a well-developed vertical flange on the ventral surface of the squamosal, as in *Phosphatochelys*, *Labrostochelys*, and *Taphrosphys*. The lateral tubercle also seen in these three genera is not determinable in *Rhothonemys*, as the anterolateral part of the squamosal is broken off.

POSTORBITAL (figs. 208–210)

Preservation: The area of the skull roof in AMNH 30521 posterior to the orbits is poorly preserved on both sides. On the right side only broken pieces of bone in the matrix are present that seem to be postorbital fragments, and no sutures are visible. On the left side, the anterodorsal and anteroventral areas of the postorbital are preserved and defined by sutures, but they are separated from each other by matrix. Posteriorly the postorbital is not clearly defined by sutures except medially, where it lies along the parietal. Most of its lateral edge is a broken margin. Posteriorly, a crack separates the postorbital from what may be the quadratojugal (see Quadratojugal) or a continuation of the postorbital. Either interpretation is possible, although the former is slightly more likely.

Contacts of lateral plate: The postorbital in *Rhothonemys* contacts the parietal medially for its entire length and the jugal anterolaterally. Posteriorly it may contact the quadratojugal (see Quadratojugal). The postorbital lateral contacts are dubious, but it is probable that there was a quadrate contact, as in *Phosphatochelys*.

Structures of lateral plate: The postorbital in *Rhothonemys* forms that posterodorsal margin of the orbit. If the quadratojugal is present behind the postorbital, then the postorbital does not reach the temporal margin. If there is no suture, however, then the postorbital extends posteriorly to the temporal margin, as in *Azabbaremys*.

Contacts and structures of medial process: The postorbital in AMNH 30521 is not well enough preserved to determine all the features of the medial process. The ventral portion of the internal postorbital surface is preserved on the left side, and it shows that the medial process is absent; there is no medial contact with another bone. The septum orbitotemporale is small or absent.

PREMAXILLA (figs. 208–211)

Preservation: The premaxilla in AMNH 30521 is present on both sides, but both lack the posterior projection.

Contacts: The premaxilla in *Rhothonemys* contacts the maxilla posterolaterally and the other premaxilla medially. A posterior contact with a vomer is indeterminate.

Structures on dorsal surface: The premaxilla in *Rhothonemys* forms the ventral margin of the very large apertura narium externa. On the midline there is a dorsal projection of both premaxillae that forms a midline separation of the apertura. This internarial process has a broken dorsal margin on both sides, but the broken area seems too small to support a complete internarial bar, particularly on the left side. It is likely that the apertura narium externa in *Rhothonemys* was not divided on the midline.

On the anterior surface of the premaxilla, the bone slopes dorsally into the apertura narium externa, very similar to *Phosphatochelys*. This condition also occurs on the maxilla of *Rhothonemys* (see Maxilla), but it is not so apparent on the *Phosphatochelys* maxilla.

Structures on ventral surface: The labial ridge on the premaxilla in *Rhothonemys* is thick in comparison to most other Taphrosphyini (e.g., *Phosphatochelys*), but it is not as thick as in *Azabbaremys*. The actual edge of the labial ridge, however, is acute, not blunt. The internal surface of the premaxilla in *Rhothonemys* is nearly vertical but slightly concave. This concave surface continues the concave surface on the maxilla. The external surface of the labial ridge is convex, curving anterodorsally to meet the low, horizontal ridge that marks the beginning of the indented surface surrounding the apertura narium externa. The medial horizontal process of the premaxilla in *Rhothonemys* is missing.

MAXILLA (figs. 208–211)

Preservation: Both maxillae are present in AMNH 30521, but both lack most of their horizontal plate.

Contacts of vertical plate: The vertical plate of the maxilla in *Rhothonemys* contacts the premaxilla anteromedially, the jugal posterodorsally, and the prefrontal anterodorsally. The posterior margin of the maxilla below the jugal is a free edge, so there is no quadratojugal or quadrate contact.

Structures of vertical plate: The orbital margin in *Rhothonemys* is an acute ridge, well dorsal to the floor of the fossa orbitalis, in contrast to the low, blunt orbit of forms like *Bothremys cooki*. The orbit is placed high on the cheek in *Rhothonemys*, so that the maxilla is unusually deep, deeper than in any other bothremydid, although *Phosphatochelys* and *Azabbaremys* approach this condition. The maxilla in *Rhothonemys* is relatively large and forms a greater part of the cheek than in any other bothremydid.

The maxilla forms the lateral margin of the apertura narium externa. This margin in *Rhothonemys* is very high and the apertura is very large, relatively larger than in any other bothremydid. The maxilla bears a slightly recessed area around the margin of the apertura narium externa, as on the premaxilla. There is a similar, indistinct recessed area around the apertura in *Phosphatochelys*, but not in other bothremydids. It is possible that this is the attachment area for a large proboscis, showing that *Rhothonemys* is really an elephant. The fossa nasalis is not completely preserved in *Rhothonemys*, but the internal surface of the maxilla shows the approximate extent. As expected from the larger apertura, the fossa nasalis is also large, although not significantly larger than in some other Taphrosphyini.

Contacts and structures of horizontal plate: Most of the horizontal or medial plate of the maxilla in AMNH 30521 is missing, but its lateral position on the vertical plate and some structures are preserved. The contacts are not preserved.

The labial ridge, actually formed more by the horizontal plate, is an acutely edged ridge that becomes thick dorsally and is slightly concave on its medial surface. The labial ridge in *Rhothonemys* is unique in shape among bothremydids; it is thicker than in *Phosphatochelys, Labrostochelys*, and *Taphrosphys* and has a different cross section than in *Arenila* and *Nigeremys*. The cross section with a broadly curved outer surface and a concave inner surface is not found in other pleurodires. The maxilla and premaxilla labial ridge morphologies are the same.

Although most of the lingual ridge is missing in AMNH 30521, a small portion is preserved on both sides. This shows a very low lingual ridge and a narrow triturating surface, broadly curved from labial to lingual ridge, similar to *Labrostochelys*. The surface, however, has a series of very low, dorsoventral ridges. The narrow triturating surface of the maxilla is consistent with the narrow lower jaw associated with the skull of AMNH 30521.

The fossa orbitalis in *Rhothonemys* (fig. 211) has a large pocket formed anterior and ventral to the orbital margin. This pocket, although smaller, also occurs in *Phosphatochelys* and *Taphrosphys*. Combined with the posterodorsal parietal pocket, the result is an unusually large fossa orbitalis in *Rhothonemys*, even larger than that in *Chedighaii*. At the posteroventral corner of the fossa orbitalis, just anterior to the jugal suture, is a large foramen leading into a canal in the maxilla. This seems to be the foramen supramaxillare, or at least the foramen identified as this in Gaffney (1979a: fig. 54).

VOMER AND PALATINE

Preservation: The vomer and the palatine are not preserved in AMNH 30521.

QUADRATE (figs. 208–210)

Preservation: Parts of both quadrates are present in AMNH 30521, but both are incomplete. The right quadrate has only the antrum postoticum portion of the cavum tympani present. The left quadrate has all of the central part of the cavum tympani, incisura columellae auris, antrum postoticum, and sulcus eustachii, but none of its margins. All of its dorsal surface is preserved, but only part of the ventral surface, and the entire processus articularis is missing.

Contacts on lateral surface: At least anterodorsally, the quadrate contacts the postorbital and the squamosal posterodorsally. Poor preservation makes the position of the quadratojugal unclear, but it is likely that the quadrate contacts it dorsally, as in *Phosphatochelys*. Because the maxilla ends posteriorly in a free edge, there is no quadrate-maxilla contact. The ventral part of the jugal is also a free edge, but there may have been a quadrate contact above it, as in *Phosphatochelys*.

Structures on lateral surface: The dorsal edge of the quadrate is a broken margin, and it looks as if the quadrate were not exposed on the temporal margin, but this is unclear.

The cavum tympani shows a centrally located incisura columellae auris that is a foramen leading medially into the canal typical of bothremydids. The sulcus eustachii is an indentation or groove in the posteroventral margin of the cavum tympani, as in *Phosphatochelys* and *Azabbaremys* and other Taphrosphyini. The antrum postoticum of *Rhothonemys* is similar in size to that in *Phosphatochelys* and *Taphrosphys*, not very small, as in *Labrostochelys*, or absent, as in *Azabbaremys*. The edges of the sulcus eustachii are damaged, but it looks as if the ventral process, as found in *Phosphatochelys*, *Labrostochelys*, and *Taphrosphys*, was present.

Contacts on dorsal and anterior surfaces: The quadrate contacts in AMNH 30521 are not entirely clear due to poor preservation and possible fusion. The quadrate contacts the opisthotic posteromedially and the squamosal posterolaterally. The area of the prootic is damaged (only the left side preserves this area), but it looks as if there is no quadrate-supraoccipital contact and that the prootic contacts the opisthotic. This would be consistent with other Taphrosphyini. The anterior surface of the quadrate is missing ventrally and is partially covered by matrix.

Structures on dorsal and anterior surfaces: The foramen stapedio-temporale and the foramen nervi trigemini in *Rhothonemys* are below the broken edge and are missing.

Contacts and structures on ventral surface: This area, containing the foramen posterius canalis carotici interni and condylus mandibularis as well as pterygoid, basisphenoid, and basioccipital contacts, is missing. The broken surface through this area is poorly preserved.

Contacts on posterior surface: The quadrate contacts the opisthotic dorsomedially, the exoccipital medially, and the squamosal dorsolaterally, but other contacts are not preserved.

Structures on posterior surface: AMNH 30521 is broken off below the level of the fenestra postotica. However, the quadrate makes up the lateral half of that foramen; it is not subdivided for the stapedial artery and lateral head vein. Lateral to the fenestra postotica is a posteroventrally facing concavity that seems to have contained a bend in the lateral head vein in *Rhothonemys*. This concavity is not seen in *Phosphatochelys* or other Taphrosphyini.

PTERYGOID

Preservation: It is likely that some of the pterygoid in AMNH 30521 is present in the broken surface of the otic chamber, but no sutures or structures can be made out.

SUPRAOCCIPITAL (figs. 208–210)

Preservation: Most of the supraoccipital in AMNH 30521 is probably present, but it is crushed and poorly preserved. The crista supraoccipitalis is preserved only at its base.

Contacts: The supraoccipital in *Rhothonemys* contacts the parietal anterodorsally. It seems to be exposed on the skull roof just behind the parietals. The supraoccipital contacts the exoccipitals posteroventrally and the opisthotics posterolaterally. Although not definite, the supraoccipital seems to contact the prootic anterolaterally with no quadrate contact.

Structures: The base of the crista supraoccipitalis in *Rhothonemys*, even though crushed, shows a plate that is lower in height than the one in *Phosphatochelys*. The foramen magnum is present but crushed, obscuring its shape.

EXOCCIPITAL (figs. 208–210)

Preservation: The dorsal part of the left exoccipital and pieces of the right one are preserved in AMNH 30521.

Contacts: The exoccipital in *Rhothonemys* contacts the supraoccipital dorsally and the opisthotic laterally. The other contacts are missing.

Structures: The left exoccipital in *Rhothonemys* preserves some of the foramen magnum margin and the dorsal half of the foramen jugulare posterius. The foramen is closed laterally and separated by bone from the fenestra postotica. The condylus occipitalis is missing.

BASIOCCIPITAL

Preservation: None of the basioccipital is preserved in AMNH 30521.

PROOTIC (fig. 210)

Preservation: The left prootic is present in AMNH 30521, but sutures defining it are questionable due to poor preservation and crushing in this area.

Contacts and structures: The prootic in *Rhothonemys* contacts the quadrate laterally and the supraoccipital posterodorsally, but the opisthotic contact is questionable. The ventral half is missing. The foramen stapedio-temporale, foramen nervi trigemini, and other structures are not preserved.

OPISTHOTIC (figs. 208–210)

Preservation: The left opisthotic in AMNH 30521 is present and only missing some of its posterior margin. The right one is preserved dorsally but broken posteriorly and ventrally.

Contacts: The opisthotic in *Rhothonemys* contacts the supraoccipital anteromedially, the quadrate anterolaterally, the squamosal posterolaterally, and the exoccipital posteromedially. There is probably an anterior contact with the prootic.

Structures: The opisthotic in *Rhothonemys* forms much of the roof of the fenestra postotica. The fenestra is not subdivided (see Quadrate). The opisthotic forms the lateral wall of the foramen jugulare posterius. There is no ventrally opening groove on the opisthotic, as in *Taphrosphys*.

BASISPHENOID

Preservation: The basisphenoid is not preserved in AMNH 30521.

Azabbaremys moragjonesi

The single skull that represents this species is a large, well-preserved, uncrushed specimen that shows internal morphology. It was described by Gaffney, Moody, and Walker (2001), which is modified and expanded here. *Azabbaremys* is the sister taxon to an undescribed skull, CNRST SUNY 199, and in turn they are sister taxa to the remaining Taphrosphyina, with *Nigeremys* and *Arenila* outside this group.

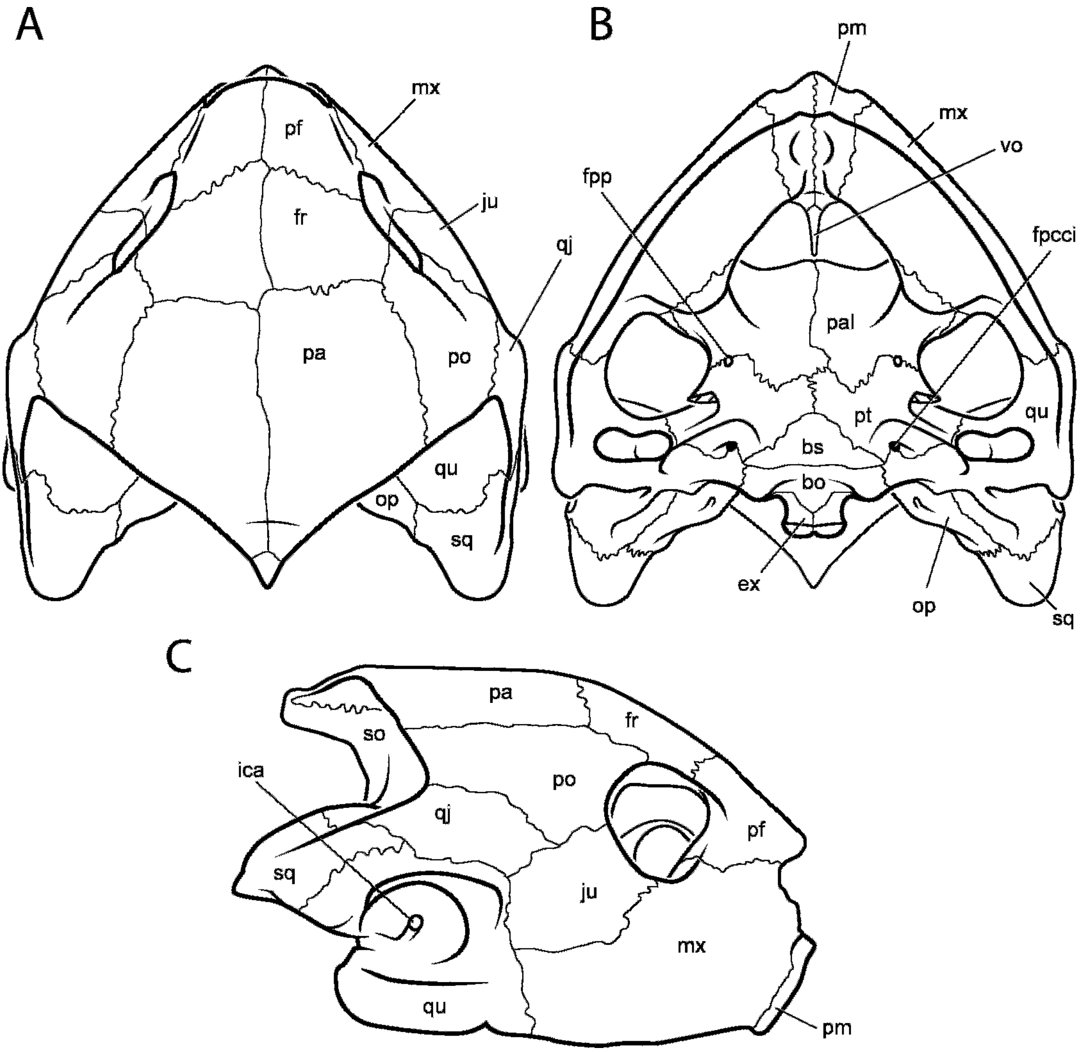

Fig. 212. *Azabbaremys moragjonesi* Gaffney, Moody, and Walker, 2001. BMNH R16370 holotype. Partially restored views of skull. **A**, dorsal; **B**, ventral; **C**, lateral. [F. Ippolito, del.]

Prefrontal (figs. 212, 215, 280A)

Preservation: Both prefrontals in BMNH R16370 are present and complete. The sutures are clearly defined and the dorsal and ventral surfaces are visible.

Contacts: The prefrontal in *Azabbaremys* contacts the maxilla anteroventrolaterally, the frontal posteriorly, and the other prefrontal medially.

Structures: The prefrontal in *Azabbaremys* is a relatively large element, forming most of the preorbital part of the skull in dorsal view. In contrast to the small prefrontals of pelomedusids and *Araripemys*, *Azabbaremys* and most bothremydids have a broad preorbital area and a large prefrontal. The dorsal surface is convex, forming most of the distinctive dorsal protuberance of the nose found in *Azabbaremys*. The ventral surface is broadly concave, without a distinctly defined sulcus olfactorius.

The prefrontal of *Azabbaremys* forms the anterior margin of the fossa orbitalis, as in other Pelomedusoides; however, in *Azabbaremys* the prefrontal has a well-developed posteroventral portion that occupies the area

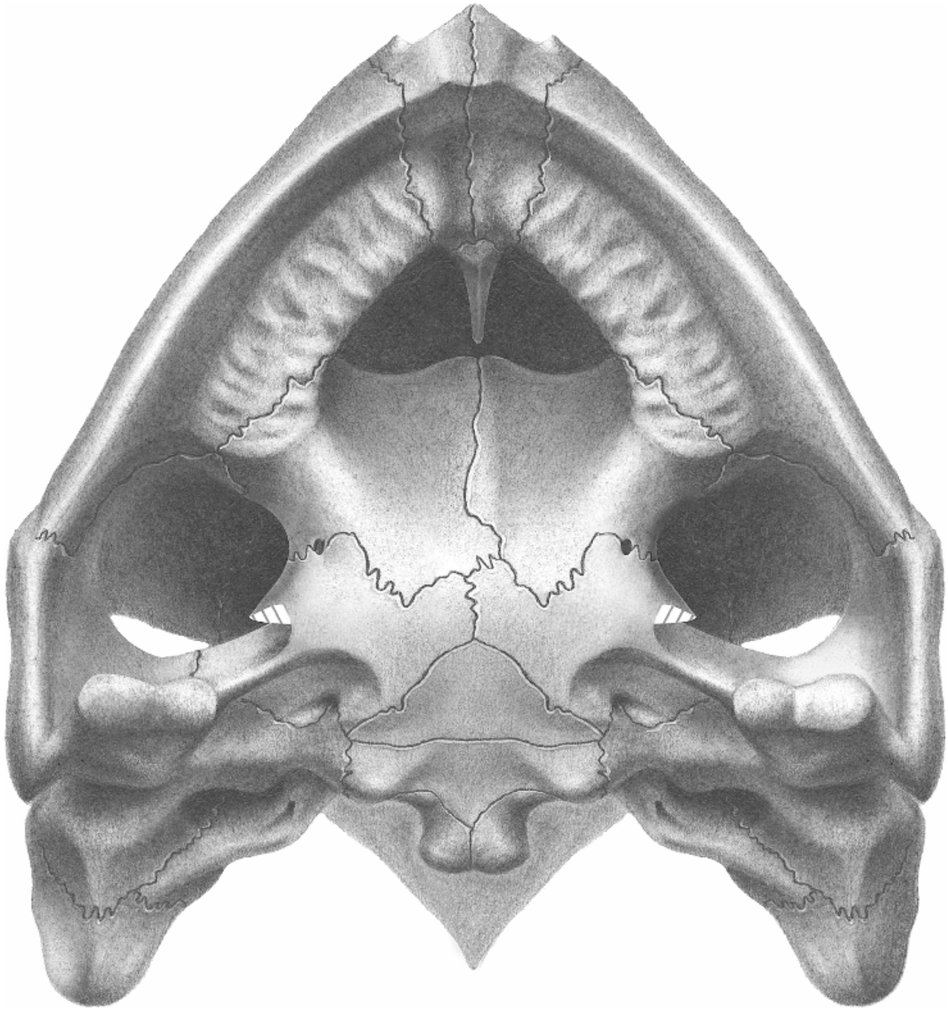

Fig. 213. *Azabbaremys moragjonesi* Gaffney, Moody, and Walker, 2001. BMNH R16370 holotype. Partially restored view of skull (modified after Gaffney, Moody, and Walker, 2001). [U. Kikutani, del.]

formed by the maxilla in other Pelomedusoides. This part of the prefrontal is comparable in extent to *Taphrosphys* and possibly *Arenila*, although the sutures are ambiguous in the latter. Ventrally the prefrontal contacts the maxilla in a nearly horizontal suture at the level of the ventral margin of the orbit. The anterior margin of the prefrontal forms the dorsal margin of the apertura narium externa, which is protuberant in *Azabbaremys* so that the dorsal margin overhangs the apertura, much as in *Taphrosphys*. The protuberance is broad, extending the entire width of the apertura.

FRONTAL (figs. 212, 215)

Preservation: Both frontals in BMNH R16370 are present and complete. The sutures are clearly defined and the dorsal and ventral surfaces are visible.

Contacts: The frontal in *Azabbaremys* contacts the prefrontal anteriorly, the other frontal medially, the parietal posteriorly, and the postorbital posterolaterally. It forms the dorsal margin of the fossa orbitalis between the prefrontal and postorbital contacts.

Structures: The dorsal surface of the frontal in *Azabbaremys* is broadly convex, continuing the convexity formed by the prefrontal.

On the ventral surface the frontal forms a deep and well-developed sulcus olfactorius. The parasagittal ridge is low anteriorly, beginning as a continuation of the prefrontal ridge that divides the fossa orbitalis from the fossa nasalis. The sulcus olfactorius ridge deepens posteriorly as it merges into the processus inferior parietalis. The orbits of *Azabbaremys* are widely separated and the margins are almost vertical, a strong contrast to other bothremydids such as *Bothremys* and *Rosasia*, which have orbits that face primarily dorsally. *Nigeremys* and *Arenila* have orbits with a more lateral orientation, but they do not approach the *Azabbaremys* condition.

PARIETAL (figs. 212, 215, 217)

Preservation: Both parietals in BMNH R16370 are present and complete. Sutures are clear on the dorsal surface. The right parietal is visible ventrally, but the left one has matrix on its ventral surface.

Contacts of dorsal plate: The dorsal plate of the parietal in *Azabbaremys* contacts the frontal anteriorly, the other parietal medially, and the postorbital laterally.

Structures of dorsal plate: The posterior edge of the parietal in *Azabbaremys* forms part of the anterior margin of the temporal emargination. The margin is a nearly straightedge trending anterolaterally along the parietal and continuing onto the postorbital. The temporal roof in *Azabbaremys* is relatively extensive, with most of the otic chamber being covered in dorsal view. In comparison to other bothremydids, the roof in *Azabbaremys* is more extensive, although *Nigeremys* approaches it. Nonetheless, the size and shape of the parietal itself are quite similar in *Azabbaremys* and *Taphrosphys*.

Contacts of processus inferior parietalis: Posteriorly the parietal in *Azabbaremys* lies above the supraoccipital, as in other turtles. The prootic contacts the parietal from midway along the supraoccipital suture and extends anteroventrally to the foramen nervi trigemini. In *Azabbaremys* the foramen nervi trigemini is preserved but damaged on both sides. As preserved, the parietal narrowly enters the foramen margin dorsally. The pterygoid forms nearly all of the anterior and ventral margins, with the prootic forming the posterior margin. The complete extent of the foramen is not known posteriorly due to damage.

Structure of processus inferior parietalis: The processus inferior parietalis in *Azabbaremys* is present on both sides, with medial and lateral surfaces being visible. It is unusually narrow, in strong contrast to pelomedusids, podocnemidids, and most bothremydids, but in common with *Taphrosphys*. The condition in *Arenila* and *Nigeremys* is indeterminate. The parietal extends ventrally, forming the processus inferior parietalis, and meets the crista pterygoidea of the pterygoid in a suture that drops anteroventrally from the foramen nervi trigemini to the edge of the processus inferior parietalis (fig. 217). The anterior margin of the processus forms the posterior margin of the foramen interorbitale. As a consequence of the high, arched palate, the deep sulcus olfactorius, and the short snout, the foramen interorbitale is relatively small in *Azabbaremys*.

JUGAL (figs. 212, 215, 280A)

Preservation: Both jugals in BMNH R16370 are present and complete. The sutures are clearly defined and the internal and external surfaces are visible except for a small area on the inside of the left jugal.

Contacts of lateral plate: The external or vertical plate of the jugal in *Azabbaremys* contacts the postorbital dorsally, the quadratojugal posterodorsally, the quadrate posteriorly, and the maxilla ventrally. The quadrate contact is found throughout the Taphrosphyini.

Structures of lateral plate: The jugal forms the posteroventral margin of the orbit in *Azabbaremys*. It is exposed to a greater extent than the jugal in *Nigeremys* and *Arenila* (Lapparent de Broin and Werner, 1998).

Contacts of medial process: The medial process of the jugal in *Azabbaremys* forms part of the septum orbitotemporale and contacts the palatine medially and the maxilla ventrally.

Structures of medial process: As in other Taphrosphyini, the jugal does not extend onto the triturating surface in *Azabbaremys*. The jugal forms part of the floor of the fossa orbitalis, contacting the maxilla anteriorly and the palatine medially (fig. 280A).

QUADRATOJUGAL (figs. 212, 215)

Preservation: Both quadratojugals are present and complete in BMNH R16370, but both have some damage due to cracking, and the sutures are not all clear.

Contacts: The quadratojugal of *Azabbaremys* contacts the postorbital dorsomedially, the jugal anteroventrally, the squamosal posteriorly, and the quadrate ventrally. In both *Phosphatochelys* and *Taphrosphys* the quadratojugal has a parietal contact, absent in *Azabbaremys*.

Structures: In the Bothremydini and Cearachelyini the quadratojugal is a large element extending from the ventral margin of the cheek to the temporal emargination on the skull roof. In *Azabbaremys* and other Taphrosphyini the quadratojugal is smaller and retracted dorsally above the quadrate, not exposed on the cheek edge, but it still enters the edge of the temporal emargination. *Rosasia* also has a retracted quadratojugal with no exposure on the cheek edge. The ventral edge of the quadratojugal in *Azabbaremys* contacts the quadrate. Just dorsal to this suture the edge of the concave cavum tympani extends up onto the quadratojugal. It is unusual in turtles to have the quadratojugal form a significant portion of the cavum tympani, and this does not occur in any other pleurodire.

SQUAMOSAL (figs. 212, 215, 218, 281, 286A)

Preservation: Both squamosals are preserved in BMNH R16370, but they are missing parts of their posterolateral margins. The right squamosal is more complete posteriorly, but it has breakage on its anterolateral process.

Contacts: The squamosal in *Azabbaremys* is the usual cone-shaped (but apparently not hollow) element sitting on the posterolateral corner of the quadrate, as in most turtles. It contacts the opisthotic medially on the dorsal, posterior, and ventral surfaces. A short process of the squamosal contacts the quadratojugal along the lateral edge of the temporal emargination. All of these contacts are as in pelomedusids, podocnemidids, and other bothremydids.

Structures: The squamosal in *Azabbaremys* is cone-shaped and relatively smooth, not flat, as in *Pelusios*. *Azabbaremys* lacks the ventral, parasagittal flange or process of the squamosal characteristic of *Taphrosphys*. The antrum postoticum is absent in *Azabbaremys*, and there is no depression on the cavum tympani (figs. 281, 286A). The squamosal is presumably solid, not hollow, as in other turtles.

POSTORBITAL (figs. 212, 215)

Preservation: Both postorbitals in BMNH R16370 are present and complete. The sutures are clearly defined and the internal surface is visible on the right side.

Contacts of lateral plate: The postorbital in *Azabbaremys* is a large, quadrangular element contacting the frontal anteromedially, the parietal posteromedially, the jugal anterolaterally, and the quadratojugal posterolaterally.

Structures of lateral plate: The postorbital forms the posterior margin of the orbit and the anterior edge of the temporal emargination. In the other Taphrosphyini in which the postorbital is completely known (*Phosphatochelys*, *Taphrosphys*, *Labrostochelys*), the postorbital is shorter and does not reach the temporal margin.

Contacts and structures of medial process: In most Pelomedusoides, the postorbital has a medial process that contacts the jugal and palatine to form the septum orbitotemporale, which is particularly large in the Bothremydini. In *Azabbaremys* this wall is absent, and the medial and ventral surfaces of the postorbital are smooth. An absent or reduced septum orbitotemporale is also seen in *Taphrosphys, Phosphatochelys*, and *Rhothonemys*, but not in *Arenila* and *Nigeremys*.

PREMAXILLA (figs. 212–216)

Preservation: Both premaxillae are preserved in BMNH R16370, being complete and visible on all surfaces.

Contacts: The premaxilla in *Azabbaremys* contacts the maxilla posterolaterally, the vomer posteriorly, and the other premaxilla medially, as in the other Taphrosphyini.

Structures on dorsal surface: The dorsal surface of the premaxilla in *Azabbaremys* forms the ventral margin of the apertura narium externa and the floor of the fossa

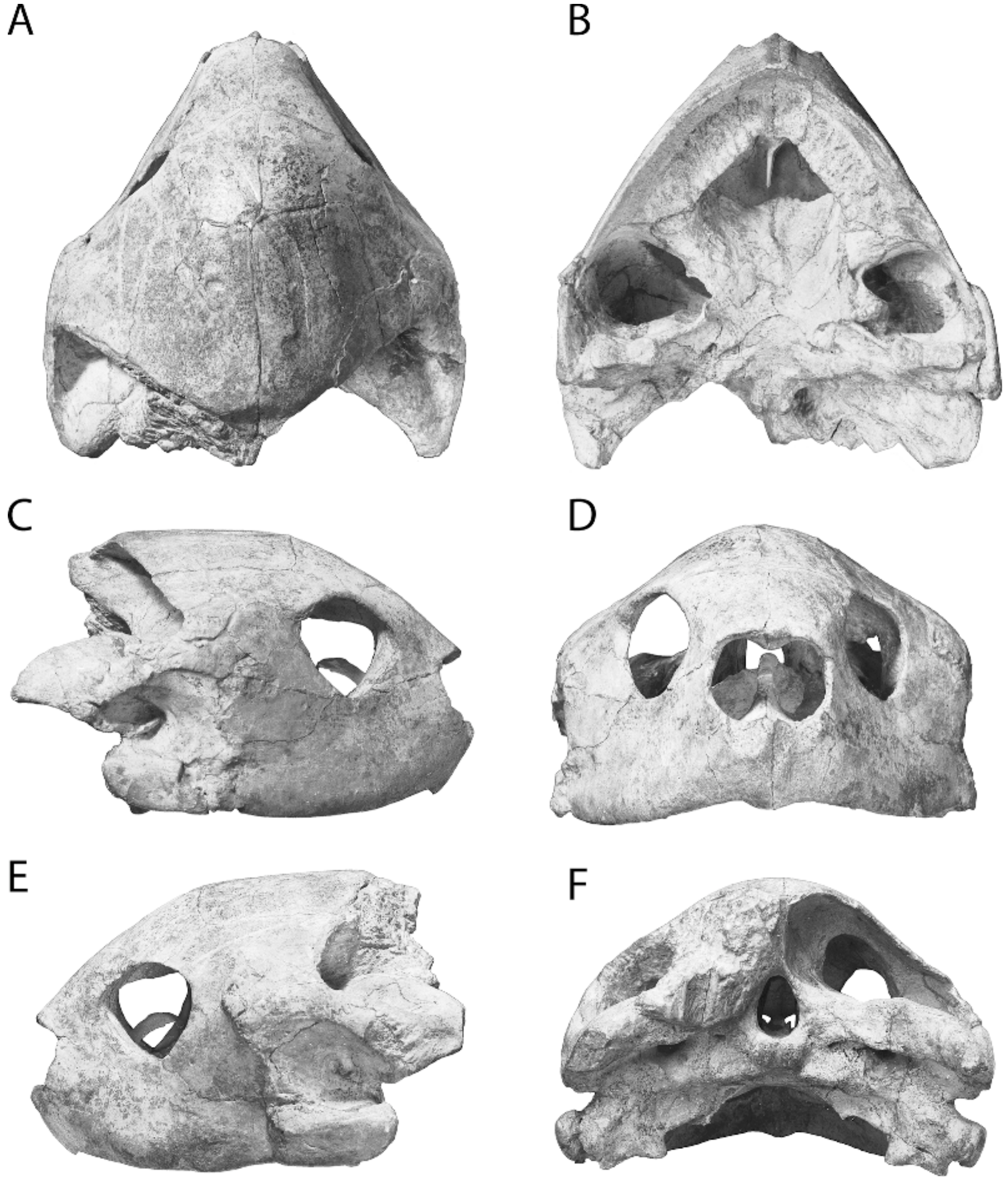

Fig. 214. *Azabbaremys moragjonesi* Gaffney, Moody, and Walker, 2001. BMNH R16370 holotype. **A**, dorsal; **B**, ventral; **C**, right lateral; **D**, anterior; **E**, left lateral; **F**, posterior (from Gaffney, Moody, and Walker, 2001). [U. Kikutani, del.]

nasalis. The apertura has paired grooves at the front that lead posteriorly into the shallow choanal channels that run posterolaterally from the fossa nasalis. Within the fossa the premaxillae on the midline are nearly flat anteriorly, but they rise dorsally very quickly to form a high, median projection dividing the choanal channels and meeting the vomer.

Structures on ventral surface: The premaxilla in *Azabbaremys* forms a deep, acute labial ridge with a median ventral process forming a short hook. On the anterior surface this hook is continuous with a low

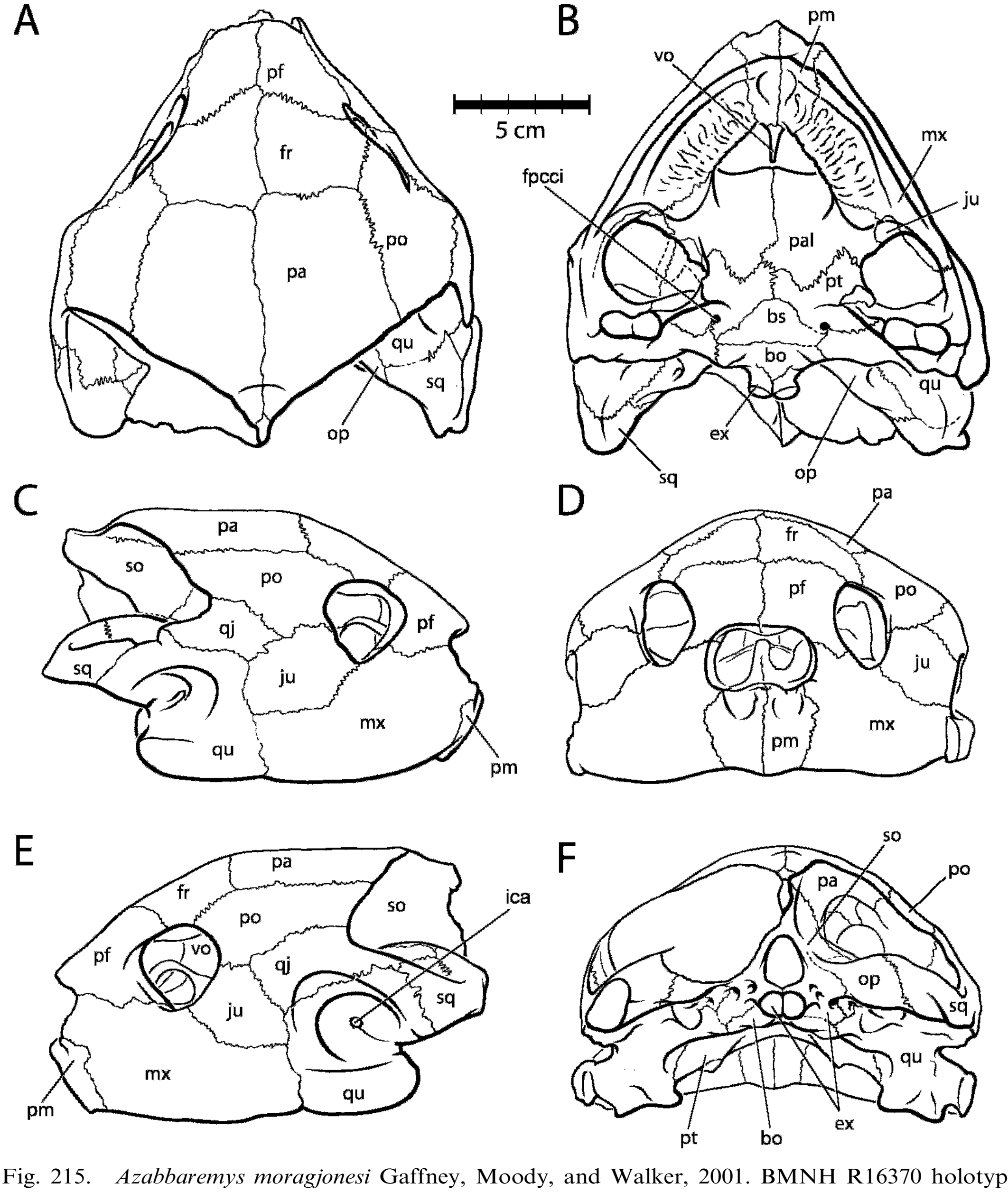

Fig. 215. *Azabbaremys moragjonesi* Gaffney, Moody, and Walker, 2001. BMNH R16370 holotype. **A**, dorsal; **B**, ventral; **C**, right lateral; **D**, anterior; **E**, left lateral; **F**, posterior (modified after Gaffney, Moody, and Walker, 2001). [U. Kikutani, del.]

ridge running on the midline dorsally to the ventral margin of the apertura narium externa. The ridge is unpaired, but at the ventral margin of the apertura, on either side of this ridge, are paired troughs that cut into the lower margin of the apertura narium externa. This premaxillary morphology is unique in turtles. The labial ridge on the premaxilla of *Azabbaremys* is relatively deep, in contrast to the shallower labial ridge in *Nigeremys*. *Nigeremys* also has a very wide and thick labial ridge with a blunt margin. In

Azabbaremys and *Taphrosphys* the ridges are much thinner and more acute. The premaxillae are missing in *Arenila*.

The premaxillae in *Azabbaremys* form a relatively deep concavity on the midline just posterior to the labial ridge. *Nigeremys* also has a midline concavity that is hemispherical rather than triangular as in *Azabbaremys*. The posterior margins of the premaxillae enter the apertura narium interna in *Azabbaremys*, but they are excluded from it in *Nigeremys* and *Arenila* by a vomer-maxilla contact.

MAXILLA (figs. 212–216, 280A)

Preservation: Both maxillae are complete and visible on all surfaces in BMNH R16370.

Contacts of vertical plate: The maxilla in *Azabbaremys* in lateral view shows a relatively flat, deep, bladelike bone, forming most of the labial ridge, the ventral part of the fossa orbitalis, and the lateral part of the fossa nasalis. The prefrontal and premaxilla contacts are clear on both sides. The maxilla has a long, roughly horizontal suture, with the jugal behind the orbit. In more typical bothremydids such as *Bothremys* and *Rosasia*, the jugal contact is not as long.

In *Azabbaremys* the posterior end of the maxilla contacts the quadrate, as in the other Taphrosphyini and most of the Bothremydini. The maxilla-quadrate contact in *Azabbaremys* is broken slightly on both sides. On the right side it is slightly broken but not displaced. The suture on the external surface can be seen ventrally, beginning in a broken part of the cheek margin and extending dorsally into an area of some breakage with a slight amount of breakage in the sutural contact itself until it reaches the jugal. On the internal surface of the right side, the maxilla-quadrate suture is less disturbed and is altered only by a slight amount of overlap between the two bones. The left side is damaged by anterior-posterior pressure forcing the maxilla and quadrate past each other so that they overlap for about a centimeter. The break did not occur precisely in the suture between the two bones, and part of the maxilla-quadrate suture is clearly visible on the internal surface running dorsally from the ventral margin of the cheek.

Structures of vertical plate: The maxilla in *Azabbaremys* is completely smooth on its external surface; there are no nutrient foramina, as in most other turtles, and there is no ridge or bone texture change indicating the position of the horny rhamphotheca. The dorsal process is wider in *Azabbaremys* than it is in *Phosphatochelys* and *Taphrosphys*; it is about the same as in *Nigeremys* and *Arenila*. The labial ridge has an acute edge and curves convex ventrally. The ridge is thinner than in *Phosphatochelys*, but thicker than in *Labrostochelys* and *Taphrosphys*.

Contacts of horizontal plate: The maxilla in *Azabbaremys* contacts the premaxilla anteromedially, the palatine posteromedially, and the jugal posterolaterally. There is no vomer contact as in *Labrostochelys, Nigeremys*, and *Arenila*.

Structures of horizontal plate: The horizontal plate of the maxilla makes up the triturating surfaces, the floor of the fossa orbitalis, and the floor of the fossa nasalis. The fossa nasalis in *Azabbaremys* is a large chamber divided posteriorly into paired choanal channels leading into the apertura narium interna. The floor of the fossa orbitalis in *Azabbaremys* lies above the choanal channel and is angled anterodorsally, forming part of the arched palate seen in *Azabbaremys*. Only a small part of the orbital floor is actually made up of maxilla; most of it is palatine and jugal.

The maxilla bears most of the triturating surface in *Azabbaremys*. It is roughly parallel-sided; the labial ridge is equidistant from the lingual margin, bordering the apertura narium interna throughout its length. There is a very small contribution of the palatine to the triturating surface posteromedially. The width of the triturating surface in *Azabbaremys* is narrower than in *Nigeremys* and *Arenila*, particularly anteriorly but comparable to *Phosphatochelys*. In *Nigeremys* and *Arenila* the maxilla is broad enough to contact the vomer and prevent narial exposure of the premaxilla. In *Azabbaremys* the maxilla does not contact the vomer and the premaxilla does enter the apertura narium interna. It is likely that in *Taphrosphys* the maxilla does not contact the vomer either. The triturating surface in *Azabbaremys* is unusual in being very rugose and formed by

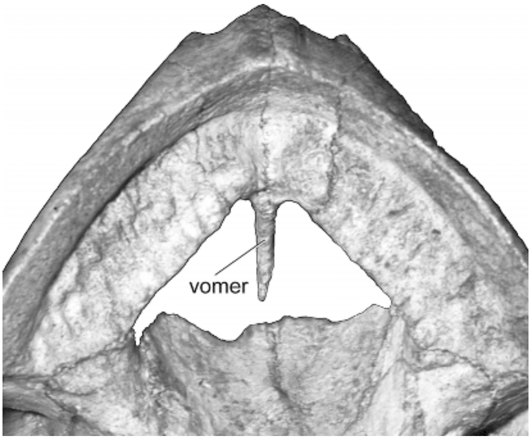

Fig. 216. *Azabbaremys moragjonesi* Gaffney, Moody, and Walker, 2001. BMNH R16370 holotype. Ventral view of palate showing vomer as originally preserved. [E.S. Gaffney, del.]

a series of rough corrugations with the shape of small teeth.

Vomer (figs. 212–216)

Preservation: The vomer was originally complete and well preserved in BMNH R16370. It may have been broken off and lost by the senior author during a misguided cleaning attempt. However, after heroic efforts by the BMNH Curator of Plumbing, it was not found down the drain. Fortunately, the cast of the skull preserves the vomer's original shape and position, and a series of photos in the AMNH archives also record its morphology (fig. 216).

Contacts: The vomer in *Azabbaremys* contacts only the premaxillae anteriorly. The posterior contact with the palatines figured in Gaffney, Moody, and Walker (2001: figs. 2B, 3) is in error. It is possible but unlikely that such a contact was been eroded away by postmortem damage, but as preserved (fig. 216), there is only the premaxillae contact.

Structures: The vomer in *Azabbaremys* is a thin, curved element, extending dorsally and posteriorly from a high midline process formed by the premaxillae. The vomer shows that the palate in *Azabbaremys* was highly arched. The dorsal margin of the vomer has a narrow groove in it, the sulcus vomeri of cryptodires that bears the septum nasalis (Gaffney, 1979a: 92). In *Labrostochelys*, *Nigeremys*, and *Arenila* the vomer is dumbbell-shaped in contrast to the thin columnar shape in *Azabbaremys*. In *Arenila* and *Nigeremys* the vomer is also unusually thick and robust. As preserved, the vomer in *Azabbaremys* is only attached anteriorly to the premaxillae. It tapers posteriorly and there is a gap between the posterior end of the vomer and the palatines. The palatines have an anterior margin that is thin and lacks an expanded area for the reception of the vomer. The anterior margin of the palatines and the posterior margin of the vomer are not finished edges, and a palatine contact could have existed.

Palatine (figs. 212–215, 280A)

Preservation: Both palatines are preserved in BMNH R16370, but their posterolateral contacts are slightly damaged and not completely clear. All of the ventral surfaces are visible, but only some of the dorsal surfaces can be clearly determined.

Contacts: The palatine in *Azabbaremys* contacts the maxilla anterolaterally, the other palatine medially, the pterygoid posteriorly, and the jugal laterally. Despite the published figures (Gaffney, Moody, and Walker, 2001: figs. 2B, 3) a vomer contact is not present as preserved. In the floor of the fossa orbitalis, the palatine contacts the maxilla anterolaterally and the jugal laterally. There is no postorbital contact, because the septum orbitotemporale is absent in *Azabbaremys*.

Structures on dorsal surface: The lateral portion of the dorsal surface of the palatine in *Azabbaremys* is complex and helps form a unique morphology. The absence of the septum orbitotemporale (see Postorbital, Jugal) considerably alters the usual pleurodire morphology in *Azabbaremys*. The palatine forms most of a ridge that extends between the inside of the cheek laterally and the base of the processus trochlearis pterygoidei medially. This ridge is really the ventral remnant of the septum orbitotemporale. The medial process of the jugal does not extend far enough medially to reach the pterygoid, as in most other pleurodires. Instead, the palatine is widely exposed in the posterior face of the septum orbitotemporale between the jugal and the pterygoid. The palatine forms most of the floor of the orbit. This area is preserved and visible on both sides of *Azabbaremys*, but the right side is damaged along the lateral palatine suture, and the left side is intact.

The palatine in the orbital floor of *Azabbaremys* is not a flat element. It is high medially and posteriorly. It slopes ventrally, forming a concavity deepest at the jugal and maxilla sutures. Posteromedially the palatine forms a dorsal process, unknown in any other pleurodire, just anterior to the contact of the pterygoid at the base of the processus trochlearis pterygoidei. This process marks the anterolateral limit of the sulcus palatinopterygoideus, a structure that in *Azabbaremys* lacks the firm base seen in other pleurodires, due to the absence of the septum orbitotemporale.

Structures on ventral surface: Only a small part of the palatine enters the triturating surface in *Azabbaremys*, about the same as in *Arenila* and *Nigeremys*. The palatine extends from a free edge anteriorly, the margin of the apertura narium interna (actually the ill-defined foramen orbitonasale), to the posterior free edge on the margin of the fossa temporalis. In nearly all other pleurodires (except some other Taphrosphyini) there is a septum orbitotemporale rather than a free margin posteriorly. Laterally the palatine contacts a short process of the jugal posterolaterally and a short process of the maxilla anterolaterally. Medially the palatine reaches the other palatine. The palatine and descending process of the prefrontal do not meet in the anteroventral part of the orbital floor; they are separated by the maxilla.

QUADRATE (figs. 212–216, 218, 281C, 286A)

Preservation: Both quadrates are present and well preserved in BMNH R16370.

Contacts on lateral surface: In lateral view the quadrate in *Azabbaremys* contacts the maxilla anteroventrally, the jugal anterodorsally, the quadratojugal dorsally, and the squamosal posterodorsally.

Structures on lateral surface: The cavum tympani in *Azabbaremys* has a completely enclosed incisura columellae auris, as in *Nigeremys* and *Arenila*. The cavum tympani is nearly circular, with a distinct notch in its posteroventral edge, presumably for the eustachian tube. The incisura columellae auris in *Azabbaremys* is a small round hole for the stapes. On the right side of the skull a remnant of the stapes is present. The cavum tympani in *Azabbaremys* is completely smooth in the area of the antrum postoticum. Neither *Arenila* nor *Nigeremys* has an antrum postoticum. Remaining Taphrosphyini do have an antrum postoticum.

The quadrate of *Azabbaremys* has a step or shelf at the ventral margin of the cavum tympani, just above the flat, vertical sheet forming the ventral margin of the quadrate. This shelf (fig. 286A) seems to be in *Nigeremys* also, although the area is not well preserved. It is indeterminate in *Arenila*. The quadrate ventral margin is a continuation of the ventral margin of the maxilla, resulting in a lateral profile for *Azabbaremys* that completely lacks any suggestion of a cheek emargination. *Nigeremys* has a shallow notch, possibly due to postmortem damage, in the cheek area. *Arenila* is missing bone in this region.

Contacts on dorsal and anterior surface: The quadrate in *Azabbaremys* contacts the prootic anteromedially, the opisthotic posteromedially, and the squamosal posteriorly. There is no supraoccipital contact, consistent with other Taphrosphyini, but in contrast to most other Bothremydidae.

Structures on dorsal and anterior surface: On the anterior face of the otic chamber the quadrate-pterygoid suture is visible on both sides but is best seen on the right. As in other turtles, the quadrate forms the lateral margin of the foramen stapediotemporalis. The margins of the foramen are eroded on both sides of *Azabbaremys*, but it is best preserved on the left side. The canalis stapedio-temporalis is free of matrix on the right side, so that the aditus canalis stapedio-temporalis can be clearly seen, as can the foramen and canalis. As in other bothremydids, the foramen stapedio-temporalis in *Azabbaremys* opens on the anterior face of the otic chamber, not more dorsally as in other pleurodires. The quadrate forms the ventral margin of the foramen stapedio-temporale and the ventral and anterior portions of the canalis cavernosus as it extends medially from the region just beneath the canalis stapedio-temporalis.

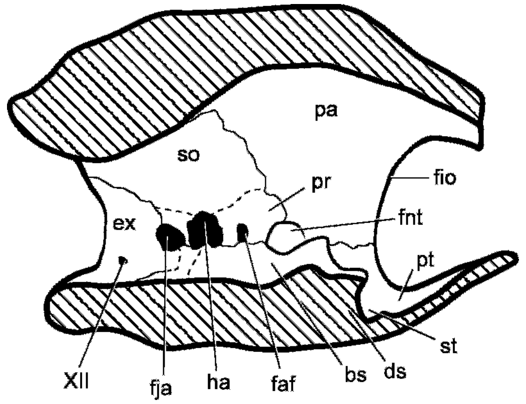

Fig. 217. *Azabbaremys moragjonesi* Gaffney, Moody, and Walker, 2001. BMNH R16370 holotype. Medial view of cavum cranii. Partially restored, based on endocast in BMNH. [A.M. Phillips, del.]

In *Azabbaremys* the region between the foramen stapedio-temporale and the processus inferior parietalis is eroded and missing some of the thin bone that covers the canalis cavernosus and forms the margins of the foramen nervi trigemini. The ventral portion of the more lateral part of this area is formed by the quadrate.

Contacts on ventral surface: In ventral view the quadrate of *Azabbaremys* forms part of the very low but distinct tuberculum basioccipitale with the basioccipital. The paired tuberculum is essentially absent in *Nigeremys* and, apparently, in *Arenila*. The quadrate has a very narrow contact with the basisphenoid between the broader contacts with the basioccipital and pterygoid. The quadrate contacts the quadrate ramus of the pterygoid in a suture extending from the basisphenoid along the processus articularis of the quadrate, as in other pleurodires.

Structures on ventral surface: The foramen posterius canalis carotici interni in *Azabbaremys* is similar in position to that in *Phosphatochelys*, in contrast to the pterygoid-basisphenoid-quadrate position of *Taphrosphys* and the quadrate-only position in *Labrostochelys*. The foramen posterius canalis carotici interni (see Pterygoid) is formed almost entirely by the pterygoid and quadrate, with a very narrow extension of basisphenoid exposed in the roof and margin of the foramen. Although it is arguable, character 74, position of the foramen posterius canalis carotici interni, has been coded as formed by the pterygoid-quadrate for *Azabbaremys*, even though the basisphenoid does enter the margin very narrowly.

The condylus mandibularis in *Azabbaremys* lies anterior to the condylus occipitalis, as in *Phosphatochelys*, but not as far anterior as in *Taphrosphys*. The fossa pterygoidea is absent in *Azabbaremys*; there is only a low ridge marking the attachment margin of the pterygoideus muscle.

Contacts and structures on posterior surface: Posteriorly in *Azabbaremys* the cone-shaped squamosal fits onto the posterodorsal part of the quadrate. The medial part of the quadrate meets the other braincase elements and forms structures enclosing the associated soft parts (fig. 218). The quadrate and opisthotic combine to form the ovoid fenestra postotica containing the stapedial artery and lateral head vein. In some forms (such as *Taphrosphys*) the fenestra is subdivided around those structures, but in *Azabbaremys* this is not the case. However, the fenestra postotica is widely separated from the foramen jugulare posterius by a well-developed opisthotic-quadrate contact medial to the fenestra postotica. Also, in *Nigeremys* the fenestra postotica is an ovoid foramen and it is widely separated from the foramen jugulare posterius. In *Azabbaremys* the quadrate contacts the exoccipital and the basioccipital ventral to the foramen jugulare posterius on the occipital surface.

PTERYGOID (figs. 212–215, 218)

Preservation: Most of both pterygoids are present in BMNH R16370, but the processus trochlearis pterygoidei is broken on both. On the right side the processus is missing entirely, but on the left side the main body is present but displaced anteriorly. The distal portions of the processus are missing on the left side also. The dorsal structures of the pterygoid are visible but so affected by damage that some areas are missing. Some of the dorsal surface sutures are unclear, although all of the ones on the ventral surface can be seen.

Contacts on ventral surface: In ventral view the pterygoid contacts are as in other bothremydids: palatine anteriorly, quadrate posterolaterally, basisphenoid posteromedially, and other pterygoid medially. The palatine contact is not transverse, as in *Arenila* and *Taphrosphys*, but is curved and concave anteriorly. The midline pterygoid contact is relatively short compared to *Taphrosphys*, but *Arenila* has the pterygoids completely or nearly separated on the midline.

Structures on ventral surface: The foramen posterius canalis carotici interni in *Azabbaremys* lies at the contact of pterygoid and quadrate (see Quadrate) at the posterior edge of the pterygoid. The anterior margin of the foramen is formed by a C-shaped indentation of the pterygoid, while the quadrate and a small extension of the basisphenoid are narrow elongations exposed in the roof and the posterior edge of the foramen. The pterygoid underlies broader exposures of the quadrate and basisphenoid. When compared with the much simpler triple meeting of these three bones in *Taphrosphys*, it seems as if the pterygoid of *Azabbaremys* had been dragged posteriorly over the other two bones, pulling the foramen with it.

Anterior to the foramen in *Azabbaremys* is a shallow concavity formed mostly by the pterygoid, with an anteromedial margin that extends right across the pterygoid. This is the scar for the M. pterygoideus, being very shallow in *Azabbaremys*. In *Arenila* and *Nigeremys* this is a concavity, the fossa pterygoidea, much deeper and fully defined, with posteromedial walls completely lacking in *Azabbaremys*.

The processus trochlearis pterygoidei in *Azabbaremys* is preserved only on the left side and its distal margins are missing. Its base has been broken and the process displaced dorsally and anteriorly. As preserved, the processus is not extensive; it would appear to be similar in shape and extent to that in the living pelomedusids and smaller than in the podocnemidids. The orientation of the processus trochlearis pterygoidei in *Azabbaremys* is posterolateral, rather than mostly lateral as in many podocnemidids. The *Azabbaremys* processus differs from Pelomedusidae in having a ridge along its ventrolateral edge, rather than being curved. The processus trochlearis pterygoidei of *Nigeremys* is present on both sides but badly damaged. Nonetheless, it is consistent with what is known in *Azabbaremys*.

The foramen palatinum posterius is formed in the pterygoid-palatine suture in *Azabbaremys*, as in most bothremydids. It is preserved only on the left side and faces ventrolaterally rather than ventrally, at least partially as a result of postmortem deformation. However, the arching of the palate in *Azabbaremys* is somewhat greater than in *Nigeremys* and *Arenila*, so that the curve from the palate around the base of the processus trochlearis pterygoidei is more pronounced. Also, the foramen palatinum posterius is located more laterally than in *Nigeremys* and *Arenila*, resulting in a foramen that opens more laterally into the fossa temporalis in *Azabbaremys* than in the others.

Contacts on dorsal surface: The anterior contacts of the pterygoid at the base of the processus trochlearis pterygoidei in *Azabbaremys* can be seen on the left side. The pterygoid-palatine contact wraps around the base of the processus from the foramen palatinum posterius dorsally to the edge of the sulcus palatinopterygoideus. The pterygoid is clearly separated from the medial process of the jugal by the palatine. This is an unusual condition; in nearly all pleurodires the jugal contacts the pterygoid in this area. The septum orbitotemporale that is formed by medial processes of the postorbital and jugal in other pleurodires is absent in *Azabbaremys* and small in all other Taphrosphyini except *Arenila* and *Nigeremys*. The enlarged palatine forms the only remaining anterior support for the base of the processus trochlearis pterygoidei in *Azabbaremys*.

Structures on dorsal surface: The dorsal surface of the pterygoid bears the crista pterygoidea and forms the floor of the canalis cavernosus and foramen nervi trigemini. The crista pterygoidea is preserved and visible on both sides in *Azabbaremys*. It rises above the level of the pterygoid plate and meets the processus inferior parietalis, making up the lower third of the braincase wall (fig. 217). The crista pterygoidea plus processus inferior parietalis are relatively short in comparison with such forms as in *Podocnemis*. The foramen nervi trigemini has been eroded along its margins as well as the anterior margin of the processus inferior parietalis.

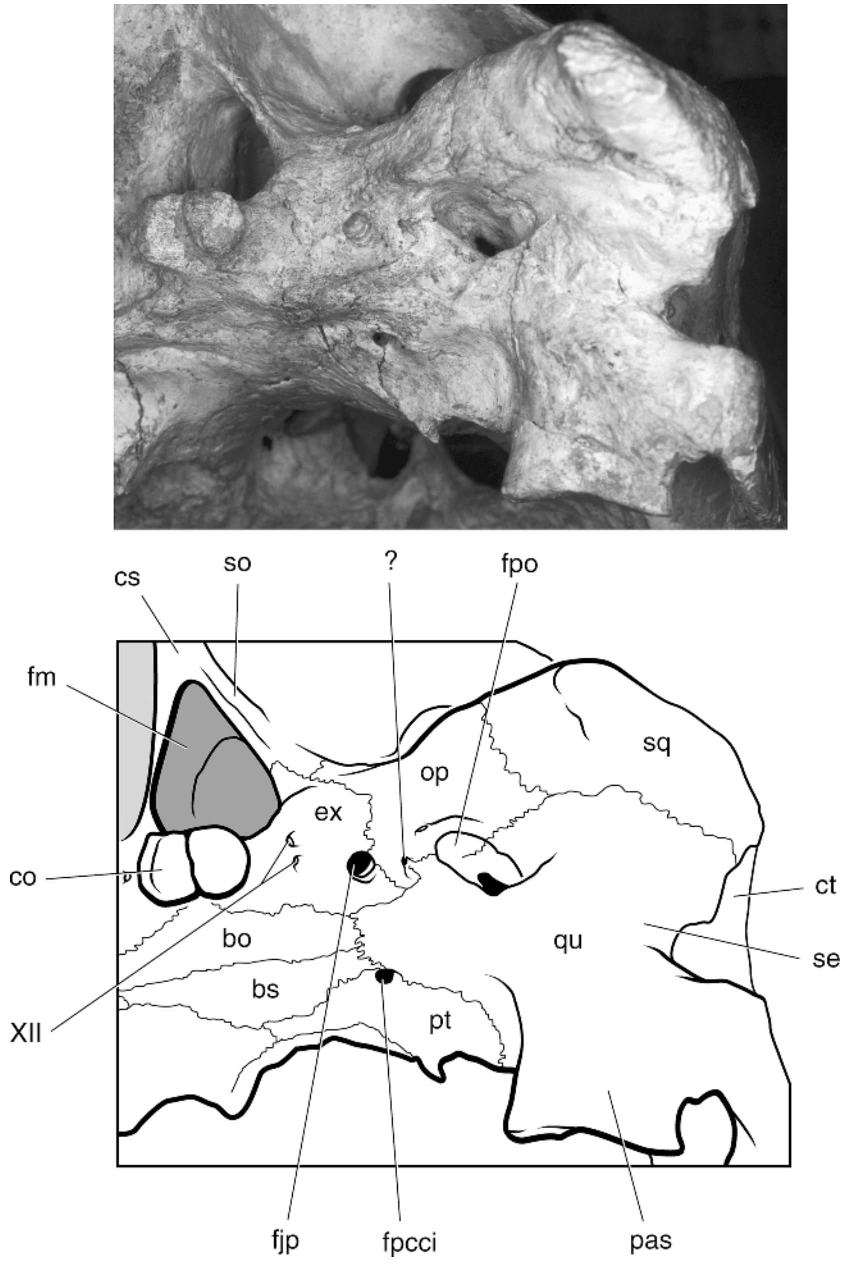

Fig. 218. *Azabbaremys moragjonesi* Gaffney, Moody, and Walker, 2001. BMNH R16370 holotype. Posterior oblique view of skull. [A. Venjara and E.S. Gaffney, del.]

However, the damage is not enough to significantly narrow this structure.

The bones, prootic plus pterygoid, making up the anterior wall of the canalis cavernosus at the anterior edge of the otic chamber are eroded, opening up the canalis on both sides. Nonetheless, the relative positions of the foramen nervi trigemini and the foramen stapedio-temporale can be determined. These foramina are relatively close to each other, as in other bothremydids.

SUPRAOCCIPITAL (figs. 212, 215, 217)

Preservation: The supraoccipital is present and nearly complete in BMNH R16370, but only the right side is visible; the left side is still covered with matrix.

Contacts: The median section of the supraoccipital underlies the two parietals along the midline. Their mutual contact slopes anteroventrally. The laterally projecting otic portion of the supraoccipital in *Azabbaremys* contacts the prootic anterolaterally, the opisthotic laterally, and the exoccipital posterolaterally. As in the other Taphrosphyini, there is no supraoccipital-quadrate contact.

Structures: The crista supraoccipitalis in *Azabbaremys* is relatively short, comparable to that in living pelomedusids, but slightly longer than in *Taphrosphys*. Although incomplete, the crista in *Arenila* seems to be longer than in *Azabbaremys*, compared to the position of the condylus occipitalis. The crista supraoccipitalis in *Nigeremys* is similar in length to *Azabbaremys* but seems to be incomplete. The crista supraoccipitalis in *Azabbaremys* is deeper anteriorly and narrows to an acute posterior end. In *Taphrosphys* the end of the crista is curved and blunt. The very end of the crista is broken off in *Azabbaremys*, but it is already very narrow and is probably missing only a small section.

EXOCCIPITAL (figs. 212, 215, 217, 218)

Preservation: Both exoccipitals are preserved in BMNH R16370; they are complete, but only the right one is entirely free of matrix. Both have clear sutures.

Contacts: The exoccipital in *Azabbaremys* contacts the supraoccipital dorsally, the opisthotic laterally, and the basioccipital ventrally and ventrolaterally. There is also a contact with the quadrate ventrolaterally between the basioccipital and opisthotic. This quadrate contact is found in all bothremydids and is absent in all other Pelomedusoides.

Structures: The exoccipital in *Azabbaremys* forms all of the condylus occipitalis; the basioccipital enters the neck of the condyle. The exoccipitals make up the condyle in all of the described bothremydids. However, this cannot be substantiated in either *Nigeremys* or *Arenila* due to poor preservation, but Lapparent de Broin and Werner (1998) described both taxa as having this feature. In *Azabbaremys* the exoccipitals are eroded on the midline, giving the condyle a bilobed appearance. The foramen jugulare posterius is formed almost entirely by the exoccipital, with a narrow section of opisthotic entering the foramen dorsolaterally. The foramen is entirely closed by bone, as in *Taphrosphys, Arenila*, and *Bothremys*, in contrast to the open condition in *Foxemys*. Between the foramen jugulare posterius and the condylus occipitalis are the two foramina nervi hypoglossi.

BASIOCCIPITAL (figs. 212–215, 217, 218)

Preservation: The basioccipital in BMNH R16370 is complete and clearly defined.

Contacts: The basioccipital is a wide but very short, triangular element in *Azabbaremys*. It makes up the medial half of the tuberculum basioccipitale along with the quadrate laterally. Its entire anterior margin is a transverse contact with the basisphenoid. Posteriorly and dorsally, the basioccipital contacts the exoccipitals, reaching only the base of the condylus occipitalis.

Structures: Between the paired tubercula basioccipitale is a shallow median concavity that extends slightly onto the basisphenoid. The basioccipital in *Nigeremys* is not clearly defined by sutures. This element in *Taphrosphys* is much larger and longer and is just as wide. *Arenila* has a longer basioccipital also, and its anterior contact with the basisphenoid is curved and concave posteriorly.

PROOTIC (figs. 212, 215)

Preservation: Both prootics are present and visible in BMNH R16370, although they are eroded in the area of the canalis cavernosus and the sutures are not always clear.

Contacts: The prootic in *Azabbaremys* contacts the supraoccipital posteromedially, the parietal medially, the pterygoid ventrally, the quadrate laterally, and the opisthotic posterolaterally. The prootic forms the medial margin of the foramen nervi trigemini, the parietal forms the anterodorsal corner, and the pterygoid forms the anterior and ventral margins.

Structures: The foramen nervi trigemini as preserved is incomplete on both sides due to erosion of the medial margin exposing the canalis cavernosus. The prootic-pterygoid suture is gone in this area, so its position and the relative amount of prootic versus pterygoid contribution to the margin of the foramen nervi trigemini is not determinable. The foramen stapedio-temporale is formed in the prootic-quadrate suture and opens directly anteriorly as in most bothremydids. Although much of the bone between the foramen stapedio-temporale and the foramen nervi trigemini is eroded away, it can be seen that these structures were relatively close together, as in *Taphrosphys* and *Bothremys*.

OPISTHOTIC (figs. 212, 215, 218)

Preservation: The opisthotic is preserved completely on both sides of BMNH R16370. It is clearly defined and visible except on the dorsal area of the left side where it is covered with matrix.

Contacts: The opisthotic in *Azabbaremys* has the usual contacts for bothremydids: supraoccipital dorsomedially, prootic anteromedially, quadrate anterolaterally, squamosal posterolaterally, quadrate (again) ventrolaterally, and exoccipital posteromedially.

Structures: The opisthotic in *Azabbaremys* forms the roof of the fenestra postotica; the ventral half of the fenestra is formed by the quadrate (fig. 218). The fenestra is an oblong oval, presumably with the stapedial artery lying in the upper part and the lateral head vein in the lower part. The processus interfenestralis of the opisthotic forms the relatively thick lateral wall of the foramen jugulare posterius, contacting the exoccipital ventromedially and the quadrate ventrolaterally. A foramen, probably the foramen externum nervi glossopharyngei, penetrates the middle of the processus interfenestralis. Above this foramen is a much smaller foramen, which could alternatively be interpreted as the foramen nervi glossopharyngei. Neither can be probed, so their identification is in doubt. Neither of these foramina is found in *Bothremys*.

BASISPHENOID (figs. 212–215)

Preservation: The basisphenoid is present and clearly defined in BMNH R16370.

Contacts and structures on ventral surface: The basisphenoid in *Azabbaremys* has the triangular shape typical for many bothremydids: wider than long, with a straight transverse posterior suture with the basioccipital, rather than the curved suture seen in *Arenila*. The lateral contact with the quadrate is relatively narrow. Anterolaterally the basisphenoid very narrowly enters the margin of the foramen posterius canalis carotici interni (see Pterygoid, Quadrate). The anterior contacts of the basisphenoid are with the pterygoids.

Contacts and structures on dorsal surface: The dorsal surface of the basisphenoid in *Azabbaremys* can be seen inside the nearly cleaned out cavum cranii. An endocast has been made to facilitate this study (fig. 217). The dorsum sellae is relatively high, compared to living Pelomedusoides and *Bothremys*. A well-developed processus clinoideus rises on each side of the dorsum, also in contrast to the lower processus clinoideus of *Bothremys* and living Pelomedusoides. The dorsum sellae in *Azabbaremys* does not overhang the sella turcica, also in contrast to the above taxa. The sella turcica is shorter due to the very short rostrum basisphenoidale, in contrast to the longer sella and very long rostrum in *Bothremys* and the living Pelomedusoides. The rostrum basisphenoidale in *Azabbaremys* is very short, with a deep concave anterior face. On either side thin walls may represent ossified portions of the trabeculae. The entire dorsal basisphenoid morphology in *Azabbaremys* is a foreshortened version of that seen in other Pelomedusoides. This is consistent with the ventral morphology, which also shows a foreshortened basisphenoid.

SUBTRIBE NIGEREMYDINA

Nigeremys gigantea

The single skull representing this taxon is nearly complete but has a very badly damaged surface, making sutures difficult or impossible to see. This skull has been described briefly by Bergounioux and Crouzel (1968), but only Lapparent de Broin and Werner (1998) actually have a useful description. *Nigeremys* is the sister taxon to the similar *Arenila*, together making up the Nigeremydina, which is the sister taxon to the Taphrosphyina.

PREFRONTAL (figs. 219, 222)

Preservation: Both prefrontals are present in MNHN (P) NIR 1, in which the surface

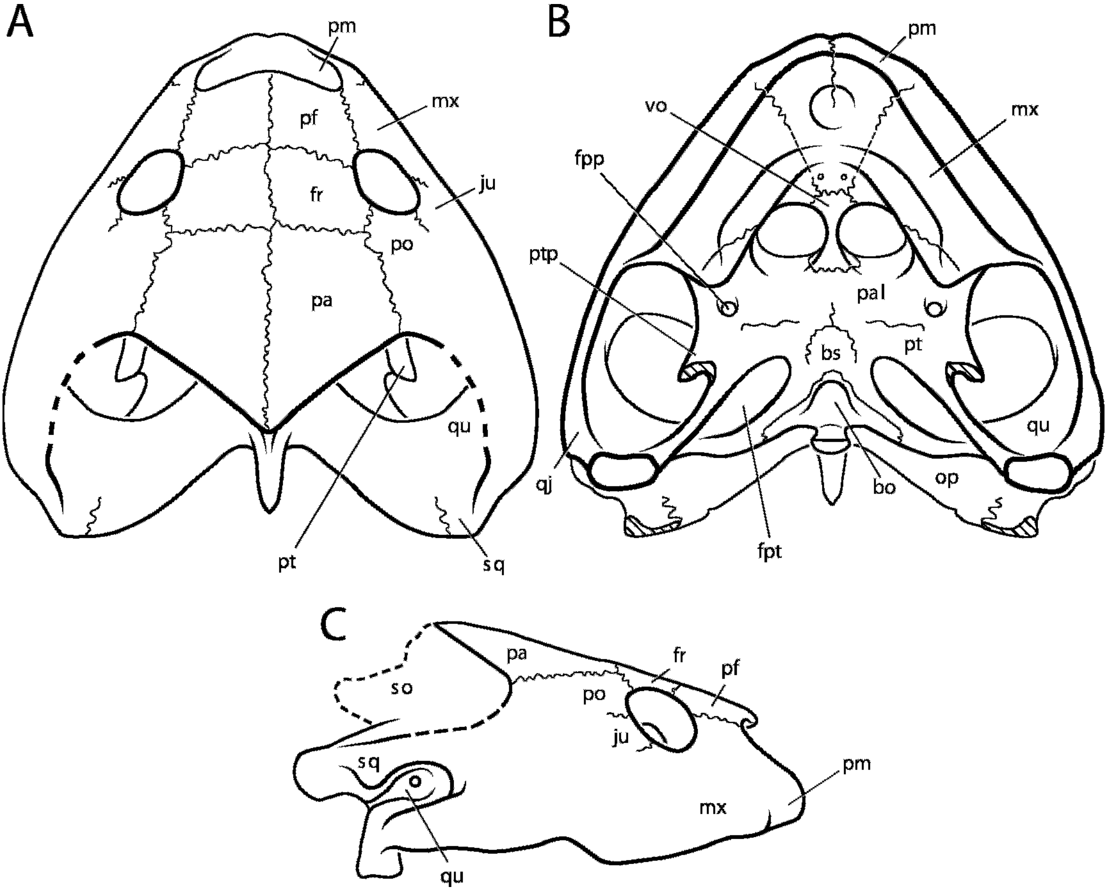

Fig. 219. *Nigeremys gigantea* (Bergounioux and Crouzel, 1968). MNHN (P) NIR 1 holotype. Partially restored views of skull. **A**, dorsal; **B**, ventral; **C**, lateral. [K. Luckenbill, del.]

is damaged by erosion and pitting, but little bone has been lost, and the marrow cavity is not exposed. The original shapes of the bones seem intact. Sutures are clear but are partially obscured by being drawn over in ink.

Contacts: The usual bothremydid contacts are present in *Nigeremys*: frontal posteriorly, maxilla anteroventrolaterally, and prefrontal medially. The contacts are similar to those in *Azabbaremys*, except that the prefrontal-maxilla contact is more dorsal in *Nigeremys* than in *Azabbaremys*. Only the posterior part of the prefrontal is present in *Arenila* and it agrees with *Nigeremys*.

Structures: The prefrontal forms a protruding dorsal margin for the apertura narium externa in *Nigeremys*, which is shaped like that in *Azabbaremys*. In *Nigeremys* the prefrontal does not extend over the premaxilla in dorsal view as it does in *Azabbaremys*. The prefrontal forms the anterior wall of the fossa orbitalis, but *Nigeremys* has less of the bone exposed in the orbital margin than in *Arenila* and *Azabbaremys*. The prefrontal exposure in the fossa orbitalis is obscured by matrix and breakage in both orbits of *Nigeremys*.

Although Bergounioux and Crouzel (1968) described paired nasal bones in "*Potamochelys*", neither Lapparent de Broin and Werner (1998) nor we have found any evidence for their presence in MNHN (P) NIR 1.

FRONTAL (figs. 219, 222)

Preservation: Both frontals are present in MNHN (P) NIR 1, in which the surface is damaged by erosion and pitting, but little

Fig. 220. *Nigeremys gigantea* (Bergounioux and Crouzel, 1968). MNHN (P) NIR 1 holotype. Partially restored ventral view of skull. [F. Ippolito, del.]

bone has been lost. There is no evidence of deformation. Most of the sutures are clear but partially obscured by being drawn over in ink. The postorbital contacts are damaged enough to make their exact position unclear, but enough is preserved to show that there is a postorbital contact.

Contacts: *Nigeremys* has the usual bothremydid contacts: prefrontal anteriorly, postorbital posterolaterally, parietal posteriorly, and other frontal medially. There is no prefrontal-postorbital contact preventing frontal exposure in the orbit, as shown in Bergounioux and Crouzel (1968: fig. 1). The frontal-parietal suture is straight, not curved. The frontal-prefrontal suture does not protrude anteriorly on the midline as much in *Nigeremys* as it does in *Arenila*, and its midline length is slightly less in *Nigeremys* than in *Arenila*.

Structures: The frontal forms the dorsal part of the orbital margin in *Nigeremys*, as in *Arenila*. The internal surface is covered by matrix.

PARIETAL (figs. 219, 222)

Preservation: Both parietals are present in MNHN (P) NIR 1, in which the surface is damaged by erosion and pitting. The posterior margin of the left parietal appears intact, but some bone is broken from the right parietal. The processus inferior parietalis is not visible due to matrix. The sutures are clear.

Contacts of dorsal plate: As in other bothremydids, the parietal of *Nigeremys* contacts the frontal anteriorly, the postorbital laterally, and the other parietal medially. The possibility of a posterolateral contact with the quadratojugal as in *Taphrosphys* and *Phosphatochelys* cannot be ruled out. The contact with the supraoccipital is at the posteromedial margin of the parietal.

Structures of dorsal plate: The posterior temporal emargination in *Nigeremys* completely exposes the otic chamber and is more emarginate than in *Azabbaremys*, *Phosphatochelys*, and *Taphrosphys*. The margin on the parietal is straight, as in *Azabbaremys*. *Arenila* could have had a very similar emargination to *Nigeremys*, but it is missing much of the edge.

Contacts and structures of processus inferior parietalis: The parietal in *Nigeremys* overlies the supraoccipital posteriorly, but the suture is unclear and none of the processus inferior parietalis is exposed.

JUGAL (figs. 219, 222)

Preservation: The area of the jugal is badly damaged with no clear sutures in MNHN (P) NIR 1. The anterior part of the jugal-postorbital contact and the jugal-maxilla contact can be seen, but we are unable to confirm the jugal contacts of either Bergounioux and Crouzel (1968) or Lapparent de Broin and Werner (1998). The latter authors showed a large jugal extending from the orbital margin to the temporal emargination, a condition unknown in any other pleurodire. This area is badly damaged by cracking and overpreparation, with a number of cracks expanded by overzealous incising of presumed sutures. Nonetheless, careful examination of the supposed jugal sutures of Lapparent de Broin and Werner (1998) has failed to corroborate them. The posterior limits of the jugal in *Nigeremys* are not determinable in our interpretation.

Contacts of the lateral plate: On both sides of MNHN (P) NIR 1, just below the orbital margin, is a contact with the maxilla. On the right side, more dorsally in the orbital margin, is the postorbital contact. Both of these become indistinguishable posteriorly. These sutures in *Nigeremys* are in about the same position in *Arenila* and in *Azabbaremys*.

Structures of the lateral plate: The jugal in *Nigeremys* enters the orbital margin; whether it entered the cheek margin is unknown.

Contacts and structures of the medial process: We have been unable to identify sutures for the medial process of the jugal in MNHN (P) NIR 1, although the area is preserved in the lower temporal fossa on both sides. Lapparent de Broin and Werner (1998) did not identify any jugal in ventral view.

QUADRATOJUGAL

Preservation: Although both Bergounioux and Crouzel (1968) and Lapparent de Broin and Werner (1998) identified a quadratojugal in MNHN (P) NIR 1, we have been unable to confirm any sutures defining this element. The cheek area where Lapparent de Broin and Werner (1998) showed quadratojugal sutures certainly has deeply incised fissures in these positions. However, microscopic examination of these cracks has revealed only broken bone fragments and glue, and they have the appearance of mechanical abrasion. It is possible that some of these fissures represent natural sutures, but this cannot be corroborated by us. It is possible that a maxilla-quadrate contact was present on the cheek in *Nigeremys*, and that the quadratojugal was placed dorsally, as in *Azabbaremys*.

SQUAMOSAL (figs. 219, 222)

Preservation: Both squamosals are present in MNHN (P) NIR 1, but the surfaces are damaged and only a few sutures are visible. The posterior surface is eroded and little if any of the original surface is preserved.

Contacts: As in other bothremydids, the squamosal of *Nigeremys* contacts the quadrate anteriorly and the opisthotic medially. The quadratojugal contact is not distinguishable.

Structures: The squamosal of *Nigeremys* is not well preserved, but it is similar in size and position to the squamosal in *Azabbaremys*. There is no ventral flange as in *Taphrosphys*. The squamosal in *Arenila* is poorly preserved also, but it seems to be longer than the one in *Nigeremys*.

POSTORBITAL (figs. 219, 222)

Preservation: The postorbital is present on both sides of MNHN (P) NIR 1, but its defining sutures are obscured by poor preservation and overpreparation. The parietal-postorbital suture and the anterior part of the jugal-postorbital are clear, but the more posterolateral sutures are ambiguous.

Structures: The postorbital of *Nigeremys* seems to extend posteriorly to reach the posterior temporal emargination, as in *Azabbaremys* and in contrast to *Phosphatochelys*. However, the bone is too poorly preserved to be sure that the quadratojugal did not contact the parietal. Lapparent de Broin and Werner (1998: fig. 4f) showed an elongate postorbital with a parasagittal jugal suture. We have been unable to confirm this suture.

PREMAXILLA (figs. 219–222)

Preservation: Both premaxillae are present in MNHN (P) NIR 1, but the sutures are unclear and are determinable only near the labial ridge. The bone surface is eroded and pitted, but it seems to be close in shape to the original bone. The dorsal end of the dorsal process is broken in both, and there is a hole in the midline concavity on the triturating surface.

Contacts: As in other bothremydids the premaxilla contacts in *Nigeremys* are with the vomer posteriorly, the maxilla posterolaterally (visible only on the labial ridge and near the vomer on the left side), and with the other premaxilla on the midline (visible only in a few places). As in *Arenila*, *Nigeremys* has an unusually long premaxilla, so the midline premaxilla contact and the posterolateral maxilla contact are unusually long.

Structures in dorsal view: Very little of the dorsal surface of the premaxilla is visible in MNHN (P) NIR 1 due to matrix and breakage. The midline dorsal process can be seen, and it is large and broad, as in *Arenila* but in contrast to other Taphrosphyini. The dorsal end of the process is broken off.

Structures in ventral view: The labial ridge on the premaxilla in *Nigeremys* is very thick, as in *Azabbaremys*. However, in *Nigeremys* the ridge is blunt in contrast to acute in *Azabbaremys*. It is possible that this is due to weathering, but the relatively even nature of the ridge suggests it is naturally blunt even though very little original bone surface is present. *Azabbaremys* has a very shallow, parasagittal groove extending vertically on the anterior face of the premaxilla (see *Azabbaremys*, Premaxilla); this groove is absent in *Nigeremys*. The anterior face of the premaxilla in *Nigeremys* is not as deep as in *Azabbaremys*.

The midline concavity formed by the premaxilla is very deep in *Nigeremys*, as it is in *Arenila* but in contrast to all other Taphrosphyini. As described by Lapparent de Broin and Werner (1998), the foramen praepalatinum is formed entirely by the premaxilla, as in *Arenila* and the other Taphrosphyini in which it is determinable.

MAXILLA (figs. 219–222)

Preservation: Both maxillae are present and nearly complete, but as with the other bones in MNHN (P) NIR 1, the maxilla surfaces are badly damaged by erosion and pitting, at least partly the result of overpreparation. The sutures are not clear, and we have not been able to confirm many of the contacts described in Lapparent de Broin and Werner (1998) (see below).

Contacts of vertical plate: In MNHN (P) NIR 1 the prefrontal contact is visible on both sides and the anterior part of the jugal suture. However, microscopic examination of the cheek does not confirm the jugal and quadratojugal contacts figured by Lapparent de Broin and Werner (1998: fig. 4f). There are grooves and fissures, but these seem to be natural cracks enlarged mechanically. It is quite possible that the quadratojugal did not contact the maxilla, and that there was a maxilla-quadrate contact, as in *Azabbaremys* and other Taphrosphyini.

Structures of vertical plate: The dorsal process of the maxilla in *Nigeremys* differs from *Arenila* and *Azabbaremys* in having a prefrontal contact that is inclined anteroventrally rather than posteroventrally, but the thickness of the process is similar in all three, and in *Azabbaremys* the maxilla forms the lateral margin of an apertura narium externa that is about as wide as it is in *Arenila* and narrower than in *Azabbaremys*.

The suborbital depth of the maxilla in *Nigeremys* is greater than in *Arenila*, but it is about the same as in *Azabbaremys*. *Arenila* has possibly been made shallower by damage

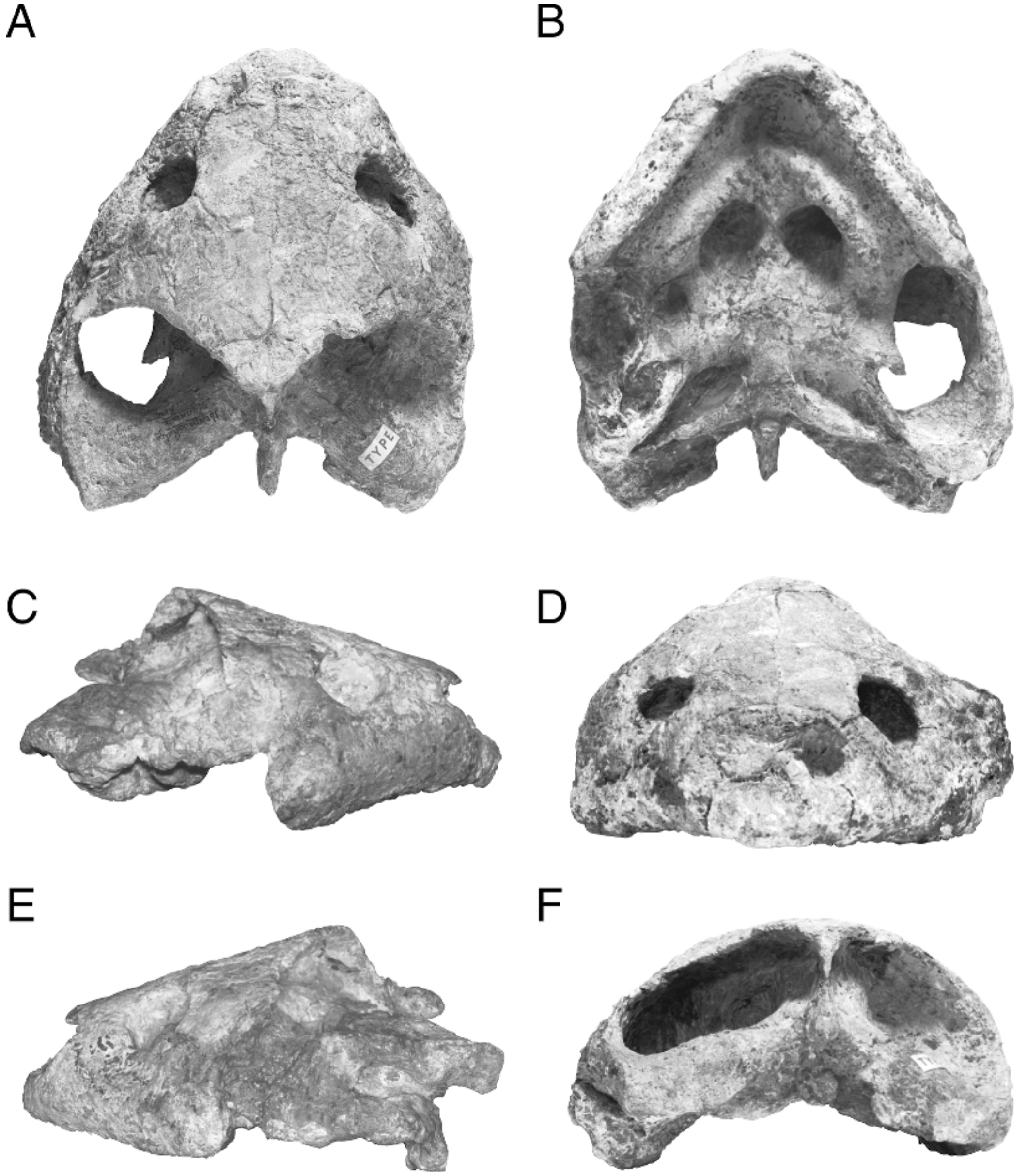

Fig. 221. *Nigeremys gigantea* (Bergounioux and Crouzel, 1968). MNHN (P) NIR 1 holotype. **A**, dorsal; **B**, ventral; **C**, right lateral; **D**, anterior; **E**, left lateral; **F**, posterior. [K. Luckenbill, del.]

(see *Arenila*, Maxilla). There is a slight emargination along the cheek margin in *Nigeremys* on the left side, and most of the right cheek margin is missing. This cheek emargination seems to have a broken edge, so it probably is not original.

Contacts of the horizontal plate: The premaxilla suture in *Nigeremys* is visible in a few places (see Premaxilla) and the vomer suture can be seen for both maxilla. *Arenila* also has a vomer-maxilla contact via a short median process of the maxilla, and both are absent in *Azabbaremys*. These sutures and the palatine sutures have been described and figured by Lapparent de Broin and Werner (1998: fig. 4b) and we can confirm

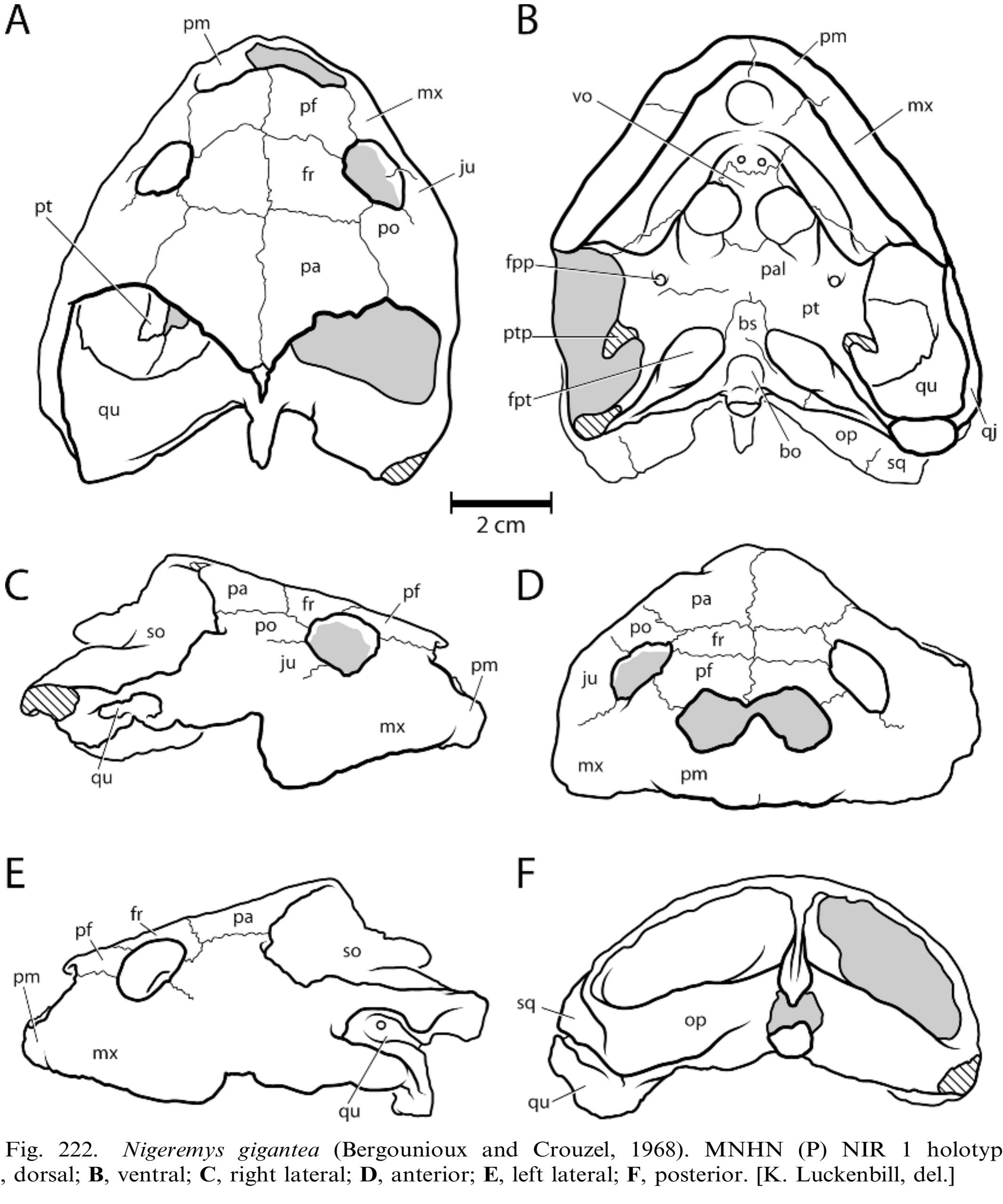

Fig. 222. *Nigeremys gigantea* (Bergounioux and Crouzel, 1968). MNHN (P) NIR 1 holotype. **A**, dorsal; **B**, ventral; **C**, right lateral; **D**, anterior; **E**, left lateral; **F**, posterior. [K. Luckenbill, del.]

them. The jugal suture, presumably exposed in the fossa temporalis inferior wall, is not discernable.

Structures of the horizontal plate: The triturating surface in *Nigeremys* has a very thick, blunt labial ridge as described and figured in Lapparent de Broin and Werner (1998) and Bergounioux and Crouzel (1968). This agrees with the very thick labial ridge of *Arenila*. *Azabbaremys* is also thick in comparison to other Taphrosphyini, but not as thick as in *Nigeremys* and *Arenila*. *Nigeremys* has a blunt margin, possibly due to postmortem erosion (see Premaxilla), in contrast to the acute edge seen in *Arenila* and *Azabbaremys*. The triturating surfaces of *Nigeremys* and *Arenila* are wider anteriorly due to a narrow medial process reaching the vomer. In both a low, thick lingual ridge is separated from the much higher labial ridge by a shallow trough. Lingual and labial ridges are parallel. Lapparent de Broin and Werner (1998) stated that the maxillary triturating surfaces are wider in *Arenila* than in *Nigeremys*, but our own measurements of the triturating surface at the position of the apertura narium interna (appendix 5) divided by the total length (partially restored for *Arenila*) results in a ratio of 4.0 for *Arenila* and 3.8 for *Nigeremys*, suggesting that they are both nearly the same.

The apertura narium interna in *Nigeremys* is very similar in size and position to that in *Arenila*. The apertura is more triangular in *Azabbaremys* and oval in *Nigeremys*.

VOMER (figs. 219–222)

Preservation: The vomer in MNHN (P) NIR 1 is nearly complete, but with the usual surface damage seen in this specimen. The sutures are relatively clear except on the right anterior edge where there is some breakage.

Contacts: *Nigeremys* has the vomer contacts seen in *Arenila*: premaxilla anteriorly, maxilla anterolaterally, and palatine posteriorly.

Structures: As in *Arenila*, the vomer of *Nigeremys* is unusually thick and wide, in contrast to *Azabbaremys* and *Labrostochelys*, the only other Taphrosphyini in which it is known. Palatal arching is much less in *Nigeremys* and *Arenila* than in *Azabbaremys* (see *Arenila*, Vomer). The apertura narium interna of *Nigeremys* is about the same size as in *Arenila* (see *Arenila*, Vomer).

PALATINE (figs. 219–222)

Preservation: Both palatines are present in MNHN (P) NIR 1, but they are damaged by surface erosion and pitting. The anterolateral sutures are clear, but the posterior and lateral ones are not. No dorsal surface morphology is visible due to matrix.

Contacts: Palatine sutures in MNHN (P) NIR 1 are not clear despite the description and figure in Lapparent de Broin and Werner (1998: fig. 4b), but we have no reason to contradict these. There is an anterolateral one with the maxilla, and, on the right side, a posterior one with the pterygoid. No sutures are visible on the dorsal surface. The midline suture is not clear.

Structures on ventral surface: The palatine in *Nigeremys* contributes only a small part to the triturating surface, as in *Arenila* and *Azabbaremys*. The choanal passage is a large, curved trough on each palatine, confluent with the apertura narium interna. The choanal passage of *Nigeremys* is almost the same as in *Arenila*, and both have a low midline ridge absent in *Azabbaremys*. The foramen palatinum posterius in *Nigeremys* seems to be completely formed by the palatine, but this is not certain due to unclear sutures. The foramen lies at the top of a cone-shaped concavity, very similar to the one seen in *Arenila* and distinct from the flat surface of *Azabbaremys*.

QUADRATE (figs. 219–223)

Preservation: Both quadrates are present in MNHN (P) NIR 1, but the bone is poorly preserved and has been further damaged by overpreparation, ink lines, and glue. The left quadrate is more complete than the right one. It is crushed slightly dorsoventrally and part of the cavum tympani is broken away. The bone surface is eroded and pitted and sutures are unclear. The right quadrate is badly crushed dorsoventrally so that the cavum tympani is barely discernable and the sulcus eustachii is not discernable. The processus articularis is broken off the right side. Although Lapparent de Broin and Werner (1998: fig. 4b, f) described sutures for the quadrate, we have been unable to confirm them.

Contacts in lateral view: The cheek on both sides in MNHN (P) NIR 1 is badly damaged and poorly preserved. We have been unable to confirm the sutures figured by Lapparent de Broin and Werner (1998: fig. 4f) showing a large quadratojugal contacting the quadrate anteriorly. There are cracks and fissures, as well as ink lines, in this area, but a careful microscopic examination has failed to distinguish sutures. However, it is quite possible to find fissures and cracks consistent with a quadrate-maxilla contact, as seen in *Azabbaremys*. We also dispute the quadrate-squamosal suture drawn by Lapparent de Broin and Werner (1998: fig. 4f). This is a crack that extends ventromedially into the cavum tympani and is not a suture.

Structures in lateral view: The cavum tympani in *Nigeremys*, visible on the left side, is unusually deep and overhung by its margins. This is probably due to dorsoventral crushing that has made the cavum lower and more oval than it was originally. It is quite possible that the cavum tympani in *Nigeremys* was originally similar in size and shape to that in *Azabbaremys*, that is, nearly circular. The incisura columellae auris in *Nigeremys* is completely closed, as in *Arenila*. The sulcus eustachii is a narrow, clearly defined trough, also similar to that in *Azabbaremys*. There is no sign of an antrum postoticum in *Nigeremys*, although the poor preservation does not preclude the presence of a small one. The antrum is absent in *Azabbaremys* also. As in most bothremydids, the fossa precolumellaris is absent in *Nigeremys*. *Nigeremys* has a well-developed shelf below the cavum tympani as in *Azabbaremys*.

Contacts in dorsal view: Sutures on the dorsal surface of the otic chamber in MNHN (P) NIR 1 are not distinguishable.

Structures in dorsal view: The foramen stapedio-temporale in MNHN (P) NIR 1 is not determinable.

Contacts in ventral and posterior views: Although Lapparent de Broin and Werner (1998: fig. 4f) showed a number of quadrate sutures in MNHN (P) NIR 1, we have only been able to confirm the basioccipital-quadrate suture. This lies about halfway along the ridge forming the posterior wall of the fossa pterygoidea. The Lapparent de Broin and Werner (1998) figure shows this suture placed more anteromedially, as a function of a very narrow basioccipital. We interpret the basioccipital as wider (see Basioccipital) and place the quadrate suture more laterally, as in *Arenila*.

Structures in ventral and posterior views: The foramen posterius canalis carotici interni in *Nigeremys* was figured by Lapparent de Broin and Werner (1998: fig. 4f) as being in the roof of the fossa pterygoidea and formed by the quadrate and pterygoid (left side) and quadrate, pterygoid, and basisphenoid (right side). We have carefully examined this area in MNHN (P) NIR 1 and have been unable to confirm the position or presence of this foramen. The two areas indicated in Lapparent de Broin and Werner (1998) are badly eroded and pitted, with a few pits more heavily prepared than others. We see no sign of natural foramina margins or sutures.

Although not identified in a figure Lapparent de Broin and Werner (1998: 179) described the "facial foramen" (i.e., the foramen nervi facialis). However, we have been unable to confirm the presence of this foramen. The fossa pterygoidea is probably formed mostly by quadrate and pterygoid in *Nigeremys*. The fossa is relatively deep and large, as in *Arenila* but in strong contrast to all the other Taphrosphyini, which lack it.

The condylus mandibularis and processus articularis are present on the left side of MNHN (P) NIR 1, but the bone surface is damaged. The right quadrate lacks the condylus and most of the processus articularis. The condylus mandibularis in *Nigeremys* lies at about the level of the condylus occipitalis, as it does in *Arenila*, but in contrast to the more anterior position in *Azabbaremys* and the other Taphrosphyini. The occipital structures are badly preserved, but the fenestra postotica (fig. 223) is discernable and seems to consist of a single opening, although markings drawn on the specimen obscure some features.

PTERYGOID (figs. 219–222)

Preservation: Both pterygoids in MNHN (P) NIR 1 are present and nearly complete, but their surfaces are pitted and eroded. Sutures are unclear. Breakage is present along the margins, particularly the processus trochlearis pterygoidei and the quadrate ramus. Only the ventral surface is visible.

Contacts on ventral surface: Only a few sutures are discernable in MNHN (P) NIR 1. We agree with Lapparent de Broin and Werner (1998: fig. 4f) in the position of the anterior palatine-pterygoid suture, the midline suture, and the general position of the basisphenoid suture. However, the basisphenoid is slightly more anterior in our interpretation, resulting in a very narrow midline contact of the two pterygoids, similar to that in *Arenila*. We are unable to confirm the pterygoid-quadrate suture figured by Lapparent de Broin and Werner (1998: fig. 4f).

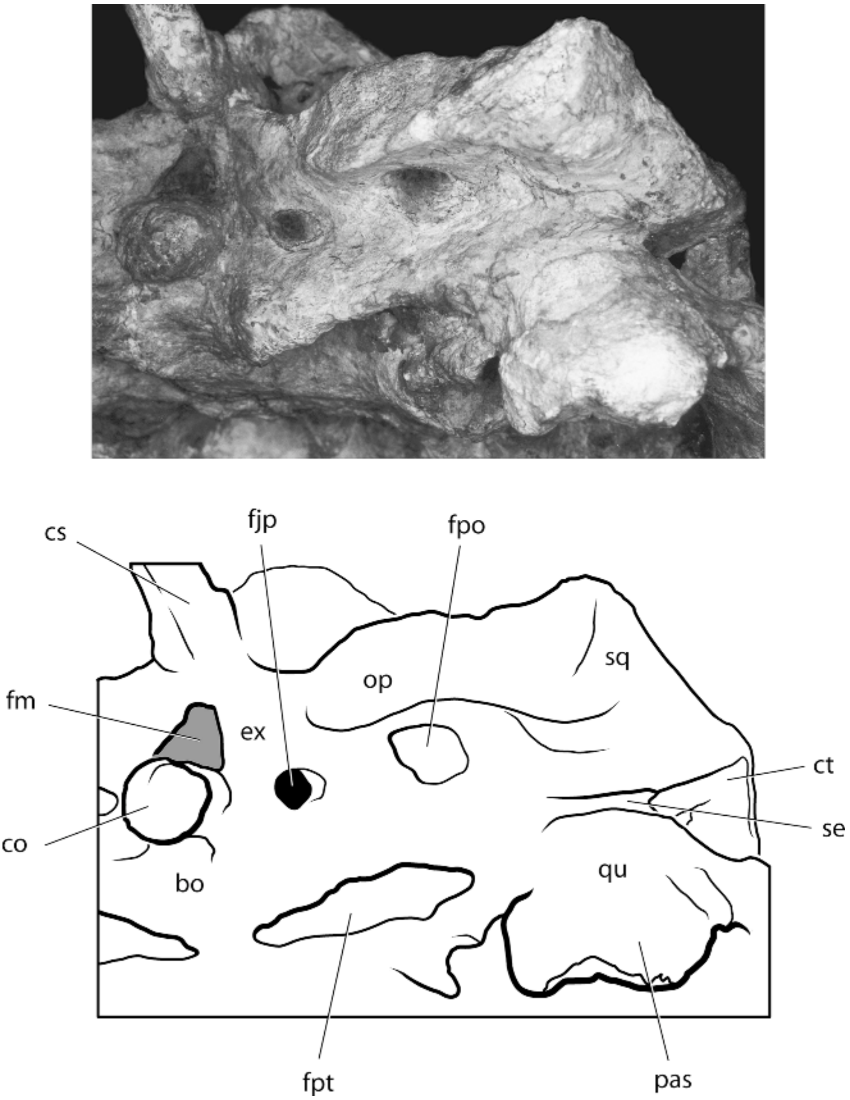

Fig. 223. *Nigeremys gigantea* (Bergounioux and Crouzel, 1968). MNHN (P) NIR 1 holotype. Posterior oblique view of skull reversed from left side. [A. Venjara and E.S. Gaffney, del.]

Structures on ventral surface: The processus trochlearis pterygoidei in *Nigeremys* trends posterolaterally, as in *Arenila* and *Phosphatochelys*. It is eroded around its margins (on both sides) but seems to be in its original position and to retain its original size. The quadrate ramus is a high wall forming the posterior margin for the fossa pterygoidea, as in *Arenila*. The fossa pterygoidea (see Quadrate) seems to be formed by the quadrate posteriorly, the pterygoid anteriorly, and the basisphenoid medially, as in *Arenila*. The foramen posterius canalis carotici interni is not identifiable (see Quadrate).

Contacts and structures on dorsal surface: The right fossa temporalis in MNHN (P) NIR 1 still contains matrix, but the left one shows the lateral surface of the processus trochlearis pterygoidei and some of the postorbital wall. Sutures are not discernable. Enough of the sulcus palatinopterygoideus can be made out to show that it is narrow, not wide as in *Azabbaremys*.

SUPRAOCCIPITAL (figs. 219, 222, 223)

Preservation: The supraoccipital in MNHN (P) NIR 1 is covered by matrix anteriorly, and much of the crista supraoccipitalis is missing. The bone is poorly preserved and badly pitted.

Contacts: No sutures are visible in MNHN (P) NIR 1.

Structures: The crista supraoccipitalis in *Nigeremys* can be seen in cross section, and the lower part is much thicker than the upper part, as in *Arenila*. The crista is broken posteriorly, so its length cannot be determined, but its longest part is at the ventral edge, which is longer than the ventral edge in *Azabbaremys*. The edges of the foramen magnum are not clear, as it is filled with matrix.

EXOCCIPITAL (figs. 219, 222, 223)

Preservation: Both exoccipitals are present in MNHN (P) NIR 1, but despite their bone surfaces being better preserved than most of the skull, sutures are not discernable.

Contacts: No sutures are visible in MNHN (P) NIR 1.

Structures: The edges of the foramen magnum in *Nigeremys* are not clear due to matrix. The bones making up the condylus occipitalis cannot be determined. Lapparent de Broin and Werner (1998: fig. 4f) showed a large basioccipital entering the condyle. However, it is just as likely that it was formed solely by exoccipitals. One foramen nervi hypoglossi could be interpreted on the right side of *Nigeremys*. The foramen jugulare posterius (fig. 223) is more certain, despite markings drawn on the specimen. The foramen is closed laterally and is separated from the fenestra postotica by a distance about the same as in *Arenila* and farther than in *Azabbaremys*.

BASIOCCIPITAL (figs. 219–222)

Preservation: The basioccipital is present and nearly complete in MNHN (P) NIR 1, but the surface is badly eroded and pitted. Nonetheless, we think that some sutures are discernable.

Contacts: Our interpretation of the basioccipital shape in MNHN (P) NIR 1 differs from that in Lapparent de Broin and Werner (1998). They showed an elongate, parallel-sided basioccipital not much thicker than the condylus occipitalis. Microscopic examination does not confirm these as sutures. In our interpretation, on the left anterior margin of the basioccipital is an anterolaterally trending suture paralleling the fossa pterygoidea. This is the basisphenoid contact, and posteriorly it is the basioccipital-quadrate contact. These sutures show that the basioccipital of *Nigeremys* is wider than long and has posterolateral processes extending along the fossa pterygoidea, all as in *Arenila*. In any case, the bone surface is poorly preserved, allowing a number of interpretations.

Structures: The contribution, if any, of the basioccipital to the condylus occipitalis cannot be determined in MNHN (P) NIR 1 (see Exoccipital). As in *Arenila*, there is no prominent tuberculum basioccipitale in *Nigeremys*. We have been unable to find a foramen posterius canalis carotici interni (see Quadrate). There is a shallow concavity on the surface of the basioccipital, as in *Arenila*. If the question of sutures is put aside, there is remarkably close agreement in the shape of the bone surface in the basicranium in both *Nigeremys* and *Arenila*.

PROOTIC

Preservation: Both prootics are presumably present in MNHN (P) NIR 1, but the absence of sutures and surface damage makes it hard to define them. The right one is still partially obscured by matrix, but the left one is visible.

Contacts: No sutures are discernable in MNHN (P) NIR 1.

Structures: Neither the foramen nervi trigemini nor the foramen stapedio temporale can be identified with assurance in *Nigeremys*. However, the dorsal surface of the left otic chamber is better preserved than most of the skull, and it seems likely that a foramen would be visible if present on the dorsal surface. The anterior surface has pits and damaged areas that could be a foramen.

OPISTHOTIC (figs. 219–223)

Preservation: Both opisthotics are present in MNHN (P) NIR 1, but their posterior surfaces are badly pitted and eroded. Most sutures are not discernable.

Contacts: The opisthotic-squamosal suture is visible on both sides in MNHN (P)

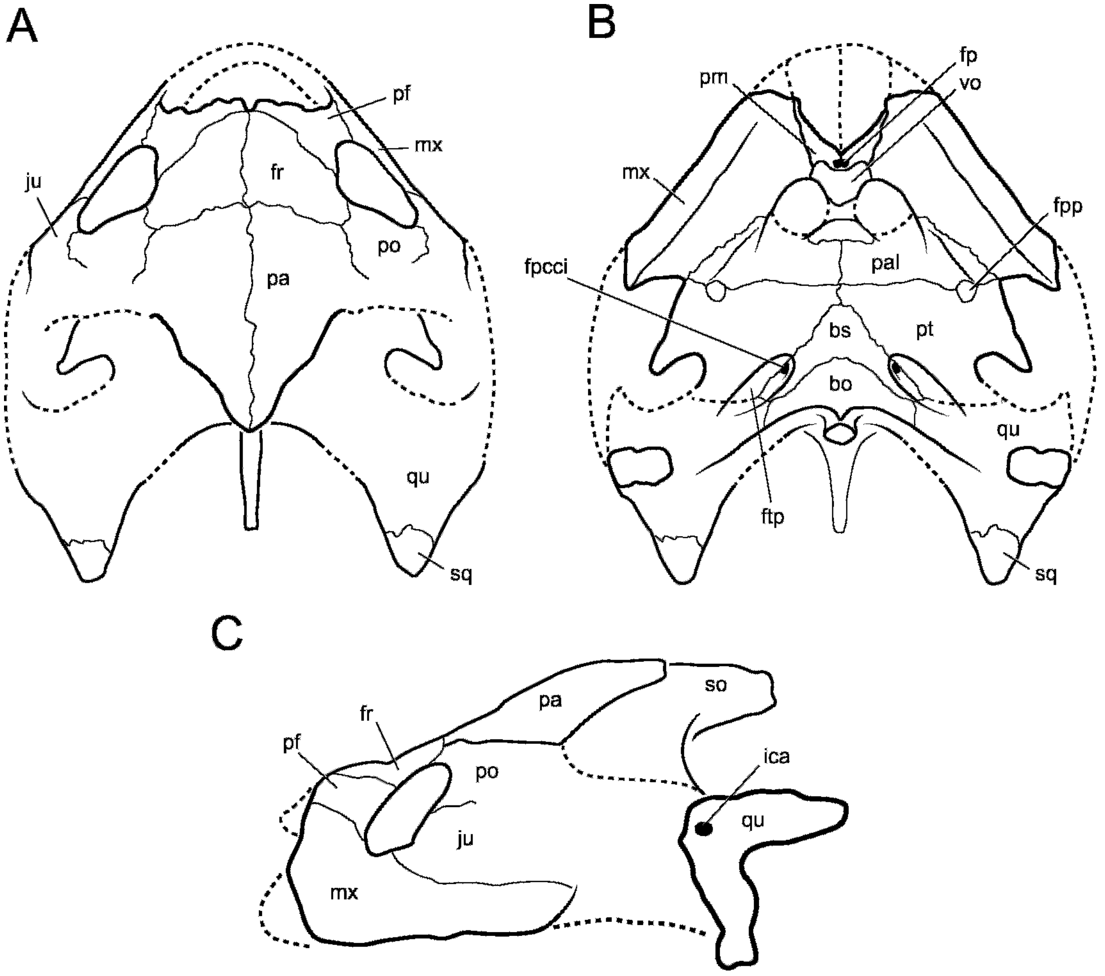

Fig. 224. *Arenila krebsi* Lapparent de Broin and Werner, 1998. TUB Vb-641 holotype. Partially restored views of skull. **A**, dorsal; **B**, ventral; **C**, lateral. [A.M. Phillips, del.]

NIR 1 but other contacts are not, despite the sutures figured in Lapparent de Broin and Werner (1998: fig. 4f).

Structures: The fenestra postotica in *Nigeremys* is a single oval placed laterally far from the foramen jugulare posterius (see Quadrate). The posterior edge of the opisthotic in *Nigeremys* has a large, horizontal ridge not found in *Azabbaremys* (the opisthotic is missing in *Arenila*). The ridge continues onto the squamosal. Some of the ridge may be missing, as the margin has the appearance of a broken edge.

BASISPHENOID (figs. 219–222)

Preservation: The basisphenoid is complete in MNHN (P) NIR 1, but its surface is damaged by pitting and erosion. Some sutures are discernable on the left side. Only the ventral surface is visible.

Contacts: On the ventral surface, the basisphenoid in *Nigeremys* contacts the pterygoid anterolaterally and the basioccipital posteriorly. Presumably, there is a posterolateral contact with the quadrate.

The basisphenoid as figured in Lapparent de Broin and Werner (1998: fig. 4f) is an elongate, parallel-sided element with a transverse basioccipital suture. The sutures we have found show the basisphenoid to be a triangular element, wider than long, with a curved basioccipital suture. The degree to which it enters the fossa pterygoidea is not determinable.

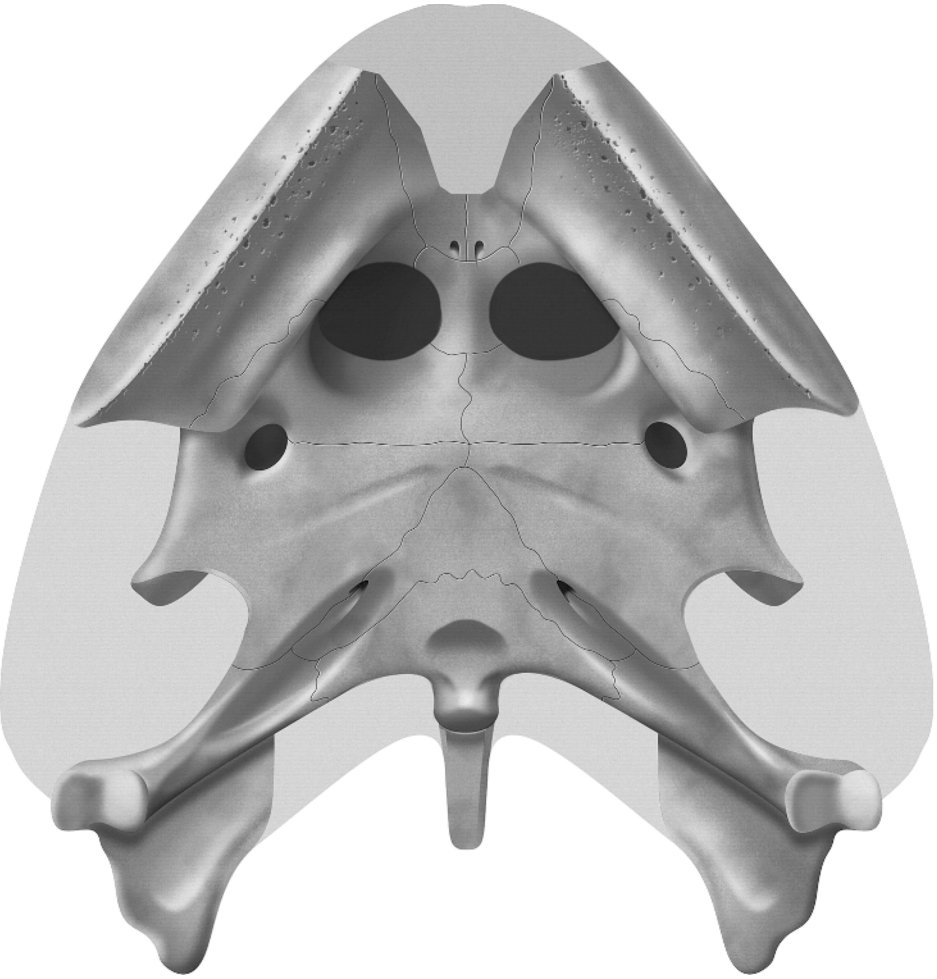

Fig. 225. *Arenila krebsi* Lapparent de Broin and Werner, 1998. TUB Vb-641 holotype. Partially restored ventral view of skull. [F. Ippolito, del.]

Structures on the ventral surface: The foramen posterius canalis carotici interni is not determinable (see Quadrate, Pterygoid). It could have been in the pterygoid-basisphenoid suture and might be one of the many pits and defects in this area. The fossa pterygoidea is probably formed medially by the basisphenoid. The roof of the fossa is particularly damaged with no clear sutures or bone surface.

Arenila krebsi

Arenila is based on one partial skull from the Maastrichtian of Egypt. Enough of the palate is present to determine most of that area, but the quadrates are poorly preserved. This skull was described by Lapparent de Broin and Werner (1998), who provided good photographs but no line drawings to go with them. To take advantage of those photographs, we provide labeled line drawings for the views in Lapparent de Broin and Werner (1998), as well as our own photographs. *Arenila* is the sister to *Nigeremys*, together making up the subtribe Nigeremydina, which is the sister group to the subtribe Taphrosphyina.

PREFRONTAL (figs. 224, 227)

Preservation: Most of the prefrontal in TUB Vb-641 is preserved on the left side, but it lacks its anterior margin. The right one is completely missing. Despite Lapparent de Broin and Werner's (1998) assertion, not enough of the prefrontal margin is preserved to show that the apertura narium externa in *Arenila* is larger than the apertura narium externa in *Nigeremys*. The sutures are clearly visible, with the bones being slightly displaced along them. The prefrontal is broken by a parasagittal crack running from the frontal suture to the anterior eroded edge of the prefrontal just medial to the midline.

Contacts: The preserved contacts in *Arenila* show the usual ones for Bothremydidae: frontal posteriorly and maxilla anteroventrolaterally. The midline contact with the other prefrontal is missing. The frontal-prefrontal suture trends anteromedially to posterolaterally to a greater degree than in *Nigeremys*, but about the same as in *Azabbaremys*.

Structures: The dorsal margin of the apertura narium externa is entirely missing and the length of the prefrontal on the midline is indeterminate. It is quite possible that the anterior margin of the prefrontal in *Arenila* was the same as in *Nigeremys*. The prefrontal part of the orbital margin is preserved with some sign of erosion, but not as much as the anterior prefrontal edge. Presumably the margin here is close to the original. Within the fossa orbitalis of *Arenila* can be seen the ventral process of the prefrontal. It forms about as much of the fossa as in *Azabbaremys*, but differs from *Azabbaremys* in having a wide maxilla contact. The prefrontal forms the lateral edge of the foramen orbitonasale, although this opening is otherwise poorly preserved.

FRONTAL (figs. 224, 227, 229)

Preservation: The left frontal is nearly complete and only slightly distorted in TUB Vb-641. The right frontal is broken off medial to the orbital margin.

Contacts: As in other bothremydids, the frontal of *Arenila* contacts the prefrontal anterolaterally, the postorbital posterolaterally, the parietal posteriorly, and the other frontal medially. The postorbital suture is short, as in *Taphrosphys* and *Nigeremys*, not long, as in *Azabbaremys*.

Structures: The frontal of *Arenila* forms the dorsal part of the orbital margin. The degree of exposure is about the same as in *Nigeremys* and *Azabbaremys*. The sulcus olfactorius is visible in lateral view with what seems to be a deep wall, as in *Azabbaremys*. The frontal is relatively thick, as in *Azabbaremys* but in contrast to *Taphrosphys* and *Phosphatochelys*.

PARIETAL (figs. 224, 227, 229)

Preservation: Most of the left parietal and a small part of the right are preserved in TUB Vb-641. As with almost the entire skull, they are broken and at least partially damaged. The left processus inferior parietalis and ventral part of the right one are preserved. The preserved lateral edge of the left parietal appears broken for its anterior half, but the posterior half has a tapered, finished edge that seems to be original, all as described in Lapparent de Broin and Werner (1998: 175).

Contacts of dorsal plate: As in other bothremydids, *Arenila* has a parietal with these contacts: frontal anteriorly, postorbital anterolaterally, and parietal medially. As in *Nigeremys* it cannot be determined due to breakage whether there was a quadratojugal contact in *Arenila*.

Structures of the dorsal plate: The degree of emargination in *Arenila* cannot be determined. The restoration shows the minimum amount of bone present, but the parietal roof was probably more extensive than shown. It could be comparable to that restored for *Nigeremys*.

Contacts of processus inferior parietalis: The processus inferior parietalis in *Arenila* contacts the frontal wall and continues the sulcus olfactorius anteriorly. The processus inferior parietalis extends ventrally along the anterior margin of the prootic to contact the pterygoid. The parietal appears to extend laterally under the parietal-frontal suture to contribute to the postorbital wall above the sulcus palatinopterygoideus. The presence of the postorbital in *Arenila* and *Nigeremys* is in contrast to the other members of the tribe Taphrosphyini. It is possible that the parietal in *Arenila* does have a descending process lateral to the sulcus palatinopterygoideus that reaches the pterygoid.

However, the required suture is at present a crack and therefore ambiguous. In the dataset *Arenila* is given a question mark for this character.

On the right side of TUB Vb 641, most of the processus inferior parietalis is missing, but its posteroventral part is present. It shows the posterior prootic contact above the foramen nervi trigemini and the ventral pterygoid contact anterior to the foramen nervi trigemini. Posteriorly the parietal contacts the supraoccipital as in other turtles.

Structures of the processus inferior parietalis: The processus inferior parietalis is relatively broad in *Arenila*, with the margin of the foramen interorbitale more anterior than in those forms with a narrow processus, *Azabbaremys* and *Phosphatochelys*. It is not known for the other Taphrosphyini.

The foramen nervi trigemini is formed by the prootic posteriorly, the parietal anteriorly, and the pterygoid ventrally, as in most Bothremydidae. In *Arenila* there is a vertical ridge anterior to the foramen that is absent in *Azabbaremys* but present in *Phosphatochelys*. It is indeterminate in the other Taphrosphyini.

JUGAL (figs. 224, 227, 229)

Preservation: The medial process and anterior part of the lateral plate of the left jugal are present in TUB Vb 641. The posterior edge of the lateral plate of the jugal is a broken margin, so its original extent is unknown. The sutures are clear but there is displacement and breakage along the sutures, particularly with the maxilla. As with other elements in TUB Vb 641, the bone surface is eroded and damaged.

Contacts of lateral plate: The jugal in *Arenila* contacts the postorbital dorsally and the maxilla ventrally, as in other Bothremydidae. The possible quadrate and quadratojugal contacts are not determinable. *Nigeremys* has poor sutures, but the lateral plate of the jugal seems to contact the postorbital and maxilla as in *Arenila*.

Contacts of medial process: The floor of the left orbit is badly fractured, but parts of the jugal-maxilla suture can be seen. In the postorbital wall, the jugal-postorbital contact runs dorsally from the pterygoid, as in most bothremydids. The jugal contacts the pterygoid and, more ventrally, the maxilla, although this area is badly broken with some displaced fragments.

Structures of medial process: As in other bothremydids, the jugal of *Arenila* forms the lateral part of the septum orbitotemporale. The septum orbitotemporale in *Arenila* and *Nigeremys* is completely formed as in the tribe Bothremydini, but in contrast to the reduced or absent postorbital wall seen in the other Taphrosphyini.

QUADRATOJUGAL

Preservation: There is no identifiable part of the quadratojugal in TUB Vb 641.

SQUAMOSAL (figs. 224, 227)

Preservation: An eroded fragment of the right squamosal is present on the posterodorsal edge of the right quadrate and is the only remnant of the squamosal in TUB Vb 641. The only original bone surface is a small section anteromedially.

Contacts: The only contact remaining in TUB Vb 641 is the anterior one with the quadrate.

Structures: The squamosal remnant is probably too incomplete laterally to retain any of the antrum postoticum if one was present. In any case, there is no sign of an antrum postoticum. The squamosal in TUB Vb 641 does extend posteriorly more than the squamosal in *Nigeremys*, but *Nigeremys* is broken in this area and may have had more of a posterior extension than is preserved.

POSTORBITAL (figs. 224, 227, 229)

Preservation: The left postorbital is preserved in TUB Vb 642, but its posterior margin is broken and the medial process is damaged by cracks and displaced fragments. The lateral plate surface is eroded. The lateral plate sutures are clear, but the medial process ones are not.

Contacts of lateral plate: As in other bothremydids, the postorbital of *Arenila* contacts the frontal anteromedially, the parietal medially, and the jugal ventrolaterally. The quadratojugal contact is missing.

Structures of the lateral plate: As preserved, the orbital margin of *Arenila* shows an orbit relatively larger than the one in *Nigeremys* and *Azabbaremys*, but compara-

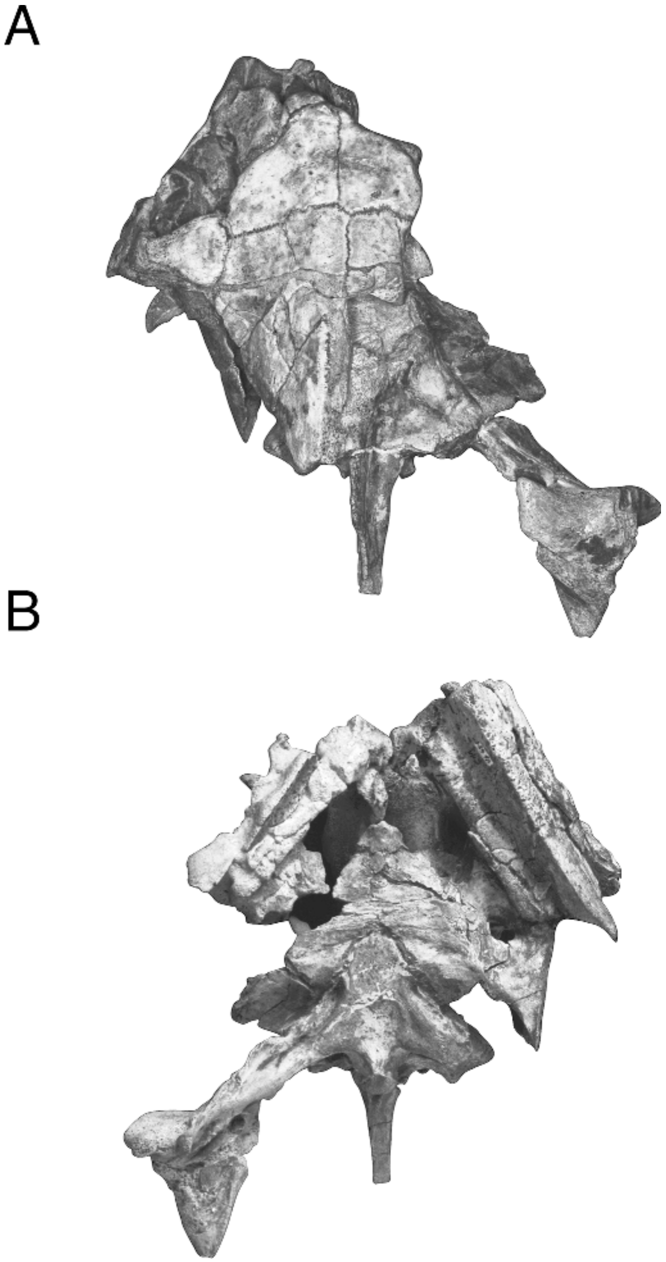

Fig. 226. *Arenila krebsi* Lapparent de Broin and Werner, 1998. TUB Vb-641 holotype. **A**, dorsal; **B**, ventral. These and the following figures are intended to coincide with figures in Lapparent de Broin and Werner (1998: pls. 6, 7). [E.S. Gaffney, del.]

ble to that in *Phosphatochelys*. Lapparent de Broin and Werner (1998) used the larger orbit of *Arenila* as a diagnostic difference from *Nigeremys*. However, close examination of TUB Vb 641 shows that all of the elements forming the orbital margin are abraded and eroded. The posteroventral elements (maxilla, jugal, and postorbital) seem to be particularly eroded and have edges exposing the cancellous marrow. The postorbital and jugal could be missing enough bone that, if restored, would result in an orbital margin of

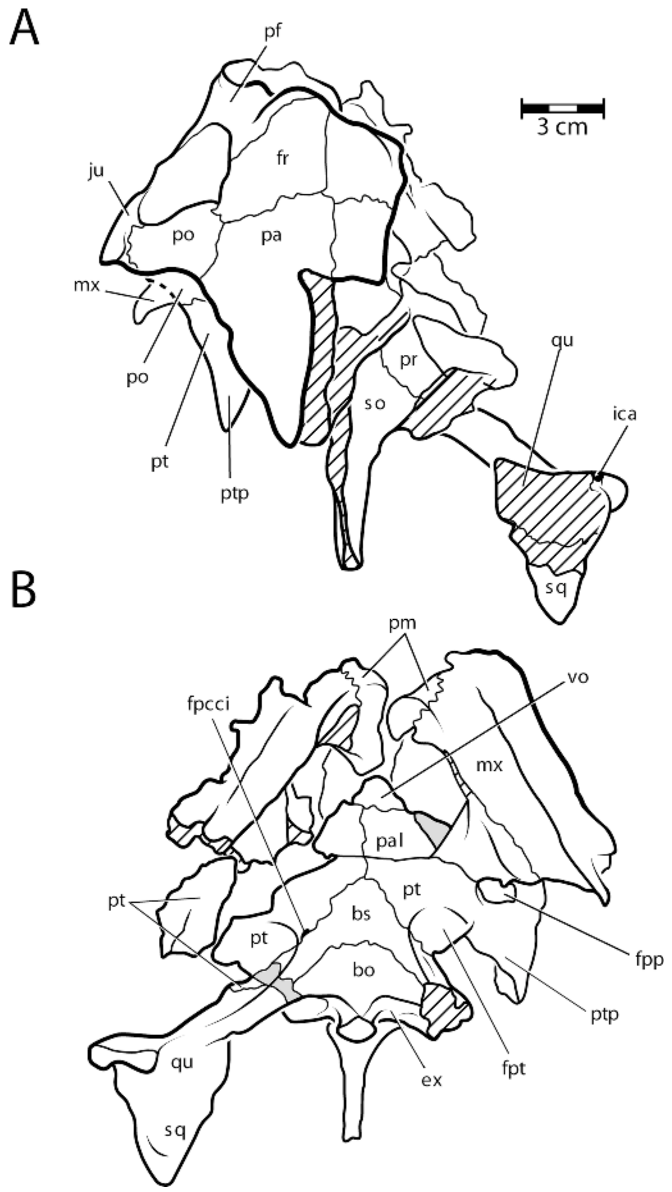

Fig. 227. *Arenila krebsi* Lapparent de Broin and Werner, 1998. TUB Vb-641 holotype. Partially restored views of skull. **A**, dorsal; **B**, ventral. [A.M. Phillips, del.]

the size seen in *Nigeremys*, removing this feature as a difference between the two taxa (Lapparent de Broin and Werner, 1998). The maxilla is also damaged and the frontal is clearly lacking its original margin. Only the prefrontal comes close to retaining an original margin. We have not compensated for these missing edges in the restoration (fig. 224), so the orbit was probably smaller than in our restoration.

Contacts of medial process: The medial postorbital process is not well preserved in TUB Vb 641, but the contacts with the pterygoid ventrally and the jugal laterally are clear. It is possible that there is a medial contact with the parietal (see Parietal) that prevents postorbital exposure in the lateral wall of the sulcus palatinopterygoideus.

Structures of medial process: The postorbital in *Arenila* forms a major part of the septum orbitotemporale. The surface exposed in the posterior wall of the fossa orbitalis is partially covered in matrix, and the sutures are not clear.

PREMAXILLA (figs. 224, 227)

Preservation: The posterior parts of both premaxillae are preserved. The right premaxilla has come to light subsequent to the description of Lapparent de Broin and Werner (1998).

Contacts: As preserved, there is the lateral contact with the maxilla, the posterior contact with a remnant of the vomer (on the right side), and the median contact with the other premaxilla.

Structures on dorsal and ventral surfaces: The dorsal surface is eroded and does not clearly show the margins of openings. Posteriorly the ventral surface forms the foramen praepalatinum and a groove entering it. The triturating surface formed by the premaxilla defines the posterior margin of the midline concavity, which is laterally and posterolaterally continuous with the lingual ridge of the maxilla. The premaxilla is unusually large, as in *Nigeremys* and in contrast to other Taphrosphyini.

MAXILLA (figs. 224, 227, 229)

Preservation: When originally described only the left maxilla was known for TUB Vb 641, but now a partial right maxilla is also available. The left maxilla is much more complete and better preserved than is the right one. The left maxilla is considerably eroded on its lateral surface. Almost all of the original bone surface is gone and the margins are broken. The labial ridge has been crushed medially and the bone displaced so that the ridge is more medial to the edge of the skull than it was premortem. The triturating surface is cracked, but most of it is not eroded.

Contacts of vertical plate: As in other bothremydids, the maxilla of *Arenila* contacts the premaxilla anteriorly, the prefrontal anterodorsally, and the jugal posterodorsally. The posterior contacts are unknown, but the restoration shows that the maxilla is relatively long in *Arenila* as it is in *Azabbaremys*, placing the known end of the maxilla close to the quadrate.

Structures of vertical plate: The anterior end of the maxilla in *Arenila* is a broken margin with no sign of the apertura narium externa. The apertura in *Arenila* could have been the same as in *Nigeremys*. The dorsal process of the maxilla in *Arenila* is about as thick and high as it is in *Azabbaremys*, in strong contrast to the conditions in *Labrostochelys* or *Phosphatochelys*. In *Nigeremys* the process is the same thickness, although the suture appears to be inclined posterodorsally rather than anterodorsally as in *Arenila*.

The size of the orbit has been discussed under Prefrontal. The maxilla edge is eroded in TUB Vb-641, but not as much as the postorbital and jugal margins. The labial ridge has been crushed dorsoventrally as well as medially. Considering both orbital erosion and labial ridge crushing, the suborbital depth of the maxilla must have been greater than it is now. One of the few differences between *Arenila* and *Nigeremys* is the suborbital depth of the maxilla, and we have not adjusted this for crushing in our *Arenila* restoration. There is no way to be sure, but it is possible that the suborbital depth was the same in both originally.

Contacts of horizontal plate: In *Arenila* the maxilla contacts the premaxilla anteromedially, the palatine posteromedially, and the jugal posterolaterally, all as in other Taphrosphyini. *Arenila* also has a small, medial contact with the vomer, very much the same as in *Nigeremys*. *Labrostochelys* also has a vomer contact, but *Azabbaremys* does not. The vomer is not known for *Phosphatochelys* and *Taphrosphys*.

Structures of horizontal plate: The triturating surface of *Arenila* is mostly formed by the maxilla with only a small posteromedial contribution by the palatine, as in *Nigeremys* and *Azabbaremys*. The labial ridge is very thick in *Arenila* and *Nigeremys*, thicker than in any other Taphrosphyini. The ridge is blunt in *Nigeremys* and acute in *Arenila*. The entire surface of the skull of *Nigeremys* has been damaged, and the labial ridge as preserved is irregular and could easily have been as acute as in *Arenila* before being damaged. The lingual ridge of *Arenila* is very low and parallel to the labial ridge, as in *Nigeremys*. Both have a very shallow trough between the ridges. The labial ridge is straight in *Arenila* and *Nigeremys*, not curved convex outward as in the other Taphrosphyini, except *Labrostochelys*. The shape of the triturating surface is similar in *Arenila*, *Nigeremys*, and *Azabbaremys*, except that *Arenila* and *Nigeremys* have a broader medial process reaching the vomer.

The apertura narium interna in *Arenila* is very similar in shape to *Nigeremys*, with the thick edge of the lingual ridge of the maxilla forming its anterolateral margin. The foramen orbitonasale is present on the left side, but the thin edges are mostly broken away.

VOMER (figs. 224, 227)

Preservation: The anterior and posterior ends of the vomer are present in TUB Vb-641, but the central bar is missing. The parts preserved show clear sutures.

Contacts: The vomer of *Arenila* contacts the premaxilla anteriorly, the maxilla anterolaterally, and the palatine posteriorly, as in *Nigeremys* and *Labrostochelys*. In *Azabbaremys* there is no vomer-maxilla contact.

Structures: Even though the vomer of *Arenila* lacks the central bar, the preserved parts show that the bar was thick and short, as in *Nigeremys* and in contrast to the very thin vomer of *Azabbaremys*. Enough of the two foramina praepalatinum are preserved on the premaxillae to show that the vomer may participate in the formation of these canals as described by Lapparent de Broin and Werner (1998).

The foramen narium interna in *Arenila* is formed by the vomer medially, the maxilla laterally, and the palatine posteriorly. As restored, the apertura in *Arenila* is about the same size as in *Nigeremys* although much of the margin is broken and the palatine edge is largely missing. Lapparent de Broin and Werner (1998: 174) used "larger choanal" to distinguish *Arenila* from *Nigeremys*, but this condition is the result of postmortem breakage. Furthermore, our examination of *Nigeremys* shows that the apertura narium interna is larger than that depicted in Lapparent de Broin and Werner (1998: fig. 4b).

Neither *Arenila* nor *Nigeremys* has the high degree of palatal arching seen in *Azabbaremys* and reflected in the vomer orientation that is more inclined in *Azabbaremys* than in *Arenila* and *Nigeremys*.

PALATINE (figs. 224, 227)

Preservation: Most of both palatines are preserved in TUB Vb 641, with some cracking along the choanal passage. A section is missing posteriorly on the right side and both palatines lack their anteromedial edges. The sutures are distinct.

Contacts: The palatine contacts in *Arenila* are with the vomer anteromedially, the palatine medially, the pterygoid posteriorly, and the maxilla anterolaterally.

Structures on the dorsal surface: Some of the contact of the palatine and the processus inferior parietalis is visible on the left side in *Arenila*, but it is too crushed to make detailed comparisons. The dorsal opening of the foramen palatinum posterius is formed anteriorly by the palatine, and on the left side a trough formed by palatine leads into it from the floor of the sulcus palatinopterygoideus. The sulcus itself is partially obscured by broken bone and matrix, but a parietal contact is possible. The palatine forms a major part of the fossa orbitalis floor and contacts the maxilla laterally and, possibly, the prefrontal anteriorly. The foramen orbitonasale is medial to the palatine here.

Structures on ventral surface: As in *Nigeremys* and *Azabbaremys*, the palatine of *Arenila* only forms a small part of the triturating surface. A large, curved choanal passage is confluent with the apertura narium interna, as in *Nigeremys*.

The foramen palatinum posterius in *Arenila* is formed anteriorly by the palatine and posteriorly by the pterygoid. As preserved, the foramen is very large, and Lapparent de Broin and Werner (1998) used this to distinguish *Nigeremys* from *Arenila*. However, discovery of a partial left palatine and close examination of the right palatine suggest that a smaller foramen was original and that the large one is a preservational artifact. The edges of the left foramen palatinum posterius are intersected by matrix-filled cracks that have enlarged and

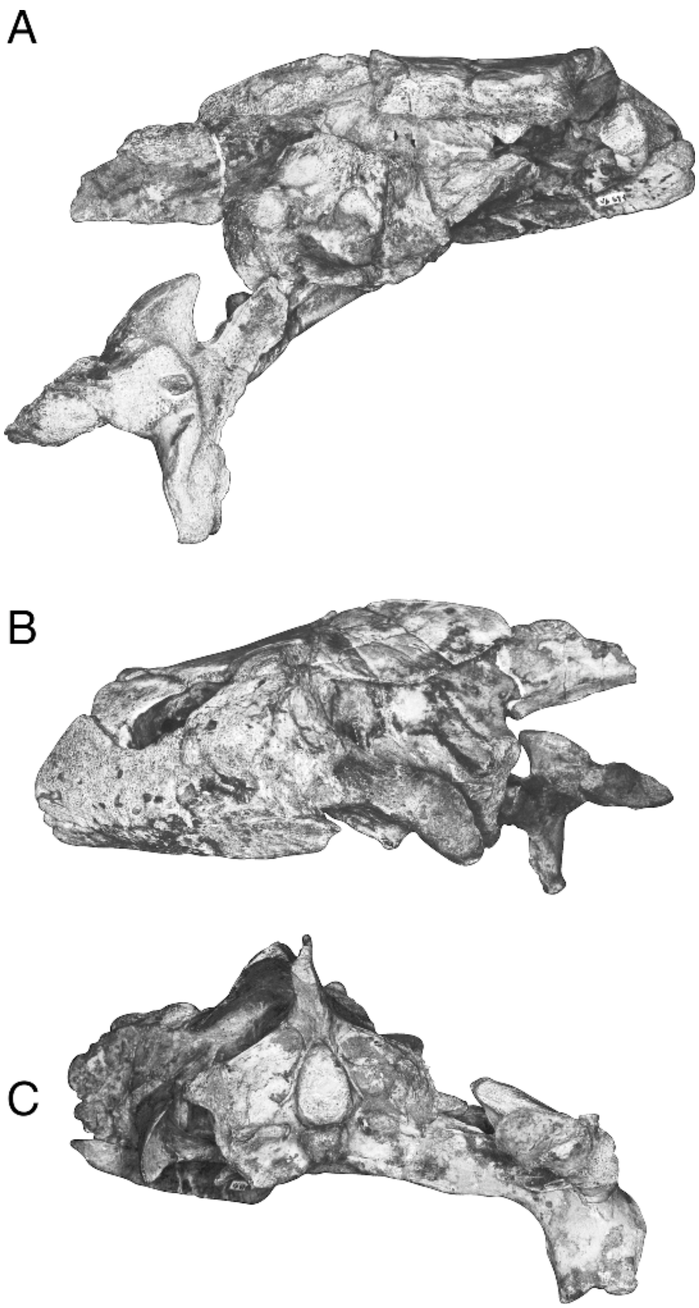

Fig. 228. *Arenila krebsi* Lapparent de Broin and Werner, 1998. TUB Vb-641 holotype. **A**, right lateral; **B**, left lateral; **C**, posterior. [E.S. Gaffney, del.]

dislocated the margins of the foramen. When the remaining original edges are adjusted for this, the foramen is less than half the size as preserved. The foramen in *Arenila* is still slightly larger than in *Nigeremys*.

QUADRATE (figs. 224–230)

Preservation: Only the left quadrate is present in TUB Vb 641and almost all of it is badly damaged by erosion that has removed a large percentage of the bone. Only a small

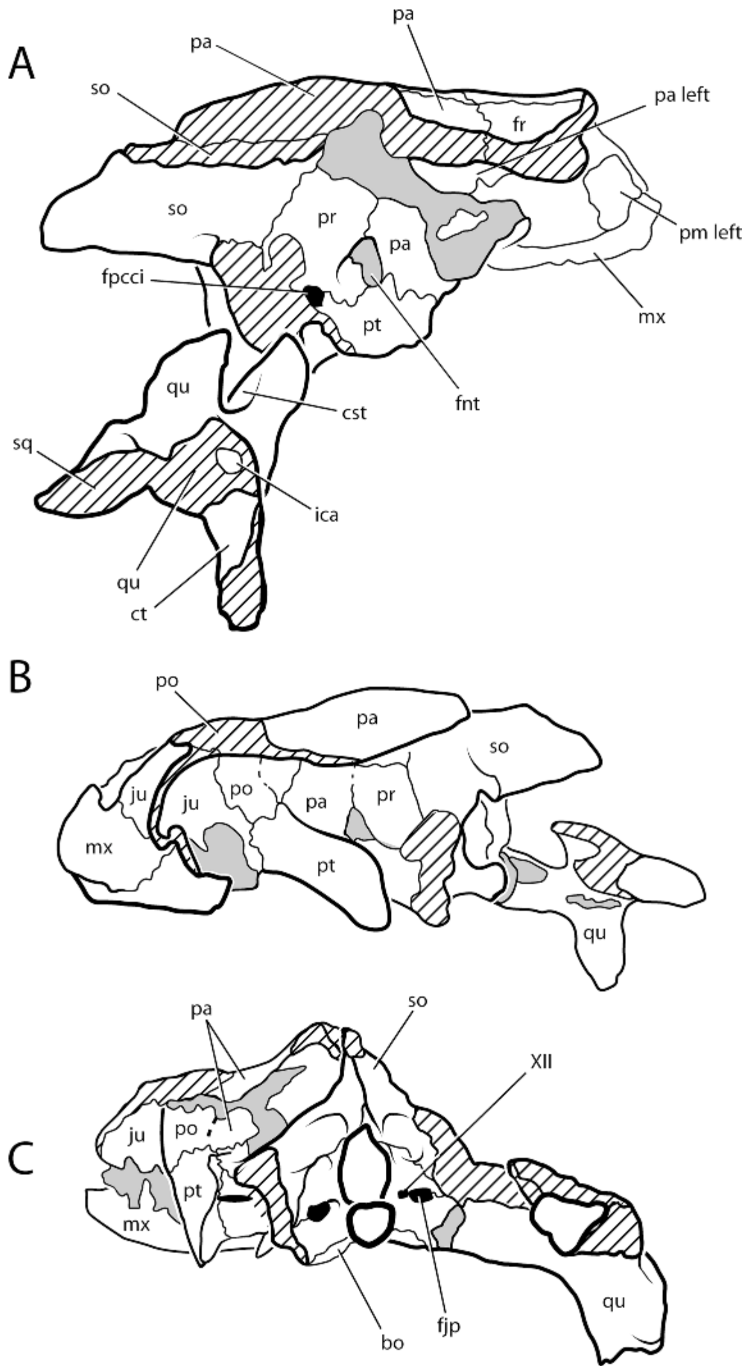

Fig. 229. *Arenila krebsi* Lapparent de Broin and Werner, 1998. TUB Vb-641 holotype. **A**, right lateral; **B**, left lateral; **C**, posterior. These figures are intended to coincide with those in Lapparent de Broin and Werner (1998: pls. 6, 7). The position of the fpcci seems anomalous, but the area is broken and the canal is revealed in this position. [A.M. Phillips, del.]

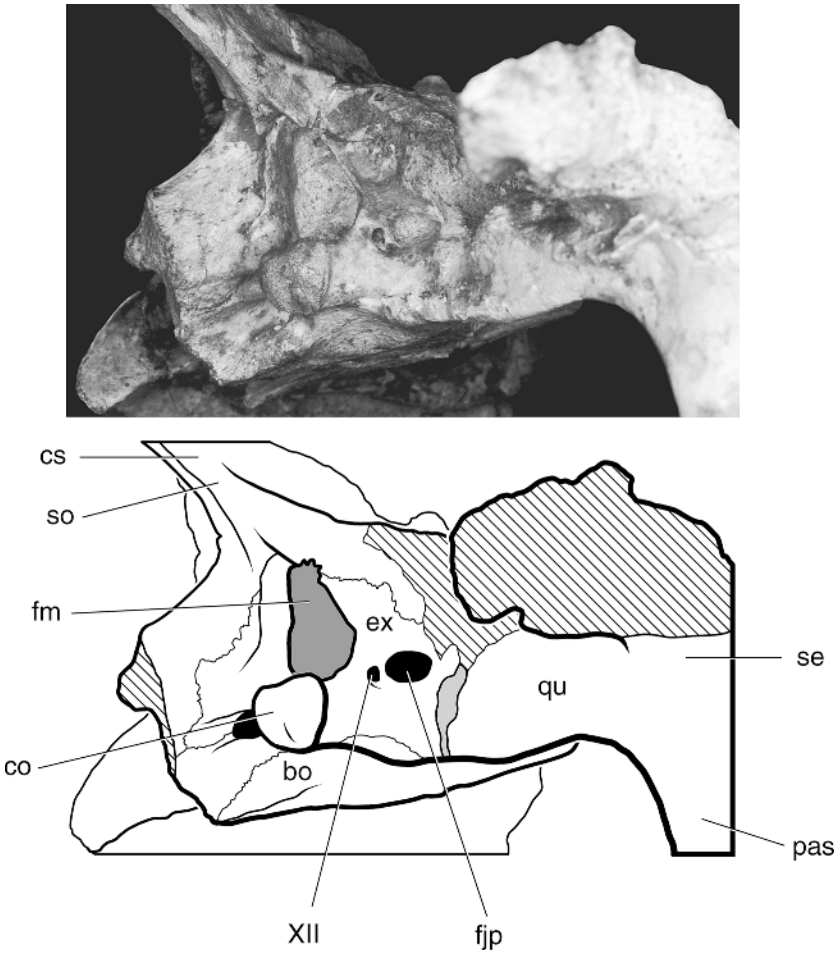

Fig. 230. *Arenila krebsi* Lapparent de Broin and Werner, 1998. TUB Vb-641 holotype. Posterior oblique view of skull. [A. Venjara and E.S. Gaffney, del.]

contact with the rest of the skull remains, and only a few areas of original bone surface are present.

Lateral view contacts: None of the cheek or skull roof contacts is preserved in *Arenila*. A block of the eroded squamosal is present on the posterodorsal part of the quadrate. Only the internal contact is preserved.

Lateral view structures: Only a small vestige of the cavum tympani is preserved in *Arenila*, and this is the medial wall of the sulcus eustachii. The canal for the columella auris is eroded away where it reaches the cavum tympani as described by Lapparent de Broin and Werner (1998). The distance between the sulcus eustachii and the stapedial canal is slightly shorter in *Arenila* than it is in *Nigeremys*, as noted by Lapparent de Broin and Werner (1998), but in neither taxon is that distance very different from that in *Azabbaremys*. The antrum postoticum is entirely missing. This may not be due only to erosion, as it is likely that if a moderate or tubelike antrum were present there would be some of it visible. It is likely that the antrum postoticum was actually absent in *Arenila* as in *Azabbaremys*.

Dorsal view contacts: The dorsal parts of the quadrate are missing due to erosion in TUB Vb 641.

Dorsal view structures: The extensive erosion of the quadrate in *Arenila* has exposed the canalis stapedio-temporalis, but the foramen stapedio-temporale has its ventral margin preserved. The foramen faces anteriorly, as in *Azabbaremys*.

Ventral and posterior view contacts: The medial contacts with the pterygoid, basisphenoid, and basioccipital are preserved at least in part on the right side in *Arenila*. There is a broken section between the quadrate and basisphenoid-basioccipital. The pterygoid has a small fragment attached to the quadrate anteriorly just lateral to the broken section, allowing restoration of the pterygoid limits. In posterior view the quadrate contacts the exoccipital ventromedially. As described by Lapparent de Broin and Werner (1998), most or all of the opisthotic is missing on both sides.

Ventral and posterior view structures: Laterally, the quadrate in *Arenila* preserves a horizontal ridge on its posterior surface that seems to continue the line formed by the sulcus eustachii. Dorsomedially, the trough above this ridge runs into the fenestra postotica. Very little of the quadrate and none of the opisthotic are preserved to show the extent and shape of the fenestra postotica in *Arenila*.

Ventrally the processus articularis and condylus mandibularis are preserved on their posterior surface, but the anterior and lateral surfaces are gone. The position of the condylus mandibularis is slightly posterior to the condylus occipitalis in *Arenila*, as in *Nigeremys* but in contrast to the more anterior position of other Taphrosphyini. The fossa pterygoidea is large and deep in *Arenila*, as it is in *Nigeremys*. The pterygoid flange of the quadrate forms the posteromedial wall of this concavity, and this is preserved in *Arenila*. The foramen posterius canalis carotici interni in *Arenila* has no contribution by the quadrate (see Basisphenoid), contrary to Lapparent de Broin and Werner (1998).

PTERYGOID (figs. 224–229)

Preservation: Parts of both right and left pterygoids are present in TUB Vb 641, but both are incomplete. The anteromedial plate is present on both sides, and on the right side most of the quadrate process is present. When described by Lapparent de Broin and Werner (1998) only the left processus trochlearis pterygoidei was present, but the right one has now been found, which helps correct a misconception about its orientation (see below).

Ventral surface contacts: As in other Taphrosphyini, the pterygoid of *Arenila* contacts the palatine anteriorly, the basisphenoid posteromedially, the quadrate posterolaterally, and other pterygoid medially. As in *Nigeremys*, the midline pterygoid contact is very narrow in *Arenila*.

Ventral surface structures: The left processus trochlearis pterygoidei in TUB Vb 641 is distorted in its position as preserved. The posterolateral end has been rotated medially, making the processus seem larger and parallel to the midline. The apparent size increase is due to matrix and bone debris filling the opened contact between the pterygoid and palatine. The distortion has also affected the size of the foramen palatinum posterius, making it larger than in its original state (see Palatine). Also, the newly discovered right processus trochlearis pterygoidei shows a more “normal” position. When restored, the processus in *Arenila* is not unusually large, similar to *Nigeremys* when its erosion is accounted for.

The fossa pterygoidea is present in *Arenila* (see Quadrate), as in *Nigeremys*. The pterygoid forms the anterolateral part of the concavity. The foramen posterius canalis carotici interni (see Basisphenoid) is formed in the pterygoid-basisphenoid suture.

Dorsal surface contacts: Some of the dorsal part of the pterygoid in *Arenila* is visible. At the base of the processus trochlearis pterygoidei, there is a lateral contact with the jugal, an anterodorsal one with the postorbital, and probably a dorsomedial one with the parietal (see Parietal). The crista pterygoidea forms the ventral margin of the foramen nervi trigemini, with the parietal forming the anterior margin and the prootic the posterior margin. The foramen is relatively large, as in *Azabbaremys* (not visible in *Nigeremys*).

SUPRAOCCIPITAL (figs. 224–230)

Preservation: Most of the supraoccipital is present in TUB Vb 641, but its posterior margin is a broken edge so its complete limits are not known.

Contacts: As in other Taphrosphyini, the supraoccipital of *Arenila* contacts the parietal dorsally, the prootic anterolaterally, and the exoccipital posteroventrally. The presumed quadrate and opisthotic contacts are not preserved.

Structures: The crista supraoccipitalis in *Arenila* is longer than in *Nigeremys* and *Azabbaremys*, although the bone in *Nigeremys* may be eroded. The crista in *Arenila* is nearly twice the length that it is in *Azabbaremys*. A low ridge is present on the crista supraoccipitalis in *Arenila*, about one-third of the way above the foramen magnum. The trough below this ridge opens into the large concavity on the exoccipital (see Exoccipital). This ridge is not in *Azabbaremys* or *Nigeremys*.

EXOCCIPITAL (figs. 224, 229, 230)

Preservation: Both exoccipitals are present in TUB Vb 641 and are nearly complete with clear sutures.

Contacts: As in other Taphrosphyini, the exoccipital of *Arenila* contacts the supraoccipital dorsally, the quadrate ventrolaterally, and the basioccipital ventrally. The presumed lateral contact with the opisthotic is missing.

Structures: The foramen magnum of *Arenila* is very similar in size and shape to that in *Azabbaremys* and *Nigeremys* (which is somewhat eroded). The condylus occipitalis is formed completely by the exoccipitals. There is one foramen nervi hypoglossi very close to the much larger foramen jugulare posterius. In *Azabbaremys*, there are two foramina nervi hypoglossi and they are separated from the foramen jugulare posterius. In *Arenila*, the foramen nervi hypoglossi is facing almost laterally, just on the margin of the foramen jugulare posterius, a condition similar to that seen in *Taphrosphys*.

BASIOCCIPITAL (figs. 224, 227, 230)

Preservation: The basioccipital in TUB Vb 641 is present, nearly complete, with clear sutures. Its posterolateral margins are damaged on both sides but not much can be missing, due to the presence of the quadrate.

Sutures: As in other Taphrosphyini, the basioccipital in *Arenila* contacts the basisphenoid anteriorly, the quadrate laterally, and the exoccipitals dorsally.

Structures: The basioccipital in *Arenila* is pinched off by the exoccipitals on the neck of the condylus occipitalis and does not reach that structure. The tuberculum basioccipitale is only a low, horizontal ridge at the posterior margin of the basioccipital, very similar to that in *Azabbaremys*. The area is damaged in *Nigeremys*. Most of the basioccipital in *Arenila* forms a broad concavity, much deeper than the one in *Azabbaremys* but similar to the poorly preserved one in *Nigeremys*. As in *Azabbaremys* and probably *Nigeremys*, the basioccipital of *Arenila* is wide and short, in contrast to the much longer one in *Taphrosphys*.

PROOTIC (figs. 224, 229)

Preservation: Both prootics are present in TUB Vb 641, but the right one is nearly complete and has clear sutures while the left one is more crushed and obscured by matrix. The right prootic has no dorsal contact and ends in a broken margin.

Contacts: As in other Taphrosphyini, the prootic of *Arenila* contacts the parietal dorsomedially (visible on left side), the supraoccipital posterodorsally, and the pterygoid ventrally. The opisthotic is missing its contacts represented by broken margins on the prootic. The left and most of the right quadrate are also missing and the possibility of a quadrate-supraoccipital cannot be excluded.

Structures: The foramen nervi trigemini in *Arenila* is formed by the usual suspects: parietal anteriorly, pterygoid ventrally, and prootic posteriorly. The foramen is oblong and, as preserved on the right side, has a larger posterior part and a smaller, anteroventral part, probably reflecting the division of the trigeminal ganglion into two branches at this point (one branch separating medially, see Gaffney, 1979a). However, the left foramen nervi trigemini (which does not seem to be as well preserved as the right one) is an oval. Although it is hard to judge the relative sizes of this foramen among skulls widely varying in size, it seems that *Arenila* and *Azabbaremys* have relatively large foramina compared to *Taphrosphys*. *Phosphatochelys* also seems to have a relatively large foramen. The opening is not visible in *Nigeremys*.

The foramen stapedio-temporale in *Arenila* is represented only by a part of the ventrolateral margin on the right quadrate. The area of the prootic-quadrate suture is damaged and the full extent of the foramen is not determinable; however, it is clearly on the anterior face of the otic chamber and close to the foramen nervi trigemini.

OPISTHOTIC

Preservation: The opisthotic is not preserved in TUB Vb 641, except possibly as fragments on the right side.

BASISPHENOID (figs. 224, 227)

Preservation: The basisphenoid in TUB Vb 641 is nearly complete, but its posterolateral margins end in broken edges. On the right side only a small amount of basisphenoid can be missing because the quadrate is separated from the basisphenoid only by a narrow gap. Only the ventral surface of the basisphenoid is visible.

Contacts in ventral view: As in other Taphrosphyini, the basisphenoid contacts in *Arenila* are: pterygoids anterolaterally, quadrate posterolaterally, and basioccipital posteriorly. The basisphenoid-quadrate contact in *Arenila* is very narrow, as in *Azabbaremys* and *Labrostochelys*. The contact is indeterminate in *Nigeremys*. The basioccipital-basisphenoid suture in *Arenila* and *Nigeremys* is curved sharply, convex anteriorly, in contrast to all other Taphrosphyini in which it is straight.

Structures in ventral view: The foramen posterius canalis carotici interni is formed mostly by the basisphenoid in *Arenila*, with the anterolateral margin formed by the pterygoid. A short groove formed by the basisphenoid leads anteromedially into the foramen. Lapparent de Broin and Werner (1998:179, fig. 12a) figured the foramen posterius canalis carotici as being at the junction of three elements: quadrate, basisphenoid, and pterygoid. Further preparation and close examination of this area confirms that the quadrate is some distance posterior to the foramen. The foramen and groove are visible on both sides. In our interpretation, the area described by Lapparent de Broin and Werner (1998) as forming the foramen posterius canalis carotici interni is the narrow gap between the quadrate and basisphenoid. Nonetheless, TUB Vb 641 is not well preserved in this area and multiple interpretations are possible.

The basisphenoid in *Arenila* forms the medial wall of the fossa pterygoidea (the "podocnemidid fossa" of Lapparent de Broin and Werner, 1998), a large concavity also found in *Nigeremys* but no other Taphrosphyini (see Pterygoid or Quadrate). At the anteriormost margin of the basisphenoid in TUB Vb 641 are small, paired foramina, just adjacent to the pterygoid suture. Preparation of these show that each leads into a small anteriorly trending canal. The contents of these foramina are unknown.

LOWER JAW MORPHOLOGY

The lower jaw in pleurodires has never been treated systematically, although Fuchs (1931), Poglayen-Neuwall (1953), and Gaffney (1979a) have useful coverage. As with the skull, the following descriptions follow a standard pattern outlined in appendix 1. Tables 20 and 21 give comparisons of lower jaws in pleurodires, particularly those described here.

FAMILY EURAXEMYDIDAE

Euraxemys essweini

MATERIAL AVAILABLE: In FR 4922 (figs. 231, 232), the right ramus of the lower jaw is complete and the left ramus is gone posterior to the coronoid process. Both rami are well preserved, free of matrix with clear sutures.

DENTARY

Preservation: The right dentary is complete; the left one is missing its posterior margin.

Contacts: The dentary in *Euraxemys* contacts the coronoid posterodorsally, the surangular posteriorly, and the angular posteroventrally. There is a narrow contact with the prearticular on the medial surface, below the coronoid.

Structures: The dentaries in *Euraxemys* seem to be separated on the midline symphysis by a suture. As preserved, they are separate, with the contact area on both rami being a mixture of what looks like a sutural surface and broken bone. The jaws are also sutured in *Araripemys* and most chelids, but not in *Emydura*, while the jaws in bothremydids and podocnemidids are fused.

The symphysis in *Euraxemys* is rounded and not pointed or protuberant as in many other pleurodires. The jaw is not greatly thickened at the symphysis. In *Araripemys* the symphysis and jaw are quite thin, similar to chelids like *Chelodina* and *Hydromedusa*. *Euraxemys* has a thicker jaw, very close in proportions to *Emydura* and *Elseya*, but without the protuberant symphysis.

The triturating surface in *Euraxemys* is roughly parallel-sided, slightly wider anteriorly and narrowing posteriorly. The labial ridge is sharp and much higher than the lingual ridge, which is only the medial edge of the triturating surface. The surface itself is slightly concave and sharply tilted medially, much as in *Elseya latisternum* (AMNH 103700).

On the external surface, the dentary of *Euraxemys* forms the processus coronoideus with the coronoid bone on the medial surface of the processus. The processus coronoideus in Pelomedusoides does not vary a great deal and its size in *Euraxemys* is about the same as in pelomedusids and *Emydura*. Just below the processus is a distinct foramen, the foramen dentofaciale majus. Posterodorsally the dentary contacts the surangular and posteroventrally it contacts the angular.

The medial surface of the dentary has a distinct groove below the triturating surface, the sulcus cartilaginis meckelii. In *Euraxemys* the sulcus becomes prominent posterior to the symphysis, as in *Elseya*, rather than extending closer to it, as in *Pelusios*. The sulcus leads posteriorly into the foramen intermandibularis medius. Within the dentary, just anterior to this foramen is the foramen alveolare inferius, as it is in chelids and other Pelomedusoides. The medial contacts of the dentary are with the coronoid posterodorsally, the prearticular posteriorly, and the angular posteroventrally.

ANGULAR

Preservation: The right angular is complete in FR 4922; the left one lacks its posterior end.

Contacts: The angular of *Euraxemys* contacts the dentary anteriorly, the prearticular dorsally, the articular posteriorly, and the surangular dorsally on the lateral surface.

Structures: The angular of *Euraxemys* is a long, thin bone that begins anteriorly on the medial surface and bends posteroventrally to end below the articular bone. The foramen intermandibularis caudalis is formed in the prearticular-angular suture and it opens into the fossa meckelii. The angular in *Araripemys* extends more anteriorly than in *Euraxemys*, which is similar in extent to *Pelusios*. In *Emydura* and *Elseya* the large

TABLE 20
Comparison of Lower Jaws 1

	Proganochelys	Chelidae	Pelomedusidae	*Araripemys*	*Euraxemys*	Podocnemididae	*Kurmademys*	*Cearachelys*	AMNH 30029
Splenial absent	no	no	yes	yes	yes	yes	yes	yes	yes
Symphysis sutured	yes	yes, no	no	yes	yes	no	no	no	?
Triturating surface wide posteriorly	no	no	no	no	no	yes, no	yes	yes	no
Fossa meckelii widely open ventrally	no	no	no	no	no	no	no	no	no
Foramen nervi auriculotemporalis present		yes	yes	yes	yes	yes	yes	yes	?
Sulcus cartilaginis meckelii open at symphysis	yes	no	no	?	no	no	no	?	?
Deep triturating pits	no	no	no	no	no	no	no	no	no
Accessory ridges on dentary	no	no	no	no	no	yes, no	no	no	no
Posterior process of dentary widely exposed laterally	yes	yes	yes	yes	yes	yes	yes	yes	yes
Surangular extends anteriorly	no	no	no	no	no	yes	no	no	no
Processus retroarticularis long	no	no	no	no	no	yes	yes	yes	?
Foramen intermandibularis oralis or caudalis defined by bone	yes	yes	yes	yes	yes	yes	yes	yes	yes
Symphyseal wedge thick	no	no	no	no	no	no	no	no	?
Processus coronoideus high	no	no	no	no	no	no	no	no	no
Coronoid with wide lateral exposure	no	no	no	yes	no	no	no	no	no

TABLE 21
Comparison of Lower Jaws 2

	Foxemys	*Araiochelys*	*Bothremys cooki*	*Bothremys maghrebiana*	*Chedighaii barberi*	*Taphrosphys congolensis*	*Rhothonemys*	*Nigeremys*	AMNH 29989
Splenial absent	yes	yes	yes	yes	yes	?	?	?	yes
Symphysis sutured	no	no	no	no	no	no	no	no	no
Triturating surface wide posteriorly	yes	no	yes	yes	yes	no	no	?	yes
Fossa meckelii widely open ventrally	yes	yes	yes	yes	yes	yes	yes	?	yes
Foramen nervi auriculotemporalis present	no	no	?	no	no	?	no	?	?
Sulcus cartilaginis meckelii open at symphysis	no	no	no	yes	no	?	no	no	no
Deep triturating pits	no	yes	yes	yes	yes	no	no	no	yes
Accessory ridges on dentary	yes	no	no	no	no	?	no	no	no
Posterior process of dentary widely exposed laterally	no	no	no	no	no	?	no	?	?
Surangular extends anteriorly	yes	yes	?	yes	yes	?	yes	?	yes
Processus retroarticularis long	yes	yes	?	yes	yes	yes	yes	?	?
Foramen intermandibularis oralis or caudalis defined by bone	yes	no	?	no	?	?	no	?	yes
Symphyseal wedge thick	no	no	yes	no	no	?	no	?	no
Processus coronoideus high	no	no	yes	no	no	no	?	?	no
Coronoid with wide lateral exposure	yes	yes	?	yes	yes	?	?	?	yes

splenial lies above the angular. In all Pelomedusoides, including *Euraxemys*, the splenial is absent. The angular in *Euraxemys* goes posteriorly to the end of the jaw separating the prearticular and surangular and curves posterodorsally to contact the surangular on the lateral surface of the jaw.

SURANGULAR

Preservation: The right surangular is complete in FR 4922; only a fragment of the left one remains.

Contacts: The surangular in *Euraxemys* contacts the dentary anteriorly, the coronoid in a narrow contact anterodorsally, the angular posteroventrally, and the articular posteromedially.

Structures: The surangular in *Euraxemys* is a large element lying on the external surface at the posterior end of the jaw. The surangular is a flat plate that forms the lateral wall of the fossa meckelii and the lateral margin of the area articularis mandibularis. The fossa meckelii in *Euraxemys* is about the same size as in *Emydura* and slightly smaller than in pelomedusids. It is much smaller than in *Proganochelys*.

On the external surface of the surangular in turtles are a series of foramina that transmit branches of the mandibular branch of the trigeminal nerve (VII_3). These foramina are particularly variable in pleurodires but the largest is usually referred to as the foramen nervi auriculotemporalis. Fuchs (1931) described this area and these nerves in *Podocnemis*, and Poglayen-Neuwall (1953) described the area in a number of cryptodires and pleurodires. The foramen nervi auriculotemporalis transmits the nervus auriculotemporalis, which has at least two branches and an anastomosis (Fuchs, 1931: figs. 8, 10). In podocnemidids the foramen and associated canals are large and complex, in other pleurodires they are usually smaller. However, in *Euraxemys*, pelomedusids, and *Hamadachelys*, the foramen approaches the podocnemidid condition. In *Emydura*/*Elseya*, and *Araripemys* the foramen is small and comparatively inconspicuous. In *Emydura*/*Elseya* the foramen is a simple hole penetrating the surangular from the fossa meckelii to the external surface. In pelomedusids the foramen nervi auriculotemporalis opens on the external surface above a short canal that extends ventrally beneath a short strap of bone to open more ventrally still on the external surface of the surangular. The contents of this short canal are presumed to be a branch of the nervus auriculotemporalis, but the canal is not described in the literature. In *Euraxemys* there is a similar canal on the right surangular (the left one is missing), but it is opened laterally by erosion and does not form a completely enclosed canal as preserved. Nonetheless, it is very similar to that canal in pelomedusids. Anteriorly, the foramen nervi auriculotemporalis penetrates medially and anteriorly into another canal in the surangular that also opens on the external surface of the surangular a short distance from the foramen nervi auriculotemporalis proper. The senior author has not seen a parallel structure in other pleurodires. This canal also is presumed to contain a branch of the nervus auriculotemporalis. Fuchs (1931) described one of the multiple foramina nervi auriculotemporalis (the largest) as being combined with the apertura lateralis canalis transversi into a larger, combined foramen that opens on the external surface of the surangular. The senior author has not been able to determine its contents, but these structures clearly vary among podocnemidids and on each side of the jaw as well.

In *Euraxemys* there is only one foramen penetrating the surangular from the external surface into the fossa meckelii. This is also the case in *Podocnemis*. There is a posterior foramen and canal just behind the foramen nervi auriculotemporalis in AMNH specimens of *Podocnemis*, and this appears to be the apertura lateralis canalis transversi of Fuchs (1931). However, this canal goes posteriorly into the articular bone and does not enter the fossa meckelii. Is this the posterior path of the nervus auriculotemporalis? Is it Fuchs' apertura lateralis canalis transversi? It does not sound like it.

The surangular forms the entire lateral wall of the fossa meckelii. The internal surface of the fossa is visible in *Euraxemys*. Its lateral wall is formed anteriorly by the dentary, which has a vertical suture with the surangular just anterior to the dorsal opening of the fossa meckelii. The anterior opening of the fossa is the foramen intermandibularis

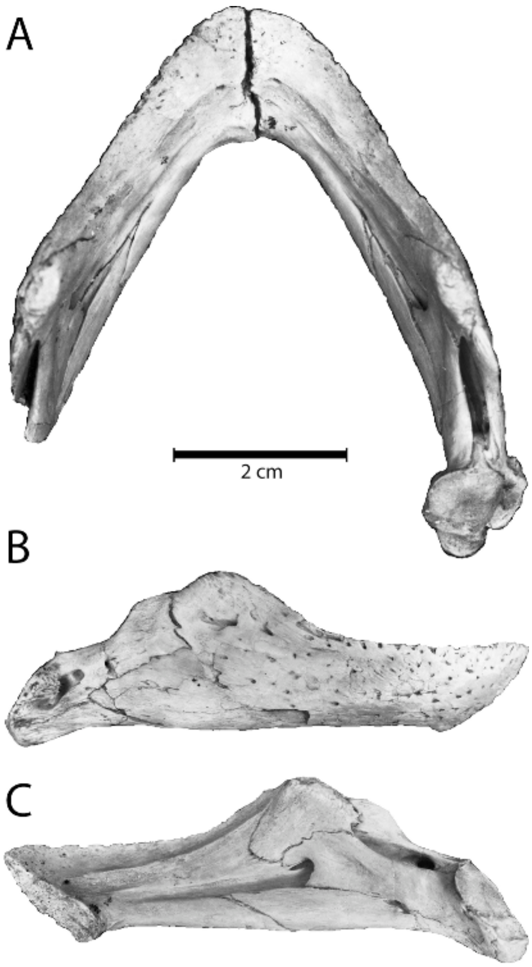

Fig. 231. *Euraxemys essweini*, n. gen. et sp. FR 4922, lower jaws. **A**, dorsal; **B**, right lateral; **C**, right medial. Scale is for parts B and C only. [E.S. Gaffney, del.]

medius formed laterally by the dentary and medially by the prearticular. The very narrow floor of the fossa slopes ventrally into the foramen intermandibularis caudalis and is mostly formed by the angular. Between the angular and prearticular is the foramen intermandibularis caudalis. The posterior wall of the fossa meckelii is formed by the articular sandwiched between the prearticular and surangular. The canal for the chorda tympani lies lateral to the articular. The surangular forms the lateral quarter or so of the area articularis mandibularis, as in most turtles. In *Euraxemys* there is a clear suture between the articular and surangular.

CORONOID

Preservation: Both coronoids are complete in FR 4922.

Contacts: The coronoid in *Euraxemys* contacts the dentary anterolaterally, the prearticular ventromedially, and the surangular posterolaterally.

Structures: The coronoid bone in *Euraxemys* lies on the medial surface of the dentary, forming the medial half of the processus coronoideus. It contacts the dentary anterolaterally, the prearticular ventromedially, and the surangular posterolaterally. The processus coronoideus does not vary a great deal in size among *Euraxemys*, *Emydura*/*Elseya*, pelomedusids, and *Araripemys*. It is slightly higher in these taxa than in *Podocnemis*. The coronoid extends anteriorly to a greater extent in pelomedusids, chelids, and *Araripemys* than it does in *Euraxemys*. As in chelids and pelomedusids, the coronoid is only barely visible in lateral view in *Euraxemys*. More of it is exposed laterally in *Araripemys*.

ARTICULAR

Preservation: The right articular in FR 4922 is complete; the left one is gone.

Contacts: The articular in *Euraxemys* contacts the surangular laterally, the angular anteroventrally, and the prearticular medially.

Structures: The articular is a triangular-shaped element lying at the posterior end of the jaw. In *Euraxemys* it is exposed dorsally and posteriorly and is sandwiched between the surangular laterally and the prearticular medially. It contacts the angular anteroventrally. As in chelids, the area articularis mandibularis of *Euraxemys* is more flat than convex and faces posterodorsally. The area is not strongly convex as in pelomedusids and podocnemidids. Rather, the surface is gently convex, dropping off laterally to the part of the surface on the surangular.

The articular pinches out anteriorly where a thin section of it forms the posterior wall to the fossa meckelii. At the posteroventral end of the fossa meckelii, laterally in the suture between articular and prearticular, is the foramen anterius chorda tympani. The foramen posterius chorda tympani is on the outside of the jaw, on the posteromedial edge of the area articularis mandibularis. It is also

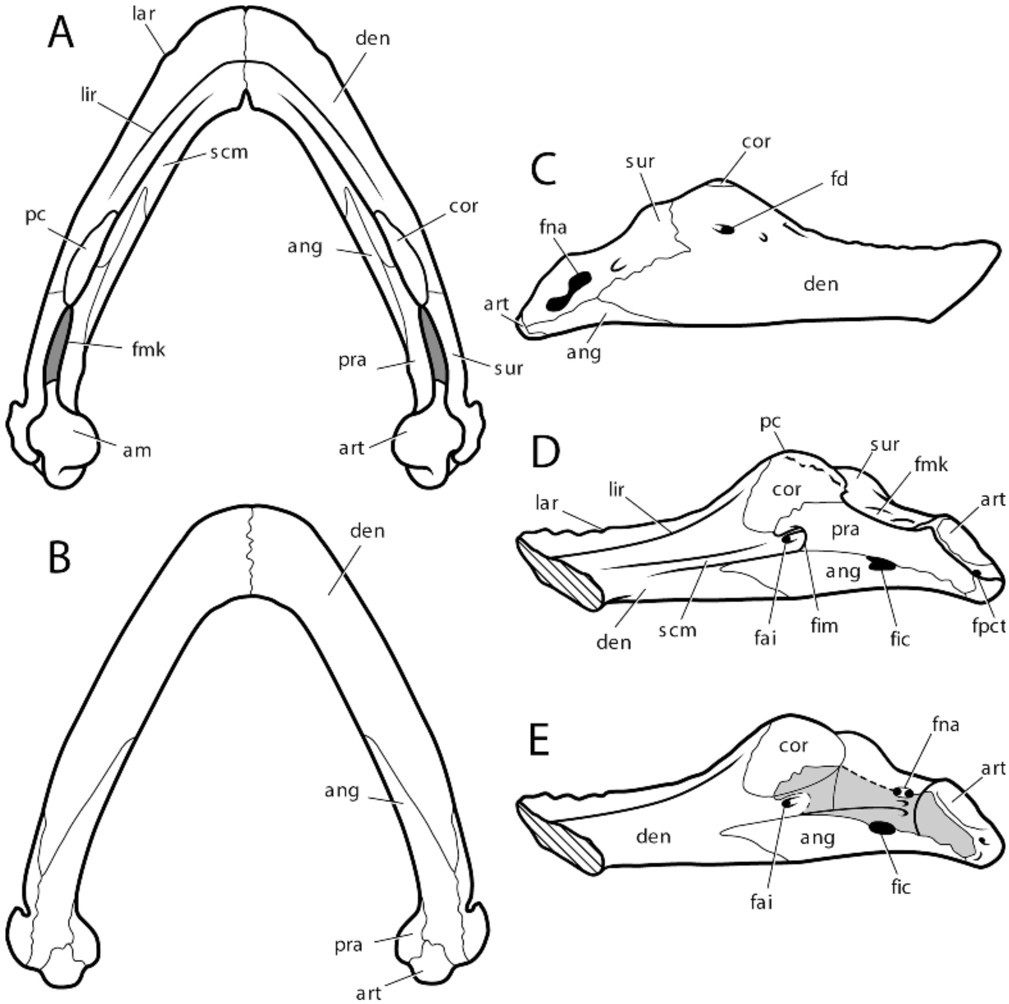

Fig. 232. *Euraxemys essweini*, n. gen. et sp. FR 4922 holotype, lower jaws. **A**, dorsal; **B**, ventral; **C**, right lateral; **D**, right medial; **E**, right medial with prearticular removed to show fossa meckelii. [E. Heck, del.]

formed by the prearticular medially and the articular laterally and lies at the base of a depression on the retroarticular process. This is similar to the chorda tympani foramina in *Hamadachelys*. In chelids and *Araripemys* the foramen posterius chorda tympani is more anterior and not adjacent to the articular surface. *Emydura*/*Elseya* and *Hamadachelys* have retroarticular processes much as in *Euraxemys*, while *Araripemys* and pelomedusids lack them. A very similar condition of the entire back end of the jaw is in AMNH 63579, *Erymnochelys madagascariensis*. However, in *Podocnemis* the retroarticular process is depressed and separated below the level of the area articularis mandibularis.

PREARTICULAR

Preservation: The right prearticular in FR 4922 is complete; the left one is missing its posterior half or so.

Contacts: The prearticular in *Euraxemys* contacts the coronoid anterodorsally, the articular posteromedially, and the angular ventrally.

Structures: The prearticular in *Euraxemys* is a long, thin sheet extending from the coronoid bone posteriorly on the medial surface to the retroarticular process. Anteriorly it forms the posterior margin of the foramen intermandibularis medius, which opens into the fossa meckelii. In *Emydura*/*Elseya* this area is formed by the splenial, but in Pelomedusoides the prearticular extends anteriorly to replace it. The prearticular in *Euraxemys* extends anteriorly farther than in *Araripemys* and pelomedusids. The dorsal edge of the prearticular forms the medial margin of the upper opening of the fossa meckelii. It is slightly higher than in *Emydura*/*Elseya* and slightly lower than in *Araripemys*.

The ventral margin of the prearticular in *Euraxemys* is a long straight suture with the angular. About halfway along it is an opening, the foramen intermandibularis caudalis. It opens between the medial jaw surface and the ventral part of the fossa meckelii. The foramen is in about the same position in chelids, pelomedusids, *Araripemys*, and *Euraxemys*. On the medial surface of the prearticular, in the floor of the fossa meckelii, the foramen anterius chorda tympani is formed between the prearticular and the articular.

The posterior end of the prearticular covers the articular laterally. It does not bear any of the area articularis mandibularis. A small part of the prearticular is exposed dorsally at the posteromedial corner of the area articularis mandibularis where it forms the medial half of the foramen posterius chorda tympani. The articular forms the lateral half of the foramen. Presumably the canalis chorda tympani is formed between the prearticular and the articular.

FAMILY BOTHREMYDIDAE

TRIBE KURMADEMYDINI

Kurmademys kallamedensis (fig. 233)

MATERIAL AVAILABLE: ISI 155E, a nearly complete jaw, lacking the left posterior end; ISI 155D, both rami and symphysis, lacking the left coronoid region and some of the triturating surface; ISI 155F, a partial right ramus.

DENTARY

Preservation: The dentary is almost entirely complete on the right side of ISI 155E, with some cracking. The left side is complete as well, except for a small part of the posterior end. In ISI 155D, the dentary is mostly present but is slightly eroded and missing the area around the left processus coronoideus and part of the right triturating surface. In ISI 155F, only the symphysis and most of the right dentary are present.

Contacts: The dentary contacts in *Kurmademys* are the same as in *Cearachelys*: coronoid posterodorsally, surangular posterolaterally, angular posteroventrally, and prearticular posteromedially. The surangular contact is vertical beneath the processus coronoideus, not as far anterior as in *Bothremys*, but more anterior than in *Euraxemys*.

Structures: The symphysis in *Kurmademys* is similar to that in *Cearachelys*, an upturned labial ridge with a U-shaped concavity behind a narrow triturating surface defined by a low lingual ridge. Based on ISI 155F and ISI 155D, the symphyseal anterior margin is projected dorsally into a curved hook, but in ISI 155E the symphysis is low, as in *Cearachelys*. The triturating surface of *Kurmademys* is very similar to that in *Cearachelys*, with a low labial ridge turned dorsally at its posterior end, and a higher lingual ridge. In ISI 155E the shallow concavity at the posterior end of the triturating surface is about as deep as it is in *Cearachelys*, but in ISI 155D the concavity is shallower and the triturating surface is narrower.

The sulcus cartilaginus meckelii does not meet on the symphysis; it is similar to that in *Cearachelys*, being formed anteriorly by the dentary, and merging with the symphyseal concavity. On the lateral surface of the dentary is the foramen dentofaciale majus, just below the posterior end of the triturating surface, as in *Cearachelys*.

ANGULAR

Preservation: A nearly complete right angular and a partial left one are present in ISI 155E. Both angulars are complete in ISI 155D, but the left one is slightly damaged. The anterior half of the right angular is present in ISI 155F.

Contacts: As in *Cearachelys*, the angular in *Kurmademys* contacts the dentary anteriorly, the prearticular dorsally, the articular posteriorly, and the surangular dorsolaterally. The prearticular contact is long, as in *Cearachelys* and *Euraxemys* but in contrast

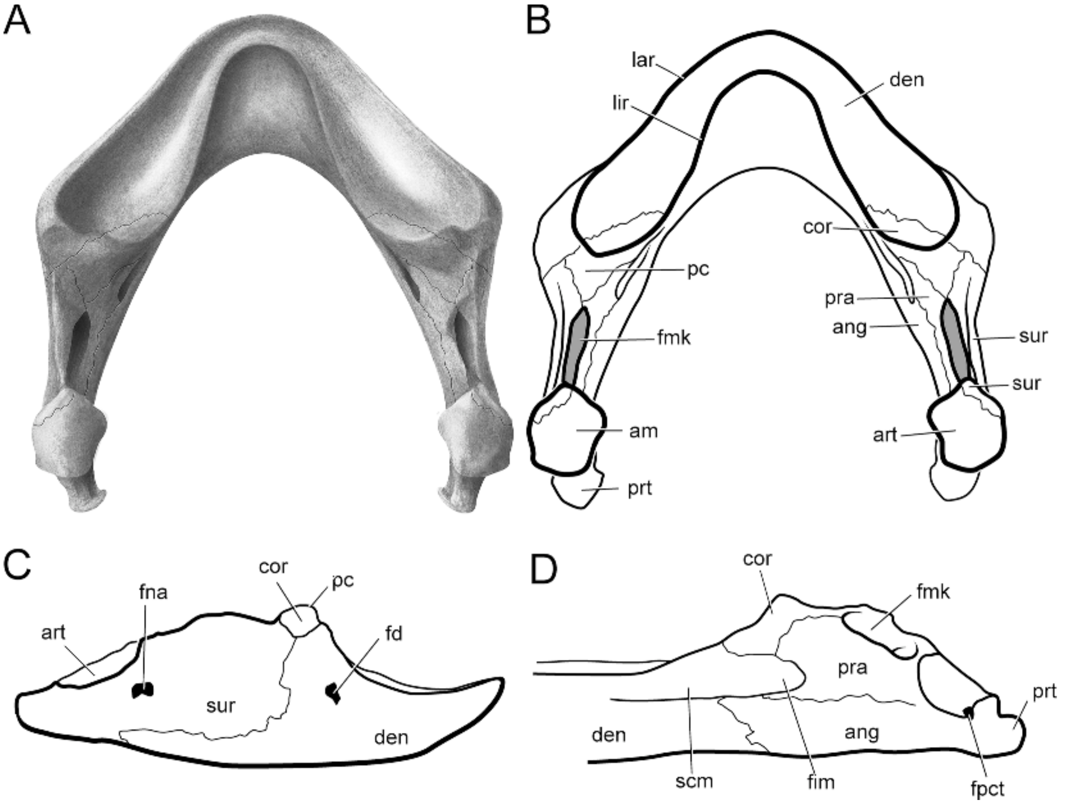

Fig. 233. *Kurmademys kallamedensis* Gaffney, Chatterjee, and Rudra, 2001. Partially restored lower jaws based primarily on ISI R155E with additions from ISI R155D and ISI R155F. **A**, dorsal [N. Hennelly, del.]; **B**, dorsal; **C**, right lateral; **D**, right medial. [A.M. Phillips, del.]

to Bothremydini and Taphrosphyini. The articular contacts are not visible.

Structures: The angular in *Kurmademys* is very similar to that in *Cearachelys*, wrapping around from the sulcus cartilaginis meckelli to the surangular laterally.

SURANGULAR

Preservation: The right surangular is complete in ISI 155E, with the left one missing posteriorly. In ISI 155D the right one is cracked and missing a few areas; the left one is only present ventrally.

Contacts: As in *Cearachelys*, the surangular of *Kurmademys* contacts the dentary anteriorly, the coronoid anterodorsally, the angular posteroventrally, and the articular posteromedially.

Structures: The surangular in both *Cearachelys* and *Kurmademys* has a shallow, laterally facing depression that covers the lateral surface of the jaw, which is better defined in *Kurmademys*. The foramen nervi auriculotemporalis is just anteroventral to the area articularis mandibularis, as in *Cearachelys*. Also as in *Cearachelys*, the surangular forms the anterolateral margin of the area. The surangular extends posteriorly on the lateral surface of the processus retroarticularis.

CORONOID

Preservation: Both coronoids are present and largely complete in ISI 155E. In ISI 155F the right coronoid is present, as it is in ISI 155D.

Contacts: The coronoid contacts in *Kurmademys* are very similar to those in *Cearachelys*. There is only a small lateral exposure of the coronoid above the dentary-surangular contact. On the medial surface the prearticular has a posteroventral contact, as in *Cearachelys*.

Structures: The processus coronoideus in *Kurmademys* is formed medially by the coronoid, as in *Cearachelys*. The processus is better defined and slightly higher in *Cearachelys* than in *Kurmademys*. The coronoid in *Kurmademys* extends anteroventrally onto the triturating surface, just dorsal to the concavity on the dentary. In *Cearachelys* the coronoid barely forms the margin of the triturating surface. A very narrow surangular-prearticular contact prevents the coronoid from entering the dorsal opening of the fossa meckelii.

ARTICULAR

Preservation: The articular is present and complete on the right side of ISI 155E and on the left side of ISI 155D.

Contacts: Most of the articular sutures in ISI 155D and ISI 155E are fused, but the surangular contact, anterolaterally, is visible.

Structures: The area articularis mandibularis in ISI 155E is slightly narrower than in *Cearachelys*, but in ISI 155D it is the same width. The surface shape is the same in both *Kurmademys* and *Cearachelys*.

PREARTICULAR

Preservation: None of the *Kurmademys* jaws has a complete prearticular, but the preserved areas are overlapping. The right prearticular in ISI 155E is the best, missing only some of the fossa meckelii margin. In the right prearticular of ISI 155D, the anterior part is missing. In ISI 155F, the anterior part is present on the right ramus.

Contacts: As in *Cearachelys*, the prearticular of *Kurmademys* contacts the coronoid anteriorly, the articular posteromedially, and the angular ventrally. The angular contact is long, as in *Cearachelys*, enclosing the fossa meckelii to a greater extent than in Bothremydini and Taphrosphyini. The foramen intermandibularis medius, therefore, is more anterior in *Kurmademys* and *Cearachelys* than in the latter tribes.

TRIBE CEARACHELYINI

Cearachelys placidoi (fig. 234)

MATERIAL AVAILABLE: THUg 1798, complete let ramus, symphysis, right ramus with articular region intact but most of remaining bone eroded away, associated with a skull and shell; BSP 1976 I 160, a nearly complete lower jaw with symphysis fragmented and distorted, associated with skull and shell.

DENTARY

Preservation: The dentary of BSP 1976 I 160 is nearly complete except for the symphysis. The left dentary in THUg 1798 is nearly complete, but most of the right one is missing.

Contacts: The dentary in *Cearachelys* contacts the coronoid posteromedially, the surangular posterolaterally, and the angular posteroventrally. The surangular contact is nearly vertical directly beneath the processus coronoideus, as in *Kurmademys*. The anterior extent of the surangular and restriction of the dentary exposure in lateral view occur in the Bothremydini, Taphrosphyini, and *Kurmademys*, but not in *Euraxemys*, chelids, or pelomedusids.

Structures: As in all bothremydids, the symphysis is fused, with no sign of a suture in *Cearachelys*. The symphyseal area in *Cearachelys* is similar to that in *Kurmademys*, with a narrow triturating surface and a deep U-shaped concavity behind it. The concavity is below the level of the triturating surface, not raised into a symphyseal wedge, as in *Bothremys cooki*.

The dentary in *Cearachelys* extends posteriorly on the lateral surface ventral to the surangular to a point below the middle of the area articularis. On the medial surface it is hidden from view below the coronoid process by contact between the prearticular and angular. The labial ridge is lower than the lingual ridge except at the symphysis. Its lateral edge is slightly concave in outline. The lingual ridge is taller than the labial ridge except where they are even at the symphysis. It is tallest where it contacts the coronoid and then becomes progressively lower anteriorly. It remains distinct to the symphysis where it produces the U-shaped central concavity.

The triturating surface in *Cearachelys* is wider posteriorly than anteriorly. There is a very weakly developed pit in the posterolateral part of the dentary. The medial and posterior walls of the pit are formed by the dentary. There is no lateral wall, no roof, and

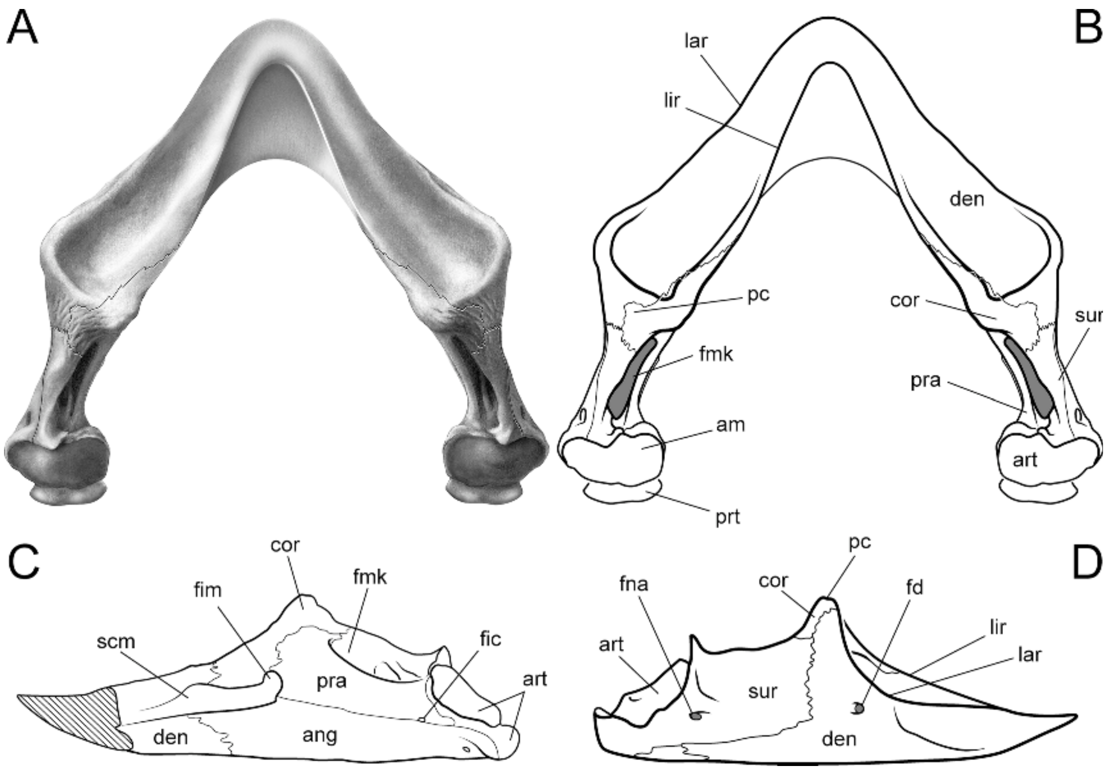

Fig. 234. *Cearachelys placidoi* Gaffney, Campos, and Hirayama, 2001. Partially restored lower jaws based on BSP 1976 I 160 with additions from THUg 1798. **A**, dorsal; **B**, dorsal; **C**, right medial; **D**, right lateral. [K. Luckenbill, del.]

no contribution by the coronoid. Although the symphysis is pointed anteriorly, there is no symphyseal hook. The symphysis is blunt, as in *Kurmademys*.

The sulcus cartilaginis meckelii in *Cearachelys* is open for a very short distance. It is closed at the symphysis and where the prearticular meets the angular ventral to the coronoid process. The foramen intermandibularis medius and the foramen alveolare inferius are not well defined. A foramen dentofaciale majus is present on the lateral side of the dentary just ventral to the small dentary pit. The presence of nutritive foramina indicates that the rhamphotheca of the mandible covered the dorsalmost part of the dentary and the adjacent coronoid.

The dentary of *Cearachelys* differs significantly from that of *Bothremys*. Well, not all that significantly. In general, the triturating surface is narrower throughout its length. Furthermore, the labial ridge of the dentary is much lower, and neither it or the coronoid contributes to the dentary pit as they do in *Bothremys*. *Cearachelys* is similar to *B. maghrebiana* but differs from *B. cooki* in having the U-shaped structure formed by the labial ridges meeting on the symphysis. The symphyseal wedge seen in *B. cooki* is absent in *Cearachelys*. This U-shaped structure is found in other bothremydid jaws, including those of *Araiochelys, Chedighaii barberi*, and AMNH 29989. It is absent from jaws of the Taphrosphyini.

The dentary of *Cearachelys* is like that of *B. cooki, Araiochelys*, and *Rhothonemys* in having the sulcus cartilaginis meckelii closed anteriorly. It is like *Araripemys* and *Kurmademys* in having the posterior limit of the sulcus below the coronoid process where it is closed by an anterior meeting of the prearticular and angular.

The dentary of *Cearachelys* is most similar to that of *Kurmademys*. They have a high lingual ridge and a low labial ridge rising posteriorly to form a distinctive, anterodorsally facing concave portion of the triturating surface. This morphology may be interpreted as primitive for Bothremydidae. A greater degree of depression at the posterior end of the triturating surface would produce the pit seen in *Araiochelys* and *Bothremys*.

The lower jaws of BSP 1976 I 160 and THUg 1798 differ in the width of the triturating surface and the posterior height of the lingual ridge. The larger jaw, BSP 1976 I 160, has a wider triturating surface posteriorly, and the lingual ridge here is higher. The jaw of THUg 1798 is about one-third smaller than that of BSP 1976 I 160 and these differences may be due to growth, as in many living turtles.

The foramen dentofaciale majus is formed entirely by the dentary, anterior to the surangular contact, and below the posterior end of the labial ridge.

ANGULAR

Preservation: The angular is nearly complete on both sides of BSP 1976 I 160 and on the left side of THUg 1798 (only part of the right one remains). The posterior sutures are unclear in both jaws.

Contacts: The angular in *Cearachelys* contacts the dentary anteromedially, the prearticular dorsally, the articular posteriorly, and the surangular dorsolaterally. These contacts are very similar to those in *Kurmademys*. In the tribes Bothremydini and Taphrosphyini the prearticular contact is much shorter. The posterior contacts are not well defined but are visible in parts of both specimens.

Structures: The angular forms the ventral margin of the fossa meckelii and its anterior continuation, the sulcus cartilaginis meckelii. As in *Kurmademys*, the sulcus stops well short of the symphysis. The angular wraps ventrally around the posterior part of the jaw. This area is very similar in both *Cearachelys* and *Kurmademys*.

SURANGULAR

Preservation: The surangular is present on both sides of BSP 1976 I 160, but there is postmortem damage in the form of pitting and cracks. The left surangular is present in THUg 1798; its surface is slightly damaged, but it is nearly complete.

Contacts: The surangular in *Cearachelys* contacts the dentary anteriorly in a nearly vertical suture below the coronoid, as in *Kurmademys*. The surangular is more extensive anteriorly than in *Euraxemys*, chelids, and pelomedusids, but not as much as in the Bothremydini. The surangular contacts the angular posteroventrally and the articular posteriorly.

Structures: In the lateral surface of the surangular, just anteroventral to the area articularis mandibularis, is the foramen nervi auriculotemporalis. The foramen can be traced within the surangular to its entrance into the fossa meckelii, anterior to the articular. The Bothremydini and Taphrosphyini seem to lack this foramen.

The surangular in *Cearachelys* extends posterolaterally around the articular and forms part of the edge of the area articularis mandibularis. It does not seem to form as much of the area as it does in *Euraxemys*. The surangular extends laterally onto the processus retroarticularis, which is almost entirely formed by the articular. The fossa meckelii in *Cearachelys* is narrow, as in other bothremydids, with the lateral surangular wall being higher than the medial prearticular wall.

CORONOID

Preservation: The coronoid is nearly complete on the left side of BSP 1976 I 160; it is slightly damaged on the right side. In THUg 1798 the left coronoid is nearly complete, but the right one is only represented by a fragment.

Contacts: The coronoid in *Cearachelys* contacts the dentary anterolaterally, the prearticular ventromedially, and the surangular posterolaterally. The coronoid is less exposed laterally in both *Cearachelys* and *Kurmademys* than it is in Bothremydini and Taphrosphyini, due to a greater coronoid-surangular contact. The coronoid-dentary contact in *Cearachelys* does not extend as far laterally as it does in *Kurmademys*.

Structures: The coronoid forms the short but distinct processus coronoideus in *Cearachelys*. The coronoid extends ventrally on the medial surface to form the dorsal edge of the sulcus cartilaginis meckelii. It does not form any of the triturating surface.

ARTICULAR

Preservation: The articular is present on both sides of BSP 1976 I 160 and THUg 1798, with some damage on the left side of BSP 1976 I 160.

Contacts: The articular contacts the surangular laterally, the angular ventrally, and the prearticular medially.

Structures: The area articularis mandibularis in *Cearachelys* is convex, with a very low ridge anteroposteriorly, as in most *Bothremys*. The area is wider in BSP 1976 I 160 than in *Kurmademys*, but in THUg 1798 it is intermediate in width. The articular forms a narrow part of the posterior edge of the fossa meckelii.

The processus retroarticularis in *Cearachelys* is short, wide, and relatively massive, similar to that in *Chedighaii*. It is as long as in *Kurmademys* but wider. There is a well-defined groove on the medial surface for the chorda tympani, which is a foramen in *Kurmademys*.

PREARTICULAR

Preservation: The prearticular is nearly complete on the left side of BSP 1976 I 160; the right one has some damage anteriorly. In THUg 1798 the prearticular is present on both sides; the left one is more complete than the right one.

Contacts: The prearticular in *Cearachelys* contacts the coronoid anterolaterally and the articular posteriorly. The angular contact runs for nearly the entire length of the prearticular, as in *Kurmademys* and *Euraxemys*, but in contrast to the much shorter contact of Bothremydini and Taphrosphyini.

Structures: The prearticular is a flat bone that forms the medial wall of the fossa meckelii, enclosing it for the entire length of the bone, in contrast to the more open fossa of Bothremydini and Taphrosphyini. In the angular-prearticular suture is a small foramen, the foramen intermandibularis caudalis.

TRIBE BOTHREMYDINI

Foxemys mechinorum (figs. 235, 236)

MATERIAL AVAILABLE: PAM 511B, lower jaws lacking articular ends, figured in Tong et al. (1998: figs. 7, 8); MC M2114, jaw lacking both articular ends; MC M2115, left ramus lacking articulation; MC M2116, left ramus lacking articulation; MC M2117, jaw lacking articular ends; MC M2118, nearly complete jaw, lacking left articular end, some cracks with displacement in symphysis.

DENTARY

Preservation: The six specimens all have most of the dentary preserved, although the preservation is best in MC M2118. In the four small jaws, MC M2114, MC M2115, MC M2116, and MC M2117, the dentary is either present only on one side or it is damaged. The largest jaw, PAM 511B, is complete on the right side but is missing the dorsal part of the left ramus. The best jaw, MC M2118, has a nearly perfect right ramus, but there is breakage with some displacement on the symphysis.

Contacts: The dentary in *Foxemys* contacts the coronoid posterodorsally, with more of the dentary being exposed ventral to the coronoid than in *Kurmademys* but not as much as in *Bothremys*. The surangular contact posterolaterally is more extensive anteriorly in *Foxemys* than in *Kurmademys*, but not as extensive as in *Bothremys*. The dentary contacts the angular posteroventrally, as in the other bothremydids.

Structures: The dentary is preserved in all six *Foxemys* jaws and it shows a size range, as measured from the symphysis to the processus coronoideus (see appendix 8), from 39 to 19 mm, presumably related to age. This increase in size is correlated with an increase in width of the triturating surface, so that the largest, PAM 511B, also has the relatively widest triturating surface. The width increase seems to be expressed in the lingual shelf in the smaller jaws. In the larger jaws, the labial edge is significantly swollen.

The symphysis of *Foxemys* has the symphyseal concavity of *Kurmademys*, but the lingual ridge on each side stops short of forming an anterior margin for the concavity, as in *Kurmademys*. The concavity is a sloping surface from the labial ridge posteriorly to the end of the symphysis. The labial ridge is upturned slightly in *Foxemys*, as in *Kurmademys*, rather than being flat, as in *Araiochelys* and *Bothremys*. The symphysis thickness is

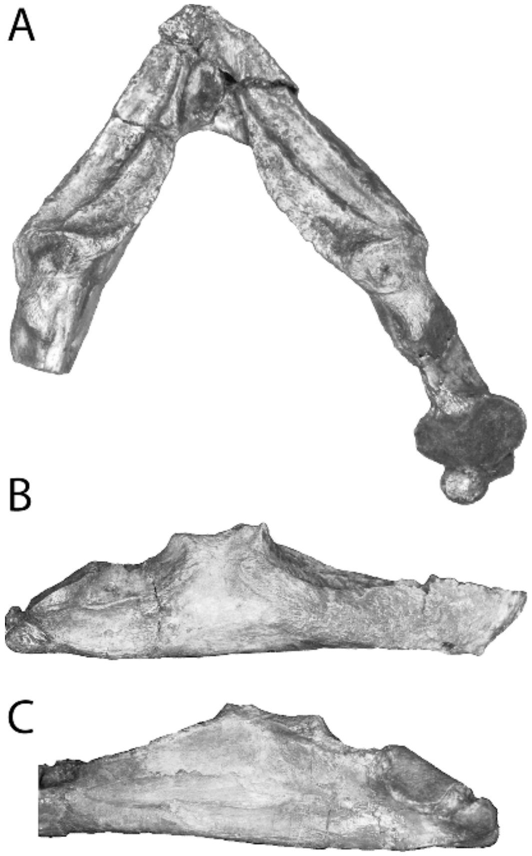

Fig. 235. *Foxemys mechinorum* Tong, Gaffney, and Buffetaut, 1998. MC M2118, lower jaws. **A**, dorsal; **B**, right lateral; **C**, right medial. [E.S. Gaffney, del.]

greater in *Foxemys* than in the other bothremydids.

The labial ridge in *Foxemys* is an acute ridge with a slight upturn that decreases in height posteriorly. In *Kurmademys, Cearachelys, Araiochelys, Bothremys*, and *Chedighaii*, the labial ridge is the edge of a relatively flat triturating surface, but in *Foxemys* the ridge is distinct on the margin of a trough that runs parallel to the ridge. None of the other bothremydids has the trough seen in *Foxemys*. Medial to the trough there is a wide, lingual shelf beginning anteriorly just behind the symphysis and sloping dorsally to the processus coronoideus. This shelf might be considered a flattened and broadened lingual ridge. The medial edge of the lingual shelf has no distinct ridge. This raised lingual shelf and parallel trough are unique to *Foxemys*. In PAM 511B (Tong et al., 1998: figs. 7, 8), the labial ridge is rounded, the trough is shallower and wider, and the lingual shelf is wider than in MC M2118.

In lateral view, the lingual shelf is higher than the labial ridge, agreeing with *Cearachelys, Kurmademys*, and other Bothremydini. The foramen dentofaciale majus lies entirely in the dentary, just anterior to the surangular contact. The medial surface of the dentary has a sulcus cartilaginis meckelii that stops short of the symphysis, as in *Kurmademys* and *Araiochelys*.

ANGULAR

Preservation: A nearly complete angular is present only on the right side of MC M2118, with the anterior part remaining on the left side. PAM 511B also has the anterior parts of both angulars. Small parts of the angular are also in MC M2114, MC M2116, and MC M2117.

Contacts: The angular in *Foxemys* is very similar to that in *Bothremys maghrebiana*. It contacts the dentary anteriorly, the prearticular dorsally, the surangular dorsolaterally, and, presumably, the articular posteriorly, although the articular sutures are fused in MC M2118, the only specimen with an articular. The angular in *Foxemys* lacks the long prearticular contact seen in *Kurmademys* and *Cearachelys*. This short contact in *Foxemys* is the same as in *Bothremys* and other Bothremydini and *Rhothonemys*.

Structures: The angular forms the ventral margin of the sulcus cartilaginis meckelii and lower edge of the jaw. The fossa meckelii has the more open condition, seen in other Bothremydini, rather than the more closed fossa of *Cearachelys* and *Kurmademys* and other pleurodires. The suture between the angular and prearticular is not perfectly preserved in MC M2118, but there is a foramen intermandibularis caudalis.

SURANGULAR

Preservation: The surangular is nearly complete only on the right side of MC M2118, but the anterior part is present on the left side as well in PAM 511B and MC M2114.

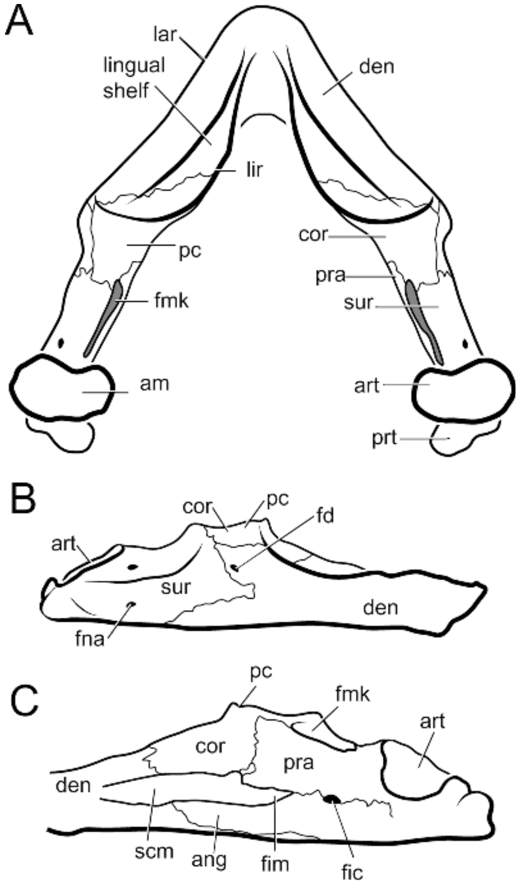

Fig. 236. *Foxemys mechinorum* Tong, Gaffney, and Buffetaut, 1998. MC M2118. Partially restored lower jaws. **A**, dorsal; **B**, right lateral; **C**, right medial. [A.M. Phillips, del.]

Contacts: The surangular in *Foxemys* contacts the dentary anteriorly, the angular ventrally, the coronoid anterodorsally, and, presumably, the articular posteromedially, although the sutures are fused.

Structures: The surangular lateral exposure in *Foxemys* is not as extensive as in other Bothremydini, but it is more extensive than in *Kurmademys* and *Cearachelys*. In those taxa the dentary-surangular contact is vertical beneath the processus coronoideus, while in *Foxemys*, the surangular sends a process anteriorly. The surangular forms the lateral wall of the fossa meckelii and the lateral margin of the upper opening to the fossa. In *Foxemys*, in contrast to other bothremydids, the surangular is very thick, and the upper opening is displaced medially and is narrower. The surangular thickening is extensive and forms an upper ventrolaterally sloping surface and a ventral, medially sloping surface with a low ridge between them, all unique to *Foxemys*, among bothremydids. There is a small foramen on the upper surface.

CORONOID

Preservation: Both coronoids are nearly complete in MC M2118. The right one is present in PAM 511B, and the left one is present in MC M2114.

Contacts: The coronoid contacts the dentary anteriorly and ventrally, the surangular posterolaterally, and the prearticular posteromedially. The surangular contact is narrow, as in *Kurmademys*, not wide, as in *Bothremys*.

Structures: The coronoid in *Foxemys* forms the posteromedial part of the triturating surface, in particular, the posterior part of the lingual shelf, ending just medial to the triturating surface trough. The posterior edge of the triturating surface is a ridge running just anterior to the very low processus coronoideus; the ridge is actually higher than the processus in lateral view. In *Bothremys*, there is no ridge at the edge of the triturating surface and the processus coronoideus is much higher. In *Kurmademys* and *Cearachelys* the morphology is more similar to that of *Foxemys*, but the processus is higher and not as distinct from the triturating surface ridge. The coronoid narrowly enters the margin of the upper opening of the fossa meckelii, as in other bothremydids.

ARTICULAR

Preservation: The articular is present only on the right side of MC M2118.

Contacts: Sutures are fused in the available jaw.

Structures: The area articularis mandibularis of *Foxemys* is roughly spherical, with the two facets separated by a low, parasagittal ridge seen in other bothremydids. The processus retroarticularis is short and broad, as in *Cearachelys*, broader than in *Rhothonemys* and much broader and shorter than in *Bothremys maghrebiana*. The foramen posterius chorda tympani is either a true foramen or a notch lateral to the processus retroarticularis; breakage prevents being sure which is the case.

Prearticular

Preservation: A nearly complete prearticular is present only on the right side of MC M2118; the anterior part of the bone is on the left ramus.

Contacts: The prearticular in *Foxemys* contacts the coronoid anterodorsally and the articular posteriorly, although no articular sutures are present. The ventral contact with the angular is only at the posterior end of the prearticular, as in the other Bothremydini and *Rhothonemys*. This is in contrast to the longer contact seen in *Cearachelys* and *Kurmademys*.

Structures: The prearticular in *Foxemys* is very similar to that bone in *Bothremys* and *Araiochelys*. In these taxa the prearticular exposes the anteroventral part of the fossa meckelii, in contrast to *Cearachelys* and *Kurmademys*, which have the fossa covered by the prearticular. Nonetheless, the *Foxemys* prearticular is slightly larger than in *B. maghrebiana* and has a small foramen anterodorsally near the foramen alveolare inferius. However, the foramen intermandibularis caudalis is also present, as in *Cearachelys* and *Kurmademys* and in contrast to other Bothremydini.

Araiochelys hirayamai (figs. 237, 238)

Material Available: THUg 3338, a nearly complete lower jaw.

Dentary

Preservation: A complete dentary is present.

Contacts: As in *Bothremys maghrebiana*.

Structures: The dentary in *Araiochelys* is closest in morphology to that in *Bothremys maghrebiana*, among the known lower jaws. There is a well-developed pit formed medially by a high lingual ridge and laterally by the labial ridge. The pit and the entire jaw ramus are narrower than in *B. maghrebiana*, or any other Bothremydini, by at least one-half. The relative height of the lingual ridge and the thickness of both ridges are comparable to those in *B. maghrebiana*, so *Araiochelys* is not simply a less ossified version of *B. maghrebiana*. The horizontal part of the triturating surface is a curved trough in *Araiochelys*, not flat, as in *B. maghrebiana* and *B. cooki*. The symphyseal wedge, low in *B. maghrebiana*, is much thinner in *Araiochelys*, although its extent on the symphysis is the same. Due to the narrower triturating surfaces in *Araiochelys*, the area posterior to the lingual ridges along the front of the symphyseal groove is wider than in *B. maghrebiana*. On the posterior and medial surface of the dentary, the sulcus cartilaginis meckelii does not meet on the midline as it does in *B. maghrebiana*.

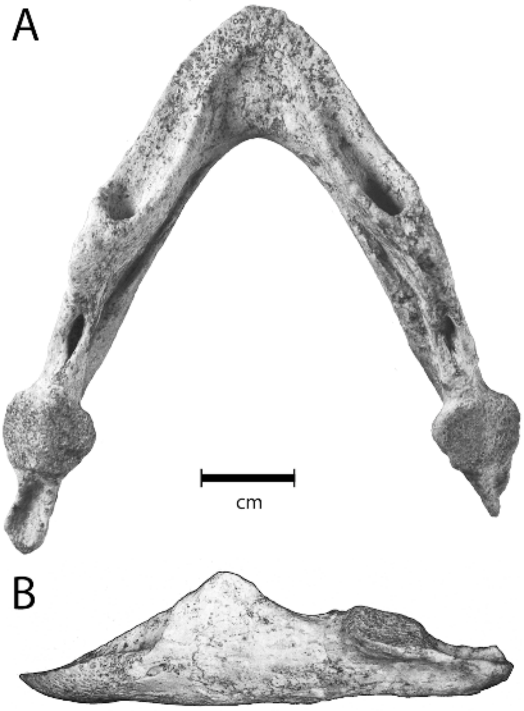

Fig. 237. *Araiochelys hirayamai*, n. gen. et sp. THUg 3338 holotype, lower jaws. **A**, dorsal; **B**, left lateral. [E.S. Gaffney, del.]

Angular

Preservation: Both angulars are present and nearly complete.

Contacts: As in *Bothremys maghrebiana*. The posterior sutures of the angular, articular, and surangular are unclear, however.

Structures: The angular in *Araiochelys* is similar to that bone in *B. maghrebiana*.

Surangular

Preservation: The surangular is complete on both sides, although the sutures are not entirely clear on the right side.

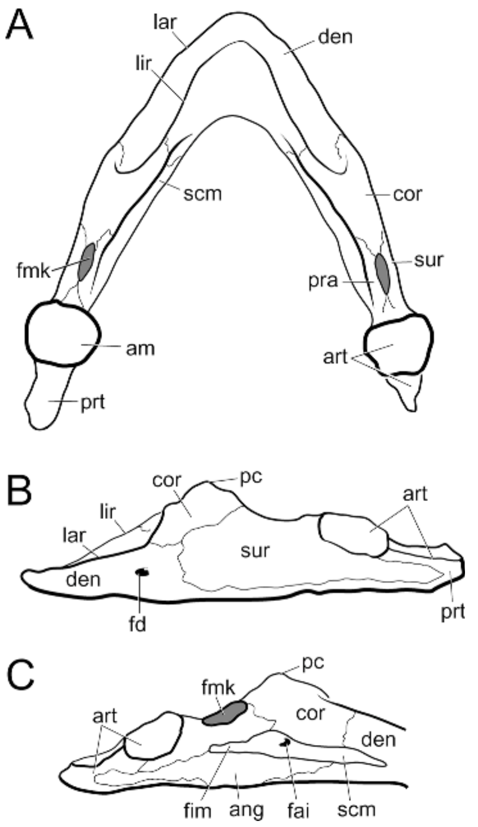

Fig. 238. *Araiochelys hirayamai*, n. gen. et sp. THUg 3338 holotype, lower jaws. **A**, dorsal; **B**, left lateral; **C**, left medial. [A.M. Phillips, del.]

Structures: The surangular of *Araiochelys* is similar to that bone in *Bothremys maghrebiana*. The extent of surangular lying on the lateral side of the processus retroarticularis in *Araiochelys* is less than that in *B. maghrebiana*.

CORONOID

Preservation: Both coronoids are complete, although the right one is slightly damaged in THUg 3338.

Contacts: As in *Bothremys maghrebiana*.

Structures: The coronoid in *Araiochelys* is very similar to that in *B. maghrebiana*.

ARTICULAR

Preservation: The left articular is complete; the right one is missing some of the processus retroarticularis.

Contacts: As in *Bothremys maghrebiana*.

Structures: The articular in *Araiochelys* is very similar to that in *B. maghrebiana*.

PREARTICULAR

Preservation: Both prearticulars in THUg 3338 are present but have some damage to their medial surfaces.

Contacts: As in *B. maghrebiana*.

Structures: The prearticular in *Araiochelys* is very similar to that in *B. maghrebiana*.

Bothremys cooki (fig. 239)

MATERIAL AVAILABLE: AMNH 2521, a lower jaw lacking the posterior ends, part of type of *Bothremys cooki* Leidy, 1865 (pl. 18, figs. 5, 8), described in Hay (1908: fig. 97, pl. 23, fig. 3) and in Gaffney and Zangerl (1968: fig. 22).

DENTARY

Preservation: The dentary and other bones of the lower jaw in AMNH 2521 are pitted and covered in places with a thin layer of plaster, presumably applied in the days of Leidy as a preservative. Both in 1966 and at the present the senior author has been unable to find any damn sutures. However, there are some cracks on the ventral surface and below the processus coronoideus in the right place for sutures. The right dentary has some pitting near the symphysis and the labial edge, and the left one has cracks and some lateral pits. The symphyseal damage is on the surface; the original morphology does not appear to have been affected significantly. On the ventral surface, the pitting is deeper and more extensive, particularly on the right side.

Contacts: Sutures are not visible.

Structures: The jaw in *Bothremys cooki* is most similar to the jaw of *B. maghrebiana*. The high lingual ridge and rising labial ridge forming the large cone-shaped pit are very similar. The extent that the pit extends posteriorly under the coronoid is the same. Where the labial and lingual ridges form the edges of the pit, they are slightly more flared in *B. cooki* than in *B. maghrebiana*.

The only prominent difference between the two jaws is in the symphyseal area. In *B. cooki* the lingual ridge is low and not defined anteriorly because of a thick wedge of bone medially. In *B. maghrebiana*, the lingual ridge is clearly defined, meeting on the midline

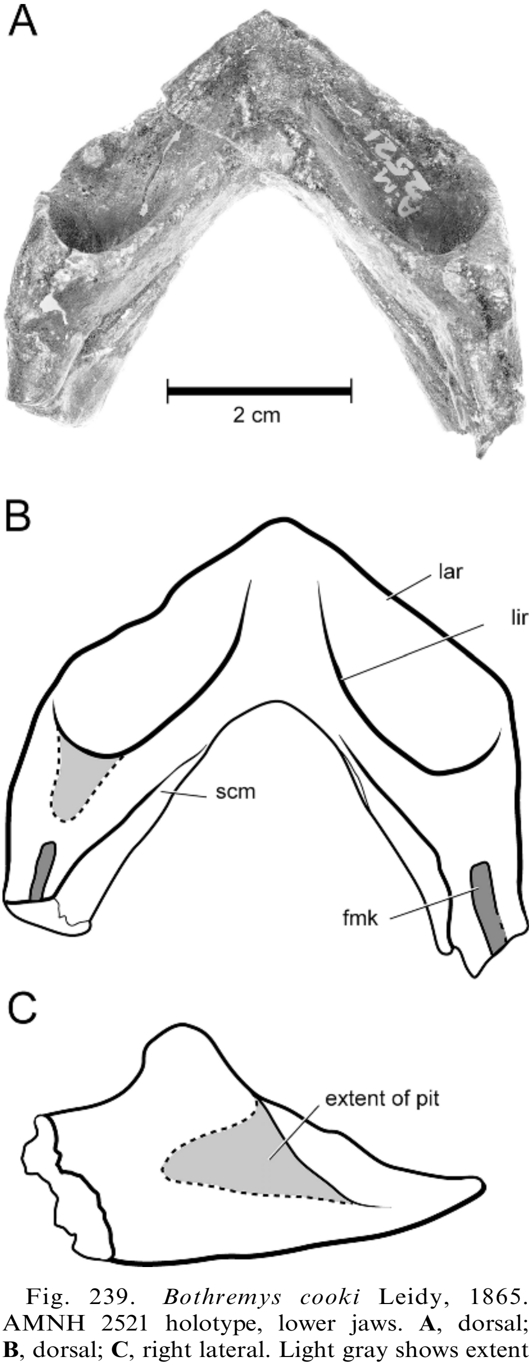

Fig. 239. *Bothremys cooki* Leidy, 1865. AMNH 2521 holotype, lower jaws. **A**, dorsal; **B**, dorsal; **C**, right lateral. Light gray shows extent of pit. [A.M. Phillips, del.]

anteriorly to define a posteromedial concavity, absent in *B. cooki*. This symphyseal wedge also occurs in UA 8708, a partial lower jaw from Madagascar (fig. 247; see also Gaffney and Forster, 2003). The anterior margin of the jaw in *B. cooki* ends in an obtuse angle with a terminal point, different from the rounded jaw margin in other Bothremydini. This point seems to be original; there is no evidence that it is a postmortem preservational or preparational artifact.

On the medial surface of the dentary, the sulcus cartilaginis meckelii does not appear to extend to the symphysis and join, as in *B. maghrebiana*. The sulcus is not well preserved, but the foramen alveolare inferius is visible on both sides.

ANGULAR

Preservation: The anterior part of the angular is present on both sides in *Bothremys cooki*, although much of this area is covered by plaster or is missing on the left side.

Contacts: Except for a suspicious crack on the ventral surface of the right ramus, there are no visible sutures for the angular.

Structures: The angular in *Bothremys cooki* forms the ventral margin of the sulcus cartilaginis meckelii and is similar to that area in *B. maghrebiana*.

SURANGULAR

Preservation: The anterior part of the surangular is present on both sides in *Bothremys cooki*, although the left side is more damaged and has a layer of plaster on it.

Contacts: Sutures are not visible.

Structures: The surangular in *Bothremys cooki* forms the lateral margin of the fossa meckelii. The anterior part of the dorsal opening of the fossa is visible on both sides in *B. cooki*. The area of the bone is very similar to that in *B. maghrebiana*.

CORONOID

Preservation: Most of both coronoids seem to be present in *Bothremys cooki*. The processus coronoideus is broken on the left side and damaged medially on the right.

Structures: The processus coronoideus of *Bothremys cooki* is higher and narrower in lateral view than in *B. maghrebiana, Chedighaii*, and *Araiochelys*. None of the bothremydid jaws, including AMNH 29989, has a high processus coronoideus.

ARTICULAR

Preservation: The articular is missing in AMNH 2521.

PREARTICULAR

Preservation: The anterior part of both prearticulars is present in *Bothremys cooki*; the right one has more bone, however.

Contacts: Sutures are not visible.

Structures: As in *Bothremys maghrebiana*, the prearticular of *B. cooki* shows an anteriorly open fossa meckelii, although the area is not well preserved.

Bothremys maghrebiana (figs. 240, 241)

MATERIAL AVAILABLE: AMNH 30522, right ramus and symphysis nearly complete, left ramus lacking labial ridge and processus retroarticularis.

DENTARY

Preservation: The dentary in AMNH 30522 is nearly complete on the right side, missing only the tip of the symphysis. On the left side the lateral one-third of the dentary is missing from the symphysis to the coronoid.

Contacts: The dentary in *Bothremys maghrebiana* contacts the coronoid posterodorsally via broad sutures both medially and laterally where the two elements join in the formation of a deep pit. It contacts the surangular posterolaterally in a relatively short vertical suture ventral to the coronoid and a long horizontal ventral suture where the dentary extends posteriorly between the surangular and the angular. The dentary contacts the angular posteroventrally along a long suture. A narrow surangular contact with the dentary in *Bothremys maghrebiana* is visible in the medial wall of the sulcus cartilaginis meckelii.

Structures: As in all Bothremydidae, the two rami of the dentary in *Bothremys maghrebiana* are fused in a long symphysis with no evidence of a suture. Dorsally, the posterior extent of the dentary is limited by the coronoid on the triturating surface; the coronoid makes up the posterior part of this surface. Ventrally, the dentary extends far more posteriorly, between the surangular and angular. It reaches posteriorly to the level of the anterior edge of the area articularis mandibularis. Within the sulcus cartilaginis meckelii the dentary can be seen to extend posteriorly below the fossa meckelii.

The labial ridge of the dentary in *Bothremys maghrebiana* is an anteriorly facing horizontal ridge, except where it rises vertically at its posterior end to the coronoid process. This very low anterior edge gives the jaw an open, plowlike profile. The lingual ridge is high adjacent to the coronoid, but becomes lower anteriorly as it approaches the symphysis. The two lingual ridges meet in a narrow but well-defined U-shaped ridge that opens posteriorly. This U-shaped structure extends anteriorly nearly to the tip of the symphysis. The symphysis in *Bothremys maghrebiana* is deeply concave between the lingual ridges, forming a moderately thick symphyseal wedge, thicker than in *Araiochelys*.

The large pits are the most obvious feature of the lower jaws, with the whole anterior half of the jaw being involved in their formation. The triturating pit in *Bothremys* has been described and commented on by Leidy (1865), Baur (1891), Hay (1908), and Gaffney and Zangerl (1968). The pit is formed mostly by the dentary. There is no distinct labial ridge anteriorly; the surface is essentially horizontal. Posteriorly the labial margin curves upward and forms the lateral side of the conical-shaped pit. The lingual ridge extends posteriorly and dorsally, forming the medial edge of the pit. The coronoid bridges the two ridges and forms most of the roof of the pit. The pit in *Bothremys maghrebiana* is very similar to that in *B. cooki*. The pit in *Araiochelys* is much narrower and occupies relatively less of the triturating surface. However, the lower jaw of AMNH 29989, unassociated with a skull, is a massive expression of the morphology seen in *Bothremys*. The lower jaws of *Chedighaii* have pits similar to *Bothremys*, and the species *barberi* was placed in *Bothremys* by Gaffney and Zangerl (1968) on the basis of the lower jaw pits.

The anterior tip of the symphysis in *B. maghrebiana* is missing, but enough is preserved to show that a symphyseal hook was absent. In posterior view the dentary can be seen to have an open sulcus cartilaginis meckelii that remains open throughout its length to the symphysis, in contrast to *Chedighaii* and *Araiochelys*.

The foramen intermandibularis medius and foramen alveolare inferius are not defined by bone, apparently because the sulcus

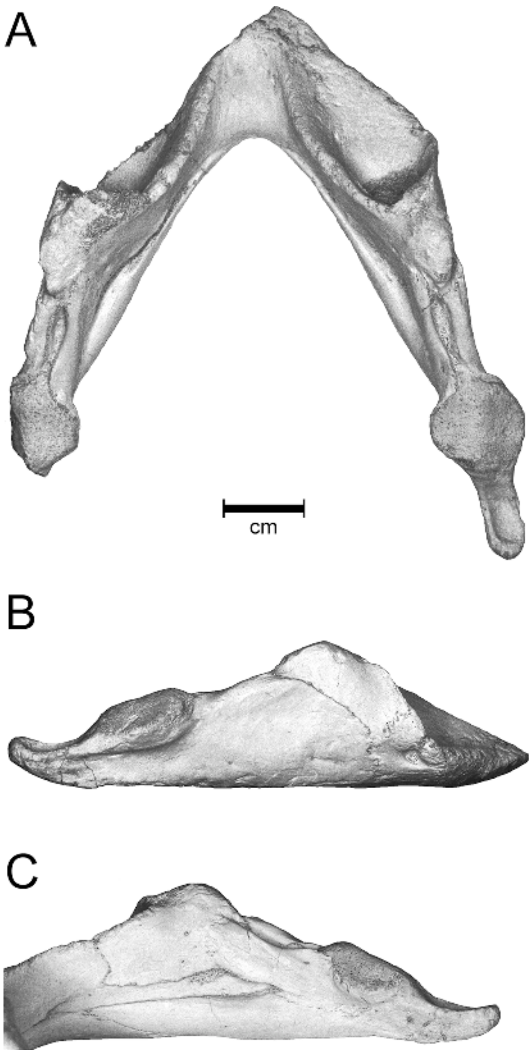

Fig. 240. *Bothremys maghrebiana*, n. sp. AMNH 30522, lower jaws. **A**, dorsal; **B**, right lateral; **C**, right medial. [E.S. Gaffney, del.]

cartilaginis meckelii is widely open between the coronoid and prearticular dorsally and the angular ventrally. A well-developed foramen dentofaciale majus is visible on the right dentary in *Bothremys maghrebiana*, ventral to the labial ridge at a point just anterior to the sutures of the surangular and coronoid.

The limits of the rhamphotheca are difficult to determine on this specimen of *Bothremys maghrebiana*. Enlarged nutritive foramina suggest that it extended posteriorly over the dentary pit and at least to the anterior edge of the coronoid. The coronoid makes up the entire dorsal quarter of the dentary pit and all of the coronoid process. Therefore, it seems unlikely that the dentary itself served as a site of insertion of the jaw adductor musculature.

Although the dentary of *Bothremys maghrebiana* is similar to that of the type of the genus, *B. cooki*, the most apparent difference is the U-shaped area formed by the lingual ridges meeting on the symphysis, the symphyseal wedge. In *B. cooki* the symphyseal wedge is much thicker than in *B. maghrebiana*, which has an excavated concavity between the ridges rather than bone that is as high as the lingual ridges as in *B. cooki*. The dentary of *B. maghrebiana* differs further from other bothremydids in having a sulcus cartilaginis meckelii that is open to the symphysis. In other bothremydids this sulcus closes posterior to the symphysis.

ANGULAR

Preservation: The angular of *Bothremys maghrebiana* is completely preserved and undistorted on the right side of the lower jaw. On the left side it is nearly complete, missing only the portion that makes up the retroarticular process.

Contacts: The angular in *Bothremys maghrebiana* contacts the dentary all along its medial surface. Ventrally there is a long diagonal suture between these elements that extends from below the anterior edge of the area articularis mandibularis nearly to the symphysis. A dorsal suture between these elements marks the ventral limit of the sulcus cartilaginis meckelii. The angular forms a suture with the prearticular dorsally. This suture is horizontal just posterior to the closure of the sulcus cartilaginis meckelii, but it turns vertically on the medial surface of the area articularis where it contacts the articular. The angular meets the surangular posteroventrally in a long suture that extends from below the anterior edge of the area articularis to the posterior end of the long retroarticular process. This suture continues dorsally and then anteriorly to the posterior edge of the articular.

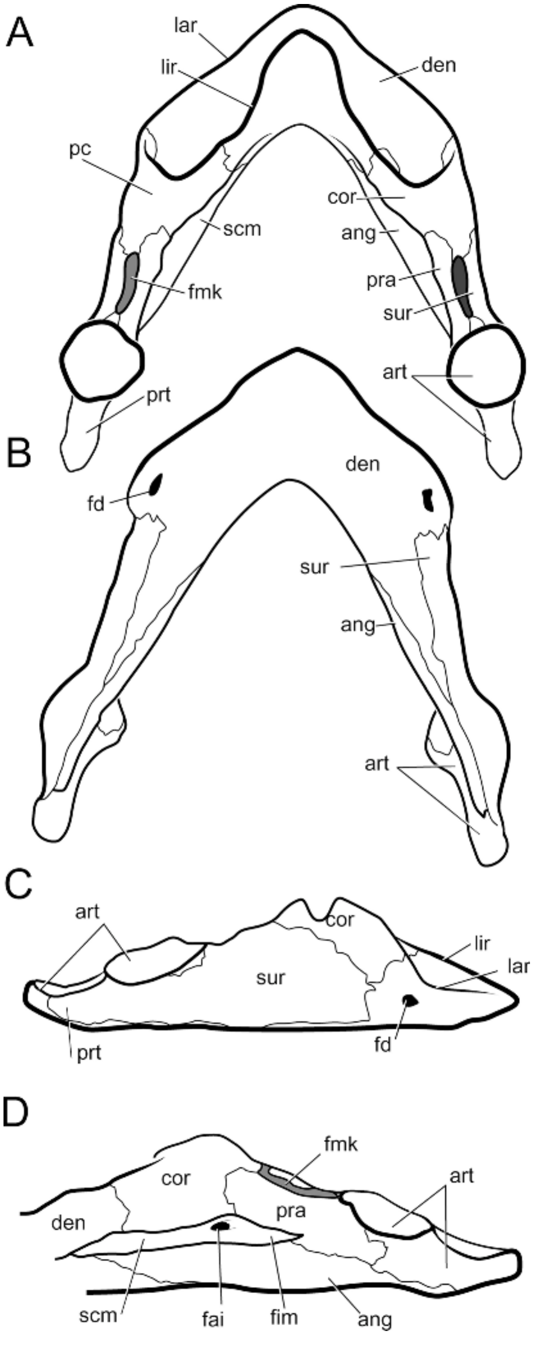

Fig. 241. *Bothremys maghrebiana*, n. sp. AMNH 30522. Partially restored lower jaws. **A**, dorsal; **B**, ventral; **C**, right lateral; **D**, right medial. [A.M. Phillips, del.]

Structures: The angular forms most of the ventral margin of the sulcus cartilaginis meckelii in *Bothremys maghrebiana*. However, since this sulcus is widely open, neither the foramen intermandibularis caudalis nor the foramen intermandibularis oralis is defined by bone. Posterior to the sulcus this element expands medially to support the medial side of the articular. The angular extends posteriorly along the ventral margin of the processus retroarticularis. The angular of *Bothremys maghrebiana* is nearly identical to the anterior portion of this element that is preserved in *B. cooki*. The angular is slightly thicker in *B. cooki* and contacts the prearticular more anteriorly. The posterior parts of the jaw of *B. cooki* are not preserved.

SURANGULAR

Preservation: The surangular of *Bothremys maghrebiana* is complete on the right side and nearly so on the left. On the left side only the portion posterior to the area articularis is missing.

Contacts: The surangular of *Bothremys maghrebiana* has a short anterior contact with the dentary just posterior to the foramen dentofaciale majus. It also has a long ventral suture with the dentary that extends posteriorly to a point below the anterior edge of the area articularis mandibularis. It has an anterodorsal suture with the coronoid that extends from near the foramen dentofaciale majus to the fossa meckelii. The surangular meets the angular posteroventrally where these elements join to form the ventral margin of the processus retroarticularis. Posteromedially the surangular meets the articular, also on the processus retroarticularis.

Structures: The surangular of *Bothremys maghrebiana* forms the lateral wall of the fossa meckelii. There is no foramen nervi auriculotemporalis visible on the lateral surface of this element. The foramen nervi auriculotemporalis is absent in Bothremydini and Taphrosphyini, but it is present in *Cearachelys* and *Kurmademys*, as well as pelomedusids, *Araripemys*, euraxemydids, and chelids. The surangular does not contribute directly to the area articularis mandibularis, but it supports the articular laterally. It also lies on the lateral wall of the processus retroarticularis, but it does not contribute significantly to this structure.

The surangular in *Bothremys maghrebiana* is a relatively large bone, extending anteriorly below the coronoid and below the processus coronoideus. This is also the case in the other Bothremydini and *Rhothonemys*, one of the Taphrosphyini. In *Kurmademys* and *Cearachelys*, the surangular is more extensive anteriorly than in *Euraxemys* and pelomedusids, but not to the degree seen in Bothremydini and Taphrosphyini. In *Cearachelys, Kurmademys*, chelids, pelomedusids, *Araripemys, Euraxemys*, and podocnemidids, the dentary extends posteriorly on the lateral surface of the jaw to separate the surangular and angular. In Bothremydini and Taphrosphyini the dentary is less extensive and more restricted to the ventral surface.

CORONOID

Preservation: The coronoid of *Bothremys maghrebiana* is completely preserved on the right side but is missing the anterolateral part that articulates with the lingual ridge of the dentary on the left side.

Contacts: The coronoid in *Bothremys maghrebiana* contacts the dentary anteriorly where it forms the dorsal part of the triturating pit. It broadly contacts the dentary both on the lingual ridge medially and on the labial ridge laterally. It contacts the surangular posterolaterally from just posterior to the foramen dentofaciale majus to the anterior end of the fossa meckelii. It also contacts the prearticular posteromedially between the fossa meckelii and the sulcus cartilaginis meckelii.

Structures: The coronoid in *Bothremys maghrebiana* forms all of the low, rounded processus coronoideus. It also forms a narrow part of the anterior end of the fossa meckelii between the surangular and the prearticular, and it contributes significantly to the mandibular triturating surface by forming the overhanging, posterodorsal one-third of the large, deep pit.

The coronoid of *Bothremys maghrebiana* is smaller than that in *B. cooki*. The coronoid extends farther anteroventrally in *B. maghrebiana*, but it has a very much lower coronoid process. It is more similar in size, height, and contacts to the coronoid of *Araiochelys*. The coronoid of *Foxemys* is smaller and lower than that in *Bothremys* and *Araiochelys*.

ARTICULAR

Preservation: The articular of *Bothremys maghrebiana* is completely preserved on the right side of the jaw, but it is missing its lateral half on the left side.

Contacts: The articular contacts the surangular laterally between the fossa meckelii and the processus retroarticularis. It contacts the angular medially and ventrally and the prearticular anteromedially. It is not possible to see any contact between the articular and the dentary.

Structures: The articular of *Bothremys maghrebiana* forms all of the area articularis mandibularis. The area is nearly round, being convex dorsally with an anteroposterior ridge in the middle. The articular also forms the posterior part of the fossa meckelii between the surangular and prearticular. It forms nearly all of the processus retroarticularis. A small foramen posterius chorda tympani is visible on the posterior suture between the articular and angular at the anterior end of the processus retroarticularis.

The area articularis mandibularis of *Bothremys maghrebiana* can be compared to only a few other bothremydids that have this element preserved. It is round in *Chedighaii barberi* (FMNH PR 247, the type) and *Araiochelys*, as well as in *B. maghrebiana*. In *Rhothonemys* the area articularis mandibularis is oval-shaped, with the long axis of the oval being oriented about 45° medial to the midline.

The processus retroarticularis in *Bothremys maghrebiana* is formed almost entirely by the articular, with a narrow layer of the angular on the ventral surface. The processus is long in *B. maghrebiana*, about as long as in *Araiochelys*. Both have a shallow concavity on the dorsal surface. In *Rhothonemys* the processus retroarticularis is shorter and broader, similar to that in *Cearachelys* and *Kurmademys*. In chelids, pelomedusids, *Euraxemys*, and *Araripemys*, the processus is very short or absent. *Chedighaii barberi* is not well preserved, but it has a large, broad processus, similar to that in *Rhothonemys*.

PREARTICULAR

Preservation: The prearticular of *Bothremys maghrebiana* is well preserved and complete on both sides.

Contacts: The prearticular contacts the coronoid anteromedially, the articular posteromedially, and the angular posteroventrally.

Structures: The prearticular in *Bothremys maghrebiana* forms the medial wall of the fossa meckelii and the posterodorsal limits of the sulcus cartilaginis meckelii and the foramen intermandibularis medius. The sulcus is widely open and, as in the other Bothremydini and Taphrosphyini, the foramen intermandibularis oralis and foramen intermandibularis caudalis are not defined by bone. The prearticular of *Bothremys maghrebiana* is comparable to that of *Araiochelys* and *B. cooki* insofar as the latter is preserved. In these forms the extent of contact between the prearticular and angular is reduced relative to that seen in *Araripemys, Kurmademys*, and *Cearachelys*. This contact is reduced to the point that the sulcus cartilaginis meckelii closes below the fossa meckelii; in the latter genera the sulcus cartilaginis meckelii closes below the coronoid process.

SPLENIAL

Preservation: The anteromedial part of the mandible of *Bothremys maghrebiana* is very well preserved and complete on both sides. It can be said confidently that it does not have a splenial.

Chedighaii barberi (figs. 242–244)
(See Note Added in Proof)

MATERIAL AVAILABLE: FMNH PR 247, complete lower jaws (fig. 242) with badly eroded surface and some edges missing, associated with partial skull and shell, jaw described and figured in Gaffney and Zangerl (1968: fig. 22); ALAB PV 2001.2, right ramus missing symphysis and posterior end, left ramus missing posterior end and part of lingual ridge (figs. 242–244), associated with skull and partial shell; CSU K-90-6-2, jaw symphysis; NJSM 12704, cast (Denton Collection) of damaged right ramus.

DENTARY

Preservation: Only the symphysis and the anterior part of the right ramus are preserved in CSU K-90-6-2. The bone surface is only slightly eroded and cracked; most of it seems to be the original surface. In FMNH PR 247 the dentary is nearly complete, lacking the anterior end, but almost the entire bone surface has been eroded. The left dentary of ALAB 2001.2 is missing the midline, the anterior part of the lingual ridge, and a small part of its posterior end, but the bone surface is well preserved. In the right ramus, the entire anterior half is missing, as is the posterior end, but the remainder is well preserved.

Contacts: Sutures are clear in ALAB 2001.2 and most are visible on one side or the other in FMNH PR 247. The dentary contacts in *Chedighaii barberi* are very similar to those in *Bothremys maghrebiana*.

Structures: The dentary of *Chedighaii barberi* that can be seen in CSU K-90-6-2 and ALAB 2001.2 has an anterior, flat surface, which is the triturating surface, marked by many nutrient foramina, and a posterior, smooth surface, with a shallow concavity, the area of the symphyseal wedge. The concavity is defined anteriorly and laterally by the lingual ridge; posteriorly there is no margin. The symphysis in CSU K-90-6-2 is very similar to that in ALAB 2001.2, which is also flat anteriorly with a posterior concavity. The anterior margin seems slightly more acute in ALAB 2001.2, but it is not complete, so this may be misleading. The triturating surface on the symphysis is slightly wider anteroposteriorly in CSU K-90-6-2 than in ALAB 2001.2. In both the area is about half the length of the concavity behind it.

The labial ridge in *Chedighaii barberi* is very low anteriorly, but the lingual ridge shows a dorsal rise, as in *Bothremys cooki* and *B. maghrebiana*. The symphyseal concavity in all the *Chedighaii* jaws does not form the thickened symphyseal wedge seen in *B. cooki*, and, to a lesser extent, *B. maghrebiana*. FMNH PR 247 seems to differ from CSU K-90-6-2 and ALAB 2001.2 in lacking a midline union of the lingual ridges, but most of this jaw is worn by abrasion (the anterior part particularly), and the anterior lingual ridges are very low, probably due to postmortem damage.

On the ventral surface of CSU K-90-6-2, the nutrient-rich area covered by the horny beak is differentiated from the smooth posterior surface by a very low ridge that

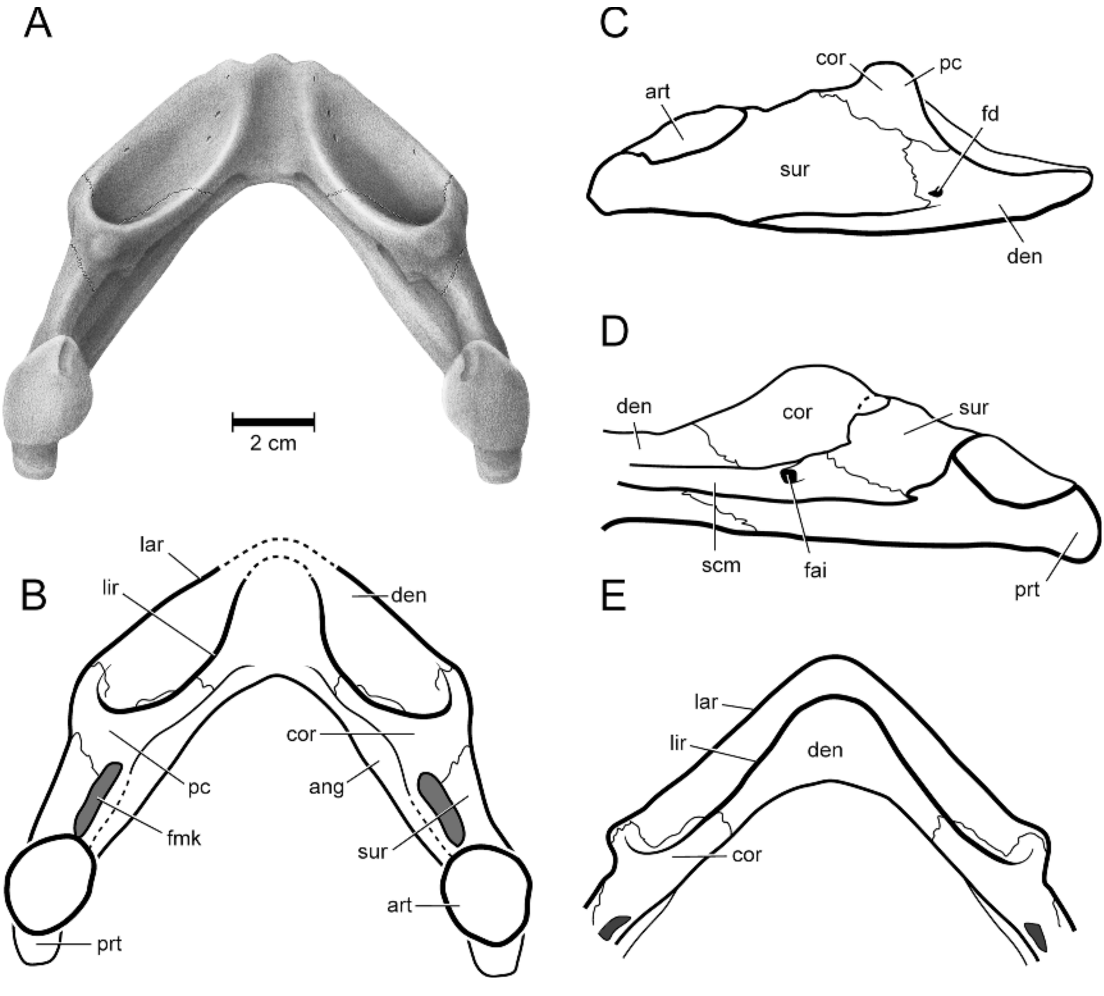

Fig. 242. *Bothremys* sp. FMNH PR247, lower jaws. **A**, dorsal; **B**, dorsal; **C**, right lateral; **D**, right medial; **E**, *Chedighaii* sp. ALAB PV 2001.2, restored lower jaws for comparison with FMNH PR247 in part B. See Note Added in Proof. [A.M. Phillips, del.]

thickens laterally. The same ridge is in ALAB 2001.2, but FMNH PR 247 seems to be smooth, although this may be due to damage, as the surface is clearly eroded. *Bothremys cooki* and *B. maghrebiana* do not have this ridge where the foramina-rich surface changes to a smooth surface. On the medial surface of the symphysis in *Chedighaii barberi*, the anteriormost part of the sulcus meckelii extends close to the symphyseal area, but it does not meet the other sulcus on the midline, as in *Bothremys maghrebiana*.

Posteriorly, the lingual ridge in *Chedighaii barberi* rises to form the medial wall of the triturating pit, as in *Bothremys*. The labial ridge is only the thickened margin of the triturating surface as it extends posteriorly, until it rises abruptly to form the lateral wall of the pit, as in *B. maghrebiana* as well. In FMNH PR 247 the ridges and pit are very similar to *B. maghrebiana* except for a greater thickness of the bone. In ALAB 2001.2, however, the lingual ridge wall is much thicker than the labial ridge wall and the pit is not as deep as in FMNH PR 247, which has the pit wall equal in thickness. The jaw width is narrower in ALAB 2001.2 than it is in FMNH PR 247. It seems best to attribute

Fig. 243. *Chedighaii barberi* (Schmidt, 1940). ALAB PV 2001.2, left ramus of lower jaw, dorsal view. [E.S. Gaffney, del.]

Fig. 244. *Chedighaii barberi* (Schmidt, 1940). Lower jaws in anterodorsal view. Upper, FMNH PR247; lower, ALAB PV 2001.2. [E.S. Gaffney, del.]

these differences to individual variation at present, in the absence of better material. NJSM 12704 is more like FMNH PR 247, but it has also been damaged by postmortem erosion. Thus, it is possible to characterize FMNH PR 247 and NJSM 12704 as having slightly wider jaws, deeper pits, and a poorly defined symphyseal concavity due to low lingual ridges, in contrast to ALAB 2001.2 and CSU K-90-6-2. It is possible that these differences represent different taxa. The incomplete nature of the specimens and the lack of supporting characters make recognizing two taxa dubious at present, and all these jaws are identified as *Chedighaii barberi*. Nonetheless, it should be kept in mind that ALAB 2001.2, the specimen with the narrower jaws and shallower pits, has a skull lacking pits and is the basis for moving the species *barberi* from *Bothremys* to *Chedighaii*. If FMNH PR 247 proves to be a jaw type that is found with a pitted skull in the future, uh oh, a change is in the wind.

ANGULAR

Preservation: Both FMNH PR 247 and ALAB 2001.2 have the angular preserved, although it is damaged on both sides. In FMNH PR 247 the bone is nearly complete but damaged on its surface.

Contacts: The angular contacts in *Chedighaii barberi* are very similar to those in *Bothremys maghrebiana*. The prearticular is missing in both *Chedighaii* specimens, however, and the articular-angular suture appears fused, as is often the case in pleurodire jaws.

Structures: The angular in *Chedighaii* is very similar to that bone in *B. maghrebiana*.

SURANGULAR

Preservation: The anterior part of the surangular is present on both sides of ALAB 2001.2. Both surangulars are nearly complete in FMNH PR 247, but they are eroded on their surfaces.

Contacts: As in *Bothremys maghrebiana*. The articular suture is not discernable.

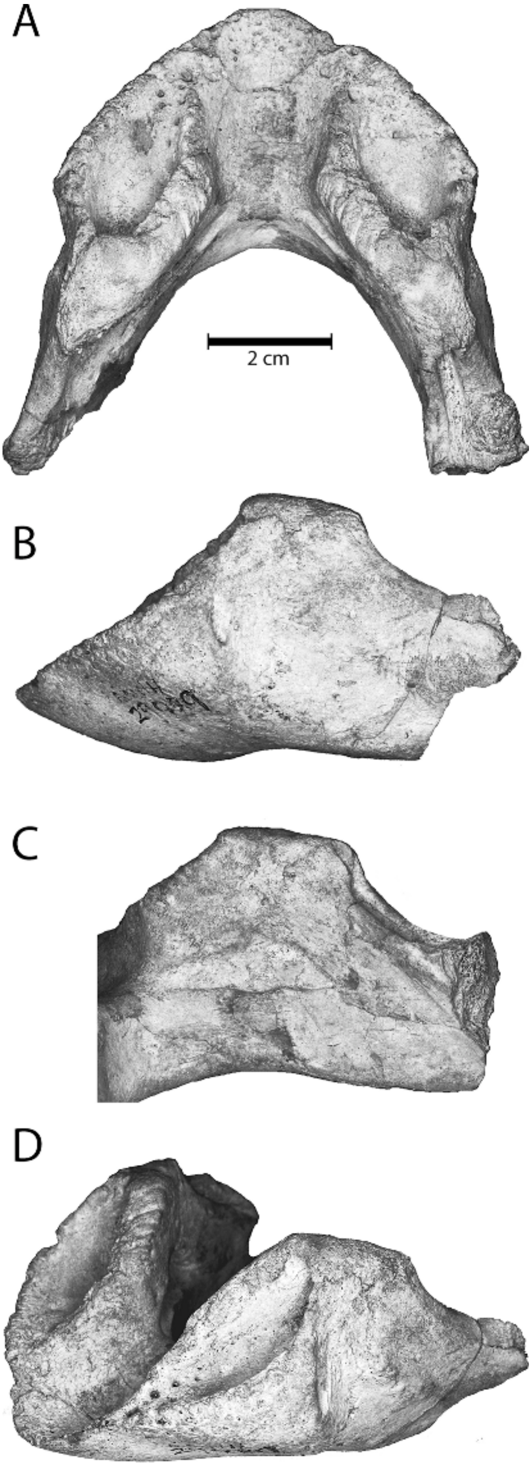

Fig. 245. Tribe Bothremydini, genus indeterminate. AMNH 29989, lower jaws. **A**, dorsal; **B**, left lateral; **C**, right medial; **D**, anterolateral oblique. [E.S. Gaffney, del.]

Structures: The foramen dentofaciale majus in *Chedighaii barberi* is in the surangular-dentary suture in ALAB 2001.2, but it seems to be in the dentary in FMNH PR 247, although poor preservation makes it hard to be sure. In *Bothremys maghrebiana* the foramen is well onto the dentary. The surangular forms the lateral wall of the fossa meckelii, which in shape and size seem to be very similar to *B. maghrebiana*. The surangular thickness, however, is much greater in *C. barberi* than it is in *B. maghrebiana* and *Araiochelys*. This is determinable only in FMNH PR 247. The lateral wall drops straight ventrally in *B. maghrebiana*, but in *C. barberi* the surangular is thicker dorsally than ventrally. *B. cooki* appears to agree with *C. barberi* in this, although the area is not well preserved.

CORONOID

Preservation: The coronoid is preserved on both sides in FMNH PR 247 and ALAB 2001.2.

Contacts: The coronoid of *Chedighaii barberi* differs slightly from *Bothremys maghrebiana* in having less lateral exposure. The prearticular is missing in all specimens, but the sutural surface shows its position to be very similar to that in *B. maghrebiana*. The dentary and surangular contacts are otherwise as in *B. maghrebiana*.

Structures: The processus coronoideus in *Chedighaii barberi* is very similar to that in *B. maghrebiana*, not as high as in *B. cooki*. The coronoid forms the roof of the triturating pit in FMNH PR 247, as in *Bothremys*, with the dentary extending into the floor. In ALAB 2001.2, however, the shallower pit is formed almost entirely by the coronoid, and the dentary does not extend into the pit floor.

ARTICULAR

Preservation: The articular is preserved on both sides of FMNH PR 247, although it is somewhat eroded and no sutures defining it are visible.

Contacts: In FMNH PR 247, sutures that define the articular are not visible, a common condition in turtles.

Structures: The area articularis mandibularis in *Chedighaii barberi* is eroded and pitted, but it appears to be the same shape as in *Bothremys maghrebiana*, rounded with

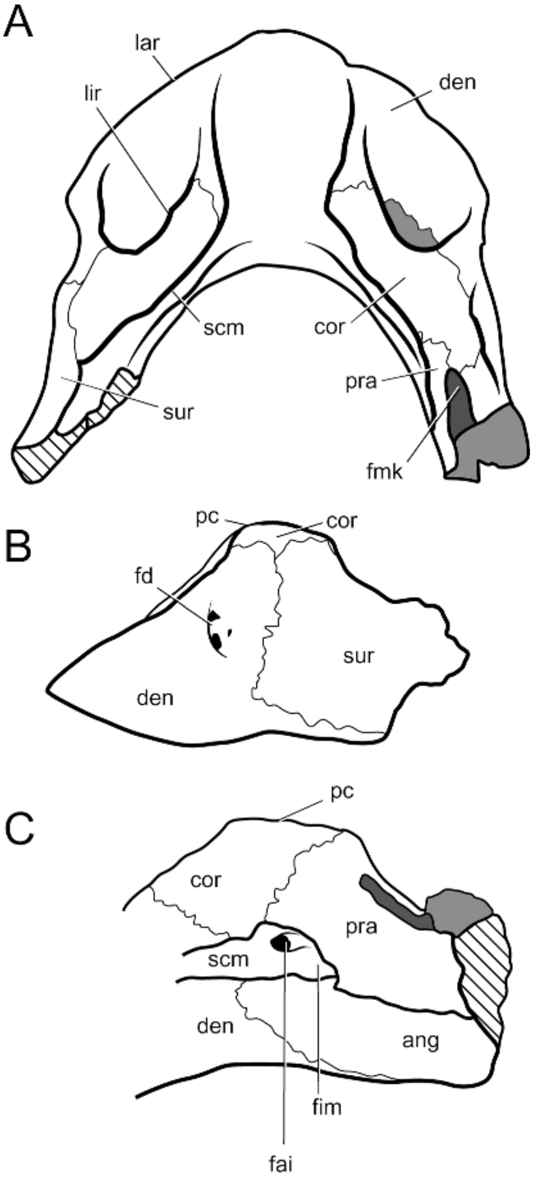

Fig. 246. Tribe Bothremydini, genus indeterminate. AMNH 29989, lower jaws. **A**, dorsal; **B**, left lateral; **C**, right medial. [A.M. Phillips, del.]

a low anteroposterior ridge. The processus retroarticularis seems to be complete on the left side. It is shorter, broader, and more massive than in *B. maghrebiana*, similar to the one in *Rhothonemys*.

Prearticular

Preservation: The prearticular is absent in all *Chedighaii barberi* specimens, but the sutural contacts in FMNH PR 247 suggest a bone very similar to that in *Bothremys maghrebiana*.

TRIBE BOTHREMYDINI
Genus indeterminate

Material Available: AMNH 29989, lower jaw lacking posterior ends (figs. 245, 246), from the Ypresian Eocene Couche 1 phosphates of Ouled Abdoun, Morocco. This specimen cannot be physically fitted into the available skull material of *Bothremys kellyi* or other known taxa and probably represents an undescribed species.

Dentary

Preservation: The dentary in AMNH 29989 is nearly complete.

Contacts: The dentary in AMNH 29989 has similar contacts to those in *Bothremys maghrebiana*, but the coronoid contact is much smaller on the lateral jaw surface. Laterally, the dentary has a long, vertical suture with the surangular, restricting the coronoid contact dorsally.

Structures: The paired pits and anteriorly open fossa meckelii in AMNH 29989 suggest a close relationship to the Bothremydini, but the massiveness and detailed triturating surface shape show that AMNH 29989 is a new taxon not represented by known cranial material.

The triturating surface in AMNH 29989 has the pit formed by labial and lingual ridges. The pit is about the same relative size as in *Bothremys*, although it is higher than wide rather than equidimensional as in *Bothremys*. The lingual ridge that forms the medial wall of the pit is much thicker than it is in *Bothremys*. The anterior continuation of the lingual ridge curves laterally and meets the labial ridge rather than meeting on the symphysis as in *B. maghrebiana* and *Araiochelys*. The area between the lingual ridges forms a deep concavity with a low transverse ridge posteriorly and an upturned labial margin anteriorly. This concavity is the symphyseal wedge, which in other Bothremydini is not as deep and is bordered by the lingual ridges anteriorly. The symphysis in

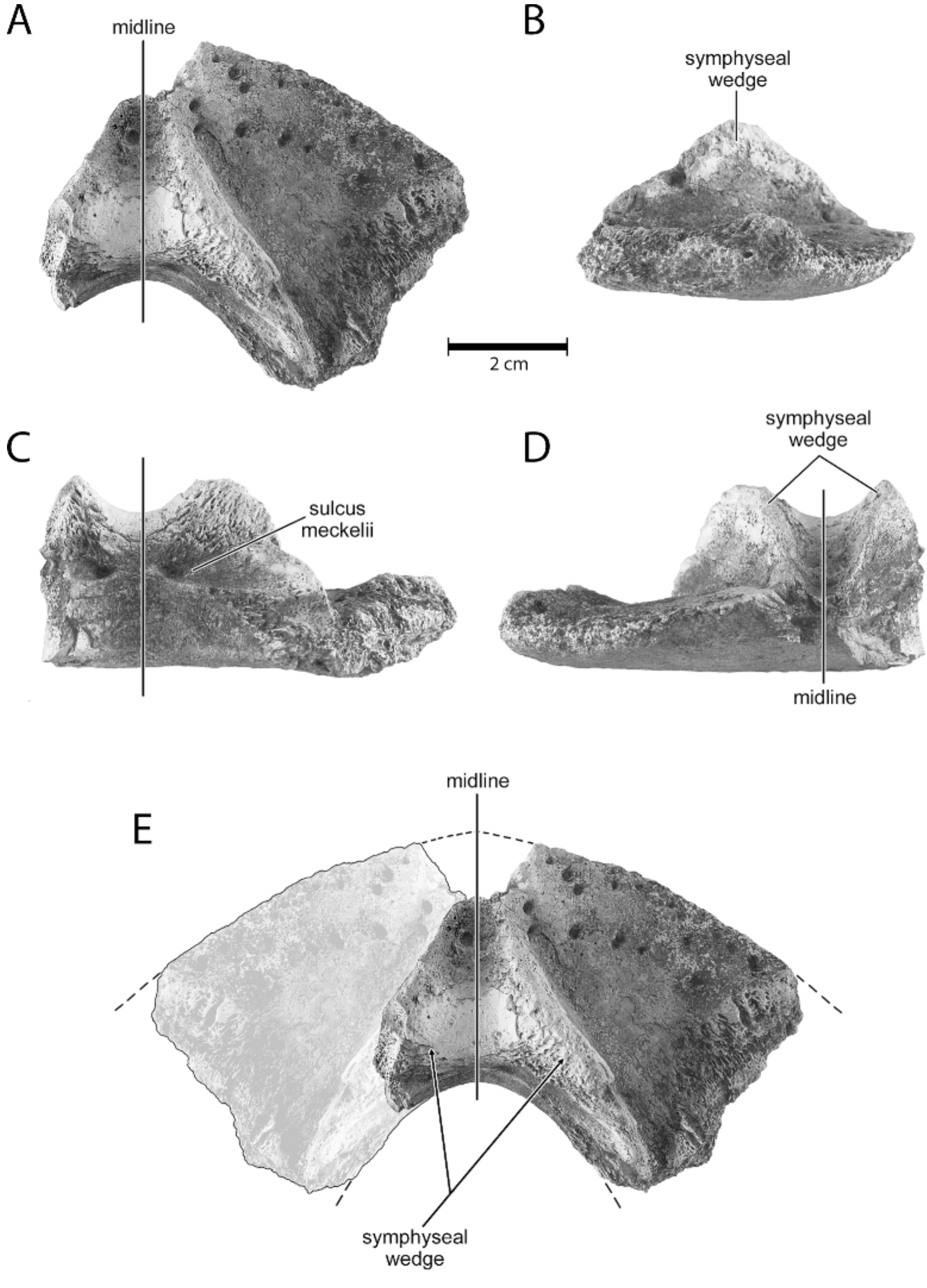

Fig. 247. Possible bothremydid lower jaw, UA 8708. **A**, dorsal; **B**, right lateral; **C**, posterior; **D**, anterior; **E**, partially restored in dorsal view (from Gaffney and Forster, 2003).

AMNH 29989 is much longer than in other bothremydids. It extends posteriorly to the level of the processus coronoideus, about twice the length of the symphysis in *Bothremys.*

The ventral surface of the dentary in *Bothremys* is relatively flat, but in AMNH 29989 it is deep posteriorly, where the bone is very thick, and tapers anteriorly to the labial margin. The symphyseal ventral surface is deeper and convex rather than flat as in *Bothremys*. The sulcus cartilaginis meckelii is relatively broad in AMNH 29989, related to the much higher and more massive jaw, compared to *Bothremys*. The sulcus does not reach the symphysis, as in *B. maghrebiana*. The foramen alveolare inferius and the contact with the surangular can be seen on the lateral wall of the fossa meckelii.

In contrast to other Bothremydini, AMNH 29989 has a highly vascularized triturating surface with nutrient foramina varying in size. The rhamphotheca-covered area does not have distinct margins, agreeing with other Bothremydini.

The foramen dentofaciale majus is formed entirely by the dentary and is contained in a shallow depression on the lateral surface of the dentary. There are what appear to be at least two foramina leading into the canalis alveolaris inferior from this depression.

ANGULAR

Preservation: The anterior part of the angular is preserved on the right side in AMNH 29989; only a small part is preserved on the left one.

Contacts: The angular in AMNH 29989 contacts the dentary in a short suture, rather than a long one as in *Bothremys maghrebiana*. The prearticular contact is more dorsal due to the greater height of AMNH 29989.

Structures: The angular in AMNH 29989 is deeper and shorter than in *Bothremys maghrebiana*, but the restricted prearticular contact still results in a relatively open fossa meckelii.

SURANGULAR

Preservation: The surangular is present on both sides of AMNH 29989, but both lack their posterior portions, broken off behind the fossa meckelii.

Contacts: The dentary contact is extensive and long, compared to *Bothremys maghrebiana*. The coronoid contact is much smaller than in *B. maghrebiana*.

Structures: AMNH 29989 is a deep and short jaw compared to *Bothremys*, and the surangular and dentary form most of the surface in lateral view. The relations of the surangular, however, are the same as in *B. maghrebiana*: it forms the lateral wall and dorsal opening of the fossa meckelii.

CORONOID

Preservation: Both coronoids in AMNH 29989 are complete.

Contacts: The coronoid in AMNH 29989 extends farther anteriorly along the lingual ridge and does not reach the labial ridge, in contrast to *Bothremys*. The medial exposure of the coronoid is less also because the dentary suture is placed more posteriorly. Laterally, the coronoid is much less extensive than in other Bothremydini because of the dorsal position of the dentary and surangular contacts.

Structures: Despite its massive form, the processus coronoideus is slightly lower than in *B. maghrebiana* and much lower than in *B. cooki.*

ARTICULAR

Preservation: A small part of articular in AMNH 29989 is exposed as a broken edge on the right side; otherwise, the bone is missing.

PREARTICULAR

Preservation: Only the right prearticular is present in AMNH 29989, and it is missing its posterior margin.

Contacts: The prearticular in AMNH 29989 contacts the coronoid anterodorsally and the angular posteroventrally.

Structures: The prearticular in AMNH 29989 is a higher, shorter bone than it is in *Bothremys*, and it is thicker and more massive. It forms the medial wall of the fossa meckelii. The fossa is more open than in *Euraxemys*, pelomedusids, and chelids, agreeing with other Bothremydini and Taphrosphyini.

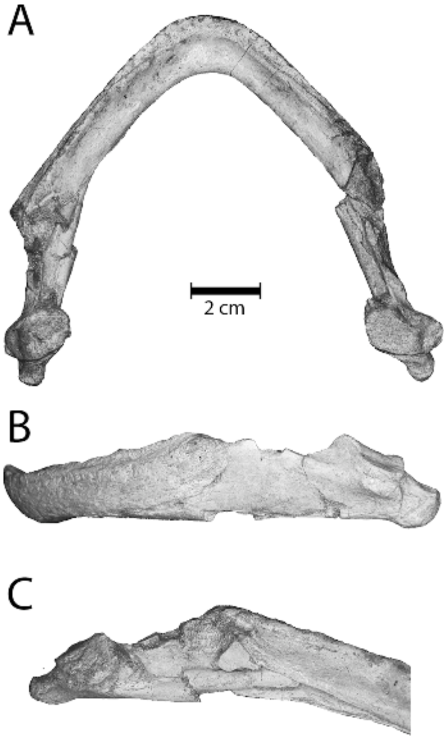

Fig. 248. *Rhothonemys brinkmani*, n. gen. et sp. AMNH 30521 holotype, lower jaws. **A**, dorsal; **B**, left lateral; **C**, left medial. [E.S. Gaffney, del.]

TRIBE TAPHROSPHYINI

Rhothonemys brinkmani (figs. 248, 249)

MATERIAL AVAILABLE: AMNH 30521, lower jaw lacking coronoid areas and both prearticulars, associated with skull.

DENTARY

Preservation: Nearly all of the left dentary in AMNH 30521 is present; the right one lacks most of its posterior contacts and is separated from the posterior jaw elements without good contacts. A posteroventral piece of dentary is present in the right posterior jaw piece.

Contacts: The dentary in *Rhothonemys* has only one piece of coronoid remaining; most of the coronoid attachment area is either broken or a sutural surface. The coronoid contact remaining is on the dorsomedial side of the dentary, just above and lateral to the fossa meckelii. Although incomplete, the coronoid contact in *Rhothonemys* appears to be less extensive medially and laterally compared to *Bothremys maghrebiana*; it seems to have been similar to that in *Euraxemys*. The surangular contact is more anterior than in *Euraxemys* and is similar to Bothremydini. In *Rhothonemys* this suture runs along the posterior edge of the foramina-rich surface for the rhamphotheca, in contrast to other Pelomedusoides. The angular contact is similar to Bothremydini as well. The prearticular is missing.

Structures: The dentary in *Rhothonemys* is fused at the symphysis, as in all other bothremydids. The dentary does not extend posteriorly to the degree seen in *Euraxemys*; it is similar to other bothremydids. The lateral side shows the foramen dentofaciale majus as a large foramen formed by the dentary anteriorly and the surangular posteriorly. The foramina-rich lateral surface extends to the posterior edge of the dentary; the surangular-dentary suture marks the limits of the rhamphotheca. This is in contrast to other bothremydids in which the rhamphotheca ends anterior to the edge of the dentary. The nutrient canal-rich area does not extend onto the ventral surface of the dentary.

The triturating surface in the lower jaw of *Rhothonemys* is very unusual for pleurodires in general and for bothremydids in particular. The dentary is roughly parallel-sided; it does not widen posterolaterally, and it is narrow. The triturating surface, as determined by foramen-rich bone and lingual and labial ridges, is very narrow, less than one-third the width of the dentary in dorsal view. The labial ridge is distinct and forms a low hook at the symphysis, but it nearly disappears posteriorly, becoming barely identifiable at the posterior edge of the dentary. The lingual ridge, very low at the symphysis, rises posteriorly so that it is the dorsalmost part of the jaw posterior to the symphysis. The lingual ridge is still blunt and low, and it barely rises above the level of the rest of the jaw. The triturating surface of *Rhothonemys* is very different from that in the Bothremydini. The surface is unusually narrow (rather than wide), it does not rise dorsally to a high processus coronoideus, and there is a symphyseal hook. The only similarity to Bothremydini is the lingual ridge that rises posteriorly to be dorsal to the labial ridge.

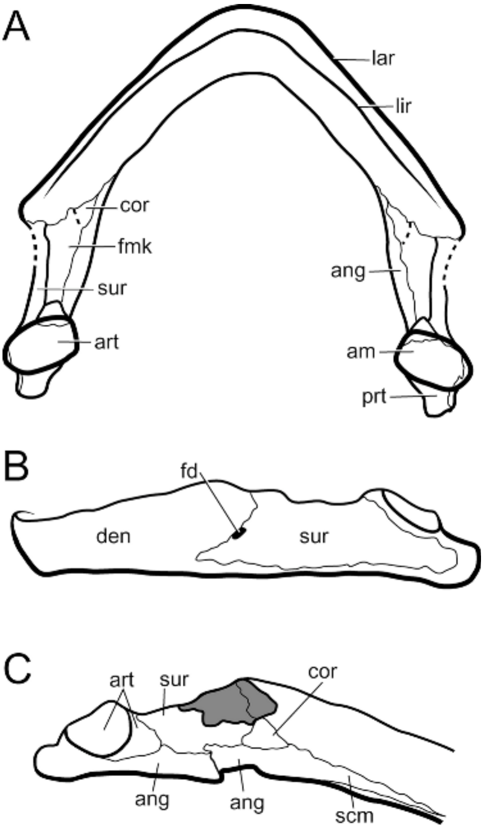

Fig. 249. *Rhothonemys brinkmani*, n. gen. et sp. AMNH 30521 holotype, lower jaws. **A**, dorsal; **B**, left lateral; **C**, left medial. [E.S. Gaffney, del.]

The dentary surface medial to the lingual ridge in *Rhothonemys* is smooth and slopes ventromedially, with a slightly concave shape. This surface is about three times wider than the triturating surface itself. On the medial surface, the dentary forms the sulcus cartilaginis meckelii, which is a sharply defined, V-shaped trough similar to that in other bothremydids, but not meeting on the midline as in *Bothremys maghrebiana*. The foramen alveolare inferius in *Rhothonemys* lies near the posterior end of the dentary on the medial surface in the region where the fossa meckelii grades into the sulcus cartilaginis meckelii. It is exposed on the right side, but on the left it is behind the displaced fragment of coronoid. Presumably, it was originally visible in medial view.

A possible tribe Taphrosphyini lower jaw is described in Bardet et al. (2000: 281, fig. 7d, e) as a "Chelonioidea gen. and sp. indet". Associated with this jaw are shell elements also described and figured (Bardet et al., 2000: 281, fig.7a–c, g), one of which (fig. 7a) has the iliac scar small, round, and at the shell margin, features probably diagnostic for the tribe Taphrosphyini. The lower jaw is very similar to those of *Rhothonemys* and *Taphrosphys congolensis* (see figs. 248–250).

ANGULAR

Preservation: Both angulars are present in AMNH 30521, but neither is complete. The right one is complete posteriorly but is missing its anterior third. The missing part can be determined from the matching sutural surface on the dentary. The left angular is more complete, but its anterior third is broken and slightly displaced from its dentary contact.

Contacts: The anterior dentary contact in *Rhothonemys* is clear and similar to that in other bothremydids. It forms a V-shaped process of the angular lying below the sulcus cartilaginis meckelii. The prearticular is missing in AMNH 30521, but the angular and articular show a short, sutural contact for it, similar in position to that in the Bothremydini. The angular merges into the articular with no sign of a suture in AMNH 30521, as in many adult pleurodires. Posteroventrally, the angular in *Rhothonemys* has a long contact with the surangular, also as in other pleurodires.

Structures: The angular in *Rhothonemys* is a splintlike element forming the ventromedial surface of the jaw, below the fossa meckelii and sulcus cartilaginis meckelii. In *Rhothonemys* the angular has a short contact with the prearticular dorsally, with a free edge exposing most of the ventral part of the fossa meckelii, all as in *Bothremys maghrebiana* and other Bothremydini and in contrast to other pleurodires. The angular in *Rhothonemys* curves dorsomedially to form the floor of the fossa meckelii. Because the fossa meckelii is relatively open anteriorly, the foramen intermandibularis medius is placed posteriorly and the foramen intermandibularis caudalis is not formed, all as in *Bothremys maghrebiana*.

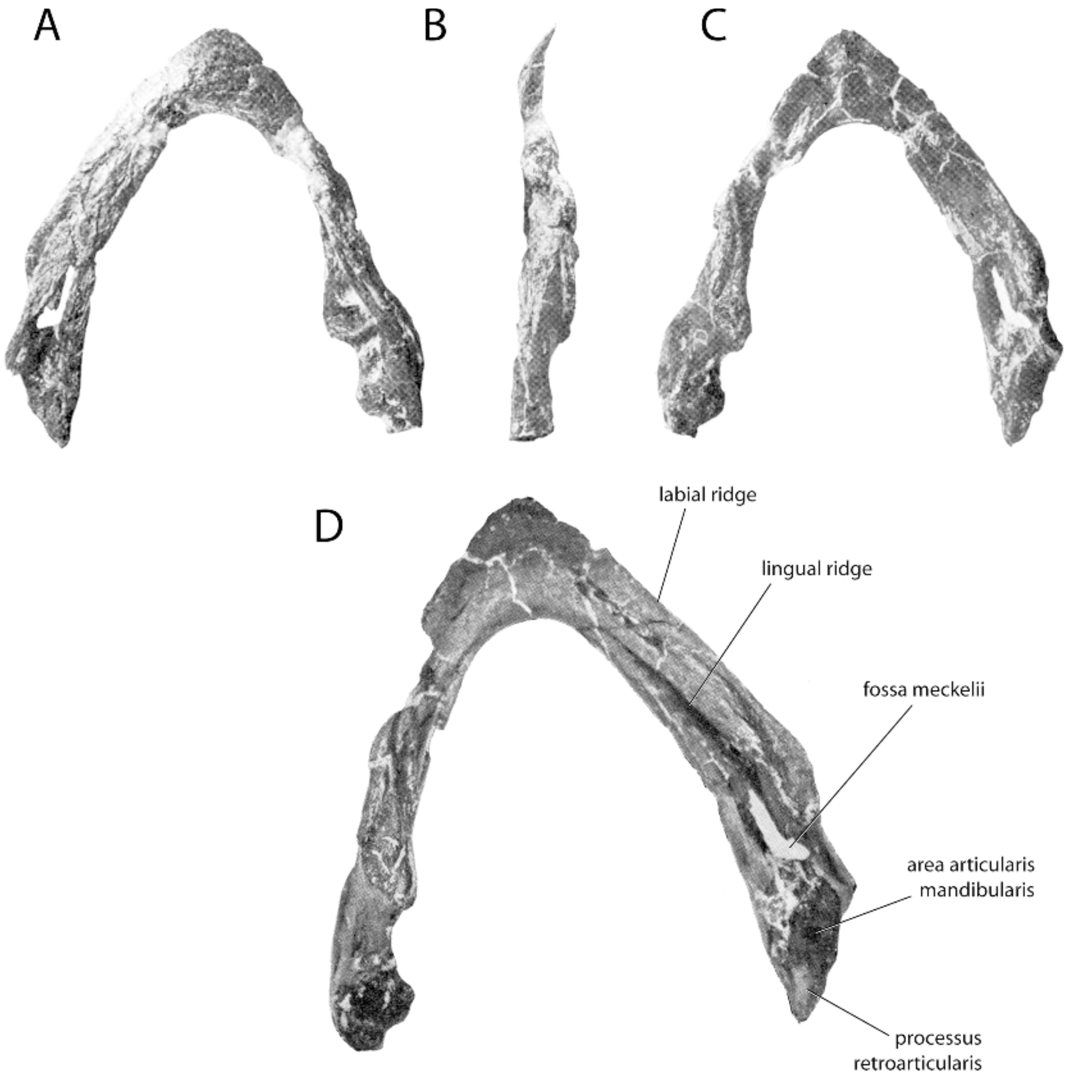

Fig. 250. *Taphrosphys congolensis* (Dollo, 1913). MRAC 3090, lower jaws. **A**, ventral; **B**, left lateral; **C**, dorsal (from Dollo,1924: fig. 1); **D**, dorsal (from Wood,1973: pl. 3), with labels added.

SURANGULAR

Preservation: The left surangular in AMNH 30521 is nearly complete, lacking only some of the dorsal margin. The right surangular is less complete, lacking its anterior and anterodorsal margins.

Contacts: The surangular in *Rhothonemys* contacts the dentary anteriorly, the angular posteroventrally, and the articular posteromedially. The coronoid is largely missing in AMNH 30521, and the surangular-coronoid contact surface is damaged.

Structures: The surangular in *Rhothonemys* is a large, sheetlike element at the posterior end of the jaw, forming the lateral wall of the fossa meckelii. As preserved, the fossa is similar to that in *Bothremys maghrebiana*, but the dorsal opening of the fossa is not preserved, so its shape is indeterminate. Posteriorly the surangular lies lateral to the blocklike articular, and in *Rhothonemys* it barely extends onto the area articularis mandibularis. The surangular extends posteriorly onto part of the processus retroarticu-

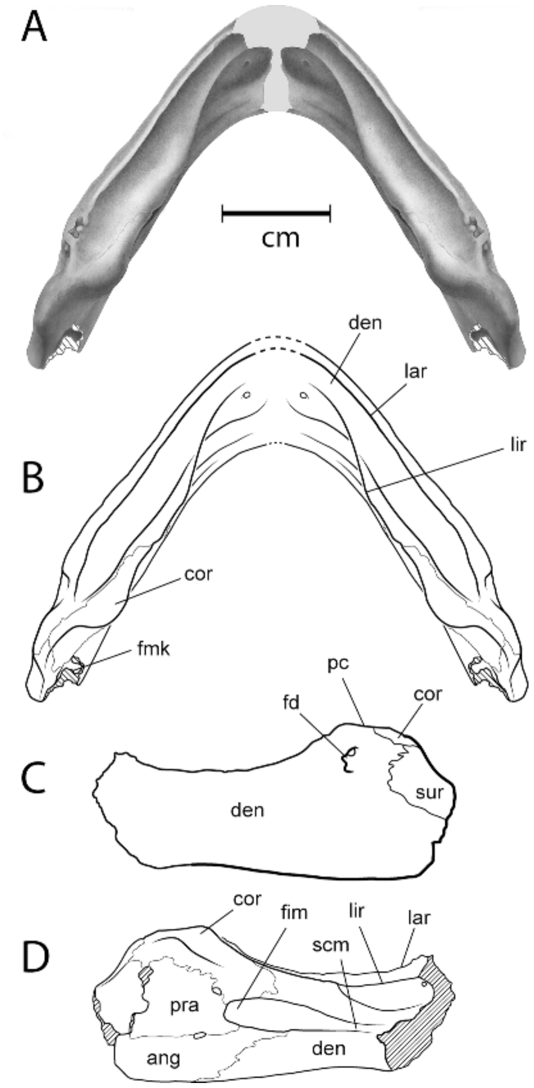

Fig. 251. *Hamadachelys escuilliei* Tong and Buffetaut, 1996. AMNH 30029, lower jaws. **A**, dorsal view partially restored by mirror image of left ramus; **B**, dorsal; **C**, left lateral; **D**, left medial. [K. Luckenbill, del.]

laris, as in other bothremydids. There is no foramen nervi auriculotemporalis.

CORONOID

Preservation: Only a fragment of the coronoid is present anteriorly on the medial surface of the left ramus in AMNH 30521. It is slightly displaced ventrally. Along with the contact area on the medial surface of the dentary, it indicates a posterodorsally sloping dentary contact in *Rhothonemys*, in contrast to the more vertical one of *Bothremys maghrebiana*.

ARTICULAR

Preservation: Both articulars are present and seem to be complete in *Rhothonemys*. Due to the fusion of some sutures, however, this is not certain.

Contacts: The articular in *Rhothonemys* contacts the surangular laterally and is fused with the angular ventrally and anteroventrally. The prearticular is missing, but a sutural surface shows a medial contact, as in other pleurodires.

Structures: The articular forms nearly all of the area articularis mandibularis in *Rhothonemys*. The surface is roughly divided into two facets by a very low anteroposterior ridge, as in *Bothremys maghrebiana*. The medial facet is larger and more anterior than the lateral one. In *B. maghrebiana* they are more equal in size.

The articular in *Rhothonemys* forms nearly all of the processus retroarticularis; the angular contribution is uncertain due to sutural fusion. The processus is large in *Rhothonemys*, much larger than in *Euraxemys* and the Pelomedusidae. In *Rhothonemys* it is shorter, broader, and not concave dorsally, in contrast to *Bothremys maghrebiana*. There is no foramen posterius chorda tympani. The articular forms the posterior wall of the fossa meckelii.

PREARTICULAR

Preservation: The prearticular is missing in AMNH 30521, but a sutural surface on the articular and angular shows that one was present.

EPIFAMILY PODOCNEMIDINURA

Hamadachelys escuilliei

MATERIAL AVAILABLE: AMNH 30029, left ramus (fig. 251), broken off approximately at or near the symphysis. This unassociated lower jaw is identified as *Hamadachelys*. Originally suspected to be the lower jaw of *Galianemys*, further preparation of *Hamadachelys* material shows that it belongs to this contemporary genus. We retain it for comparison with bothremydids.

DENTARY

Preservation: The left dentary in AMNH 30029 lacks the posterior ventral process and is preserved up to what seems to be the midline, although it is hard to be sure.

Contacts: The dentary in AMNH 30029 contacts the coronoid posterodorsally, the surangular posteriorly, but more dorsally than in *Cearachelys* or *Kurmademys*, and the angular posteroventrally. The surangular contact is vertical dorsally, but it becomes horizontal midway in its height, rather than at the bottom edge.

Structures: The symphyseal area as preserved in AMNH 30029 seems to be very similar to *Kurmademys*, particularly ISI 155D, which has a symphyseal hook. The hook is likely in AMNH 30029 because the labial ridge is rising at its broken edge. The narrow triturating surface, defined posteriorly by a U-shaped concavity with a low lingual ridge as its border, is very similar to this area in *Cearachelys* and *Kurmademys*. The labial ridge is slightly higher than the lingual ridge anteriorly, as in *Cearachelys*, THUg 1798. Also as in this *Cearachelys* specimen, the triturating surface is narrower than in *Cearachelys*, BSP 1976 I 160, and *Kurmademys*, although clearly there is variation in this in both *Cearachelys* and *Kurmademys*. The lingual ridge in AMNH 30029 rises posteriorly and is higher than the labial ridge, as in bothremydids. The triturating surface is slightly concave along its length, similar to that in *Kurmademys* and *Cearachelys*, except it is not as flat anteriorly. The jaw ramus is slightly deeper and more massive than in *Cearachelys*, similar to *Kurmademys*.

The sulcus cartilaginis meckelii is similar to that in *Kurmademys* and *Cearachelys*. The foramen dentofaciale majus is at the upper edge of the ramus, in the processus coronoideus, rather than more ventrally, as in *Kurmademys* and *Cearachelys*.

ANGULAR

Preservation: The anterior half of the left angular is present in AMNH 30029.

Contacts: The angular in AMNH 30029 contacts the prearticular dorsally and the dentary anteriorly and ventrally. The prearticular contact is long, as in *Kurmademys* and *Cearachelys*.

Structures: The angular in AMNH 30029 borders the sulcus cartilaginis meckelii, as in *Kurmademys* and *Cearachelys*. The angular wraps ventrally around the jaw, as in other pleurodires.

SURANGULAR

Preservation: Only a small part of the surangular, just posterior to the processus coronoideus, is present in AMNH 30029.

Contacts: The surangular in AMNH 30029 contacts the dentary anteriorly and dorsally and the coronoid anteromedially, as in *Kurmademys* and *Cearachelys*.

Structures: The surangular forms the lateral wall and dorsal margin of the fossa meckelii, the anterior part of which is present in AMNH 30029. The dentary and surangular form the lateral side of the processus coronoideus. There is not enough of the surangular preserved to determine other features.

CORONOID

Preservation: All of the coronoid is present in AMNH 30029.

Contacts: The coronoid in AMNH 30029 contacts the dentary anteriorly, the prearticular posteroventrally, and the surangular posteriorly.

Structures: The processus coronoideus in AMNH 30029 is slightly lower than that in *Kurmademys* and *Cearachelys*, but its shape is still similar to that in those taxa. The coronoid forms part of the dorsal edge of the foramen intermandibularis medius. The coronoid does not extend onto the triturating surface to the extent seen in *Kurmademys*, but it does form part of the medial margin and lingual ridge as in *Cearachelys*.

ARTICULAR

Preservation: The articular is missing in AMNH 30029.

PREARTICULAR

Preservation: The anterior part of the prearticular is present in AMNH 30029.

Contacts: The prearticular in AMNH 30029 contacts the coronoid dorsally and the angular ventrally. Other contacts are not preserved.

Structures: The prearticular in AMNH 30029 has the anterior extent seen in *Kurmademys* and *Cearachelys* and is not short as in the Bothremydini and Taphrosphyini.

SHELL MORPHOLOGY

FAMILY EURAXEMYDIDAE
Euraxemys essweini, n. gen. et sp.
(figs. 252–254)

MATERIAL AVAILABLE: FR 4922, a nearly complete shell. The shell of *Euraxemys* was originally in a concretion broken in half transversely (not into part and counterpart, the usual pattern for Santana fossils), and it was repaired with a solvent-based putty that also covered the ventral surface before being acquired by the Senkenburg Museum. This putty was removed at AMNH, the entire surface cleaned, and the rearticulated shell was embedded in a clear plastic that covered the carapace. Before embedding in plastic, a cast, AMNH 30568, was made of the carapace. With the ventral surface exposed, the shell was acid prepared using techniques described in Rutzky et al. (1994). The outline and margins of FR 4922 do not appear to be distorted, as the plastron and bridge have what seem to be their natural curvature. The central area of the carapace, however, is crushed ventrally with much of the bone broken. The original curvature is retained along the posterior margin. Due to the fragmented condition of the bone of the carapace, complete removal of the matrix was halted in order to leave a layer just beneath most of the carapace. Despite the breakage, many of the carapacial sutures are visible, but the scale sulci are largely obscured except along the well-preserved posterior margin. The anterior part of the ventral surface is visible in FR 4922, but the posterior area medial to the peripherals is covered by matrix.

The published reconstruction of the shell (Gaffney and Meylan, 1991) is incorrect in a number of areas, and a new description is presented here (fig. 254).

CARAPACE

Shell surface texture is largely obscured by breakage in FR 4922, but the distal portion of left costals 1–3 has the surface preserved (particularly visible on the cast). The surface texture has the form of low ridges and troughs roughly parallel to the lateral margins of the pleural scales, a surface ornamentation commonly seen in cryptodires (cf. Ernst et al., 1994: pl. 24, *Clemmys muhlenbergii*) but not often in pleurodires. Nonetheless, it is a common chelonian pattern seemingly related to growth of the pleural scales.

Although damaged, the nuchal bone can be restored because its right lateral and posterior limits are determinable. It has the common six-sided shape of most Pelomedusoides, such as *Taphrosphys*, but it does not have the slight nuchal embayment seen in *Chedighaii* or in the original reconstruction of FR 4922 (Gaffney and Meylan, 1991), which also shows the nuchal as too long. The first two peripheral bones can be made out on the left side of FR 4922, and they are very similar to most other Pelomedusoides, such as *Taphrosphys*. They differ significantly from *Araripemys*, which has greatly reduced the anterior peripherals and lost contact with the nuchal. The bridge peripherals in FR 4922 are damaged on the dorsal surface but are better preserved ventrally, particularly on the left side. The bridge peripherals do not have guttering, and there is no indication of fontanelles as in *Araripemys*. The posterior peripherals 8–11 and pygal are well preserved and show the original shell curvature.

Peripheral 11 has an undercut separating the external and internal surfaces on the ventral side. The body wall margin separates these two surfaces. The internal surface is concave anteriorly and is nearly vertical. On the dorsal surface the pygal and posterior peripherals have a distinct flare that curves dorsally, suggesting that the shell may have been higher domed than in *Cearachelys* and was similar to the higher domed *Pseudemys* species. The crushing has greatly altered the original curvature.

Euraxemys has eight pairs of costals, with 2–7 being parallel-sided. The first costal is expanded anteriorly, as in nearly all turtles, and the eighth costal is slightly expanded distally. Many of the costal sutures are indeterminate due to breakage, but some of their limits can be determined by assuming bilateral symmetry and restoring by transposition. Costals 3–5 are particularly poorly preserved because this is the region where the concretion containing the skeleton was broken in half transversely. None of the costals

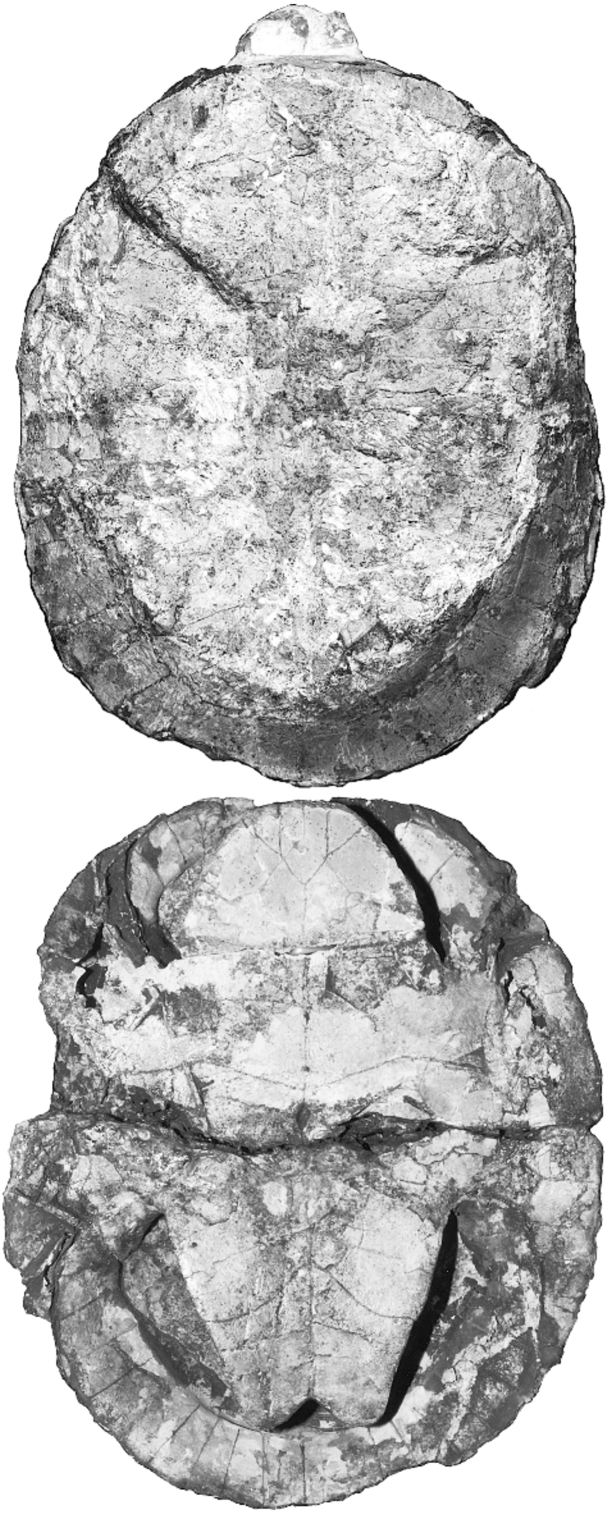

Fig. 252. *Euraxemys essweini*, n. gen. et sp. FR 4922 holotype, shell. Upper, dorsal (figure courtesy FR); lower, ventral. [E.S. Gaffney, del.]

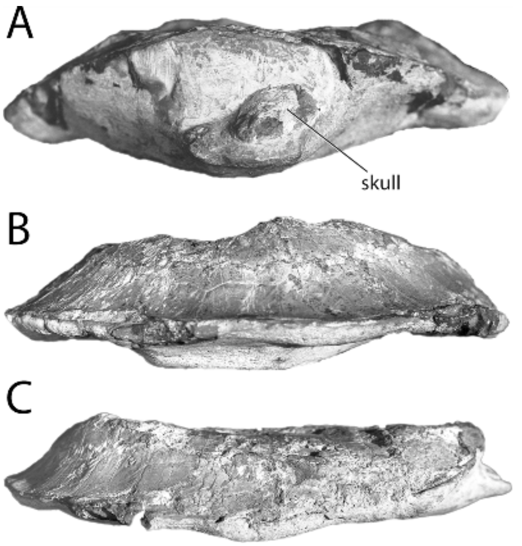

Fig. 253. *Euraxemys essweini*, n. gen. et sp. FR 4922 holotype, shell. **A**, anterior showing position of skull before preparation; **B**, posterior; **C**, right lateral. [Figures courtesy of F.R.]

meets on the midline. The suprapygal is six-sided, contacting the eighth neural anteriorly, the eighth costals laterally, the eleventh peripherals in a narrow pair of contacts, and the pygal posteriorly. The pygal is four-sided and nearly square, as in many Pelomedusoides butin contrast to the long pygal of *Araripemys* and the short pygal of *Notoemys*.

The neurals of *Euraxemys* are a complete set of eight with the common Pelomedusoides condition of $4 < 6 < 6 < 6 < 6 < 6 < 6 < 6$. Although many of the neurals are not well preserved, their shapes have been determined by reconstruction that assumes bilateral symmetry. The shortest neural is probably the seventh, with the eighth being about the length of the sixth. The first neural is the common shape seen in living Pelomedusoides, that is, rectangular with slightly curved margins. Neurals 2–5 are "coffin-shaped" hexagonal: neural 6 is wide and short, neural 7 is wider than long, and neural 8 is similar in shape to neural 2 but smaller.

The ventral surface of the carapace in FR 4922 shows some morphology, although the area largely consists of finely broken bone. The nuchal, peripherals 1–4, costal 1, and the first neural can all be made out. Although broken, the first thoracic centrum is preserved. The anterior articulation and zygapophyses are missing, but its ventral surface is flat. The first thoracic ribs are preserved and they extend sharply posterolaterally, as in pelomedusids. Distally they curve laterally and are longer than in pelomedusids. In pelomedusids and all other living pleurodires the ribs are relatively flat and more closely sutured to the first costal than in *Euraxemys*, which has ribs that are rounded and seem to be free of the costal for a greater length. The *Euraxemys* rib does not have the short anterior projection seen in *Pelomedusa*. The posterior contact with the second thoracic is a flat ankylosis, with the first costal rib contacting both the first and second thoracic centra as in all other pleurodires.

The scale pattern on the carapace of *Euraxemys* is clear around the posterior edge but is not well preserved elsewhere. There does not seem to be a cervical scale, and there is the normal set of 12 marginals as in other Pelomedusoides. Marginals 1, 2, and 8–12 are determinable and lie entirely on the peripherals. The elongate marginal 2 of the Gaffney and Meylan (1991) reconstruction was in error. This marginal is similar in size to the first. The only vertebral scales that have margins preserved are the second and the fifth. The sulci for the second vertebral are visible laterally on the right and left sides where they cross the costal 1–2 suture and anteriorly where it crosses the neural 1. The second vertebral is similar in width to that in other Pelomedusoides such as *Taphrosphys*. The fifth vertebral is also similar to *Taphrosphys* but it may be slightly wider. The new reconstruction of FR 4922 indicates wider vertebrals than in the Gaffney and Meylan (1991) figure. The pleural scales are poorly preserved, and only the pleural 1–2, 3–4, and 4–5 sulci are preserved. There are no supramarginal scales as in *Proterochersis* and *Platychelys*.

PLASTRON

The plastron of *Euraxemys* is made up of the usual 11 bones found in most Pelomedusoides. The anterior lobe is shorter than the posterior lobe, but it reaches the anterior edge of the carapace, similar to that in *Dortoka*. The size and shape of the entoplastron, epiplastra, and anterior lobe in Gaffney

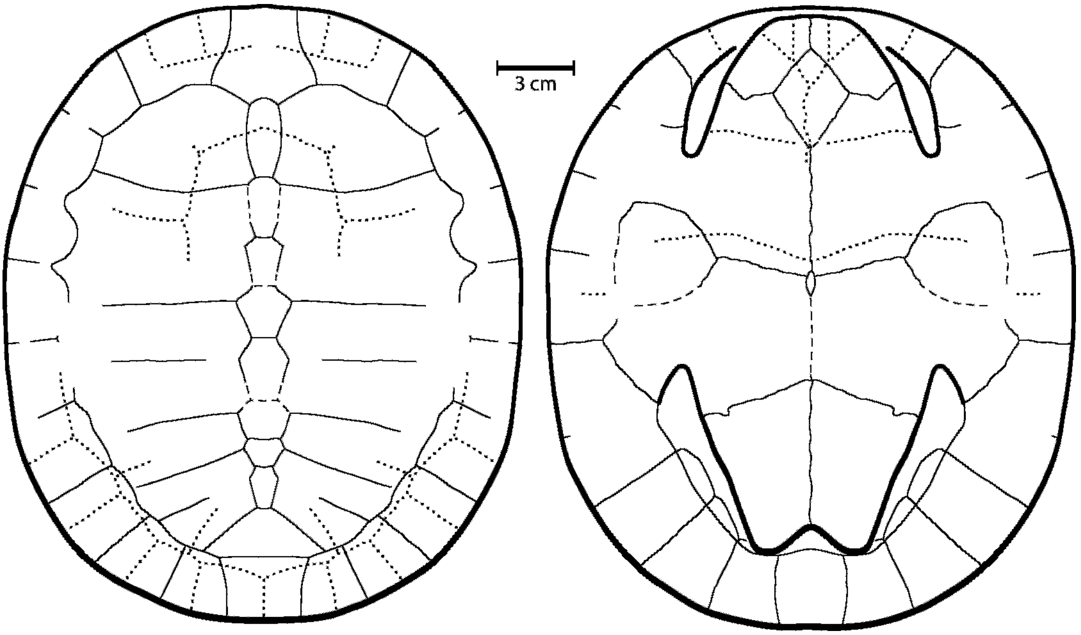

Fig. 254. *Euraxemys essweini*, n. gen. et sp. FR 4922 holotype. Partially restored shell. Left, dorsal; right, ventral. [J. Kane, del.]

and Meylan (1991) are incorrect (fig. 254). There is a relatively short midline contact of the epiplastra, as in most Pelomedusoides. The entoplastron of *Euraxemys* is quadrangular, as in most pleurodires. It is slightly longer than wide, in contrast to *Chedighaii* and *Taphrosphys* in which it is slightly wider than long. The hyoplastron forms the axillary notch. The hypoplastron forms the inguinal notch, which is relatively open. Neither notch is as open as in *Araripemys*, however.

Euraxemys has paired, laterally placed mesoplastra, in contrast to *Araripemys*, *Dortoka*, and chelids, which lack them, and in common with all other Pelomedusoides. Although neither mesoplastron in FR 4922 is complete, their limits can be reconstructed. The mesoplastron is slightly larger than in such forms as *Bothremys*, *Pelomedusa*, and *Podocnemis*. The mesoplastron does not extend farther medially than in most Pelomedusoides. There are no fontanelles in the *Euraxemys* plastron, and there are no foramina for musk ducts visible.

The xiphiplastron in *Euraxemys* forms most of the posterior lobe, which tapers posteriorly as in *Platychelys* and *Notoemys* and in contrast to forms like *Taphrosphys*, which are roughly parallel-sided. The posteriorly tapering plastron of *Euraxemys* is nearly the only similarity it has to that of *Araripemys*. There is a shallow anal notch, also similar to *Araripemys* and *Platychelys* and distinct from the deeper notch commonly seen in other Pelomedusoides.

There is the common Pelomedusoides complement of 13 scales on the plastron of *Euraxemys*, with no indication of axillary, inguinal, or inframarginal scales. There is a large, parallel-sided, intergular overlapping onto the entoplastron completely separating the smaller gulars and partially separating the humerals. This is essentially the same pattern seen in *Pelusios*, *Podocnemis*, and bothremydids like *Cearachelys*, *Foxemys*, *Chedighaii*, and *Polysternon*, but distinct from forms like *Taphrosphys*, which has a larger intergular scale completely separating the humeral scales, and *Pelomedusa*, which has very large humerals only slightly separated by the intergular. The gular scales in *Euraxemys* lie entirely on the epiplastra and are triangular.

The humeral scales are separated anteriorly by the gulars and intergular and are in contact medially for about half their length. The humeral scales extend onto the entoplas-

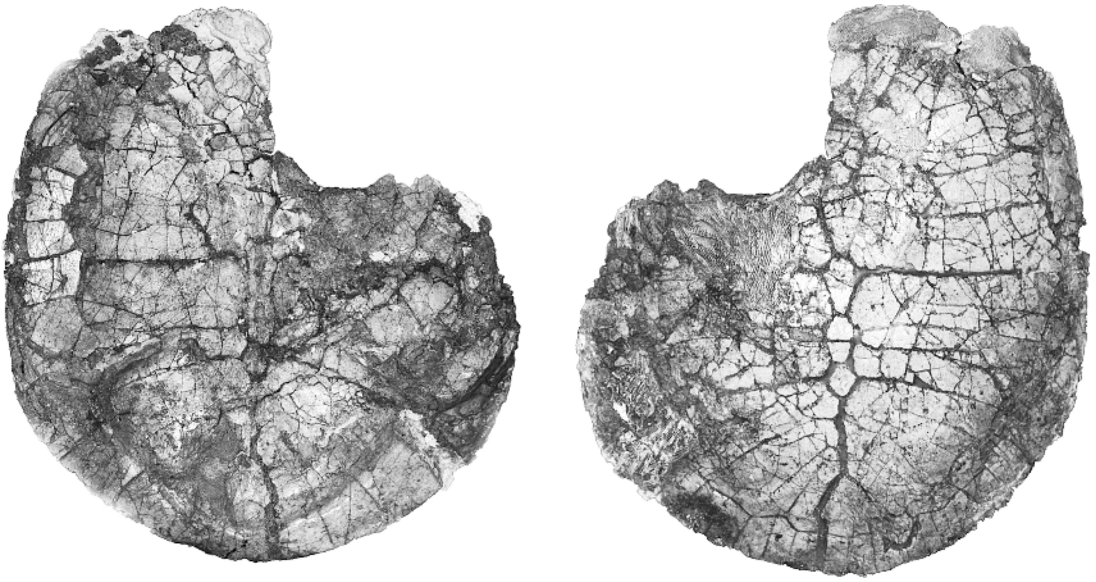

Fig. 255. *Kurmademys kallamedensis* Gaffney, Chatterjee, and Rudra, 2001. ISI R278, carapace in ventral (left) and dorsal (right) views. [E.S. Gaffney, del.]

tron. The humeral-pectoral sulcus is more posterior in *Euraxemys* than in forms like *Bothremys*, so that the humeral scale dominates the anterior lobe margin. The pectoral scales do not overlap onto the posterior half of the entoplastron, in contrast to the reconstruction of Gaffney and Meylan (1991). The pectoral-abdominal sulcus runs along the posterior part of the hyoplastra onto the mesoplastra. The abdominal and femoral scales in *Euraxemys* are similar to those in *Cearachelys* and most Pelomedusoides, as these scales do not exhibit much variation. The femoral-anal sulcus runs anteromedially rather than straight transversely in *Euraxemys*.

FAMILY BOTHREMYDIDAE
TRIBE KURMADEMYDINI
Kurmademys kallamedensis (figs. 255–257)

MATERIAL AVAILABLE: ISIR 278, partial shell; ISIR 152A, left costal 1; ISIR 152B, left costal 4; ISIR 152C, left costal 2; ISIR 152D, right hypoplastron; ISIR 152E, hyoplastron fragment; ISIR 152F, left ninth or tenth peripheral; ISIR 152G, left tenth or eleventh peripheral; ISIR 152H, costal fragment; ISIR 152I, nuchal; ISIR 152J, right costal 3; ISIR 152K, right peripheral 3; ISIR 152L, right peripheral 8; ISIR 152M, costal; ISIR 152N, bridge peripheral; ISIR 152O, right costal 1; ISIR 152Q, left hypoplastron; ISIR 152R, left hypoplastron; ISIR 152S, right hyoplastron; ISIR 152T, right peripheral 2; ISIR 153A, left costals 1 and 2, peripherals 3 and 4; ISIR 153B, neural 3; ISIR 153C, right costal 1; ISIR 153E, right costal 1; ISIR 153F, left peripheral 7; ISIR 153G, right costal 1; ISIR 153H, right xiphiplastron; ISIR 157B, right hyoplastron; ISIR 157D, costal fragment; ISIR 157E, left costal 1; ISIR 157F, costal fragment; ISIR 157G, right? eighth peripheral; ISIR 157H, costal; ISIR 157I, buttress or peripheral; ISIR 157J, buttress; ISIR 157K, buttress; ISIR 157L, right xiphiplastron; ISIR 157M, mesoplastron; ISIR 157P, costal 5; ISIR 157Q, costal 5; ISIR 157R, right costal 1; ISIR 157U, left costal 1; ISIR 157V, costal fragment; ISIR 157W, left costal 1; ISIR 157X, costal; ISIR 157Y, peripheral; ISIR 157Z, costal; ISIR 157AA, costal; ISIR 157AB, right hypoplastron; ISIR 157AC, neural 3 or 5?; ISIR 157AD, peripheral 9 or 10?; ISIR 157AE, neural 3 or 5?; ISIR 157AF, peripheral 2; ISIR 157AG, bridge peripheral; ISIR 157AH, neural; ISIR 157AJ, neural; ISIR 157AK, peripheral; ISIR

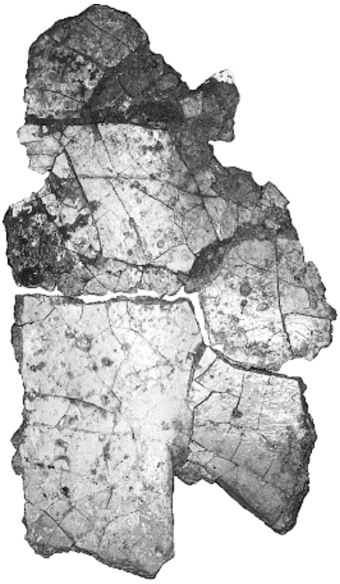

Fig. 256. *Kurmademys kallamedensis* Gaffney, Chatterjee, and Rudra, 2001. ISI R278, plastron in ventral view. [E.S. Gaffney, del.]

157AL, costal; ISIR 157AM, peripheral; ISIR 157AN, costal; ISIR 157AO, left xiphiplastron; ISIR 157AP, left peripheral 6; ISIR 157AQ, left hypoplastron; ISIR 157AS, costal 5; ISIR 157AT, bridge peripheral; ISIR 157AU, right costal 1; ISIR 157AV, costal 5; ISIR 157AW, peripheral 8; ISIR 157AX, neural; ISIR 157AY, neural; ISIR 157AZ, right costal 5; ISIR 157BA, right costal 7; ISIR 157BB, first neural; ISIR 157BC, fourth neural; ISIR 157BD, second neural; ISIR 157BE, nuchal; ISIR 157BH, left costal 5; ISIR 157BI, right peripheral 2; ISIR 157BJ, left costal 1; ISIR 157BK, right hypoplastron; ISIR 157BL, neural; ISIR 157BM, right costal 1; ISIR 157BN, left costal 5; ISIR 157BO, right xiphiplastron; ISIR 157BS, costal; ISIR 157BT, costal 1; ISIR 157BU, costal.

CARAPACE

The shell of *Kurmademys* has not previously been illustrated. The carapace is incomplete in ISIR 278; the anterior part is damaged. The reconstruction is also based on ISIR 157BE (nuchal), ISIR 157W (costal 1), ISIR 152T (peripheral 2), and ISIR 152K (peripheral 3). The carapace is oval in shape and apparently lower than in most bothremydids, although crushing may obscure its original depth. The shell surface shows the "pelomedusoid" pattern to some extent (Broin, 1977), at least on the bridge region.

The carapace consists of one nuchal, six neurals, one suprapygal, one pygal, eight pairs of costals, and 11pairs of peripherals, although the first peripheral is not known. The nuchal is pentagonal in shape without nuchal emargination, and it is wider than long as in *Chedighaii*. The first neural is more elongated than the following neurals and is roughly rectangular in shape. It does not contact the second costal, as in most bothremydids. The second to fifth neurals are all elongated and six-sided with the short anterolateral sides. The sixth neural is five-sided and as long as wide; it does not contact the suprapygal. The first costal is about as long as the second and the third costals together. Its inner side bears the axillary buttress scar, where a rounded swelling links the scar to the first and second thoracic rib head. The fifth costal bears the inguinal buttress scar on its inner side, which extends nearly half the width of the plate along its center, as in most bothremydids. The posterior part of the sixth costal and the seventh and eighth costals meet on the midline, separating the neural series from the suprapygal. The suprapygal is triangular in shape, as in other bothremydids. The pygal is slightly longer than wide.

The carapacial scales of *Kurmademys* do not differ significantly from those in *Chedighaii* and other bothremydids. The cervical scale is absent.

PLASTRON

The plastron in ISIR 278 consists of the posterior part of the left hyoplastron, left hypoplastron, left mesoplastron, and partial right hypoplastron. Other elements of this specimen are too badly broken to be recognizable. The plastron reconstruction is based mainly on ISIR 278, with information from ISIR 152S (right hyoplastron) and ISIR 157L (xiphiplastron). The entoplastron and both epiplastra are not known.

The anterior lobe in *Kurmademys* is probably relatively long, as in *Cearachelys*, not short, as in the Bothremydini and Taphrosphyini, based on the lateral edges of the hyoplastra. The mesoplastron is equidimen-

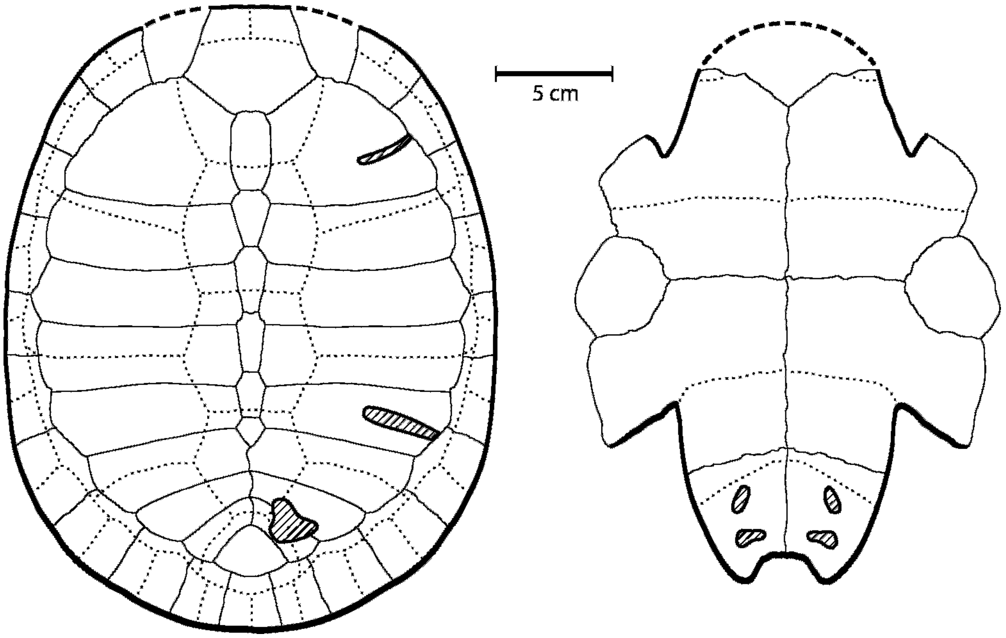

Fig. 257. *Kurmademys kallamedensis* Gaffney, Chatterjee, and Rudra, 2001. Partially restored shell based on ISI R278 plus other elements as discussed in text, in dorsal (left) and ventral (right) views. [J. Kane, del.]

sional but larger than that bone in *Chedighaii*. The posterior lobe is wide, as in *Chedighaii*, with a semicircular-shaped anal notch.

The plastral scales of *Kurmademys* are not well preserved. Only a lateral portion of the humeropectoral sulcus is present, and its position is very similar to that in *Araiochelys*, suggesting that the pectoral scale covers a small part of the epiplastron and a large part of the entoplastron. The pectoroabdominal sulcus is placed far anterior to the mesoplastron, also as in *Araiochelys*. The pelvic scars are similar to those in *Chedighaii*; the ischiac scar is triangular in shape and situated anterior to the posterior margin of the plastron.

TRIBE CEARACHELYINI

Cearachelys placidoi (fig. 258, table 22)

MATERIAL AVAILABLE: THUg 1798 (Gaffney, Campos, and Hirayama, 2001: figs. 8, 9), a complete shell; BSP 1976 I 160, a complete shell; MPSC uncatalogued, type specimen (Gaffney, Campos, and Hirayama, 2001: figs. 6, 7), plastron and partial carapace.

CARAPACE

The carapace of *Cearachelys* is nearly complete in THUg 1798 and BSP 1976 I 160. Fragments of the left and right bridge peripherals are present in the MPSC specimen.

The carapace of *Cearachelys* is moderately domed, much as in recent *Pelomedusa*. The carapace is composed of a nuchal, eight neurals, eight pairs of costals, 11 pairs of peripherals, a single suprapygal, and a single pygal. There are no fontanelles as in *Araripemys*, and all the bones are tightly sutured as in most pleurodires. The principal distinguishing features of the carapace in *Cearachelys* lie in the neural bones. The first neural in most Pelomedusoides is four-sided and contacts only the nuchal, first costals, and second neural. In *Cearachelys* the first neural is six-sided and has short, paired contacts with the second costals. In THUg 1798 the second neural is four-sided, rather than six-sided as in most Pelomedusoides, and as a consequence it does not contact the first costals. In *Araripemys* the second neural also does not contact the first costals.

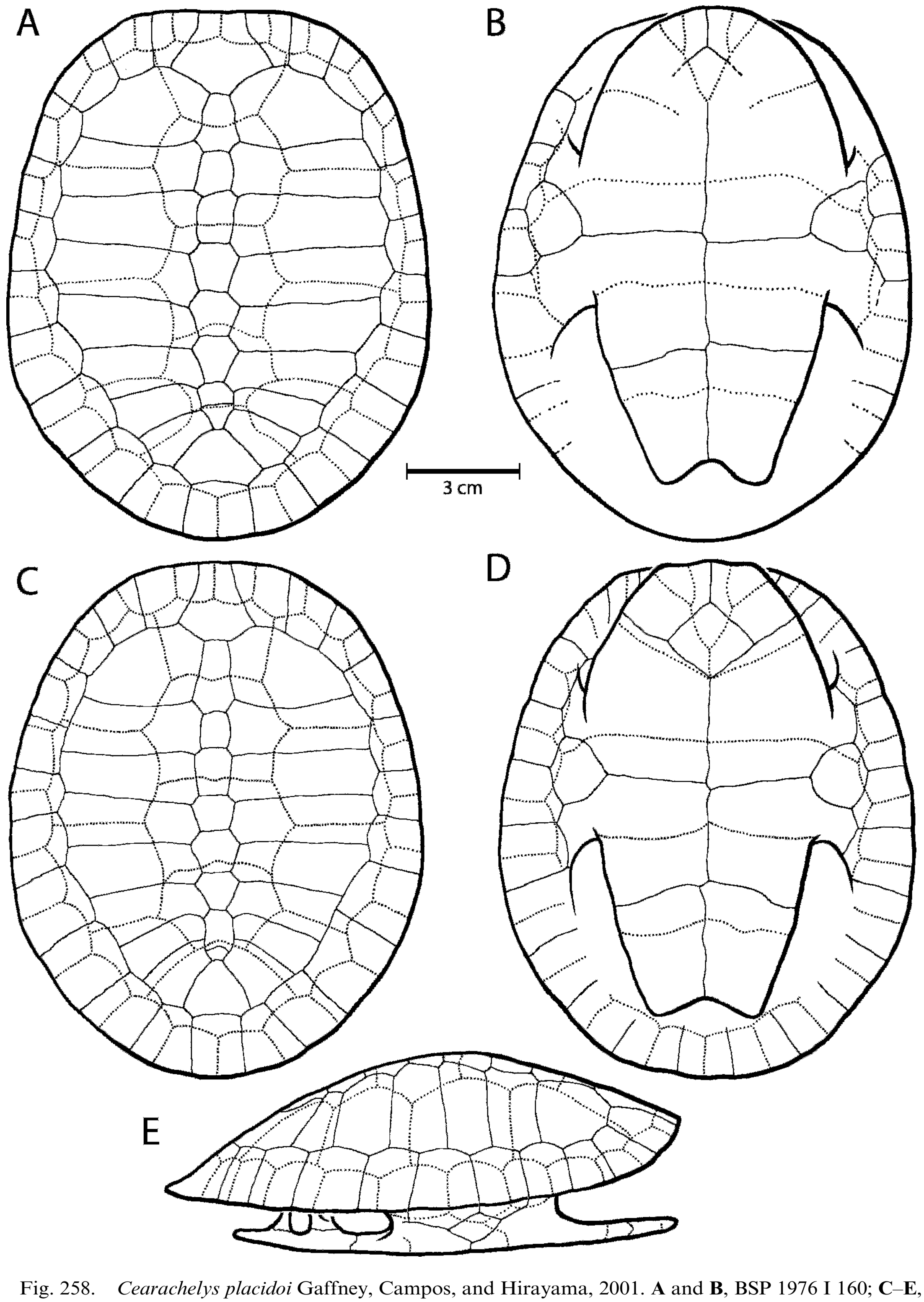

Fig. 258. *Cearachelys placidoi* Gaffney, Campos, and Hirayama, 2001. **A** and **B**, BSP 1976 I 160; **C**–**E**, THUg 1798 (from Gaffney, Campos, and Hirayama, 2001). [L. Redniss, del.]

TABLE 22
Possible Cearachelyini Shells

	AMNH 30551	AMNH 30550	*Cearachelys*
Size	large (56 cm)	large (55 cm)	small (13–20 cm)
Shape	oval	oval	oval
1st neural 6-sided with short posterolateral sides	yes	yes	yes
2nd neural 4-sided	yes	yes	yes
Neural series	8 neurals	6 neurals	8 neurals
Neural-suprapygal contact	absent	absent	present
8th pair of costals meeting on midline	yes	yes	no
7th pair of costals meeting on midline	no	yes	no
Anterior lobe	short, wide at base	short, wide	long, wide at base
Bridge length	bridge > posterior lobe > anterior lobe	same as AMNH 30551	posterior lobe > bridge > anterior lobe
Intergular	small, narrow	large, wide	large, wide
Gular much wider than intergular	yes	no	no
Humeropectoral sulcus posterior to epihyoplastral suture and entoplastron	yes	yes	yes
Pectoroabdominal sulcus cutting mesoplastron	yes	no	yes
Locality and horizon	Kem Kem, Morocco	Kem Kem, Morocco	Santana Fm, Brazil

However, in BSP 1976 I 160 the second neural also does not contact the first costals. However, in Munich BSP I 160 the second neural is asymmetric with five sides and a third costal contact only on the left side. The third neural in this shell is also asymmetric with five sides and a second costal contact only on the right side. Neurals 4–6 are the usual six-sided, coffin-shaped bones. Neurals 7 and 8 are smaller and more irregular, varying in the two carapaces. Neural 7 is six-sided, but the two lateral sides are nearly parallel rather than converging as in the other neurals. In both shells neurals 7 and 8 occupy the area between costals 7 and 8, but the neurals vary in size. In THUg 1798, neural 7 is much longer than neural 8 while in BSP 1976 I 160 they are nearly the same length. The triangular suprapygal contacts the last neural and is a bit wider in BSP 1976 I 160 than in THUg 1798.

The eight costals of *Cearachelys* are similar to those in *Chedighaii* and *Taphrosphys* as well as *Euraxemys*. The 11 peripherals are also similar to the other bothremydids, being wider posteriorly. The carapacial scales of *Cearachelys* are quite similar to the generalized condition for Pelomedusoides seen in *Chedighaii*, *Taphrosphys*, and *Podocnemis*. Because of a complete neural series, the sulcus between vertebrals 4 and 5 falls on the seventh neural in THUg 1798 and nearly on the seventh-eighth neural suture in BSP 1976 I 160. As expected, the scales in *Cearachelys* differ from the unique condition in *Araripemys* in which the first vertebral enters the nuchal emargination and the first two marginals are widely separated.

PLASTRON

The plastron in *Cearachelys* is known in all three specimens. The plastron in BSP 1976 I 160 is complete, but the bone surface is damaged in some areas, precluding sulci preservation. THUg 1798 is nearly complete with all sutures and sulci preserved. The MPSC specimen is missing some of the anterior edges of the plastron, and the posterior margins of the xiphiplastra are broken off.

The plastron of *Cearachelys* has a broad, semicircular anterior lobe and a tapering posterior lobe with a shallow xiphiplastral notch. The anterior lobe in *Cearachelys* is much broader than in *Euraxemys* and

Araripemys. It agrees with *Euraxemys* and most pleurodires in being rounded and differs strongly from that in *Araripemys*, which is pointed. The epiplastra in *Cearachelys* meet on the midline for a length that is much more than in *Araripemys* but less than in *Euraxemys*. The entoplastron in *Cearachelys* is trapezoidal, not V-shaped as in *Araripemys*, and it does not have a curved posterior margin as in *Euraxemys*. The anterior lobe in *Cearachelys* is not as short as in the Taphrosphyini and Bothremydini, agreeing with *Kurmademys*.

Paired, laterally placed mesoplastra are present in *Cearachelys*, as in *Euraxemys* and in contrast to *Araripemys*, which lacks them. The mesoplastra of *Cearachelys* are similar in size and shape to those in *Podocnemis*, *Taphrosphys*, and *Chedighaii* and are not very large as in *Euraxemys*. The axillary and inguinal buttress attachments are not visible in any of the specimens at their current stage of preparation. The xiphiplastron has a moderate posterior projection and a shallow xiphiplastral notch, much as in *Chedighaii* but in contrast to the pointed projections and C-shaped notch in *Taphrosphys*.

The plastral scales in *Cearachelys* are much as in other Pelomedusoides. The intergular is roughly V-shaped and extends onto the entoplastron partially separating the humerals, as in *Chedighaii* and *Podocnemis*. The intergular extends onto the entoplastron slightly more than in *Euraxemys* but not as much as in *Taphrosphys* in which the intergular is large and completely separates the humerals. The humero-pectoral sulcus is behind the entoplastron, as in *Euraxemys* and *Rosasia*, but not crossing it, as in *Foxemys, Polysternon*, and *Taphrosphys*. The pectoral-abdominal sulcus crosses the anterior part of the mesoplastron, as in *Chedighaii* and most other Pelomedusoides. The other plastral scales are very similar to those in *Chedighaii*.

TRIBE BOTHREMYDINI

Foxemys mechinorum (fig. 259)

MATERIAL AVAILABLE: MDEt 10, shell (figured in Tong et al., 1998: figs. 1, 2); PAM 548, shell (figured Tong et al., 1998: figs. 9, 10); MDEt 09, complete plastron; MDEt 11, right scapuloprecoracoid and several isolated plates (Tong et al., 1998); MDEt uncatalogued, nearly complete shell; MHNM uncatalogued specimen, a nearly complete shell.

CARAPACE

The shell morphology of *Foxemys* is very similar to that in *Polysternon*, although there are some differences (see Tong et al., 1998: table 1). The surface of the carapace and plastron in *Foxemys* is covered by the so-called "pelomedusoid" ornamentation, state 1 of character 175, that consists of fine forking and irregular vascular grooves, but the parallel striations seen in *Polysternon* are absent in *Foxemys*. The carapace outline is an elongated oval rather than more rounded, as in *Polysternon* and most other bothremydids, with a straight anterior margin and without a nuchal emargination. A wide posterior emargination on the carapace is present on the holotype (Tong et al., 1998), which is apparently an individual anomaly and is absent in other specimens.

The nuchal is trapezoidal with a straight anterior margin. The anterior portions of the lateral margins of the nuchal are nearly parallel to each other in most specimens. The greatest width of the nuchal is usually about two times its anterior margin. There are seven neurals; their size and shape are similar to *Polysternon*, with the seventh and eighth pairs of costals meeting on the midline. The first neural is the largest and is roughly rectangular with slightly convex lateral margins. Its posterior end is usually slightly wider than the anterior end. The single, triangular suprapygal contacts the pygal and eleventh peripherals posteriorly. Eleven peripherals are present. The first one is roughly triangular with a short contact to the first costal.

There is no cervical scale, as in all Pelomedusoides. The vertebral scales are all slightly wider than long. The first vertebral is restricted to the first peripheral in most specimens, but some shells, such as PAM 548 and the MHNM specimen, have the first vertebral extending onto the second peripheral plate. The second vertebral is as wide as the first in all *Foxemys* specimens, while the second vertebral is clearly narrower than the first one in the *Polysternon* from the Fuveau

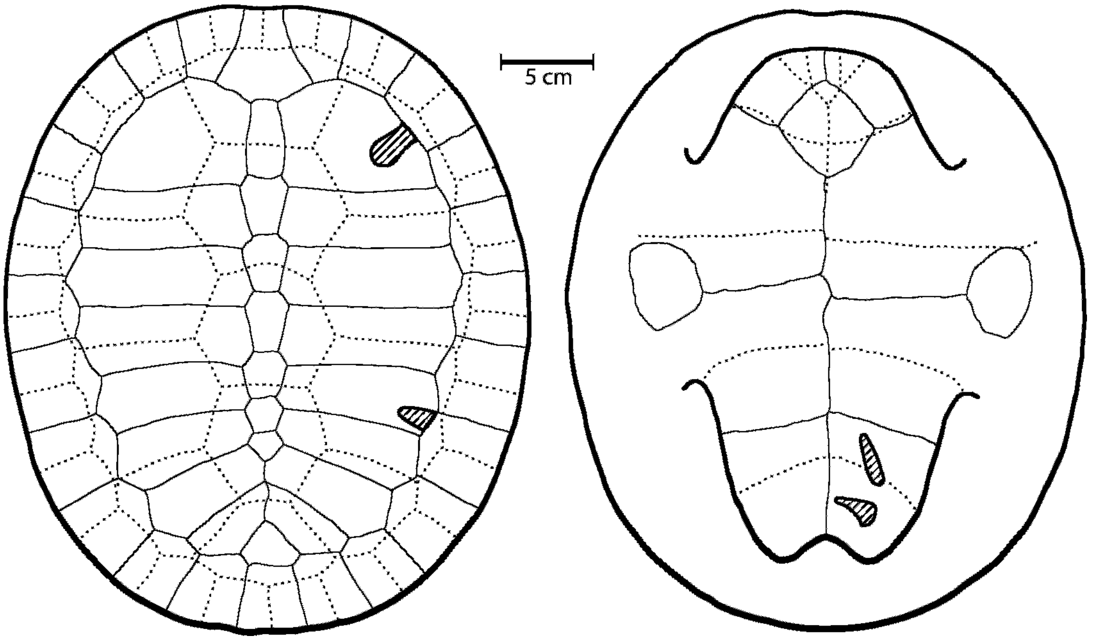

Fig. 259. *Foxemys mechinorum* Tong, Gaffney, and Buffetaut, 1998. Partially restored shell based on PAM 548, MDE t 10 holotype, and MDE t 09 in dorsal (left) and ventral (right) views. [J. Kane, del.]

Basin. All marginal scales are restricted to the peripheral bones.

Plastron

The axillary buttress in *Foxemys* is large and inserts on the lateral part of the first costal plate. On the inner side of the first costal plate, a low, blunt, posteriorly convex ridge links the axillary scar to the first and second dorsal rib heads. The inguinal buttress contacts the eighth peripheral plate and the lateral third of the fifth costal.

The plastron is slightly shorter than the carapace. The anterior lobe is short and wide at the base, as in other Bothremydini, with a nearly straight anterior margin. The bridge is longer than the posterior lobe, and the posterior lobe is longer than the anterior one. The lateral margins of the posterior lobe of *Foxemys* are less rounded than in *Polysternon.* The anal notch is large and wide, wider than in *Polysternon.*

The length of the epiplastral symphysis is about one-third to one-half that of the entoplastron. The large and diamond-shaped entoplastron is wider than long in most specimens, but some of them, such as the MHNM specimen and MDEt 09, have the entoplastron as long as wide. The posterior end of the entoplastron reaches the level of the bridge, as in *Polysternon*, but differs from *Rosasia*, in which the entoplastron is more anteriorly placed. The hyoplastra and hypoplastra are about the same length. The mesoplastron is roughly semicircular in shape and longer than wide. The size of the mesoplastron varies compared to the entoplastron, from smaller (MDEt 10) to equal (MDEt 09, MNHM specimen, and PAM 548). On the inner side of the xiphiplastron, the pubic scar is an anteromedially orientated, elongate oval, with an acute anterior tip. The ischiac scar is elongated and triangular in shape. Its anterior margin is transverse and its posterior tip is anterior to the anterior margin of the anal notch.

The plastron has the usual 13 scales. The gular scales are large and triangular in shape, reaching but not crossing the anterior margin of the entoplastron. In PAM 548, MDEt 09, and most other specimens, the intergular is large, widely separating the gulars and extending for half the length of the entoplastron. In contrast, the shells in MDEt 10 and the MHNM specimen have a smaller intergular scale that reaches only the anterior third of the entoplastron. The humeral scale has a variable but short midline length, from 40% to 8% of the entoplastral length. The humeropectoral sulcus crosses the entoplastron posteriorly, about one-third to one-fourth of the length of the entoplastron, and then crosses the epihyoplastral suture about halfway along the length of the suture. The humeropectoral sulcus is entirely anterior to the epihyoplastral suture in MDEt 10. The pectoral scales cover the anterior two-thirds of the hyoplastra. The pectoroabdominal sulcus is straight and does not reach or barely reaches the mesoplastra. The abdominals are the largest plastral scales. They cover the posterior third of the hyoplastra and the anterior half of the hypoplastra and mesoplastra. The abdominofemoral sulcus is straight or slightly convex anteriorly, with the lateral ends curved posteriorly. The femoral scales cover the posterior half of the hypoplastra and the anterior part of the xiphiplastra. The femoroanal sulcus is convex anteriorly. The anal scales cover the posterior half of the xiphiplastra.

Polysternon provinciale (fig. 260)

Material Available: Two shell fragments including an anterior portion of carapace (MHNM 1982-853), from "lignite de la grande Mène", Matheron collection (Matheron, 1869; Broin, 1977: fig. 1, pl. 1, fig. 3a,b; the other specimen was already lost when Broin [1977] reviewed the material); uncatalogued partial shell in the collection of the Musée Cantonal de Géologie de Lausanne (Portis, 1882); MHNM 1982-857, holotype of "*Elochelys major*" (Nopcsa, 1931: pl. XIII; Broin, 1977: fig. 2, pl. 1, fig. 1); MHNM 1982-855, internal cast showing the plastron with pubic and ischiac scars, collection Comte de Gérin-Ricard (Nopcsa, 1931: fig. 1; Broin, 1977: pl. 1, fig. 2, from "Valdonne"); Costa collection, a complete shell (Buffetaut et al., 1996: fig. 4) and numerous plates.

Carapace

The shell surface ornamentation is figured by Portis (1882: pl. 28) and Broin (1977: pl. 1, fig. 3b). It consists of anteroposteriorly directed, thin parallel striations, along with the "pelomedusoid" texture pattern, consisting of fine forking and irregular vascular grooves (state 1, character 175). The parallel striations, state 3, are unique among bothremydids; they are well marked and cover the entire surface of the carapace on the Portis specimen. On the holotype and Villeveyrac specimens, they are well marked on the neurals and the medial part of the costals. They are weaker on the plastron than on the carapace and absent on the plastron. The "pelomedusoid" ornamentation is also visible on the peripherals and the plastron.

The shell is low and a shortened oval in outline, different from that in *Foxemys*, which is an elongated oval. The nuchal emargination is present and shallow. The nuchal is trapezoidal and roughly as long as wide. There are seven neurals, with the first being the longest and having the laterally convex lateral margins as in *Foxemys*. The lengths of the neurals decrease from the front to the back. The second to sixth neurals are six-sided with short anterolateral sides. The seventh neural is five-sided and smaller. Eight costals are present; the first is the longest, but not as long as in *Taphrosphys*. The seventh and eighth pairs of costals meet on the midline. A single, triangular suprapygal contacts the pygal and the eleventh peripheral posteriorly, except in the Villeveyrac specimen, in which the suprapygal is narrower and does not contact the eleventh peripheral. There are 11 peripherals, all longer mediolaterally than anteroposteriorly in the Villeveyrac specimen, and the preserved posterior peripherals in Portis' specimens (Portis, 1882: pl. 28). The first peripheral is roughly triangular with a short contact with the first costal, as in *Foxemys* but in contrast to *Cearachelys*, *Chedighaii*, and *Rosasia* in which the first peripheral is more rectangular with a longer contact with the first costal.

The cervical scale is absent, as in all Pelomedusoides. The first vertebral is wider than the second one, in contrast to *Foxemys*, in which it is as wide as the second vertebral, and *Cearachelys*, *Taphrosphys*, *Elochelys*, and *Rosasia*, in which the first vertebral is narrower than the second one. The vertebrals

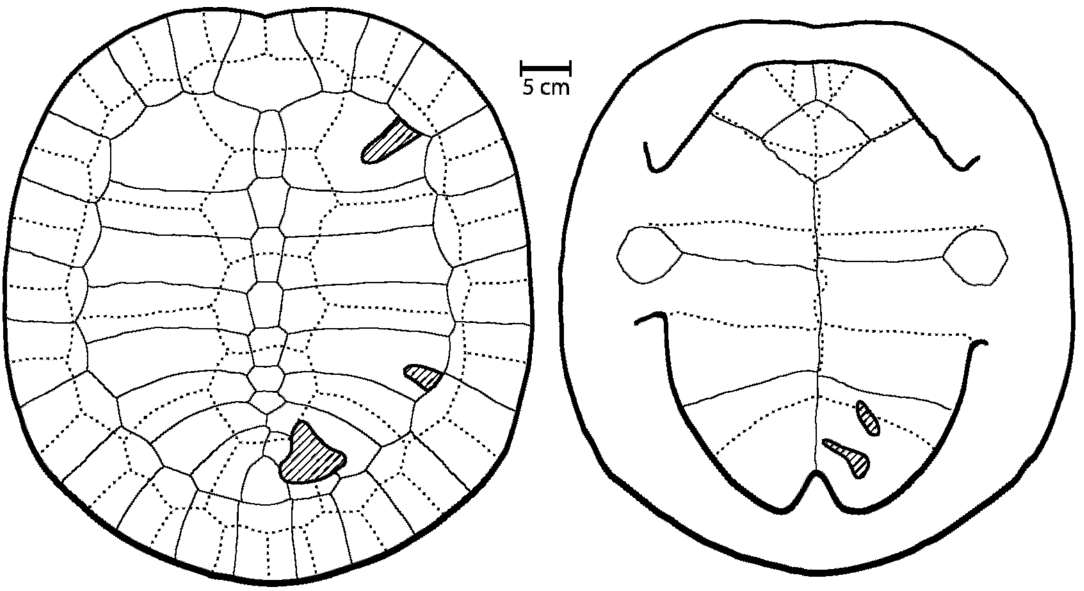

Fig. 260. *Polysternon provinciale* (Matheron, 1869). Partially restored shell based on specimen in Costa Collection. Dorsal (left) and ventral (right) views. [J. Kane, del.]

2–4 are longer than wide in the type shell, but wider than long in the Villeveyrac specimen.

Plastron

The plastron is shorter than the carapace. The anterior lobe is relatively short and wide at the base, as in other Bothremydini and Taphrosphyini. The bridge is longer than the posterior lobe; the latter is longer than the anterior lobe. The posterior lobe is wide with laterally convex lateral margins, differing from the nearly straight lateral margins of *Araiochelys*. The anal notch is deep and narrow. The pubic and ischiac scars are similar to those in *Foxemys*. The epiplastron is large with a rather long midline suture. The large entoplastron is diamond-shaped and slightly wider than long. The mesoplastron is laterally placed and smaller than the entoplastron.

Thirteen scales cover the plastron. The intergular scale is roughly as wide as the gular scale and covers little of the entoplastron. The gular scale reaches the entoplastron but does not overlap it in the type. In the Villeveyrac locality, among seven epiplastra preserved, only one has the large gular scale reaching the entoplastron; on the others the gular scale is smaller and does not reach the entoplastron. The humeropectoral sulcus is located half to a third of the length along the entoplastron and close to the epihyoplastral suture, in contrast to *Cearachelys, Galianemys*, and *Rosasia* in which the humeropectoral sulcus is located far behind the epihyoplastral suture and posterior to the entoplastron. The pectoroabdominal sulcus barely reaches the mesoplastron or is located slightly anterior to it, in contrast to *Araiochelys* and *Kurmademys* in which this sulcus is located well anterior to the mesoplastron.

Rosasia soutoi (fig. 261)

Material Available: Museu Minerologico e Geologico de la Faculdade de Ciencias, Universidade do Porto, uncatalogued type shell (figured in Carrington da Costa, 1940: pls. I, III); Universidade Nova de Lisboa, Portugal, MTA 1, shell (Antunes and Broin, 1988: pl. 3, figs. 1, 2), MTA 2, shell (Antunes and Broin, 1988: pl. 4, figs. 1, 2); two shells (only one figured) in the Serviços Geológicos de Portugal Lisbonne (Carrington da Costa, 1958: pls. 3, 4); one shell in the Faculdade de Ciencias e Tecnologia, Universidade de Coimbra (Carrington da Costa, 1958: pls. 5, 6).

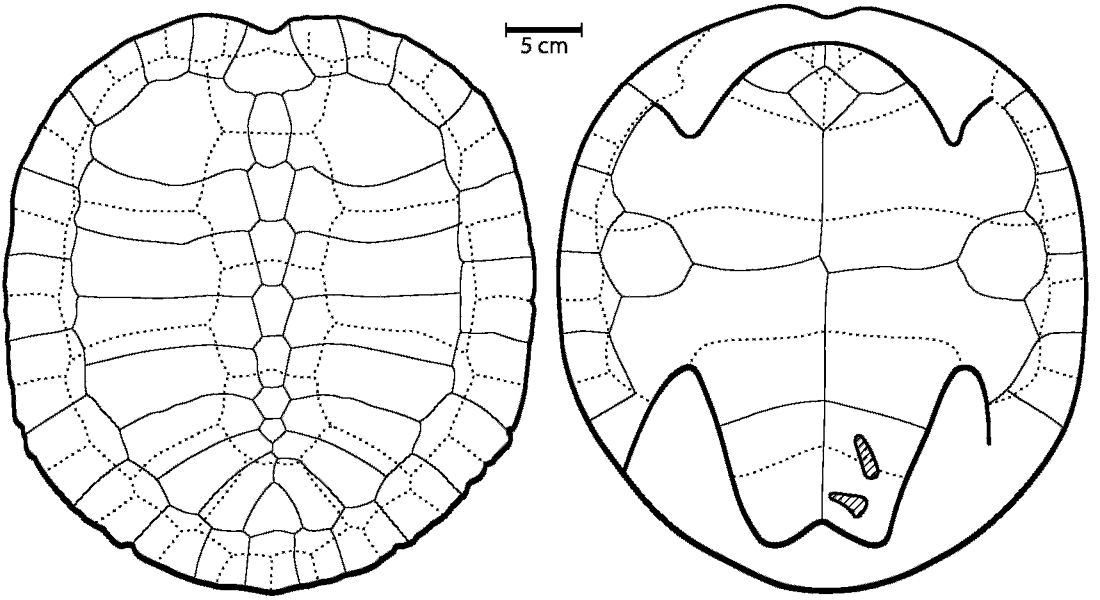

Fig. 261. *Rosasia soutoi* Carrington da Costa, 1940. Partially restored shell based on Fuentes (1985) in dorsal (left) and ventral (right) views. [J. Kane, del.]

Carapace

The present description is based on the descriptions and illustrations of Carrington da Costa (1940, 1958) and Antunes and Broin (1988). The shell surface of *Rosasia* is figured in detail by Carrington da Costa (1940: pl. II; 1958: pl. II). The texture is the "pelomedusoid" pattern, fine forking and irregular vascular grooves, as in many Pleurodira, especially bothremydids, but not as dense as in *Taphrosphys* (Antunes and Broin, 1988).

The shell is low, with a rounded outline. The nuchal emargination is narrow and deep, mostly involving the nuchal. Antunes and Broin (1988) mentioned the absence of the nuchal emargination in the specimen of Coimbra; this may be due to damage of the anterior margin of the shell. The nuchal is wider than long, but the anterior margin is roughly equal to half of the maximum width. There are seven neurals: the first is four-sided, the following ones are six-sided with short anterolateral sides, and the last neural is five-sided. The seventh and eighth pairs of costals meet on the midline. The suprapygal is small and triangular in shape, with its length slightly larger than the width. The pygal is slightly longer than wide. The first costal is longer than the second and third costals together. The first peripheral is roughly rectangular in shape, with the anterior margin being only slightly longer than the posterior one, in contrast to *Polysternon* and *Foxemys* in which the first peripheral is more triangular.

The cervical scale is absent, as in all Pelomedusoides. The second and third vertebral scales are roughly as long as wide. All marginal scales are restricted to the peripheral plates. The carapace has strong buttresses, as in podocnemidids and other bothremydids. The axillary buttress extends to the lateral half of the first costal plate and the inguinal buttress attaches to the fifth costal plate (Antunes and Broin, 1988). The pelvic girdle is sutured to the shell, as in all Pleurodira. Its contact with the carapace cannot be seen. The pubic scar is oval in shape, oblique, and relatively short and wide, not elongated, as in *Taphrosphys*. The ischiac scar is roughly triangular in shape and placed anterior to the anal notch.

Plastron

The anterior lobe of the plastron is short and wide at its base, as in most bothremydids, with a semicircular outline. The bridge is long, longer than the posterior lobe and longer than in other bothremydids. The posterior lobe is longer than the anterior one and has straight lateral margins convergent posteriorly. The anal notch is very shallow and wide. The entoplastron is small, diamond-shaped, and as long as wide. Its posterior end does not reach the level of the axillary notch. The mesoplastron is larger than the entoplastron and is slightly wider than it is long.

The plastron is covered by 13 scales. The intergular scale overlaps about a third of the entoplastron. The gular scale is small and does not reach the entoplastron. The humeropectoral sulcus crosses the hyoplastron just posterior to the end of the entoplastron and is placed far behind the epihyoplastral suture, as in *Cearachelys* and *Galianemys*. The pectoroabdominal sulcus crosses the anterior part of the mesoplastron. The abdominofemoral sulcus is about midway along the hypoplastron, as in *Cearachelys, Polysternon*, and *Foxemys*, while in *Araiochelys* and *Taphrosphys* it is more anterior. The femoroanal sulcus is as in other bothremydids, crossing the xiphiplastron about midway.

Araiochelys hirayamai (figs. 262, 263)

MATERIAL AVAILABLE: THUg 3338, partially disarticulated shell (fig. 262), including left first and fifth costals, left third, seventh, and eighth peripherals and other fragments, nearly complete plastron and limb bones; MDEt 25, an incomplete and disarticulated shell, neurals 1–2, left costals 1–4 (the fourth is incomplete), right costals 2–5 (costals 3 and 5 are incomplete), left tenth and eleventh peripherals, one peripheral of bridge region, right hypoplastron and xiphiplastron, and other fragments. MDEt 25 is tentatively identified as *Araiochelys hirayamai* because of the similar size, the shape and the structure of the first and fifth costal plates, similar development of the axillary and inguinal buttress scars, the shape of the posterior lobe of the plastron, and the shape and position of the pubic and ischiac scars. Both MDEt 25 and THUg 3338 are from the Danian beds of the Ouled Abdoun Basin, Morocco. None of the plastron and only part of the carapace restoration are dependent on the identification of MDEt 25 as *Araiochelys*.

CARAPACE

The surface texture of the carapace and plastron is the usual network of fine furrows, the "pelomedusoid" texture (state 1, character 175). This pattern is less pronounced than that seen in *Taphrosphys*; the polygonal areas delimited by the furrows are flat rather than raised, as in *Taphrosphys*. The carapace is very thin in MDEt 25, measuring from 6 mm for neurals to less than 2 mm for the lateral end of the costal plates. In MDEt 25, only the first and the second neurals are preserved. The first neural is elongated and roughly rectangular in shape; it is slightly expanded at the midpoint and does not contact the second costal. The second neural is much shorter than the first and is pentagonal in shape with short anterolateral sides. It is in contact with the first neural anteriorly and the first costal anterolaterally. The following neurals are not preserved, but the complete medial margin of the second to fifth costal plates allows the reconstruction of the third to fifth neurals. The third to fifth neurals are all diamond-shaped and longer than wide, with their size decreasing from front to back. The posterior part of the second to fifth costals meets on the midline between the neurals. The sixth neural was present but not preserved, judging by the posteromedial margin of the fifth costal. It is probably smaller than the fifth neural.

The complete left first costal is preserved in THUg 3338. In MDEt 25 the left first costal is nearly complete, but only a small fragment of the right one is preserved. The first costal is relatively long, with its length being greater than that of the second and third costals together, as in *Taphrosphys sulcatus* (Gaffney, 1975a). The inner surface of this plate bears a large scar for axillary buttress insertion that reaches halfway along the costal. A posteriorly convex, low ridge with an acute anterior edge links the axillary buttress scar to the first and second dorsal rib heads. This structure is present on both THUg 3338 and MDEt 25. The second to fourth costals are short, as in *Taphrosphys* and *Chedighaii*. The fifth costal is preserved in both THUg 3338 and MDEt 25, in which it widens distally; the inguinal buttress reaches its midpoint on the ventral side. The third peripheral is rectangular and longer

Fig. 262. *Araiochelys hirayamai*, n. gen. et sp. THUg 3338 holotype before preparation showing skull, jaws, plastron, and carapace elements in situ. [E.S. Gaffney, del.]

than wide. The seventh, eighth, and tenth peripherals are roughly square in shape. The eleventh peripheral is wider than long. The posterior margin of the carapace is undulant.

The scute sulci of the carapace are shallow but easily distinguishable. The first vertebral scale is not complete; only the posterior part of the left side is preserved. The first vertebral is clearly narrower than the second one. The second vertebral scale is very large and longer than wide. It is much larger than the third vertebral scale, with its posterolateral corner reaching the posterior margin of the third costal, which is a unique feature among bothremydids. The third vertebral scale is roughly square in shape. The intervertebral sulci cross the first neural medially, just anterior to the fourth neural and just posterior to the fifth neural.

PLASTRON

The plastron of THUg 3338 lacks the epiplastra and entoplastron; the anterior edge of both hyoplastra is damaged. In MDEt 25, the right hypoplastron and xiphiplastron are preserved. The hyoplastron is slightly widened at its anterior part. The mesoplastron is not completely known, but it seems to be slightly wider than long. The posterior lobe is narrow with nearly straight lateral margins. There is a shallow notch on the lateral border of the xiphiplastron at the lateral limit of the femoroanal scute sulcus in both THUg 3338 and MDEt 25. The anal notch is V-shaped, deep, and broad in THUg 3338. It has more curved borders in MDEt 25, which may be sexual dimorphism or may indicate a separate taxon. Both hypoplastron and xiphiplastron are much longer than wide. On the dorsal side of the xiphiplastron, the pubic scar is an elongated oval; it is less oblique and is placed closer to the lateral margin of the plastron than in *Taphrosphys sulcatus* (Gaffney, 1975a). The ischiac scar is roughly triangular in shape. It is posterior to the anterior margin of the anal notch, which differs from the

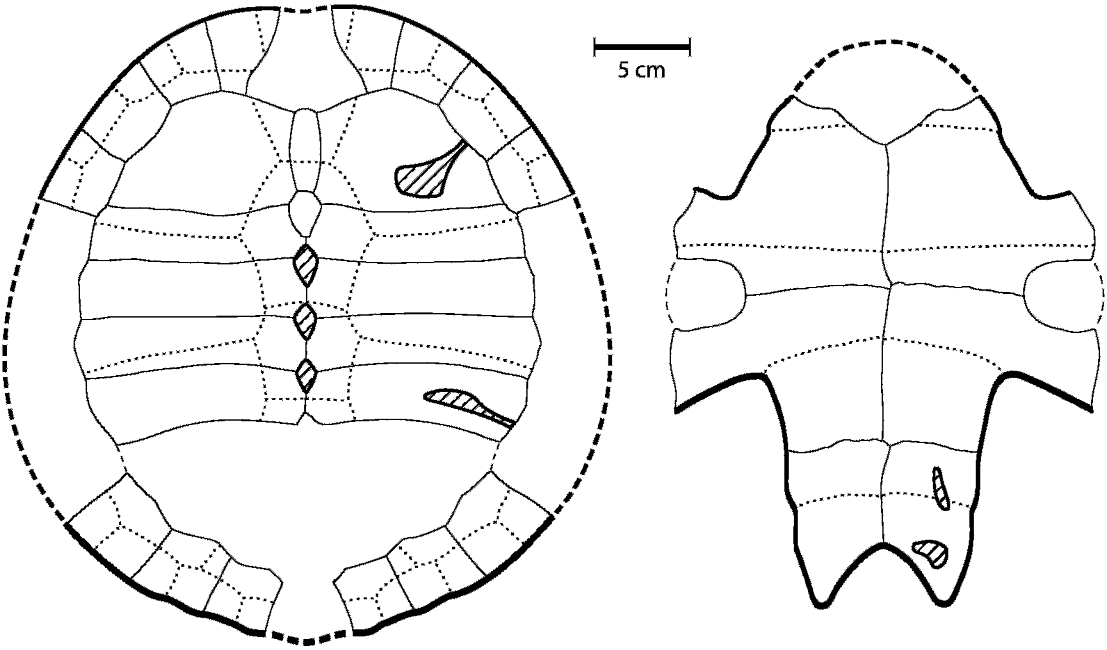

Fig. 263. *Araiochelys hirayamai*, n. gen. et sp. Partially restored shell based on THUg 3338 holotype and MDEt 25 in dorsal (left) and ventral (right) views. [J. Kane, del.]

condition in *Foxemys*, but it is not as close to the posterior margin of the plastron, as in *Taphrosphys*.

The humeropectoral sulcus is preserved on the right hyoplastron of THUg 3338; it is posterior to the epihyoplastral suture, as in *Taphrosphys* and *Chedighaii*, but it probably crosses the entoplastron. The pectoroabdominal sulcus is preserved on the left hyoplastron; it is nearly straight and placed well anterior to the mesoplastron. The abdominofemoral sulcus is slightly convex anteriorly, crossing the midline at about one-third of the length of the hypoplastron. The femoroanal sulcus crosses the midline near the middle of the xiphiplastron.

Chedighaii barberi (fig. 264, table 23)

MATERIAL AVAILABLE: FMNH P 26055, shell (Schmidt, 1940: figs. 1–5); FMNH P2769, shell (Zangerl, 1948: fig. 3); FMNH P27372, shell (Zangerl, 1948: figs. 4, 7, 9,10); FMNH 27370, shell (Zangerl, 1948: figs. 5, 6, 11, 12, pl. 4, fig. 1); FMNH 27331, shell; FMNH P27405, shell; FMNH PR 247, shell (Gaffney and Zangerl, 1968: figs. 2, 3); ANSP 15902, shell (Gaffney and Zangerl, 1968: figs. 408); YPM 3608, shell (Gaffney and Zangerl, 1968: figs. 9–12); ALAB PV 2001.2, partial shell.

CARAPACE

Shell surface texture is the "pelomedusoid" pattern (Broin, 1977). The carapace is broadly rounded and low, as in *Taphrosphys*. The lateral margins converge posteriorly, with the widest point at the level of the seventh to eighth peripherals, then becoming narrower posteriorly.

The posterior end of the carapace tapers to a blunt curve at the rear. It is wider than long (FMNH P27369, FMNH P27370, FMNH P27372, FMNH PR 247) or as long as wide (FMNH P26055). This is more like the shell of *Taphrosphys* (Gaffney, 1975a) but different from that of *Galianemys* and *Cearachelys*, in which the shell is an anteroposteriorly elongated oval. The nuchal emargination is present in all specimens with this part available, although its size and shape vary. In FMNH P26055, FMNH PR 247, and FMNH P27370, the nuchal emargination is narrow and deep, while FMNH P27369 and YPM 3608 have a shallower emargination.

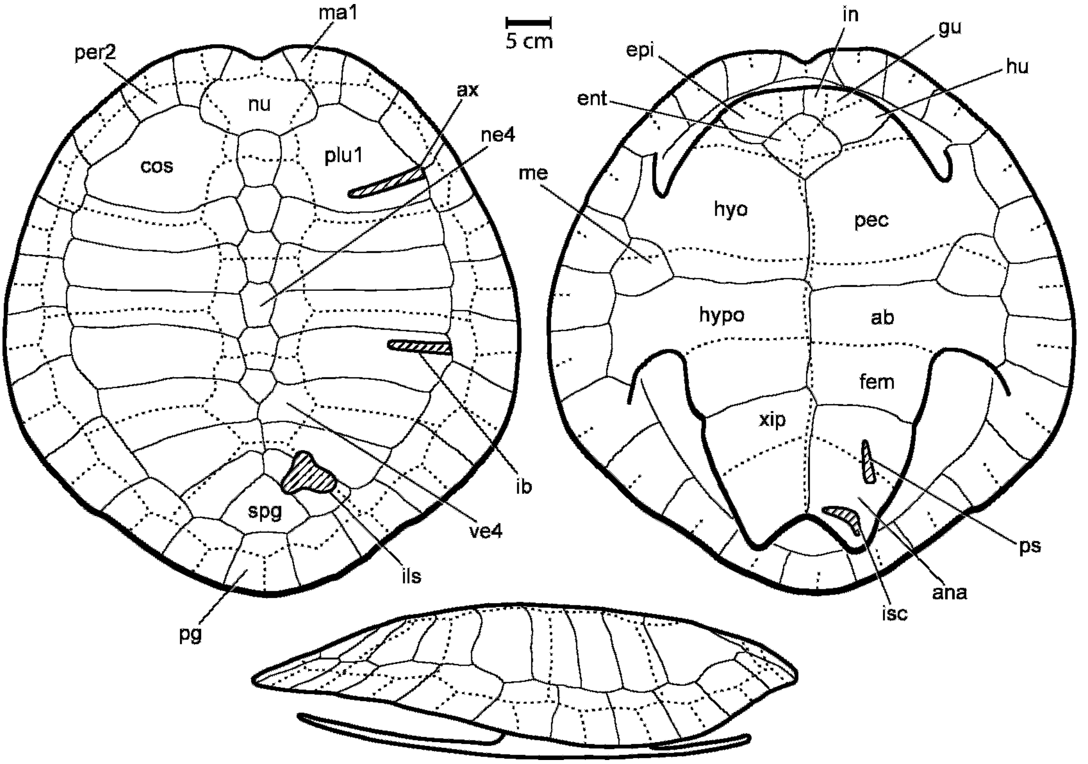

Fig. 264. *Bothremys* or *Chedighaii barberi* (Schmidt, 1940). Partially restored shell based mostly on FMNH P26055, the holotype of "*Podocnemis*" *barberi* Schmidt, 1940. Upper left, dorsal view; upper right, ventral view; lower, right lateral view. See Note Added in Proof. [J. Kane, del.]

The carapace of *Chedighaii barberi* is composed of one nuchal, six or seven neurals, eight pairs of costals, 11 pairs of peripherals, one suprapygal, and one pygal, as in other Pelomedusoides. The nuchal is six-sided and short; it is clearly wider than long. Six neurals are present in FMNH P26055, FMNH P27370, FMNH P27372, FMNH P27331, and ANSP 15902, while FMNH PR 247, FMNH P27369, and YPM 3608 have seven neurals. The first neural is rectangular and only slightly longer than the second neural, except YPM 3608, which has a longer first neural. In most other bothremydids, the first neural is much longer than the second one (*Cearachelys, Galianemys, Kurmademys, Foxemys, Polysternon*). The second to fifth neurals are six-sided with short anterolateral sides. The sixth neural is as wide as long; it is five-sided when it is the last neural or six-sided when seven neurals are present. In both cases the sixth neural is as wide as the fifth one. The seventh neural, when present, is clearly smaller than the sixth. The first costal is longer than the second and third costals together, as in *Taphrosphys*. The sixth to eighth pairs of costals meet on the midline, separating the last neural from the suprapygal, when six neurals are present. In specimens with seven neurals, the seventh and eighth costals meet on the midline. The suprapygal is triangular, as in other Pelomedusoides. The first peripheral is four-sided, with the posterior margin being much shorter than the anterior one. The size of the peripherals increases from front to back, reaching the maximum size at the eighth and ninth peripherals. The tenth and eleventh peripherals are much smaller than the ninth one. The tenth and eleventh peripherals are also small in *Taphrosphys*, but the peripherals are generally narrower in it (Gaffney 1975a). The pygal is four-sided and nearly square, as in many Pelome-

TABLE 23
Comparison of *Chedighaii barberi* Shells

	FMNH P26055	FMNH PR 247	FMNH P27369	FMNH P27370	FMNH P27372	ANSP 15902	YPM 3608	FMNH P27331
Carapace shape	as long as wide	wider than long	wider than long	wider than long	wider than long	?	?	?
Nuchal emargination	deep, narrow	deep, narrow	very shallow	deep, narrow	?	?	very shallow	?
Neural number	6	7	7	6	6	6	7	6
1st neural > 2nd neural	slightly longer	slightly longer	slightly longer	slightly longer	slightly longer	slightly longer	much longer	slightly longer
Vertebrals	narrower	?	?	wider	wider	narrower	narrower	wider
Anterior lobe	semicircular	semicircular	trapezoidal	semicircular	?	semicircular	trapezoidal	?
Epiplastral symphysis	longer	very short	very short	very short	?	very short	longer	?
Entoplastron shape	wider than long	wider than long	wider than long	wider than long	?	as long as wide	wider than long	?
Mesoplastron shape	as wide as long	wider than long	?	wider than long	?	wider than long	?	?
Anal notch	V-shaped	V-shaped	V-shaped	U-shaped	?	U-shaped	?	?
Environment	marine	marine	marine	marine	marine	marine	marine	marine

dusoides, with the posterior margin being longer than the anterior one.

The scale sulci on the carapace are preserved and figured in Schmidt (1940: fig. 2, FMNH P26055) and Zangerl (1948: pl. 4, fig. 1, AMNH P27370). They are partly visible in ANSP 15902 (Gaffney and Zangerl, 1968: fig. 4) and YPM 3608 (Gaffney and Zangerl, 1968: fig. 9). The general pattern of the scales of *Chedighaii barberi* agrees with that in other Pelomedusoides. The cervical scale is absent, as in all Pelomedusoides. The vertebral scales are all wider than long in FMNH P27370, FMNH P27372, and FMNH P27331, with strongly angled lateral margins. In FMNH P26055, ANSP 15902, and YPM 3608, the first to fourth vertebrals are narrower, with only slightly angled lateral margins. The first marginal is much wider than long ,as in *Galianemys* but in contrast to *Taphrosphys* and *Cearachelys* in which it is square. All marginals are restricted to the peripherals, as in other bothremydids.

On the inner side of the carapace, the axillary buttress scar lies on the lateral half of the first costal, near its posterior margin (Zangerl, 1948: fig. 7; Gaffney and Zangerl, 1968: figs. 5, 10). In *Taphrosphys*, the axillary scar is even more posteriorly placed (Gaffney, 1975a: fig. 4). The inguinal scar is less than half the width of the fifth costal, as in *Taphrosphys*. The iliac scar is placed on the posterior part of the seventh costal and eighth costals, overlapping slightly onto the suprapygal (Zangerl, 1948: fig. 9), as in *Taphrosphys*.

PLASTRON

The plastron in *Chedighaii* is shorter than the carapace, with the anterior margin posterior to that of the carapace, unlike *Cearachelys* and the possible *Galianemys* shells. The anterior lobe is short and wide, with a semicircular outline in FMNH P26055, ANSP 15902, FMNH PR 247, and FMNH P27370, in contrast to YPM 3608 and FMNH P27369, which have a more trapezoidal-shaped anterior lobe. The bridge is longer than the anterior lobe and shorter than the posterior lobe. The bridge is wide, as in *Taphrosphys* but in contrast to *Galianemys*, *Foxemys*, *Polysternon*, and *Rosasia* in which it is narrower. The posterior lobe is narrower than the anterior lobe, with the lateral margins tapering posteriorly, unlike *Taphrosphys*, which has the posterior lobe nearly as wide as the anterior one with nearly parallel lateral margins. The anal notch is deep and wide. It has an inverse V-shape in FMNH PR247, FMNH P26055, and FMNH P27369 and a more U-shape in ANSP 15902.

The plastron is composed of 11 plates, as in other podocnemidoids. The epiplastron is similar to *Taphrosphys*, with a comparatively short midline suture, except in YPM 3608 (Gaffney and Zangerl, 1968) and FMNH P26055. In *Cearachelys* the midline suture of the epiplastron is longer. The entoplastron is diamond-shaped and wider than long in most specimens (except ANSP 15902), as in *Taphrosphys* but differing from *Galianemys* in which it is as long as wide. The hyoplastron and hypoplastron are similar in length. The xiphiplastron is much longer than wide, as in most other bothremydids but in contrast to *Taphrosphys* in which this plate is equidimensional.

On the inner side of the plastron, the pubic scar (Zangerl, 1948: fig. 11, pl. 4, fig. 2; Gaffney and Zangerl, 1968: figs. 8, 12) is oval and elongated, similar to that of *Araiochelys*. In *Taphrosphys*, the pubic scar is longer and narrower (Gaffney, 1975a: fig. 11). The ischiac scar of *Chedighaii barberi* is similar to that of *Podocnemis*. It is triangular, wider than long, and placed far anterior to the posterior margin of the plastron. In *Taphrosphys*, the ischiac scar is nearly rounded and is situated near the posterior margin of the plastron.

The scale sulci on the plastron are only partly visible in FMNH P27369 (Zangerl, 1948: fig. 3), FMNH PR 247 (Gaffney and Zangerl, 1968: fig. 3), and YPM 3608 (Gaffney and Zangerl, 1968: fig. 11). There are some visible on ANSP 15902 (Gaffney and Zangerl, 1968: fig. 7) but only a few on the type specimen (although none figured, Schmidt, 1940: fig. 5). When all specimens from the Selma Formation at the Field Museum are taken together, all the scales are known for a composite reconstruction (fig. 264). The intergular scale is similar to that in *Foxemys*, extending about half the length of the entoplastron. The gular scale is triangular and wider than long, reaching the entoplastron but not crossing it. The humeropectoral sulcus is entirely posterior to the epihyoplastral suture, extending through the posterior third of the entoplastron. The pectoroabdominal sulcus is similar to that of *Galianemys*, crossing the mesoplastron. The abdominofemoral sulcus lies along the midpoint of the hypoplastron. The femoroanal sulcus is similar to that in *Taphrosphys*.

TRIBE TAPHROSPHYINI

Taphrosphys sulcatus (fig. 265, table 24)

MATERIAL AVAILABLE: YPM PU 18706, partial shell collected by Regensburg and Dilkes, August, 1960, MFL Hornerstown Formation, Sewell, New Jersey (Gaffney, 1975a); YPM PU 18707, partial shell with associated limb and skull fragments, same data as in YPM PU 18706; YPM PU 18708, left xiphiplastron, same data as in YPM PU 18706; ANSP 15544, carapace with partial skull and limb elements, collected by Keith Madden and James Maddox from the MFL Hornerstown Formation, Inversand pits, Sewell, New Jersey (Richards and Gallagher, 1974; White, 1972); NJSM 10410, a plastron, no data; AMNH 1347, nuchal and first peripherals, "Cretaceous, New Jersey" (label), Cope Collection; AMNH 1470 (Hay, 1908: 119, fig. 119), neural bones, nuchal, and other shell fragments, "Barnsboro, 9/8 1870" (label), Cope Collection; AMNH 1472 (type of *Taphrosphys molops* Cope, figured in Cope, 1870: pl. 7, fig. 16; text-figs. 43, 44; Hay, 1908: figs. 112–116), nearly complete anterior lobe, incomplete xiphiplastron and other shell fragments, West Jersey Marl Company pits, Barnsboro, New Jersey, August 25, 1868, Cope Collection; AMNH 1474 (Hay, 1908: figs. 117, 118), partial plastron with incomplete right and left hypoplastra, complete left xiphiplastron and other fragments, Birmingham, New Jersey, Cope Collection; AMNH 1477 (Hay, 1908: fig. 120), shell fragments, West Jersey Marl Company pits, Barnsboro, New Jersey, 1855, Cope Collection; AMNH 1471 (Hay, 1908: fig. 106), anterior plastral bones, mixed with AMNH 1470 (label), Cope Collection; AMNH 1467 (type of *Taphrosphys leslianus* Cope, figured in Hay, 1908: figs. 103–105), partial shell, Hornerstown, New Jersey, collected by Dr. S. Lockwood, Cope Collection; AMNH 1125 (only the right first costal is labeled as 1124) (type of *Taphrosphys longinuchus* Cope, figured in Hay, 1908: figs. 101, 102), partial shell with limb fragments (this specimen was apparently mixed with the type of *Adocus agilis* Cope, AMNH 1135), David Haine's marl pit, Medford, New

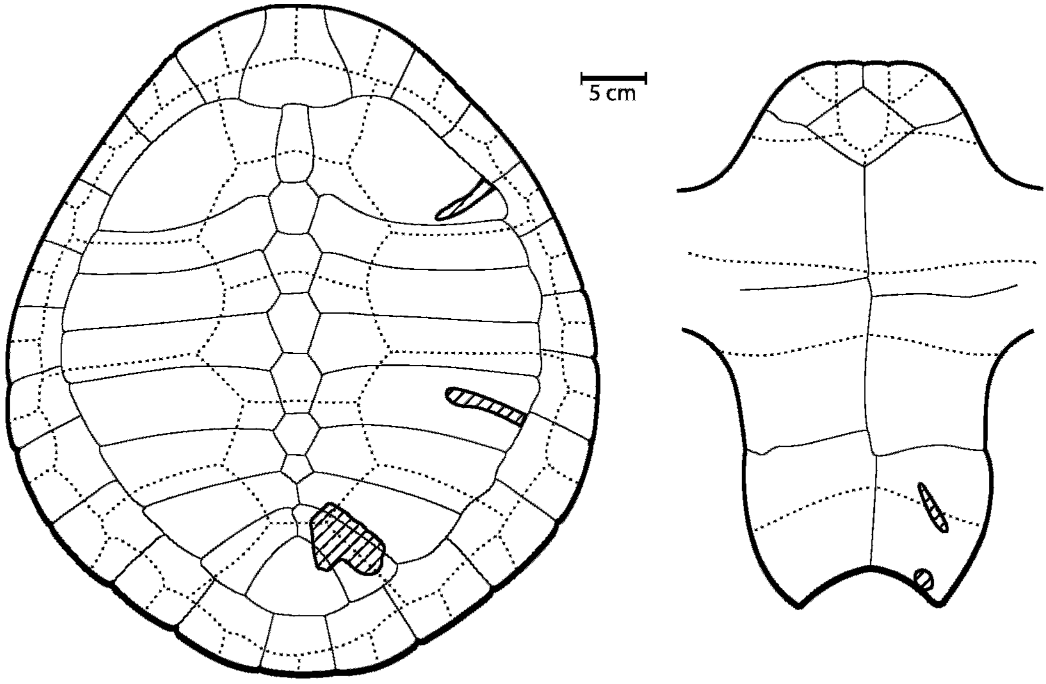

Fig. 265. *Taphrosphys sulcatus* (Leidy, 1856). Partially restored shell based mostly on YPM PU 18706 (from Gaffney, 1975a). Dorsal view of carapace (left) and ventral view of plastron (right). [J. Kane, del.]

Jersey, March 15, 1870, Cope Collection; AMNH 1468 (Cope, 1870: 166, fig. 45; not that two consecutive figures in Cope [1870] are both labeled fig. 45 but illustrate different specimens; Hay, 1908: figs. 99, 100), shell fragments, Barnsboro, New Jersey, Cope Collection; AMNH 1469, shell fragments, West Jersey Marl Company pits, Barnsboro, New Jersey, 1869, Cope Collection; AMNH 2524 (Cope, 1870: 165, fig. 45), nuchal bone, Barnsboro, New Jersey, in the Rutgers University Cook Collection until 1970; AMNH 1126, plastron fragments, incomplete ilium and humerus, and other shell fragments, type of *Taphrosphys strenuous*, "?Hornerstown Formation (Upper Greensand), Barnesboro, Gloucester Col, New Jersey, Cope Collection" (label); AMNH 1128, shell fragments, including one neural and several fragments of costals, "*Taphrosphys molops*, Cope Collection" (label); AMNH 14754, incomplete nuchal and first peripherals, one neural, incomplete xiphiplastron, and other shell fragments; *Taphrosphys sulcatus*, shell fragments, MFL Hornerstown Formation, HT-1, Hornerstown type locality, Hornerstown, Monmouth Co., New Jersey, coll. E. S. Gaffney.

CARAPACE

The best previously published reconstructions of *Taphrosphys sulcatus* are those based on AMNH 1125 by Hay (1908: figs. 101, 102) and YPM PU 18706 by Gaffney (1975a). The two best preserved shells, YPM PU 18706 and YPM PU 18707, were described in Gaffney (1975a). Most of the material of *Taphrosphys*, particularly in the AMNH, YPM, NJSM, and ANSP collections, is fragmentary. *Taphrosphys sulcatus* has prominent surface texture on both carapace and plastron, consisting of irregular raised polygons separated by a network of deep furrows. This kind of sculpture (state 2, character 175) is different from the more common "pelomedusoid" texture (state 1) defined by Broin (1977) and found in other bothremydids. The carapace of *Taphrosphys* is a short oval, with a narrow anterior end and the lateral margins diverging posteriorly, reaching their widest point at the level of the seventh peripherals and then narrowing to a blunt posterior end.

TABLE 24
Comparison of Taphrosphyini Shells

	T. sulcatus	*T. congolensis*	*"T." olssoni*	*"T." ambiguus*	*Ummulisani*
Carapace shape	short, oval	?	short, oval	?	?
Surface texture irregular raised polygons delimited by deep furrows	yes	yes	yes	yes	yes
Neural number	7	7	7	?	?
Plastron midline length	370 mm	510 mm	235 mm	305 mm	780 mm.
Plastron	narrow	wider	wider	narrow	wider
Anterior lobe very short	yes	yes	yes	yes	yes
Anterior margin of anterior lobe	nearly straight	nearly straight	rounded	nearly straight	rounded
Bridge	wide	narrower?	wide	wide	wide
Posterior lobe same width as anterior lobe	yes	yes	yes	yes	yes
Lateral margins of posterior lobe	parallel	tapering	convex	parallel	parallel
Anal notch	wider	wide	deeper	wider	?
Xiphiplastral points	wider	wider	closer	wider	?
Intergular very large	yes	yes	yes	yes	yes
Intergular separating gulars and humerals	yes	yes	yes	yes	yes
Intergular longer than wide	yes	no	yes	yes	yes
Gular	large	large	small	large	large
Gular as wide as intergular	yes	yes	no	yes	no
Gular reaching entoplastron	yes	yes	no	yes	yes
Humeropectoral sulcus behind epihyoplastral suture & cutting entoplastron	yes	yes	yes	yes	yes
Pubic scar very long, narrow	yes	yes	yes	yes	yes
Ischiac scar small, round	yes	yes	yes	yes	yes
Ischiac scar lying near anal notch margin	yes	yes	yes	yes	no
Locality	USA	Angola	Peru	France	Morocco

This shape is very similar to *Chedighaii*, unlike the oval carapace in *Galianemys, Cearachelys, Kurmademys*, and *Foxemys*.

The nuchal is trapezoidal and as long as wide in AMNH 1125 and YPM PU 18706, but wider than long in ANSP 15544 (Gaffney, 1975a). Another complete nuchal is preserved in AMNH 1347 and an incomplete nuchal is preserved in AMNH 1467 and AMNH 14754. The nuchal emargination is absent in all these specimens with the nuchal preserved; the front margin of the nuchal is straight or slightly convex anteriorly. The neural series consists of seven continuous neurals, based on ANSP 15544, YPM PU 18706, and YPM PU 18707 (Gaffney, 1975a), as in *Foxemys*, *Polysternon*, and *Rosasia*. The first neural is clearly longer than the second one. It is four-sided with the convex lateral margins, as in *Foxemys* and *Polysternon*. The second to fifth neurals are six-sided with short anterolateral sides and are longer than wide. The sixth neural is nearly equidimensional. The seventh neural is five-sided and much smaller than the sixth neural. AMNH 1463 has the last neural preserved and the seventh and eighth costals meeting on the midline. The first costal is longer than twice the length of the second costal, as in *Chedighaii* and *Araiochelys*. The seventh and eighth costals meet on the midline, separating the neurals from the suprapygal. The suprapygal is triangular and nearly as long as wide. The pygal, preserved in YPM PU 18707, is wider than long with a convex posterior margin.

On the visceral surface of the shell, the axillary buttress scar is on the lateral half of

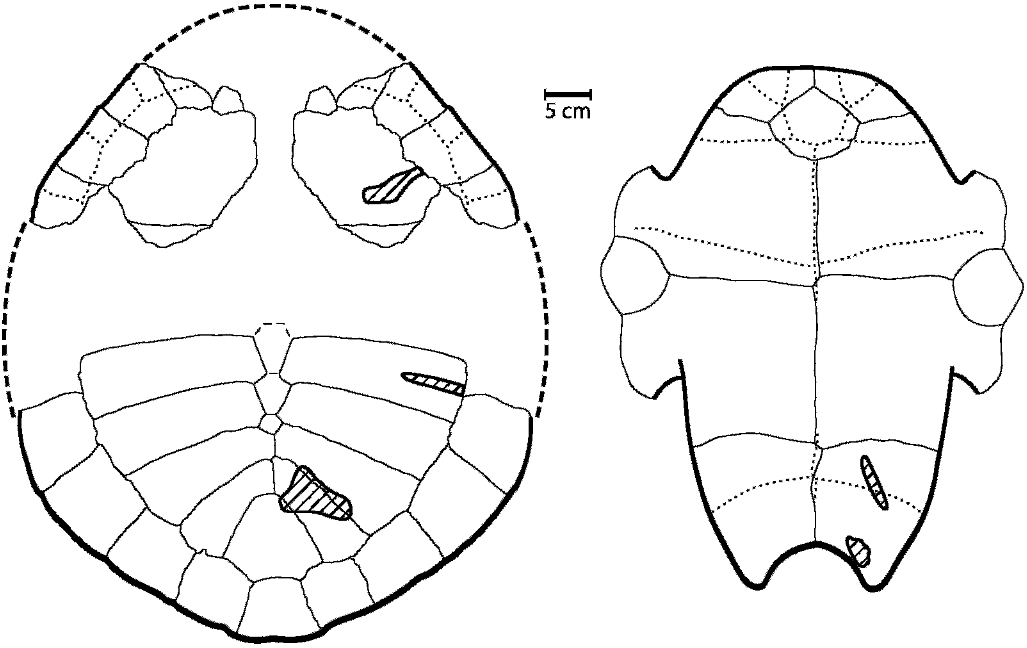

Fig. 266. *Taphrosphys congolensis* (Dollo, 1913). Partially restored carapace (left) based on MRAC 4795 and the MRAC uncatalogued type specimen (Dollo, 1913: pl. 7, figs. 1, 2). Partially restored plastron (right) based on MRAC 4794 and Wood (1975: fig. 2). [J. Kane, del.]

the first costal, near the posterior margin of the plate. The first rib head is smaller than the second one. The inguinal buttress reaches about half the width of the fifth costal. The iliac scar covers the posterior part of the seventh and eighth costals and slightly overlaps onto the suprapygal in AMNH 1468, YPM PU 18706, and YPM PU 18707, but in

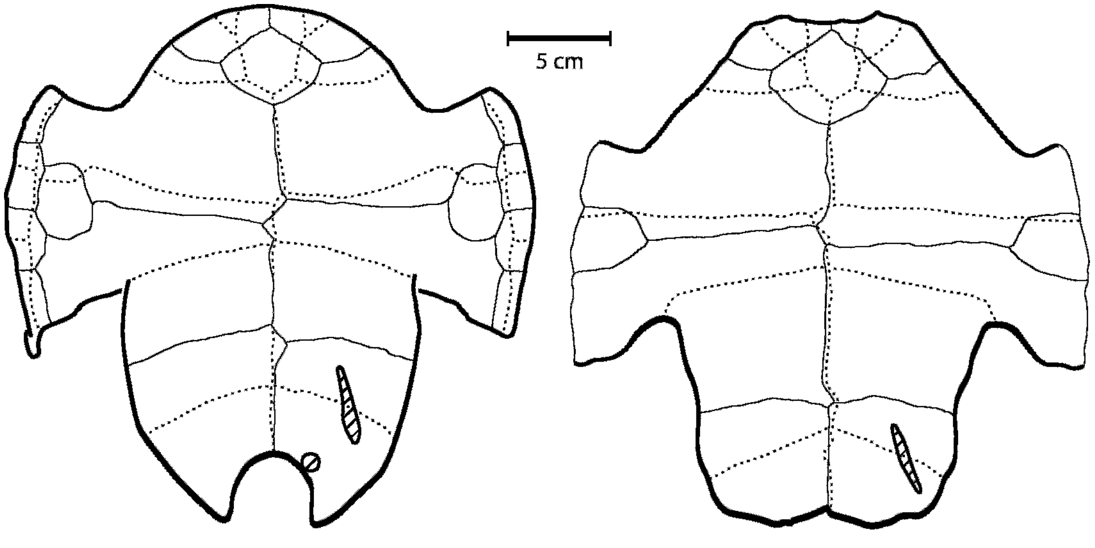

Fig. 267. Tribe Taphrosphyini, incertae sedis, partially restored ventral views of plastra. Left, "*Taphrosphys*" *olssoni* (Schmidt, 1931), based on Zangerl (1947: fig. 12); right, "*Taphrosphys*" *ambiguus* (Gaudry, 1890), based on Broin (1977: fig. 4). [J. Kane, del.]

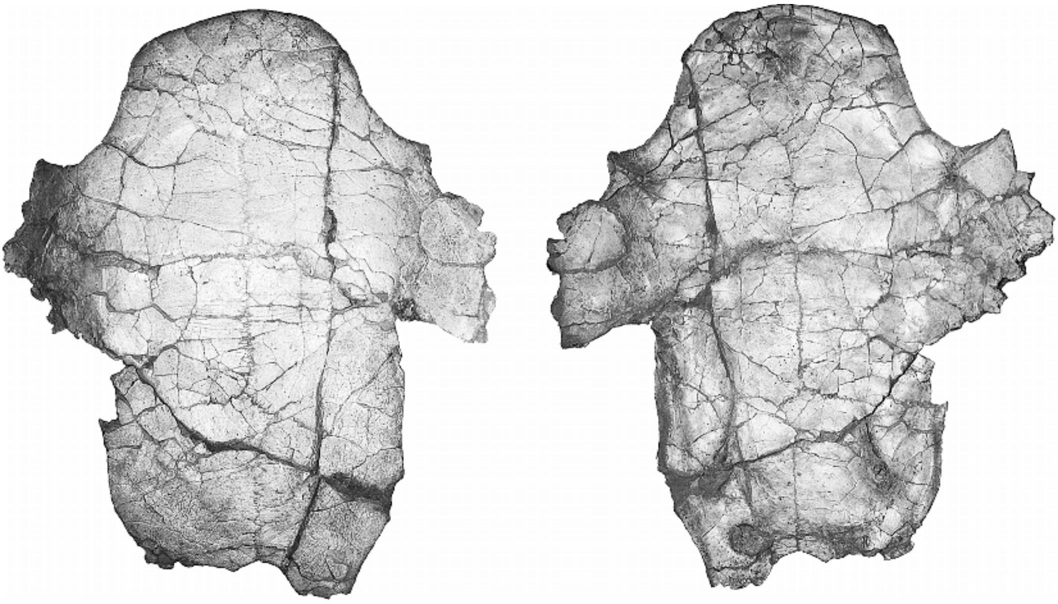

Fig. 268. *Ummulisani rutgersensis*, n. gen. et sp. AMNH 30562 holotype, plastron. Left, ventral; right, dorsal. [E.S. Gaffney, del.]

AMNH 1125, the iliac scar reaches the anterolateral margin of the suprapygal but does not overlap onto it.

The cervical scale is absent, as in all Pelomedusoides. As in the reconstruction in Hay (1908: fig. 101) and Gaffney (1975a: fig. 1), the first vertebral is narrow; it is narrower than the second and third vertebrals, especially in YPM PU 18706. The second and third vertebrals are wider than long and the fourth vertebral is narrower. The marginal scales are restricted to the peripheral bones, as in all Pelomedusoides.

PLASTRON

The plastron of *Taphrosphys sulcatus* is composed of 11 plates, as in other bothremydids. The plastron is shorter than the carapace; its front margin does not reach the anterior margin of the carapace, as in *Chedighaii*, *Polysternon*, and *Foxemys* but in contrast to *Galianemys* and *Cearachelys*.

The plastron of *Taphrosphys sulcatus* has a very short and semicircular anterior lobe, as in *Chedighaii*. The bridge is longer than the anterior lobe and shorter than the posterior one, also as in *Chedighaii*. The bridge is relatively wide, as in *Chedighaii* and *Araiochelys*, not as narrow as in most other bothremydids. The posterior lobe is relatively wide, nearly as wide as the anterior lobe, with nearly parallel lateral margins, in contrast to *Chedighaii* in which the posterior lobe tapers posteriorly. The anal notch is rounded and very broad.

The epiplastron has a short midline suture, much shorter than the entoplastral length. The entoplastron is complete in AMNH 1472 and YPM PU 18706. It is diamond-shaped and clearly wider than long. The mesoplastron is not preserved in any of the specimens. The xiphiplastron is broad, being nearly as wide as long (YPM PU 18708, AMNH 1125), or slightly longer than wide (AMNH 1474 and YPM PU 18706), in contrast to Bothremydini in which it is much longer than wide.

The plastron in *Taphrosphys sulcatus* is covered by 13 scales, as in all Pelomedusoides. The intergular, preserved in YPM PU 18706 (Gaffney, 1975a: fig. 2) and AMNH 1472 (Hay, 1908: fig. 116), is very large, completely separating the gulars and humerals, as in *Taphrosphys congolensis* and *Ummulisani* but in contrast to all other bothremydids (except *Elochelys*). The gular

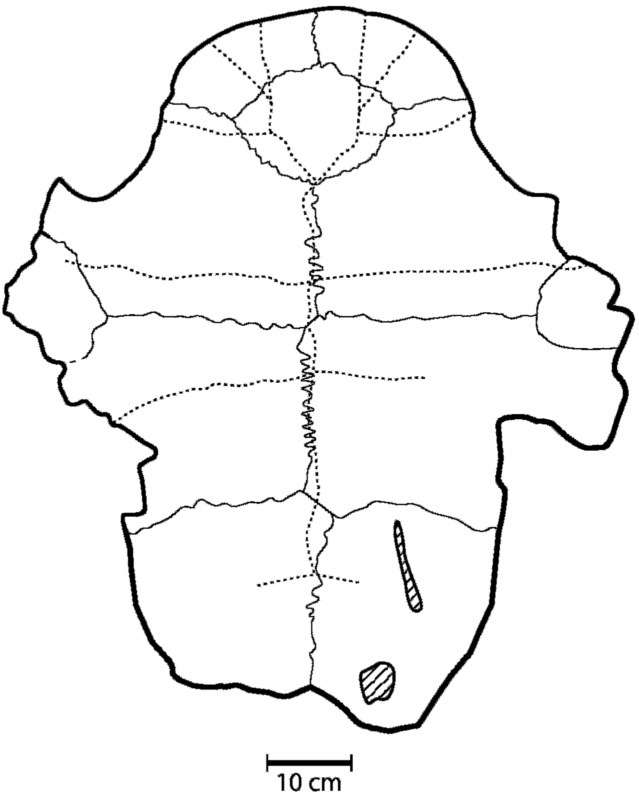

Fig. 269. *Ummulisani rutgersensis*, n. gen. et sp. AMNH 30562 holotype, ventral view of plastron. [G. Giardina, del.]

scale, preserved in YPM PU 18706 (Gaffney, 1975a: fig. 2) and AMNH 1471 (Hay, 1908: fig. 106), is triangular; it reaches the entoplastron but does not cross it. The humeropectoral sulcus is behind the epihyoplastral suture, crossing the entoplastron, as in *Chedighaii*. As in *Taphrosphys congolensis* and *Ummulisani, T. sulcatus* has a very short abdominal scale, with the pectoroabdominal sulcus lying near the hyohypoplastral suture, in contrast to all other bothremydids (except "*T.*"*olssoni* and "*T.*" *ambiguous*, fig. 267).

On the inner side of the plastron, the pubic scar is long and narrow. The ischiac scar is very small and rounded, placed very near the margin of the anal notch (Gaffney, 1975a).

Taphrosphys congolensis (fig. 266, table 24)

MATERIAL AVAILABLE: This description is based primarily on the description and illustrations of Dollo (1913) and Wood (1975), although one of us (E.S.G.) has seen the material.

CARAPACE

The shell surface of *T. congolensis* is covered by "a network of deeply inscribed anastomosing vermiculations", as described by Wood (1975: 139), as in *Taphrosphys sulcatus*. The carapace is known only from the anterior portion and the posterior third. The preserved part is very similar to *T. sulcatus*. On the lectotype of *T. congolensis* (Dollo, 1913: pl. VII, figs. 1, 2; Wood, 1975: fig. 1), the nuchal and the first peripheral are represented only by fragments and their shapes are therefore undeterminable. The second peripheral is roughly square and the third one is longer than wide, as in *T. sulcatus* (YPM PU 18706 and YPM PU 18707, Gaffney, 1975a: figs. 1, 6, 8). The first costal is as long as in *T. sulcatus*. On the inner side, the axillary buttress attaches to the third peripheral and the lateral half of the first costal, although its position appears to be more anterior than in *T. sulcatus* (Gaffney, 1975a: fig. 4). A posterior portion of cara-

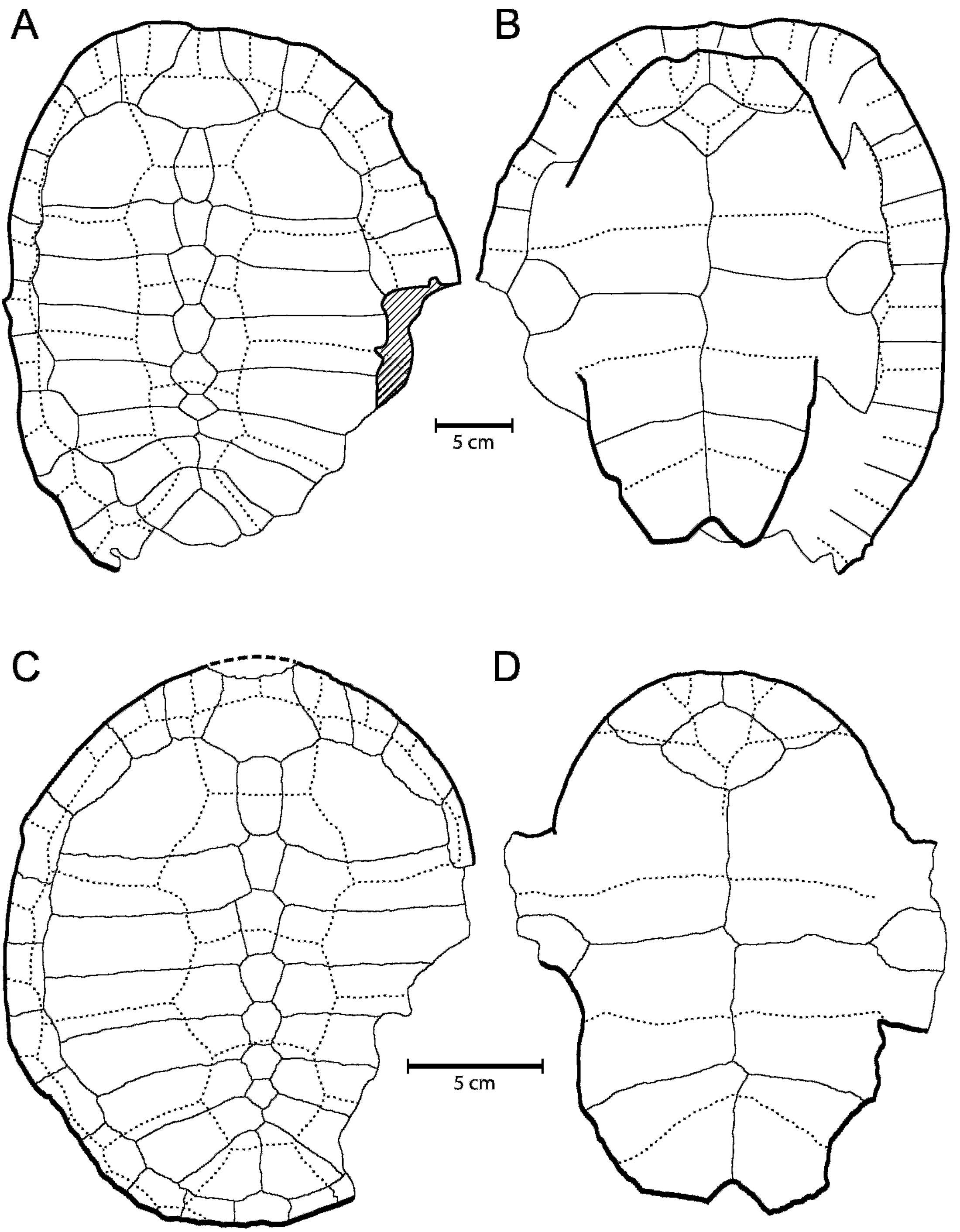

Fig. 270. **A**, **B**, *Elochelys convenarum* Laurent, Tong, and Claude, 2002. **A**, carapace; **B**, plastron (after Laurent et al., 2002). **C**, **D**, *Elochelys perfecta* Nopcsa, 1931. **C**, carapace; **D**, plastron (after Nopcsa, 1931). [J. Kane, del.]

pace (MRAC 4795) consists of the last neural, right fifth to eighth costals, left seventh and eighth costals, suprapygal, pygal, and right eighth to eleventh peripherals (Wood, 1975: pls. 1, 2). The preserved neural, between the sixth and seventh costals, is the seventh neural. It is therefore likely that seven neurals are present in *T. congolensis*, as in *T. sulcatus*. The last neural is small and short, as in *T. sulcatus*.

On the inner surface of the carapace, the inguinal buttress attaches to the eighth peripheral and the fifth costal. The iliac scar is on the seventh and eighth costals and covers a small part of the suprapygal, all similar to *T. sulcatus*.

PLASTRON

A nearly complete plastron (MRAC 4794) and two more-or-less complete xiphiplastra are figured in Wood (1975: pls. 3, 4, 6). The general morphology of the plastron of *T. congolensis* is similar to that of *T. sulcatus*. However, the plastron of *T. congolensis* seems wider than that of *T. sulcatus*. The reconstruction by Wood (1975: fig. 2) shows a narrow bridge relative to that of *T. sulcatus*. The posterior lobe has the lateral margins slightly tapering posteriorly, instead of nearly parallel as in *T. sulcatus*. The xiphiplastron is slightly longer than wide in MRAC 4794, while the complete xiphiplastron in plate 6 (Wood, 1975) is broader. Another diagnostic feature of *T. congolensis* pointed out by Wood (1975) is that its intergular is hexagonal and wider than in *T. sulcatus*. It is nearly as broad as long; while in other *Taphrosphys* species, the intergular is much longer than wide. The comparison of species referred by various authors to *Taphrosphys* is shown in table 24.

Ummulisani rutgersensis (figs. 268, 269)

MATERIAL AVAILABLE: AMNH 30562, a nearly complete plastron associated with skull and jaws.

PLASTRON

The plastron of *Ummulisani* has the usual 11 bones and 13 scales and is very similar to the plastron of *Taphrosphys*. The epiplastra are slightly larger relatively in *Ummulisani* than in *Taphrosphys*, and the anterior plastral lobe is relatively wider. The entoplastron in *Ummulisani* is wider than long, as in *Taphrosphys*. The hyo- and hypoplastra are very similar in both genera. The mesoplastron in *Ummulisani* lacks the lateral edges, but it seems to be larger than the mesoplastron in *Chedighaii*. The xiphiplastron in *Ummulisani* has the narrow posterior projection and broad, semicircular anal notch of *Taphrosphys*, but it is slightly narrower posteriorly.

On the visceral surface, the buttresses are mostly broken away. The pubic scar is long and narrow in *Ummulisani*, as in *Taphrosphys*. The ischiac scar is round as in *Taphrosphys*, but it is not right on the edge of the xiphiplastron as in *Taphrosphys*.

The plastral scales of *Ummulisani* are similar to those in *Taphrosphys*. There is a large intergular that occupies most of the entoplastron, widely separating the gular and humeral scales. In contrast to *Taphrosphys*, the gular scales extend onto the entoplastron a short distance in *Ummulisani*. The abdominal scales are narrow and the femorals are large, as in *Taphrosphys*.

PELOMEDUSOIDES INDETERMINATE

?*Galianemys* sp. (table 22, figs. 271–274)

MATERIAL AVAILABLE: AMNH 30550, nearly complete shell (figs. 273, 274), Cenomanian, Kem Kem, Morocco; AMNH 30551, nearly complete shell (figs. 271, 272), Cenomanian, Kem Kem, Morocco. There are differences between these two shells (table 22), and it is possible they represent two taxa (see below). The named turtles known from skulls occurring in the Kem Kem Campanian of Morocco are *Galianemys emringeri*, *Galianemys whitei, Hamadachelys*, and *Dirqadim*, but a phylogenetic analysis including these shells (fig. 294) places them in the tribe Cearachelyini, suggesting that they may be the shells for one or both *Galianemys* species.

CARAPACE

The two shells have an oval outline, slightly expanded posteriorly. There is no nuchal emargination. AMNH 30551 has eight neurals with costal 8 meeting on the midline. AMNH 30550 has six neurals with costals 7 and 8 meeting on the midline (see table 22). In AMNH 30551 the nuchal is

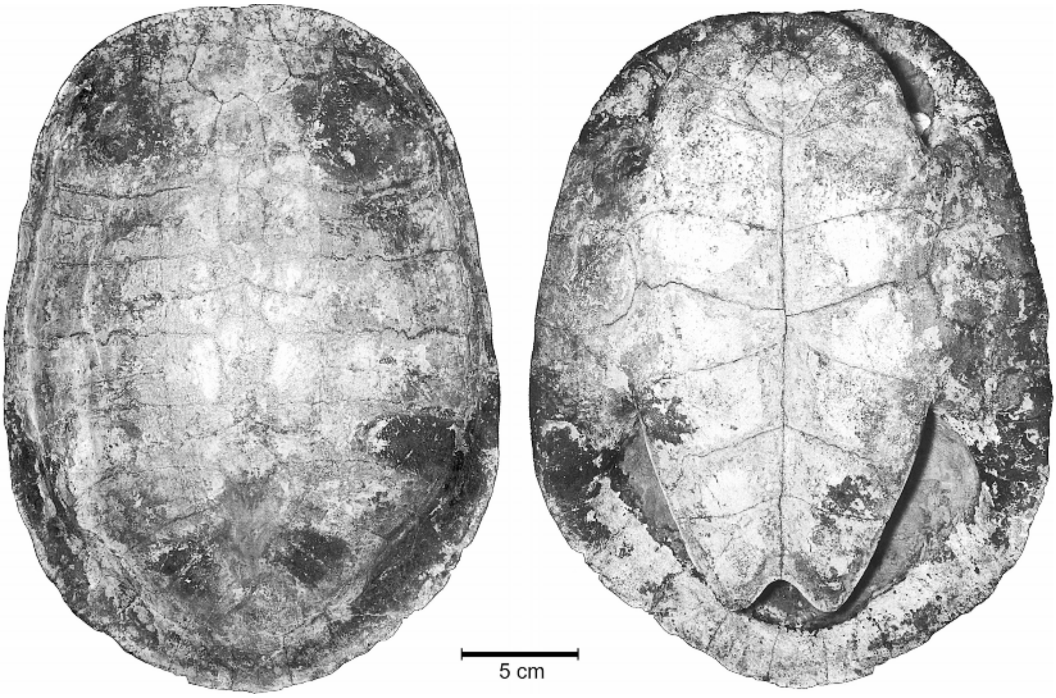

Fig. 271. Pelomedusoides incertae sedis, ?*Galianemys*, shell. AMNH 30551. Dorsal (left), ventral (right). [E.S. Gaffney, del.]

slightly wider than it is long, with a long anterior margin. The first neural is six-sided with short posterolateral sides contacting the second costal as in *Cearachelys* and different from all other bothremydids. The second neural is four-sided and short, as in *Cearachelys*. The third to fifth neurals are six-sided with short anterolateral sides and are longer than wide. The sixth and seventh neurals are wider than long and the eighth neural is reduced and pentagonal in shape; it does not contact the suprapygal. The first costal is similar to that of *Cearachelys*, being shorter than the length of the second and third costals together. The eighth pair of costals meets on the midline in AMNH 30551 and the seventh and eighth pairs of costals meet on the midline in AMNH 30550 between the neural series and the suprapygal, in contrast to *Cearachelys* in which the costals are completely separated by the neural series. The suprapygal is roughly triangular in shape, as in other Pelomedusoides; it is wider than long.

The carapace scales are similar to the generalized scale pattern of other Pelomedusoides. The cervical is absent. The second and third vertebrals are roughly as long as wide, different from *Cearachelys* in which these two scales are wider than long. The marginals are restricted to the peripherals as in all Pelomedusoides.

PLASTRON

The plastron is sutured to the carapace. The plastron is long; its anterior margin reaches the anterior margin of the carapace, as in *Cearachelys*. The anterior lobe is short and wide at the base, with a semicircular outline, as in most bothremydids but different from *Cearachelys*, which is longer. The mesoplastron is laterally placed and longer than wide. The bridge is long, longer than the posterior lobe, in contrast to *Cearachelys*, in which the bridge is shorter than the posterior lobe. The anal notch is V-shaped.

The plastron scale pattern differs between the two shells. The intergular scale is narrow

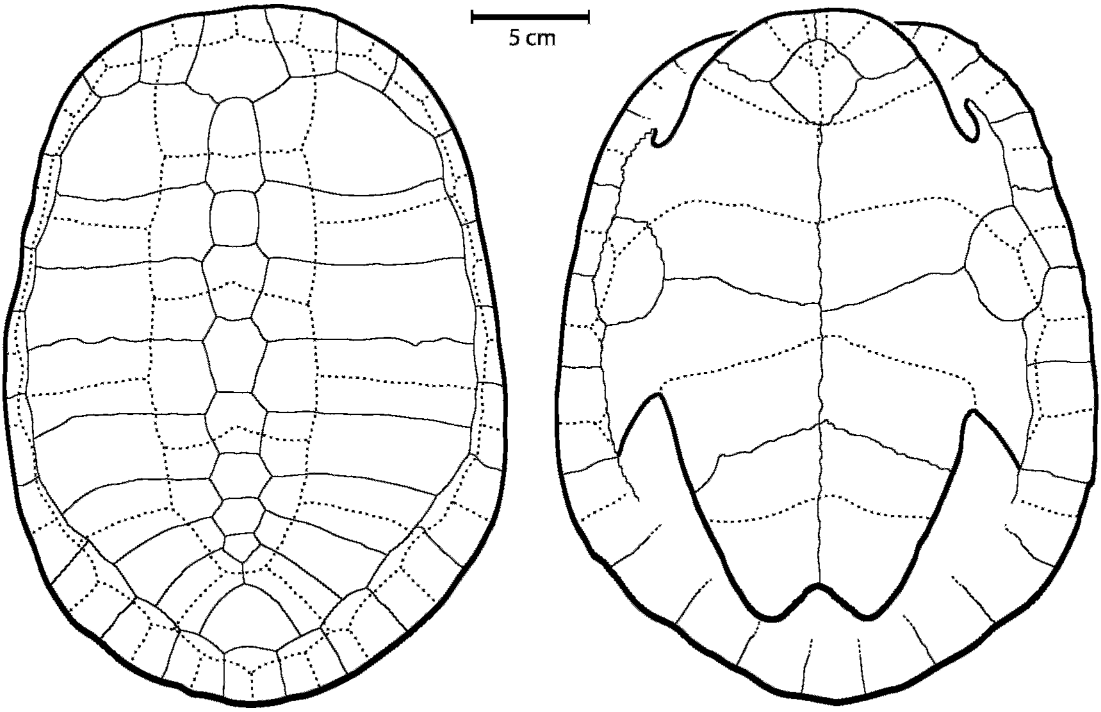

Fig. 272. Pelomedusoides incertae sedis, ?*Galianemys*, shell. AMNH 30551. Dorsal (left), ventral (right). [J. Kane, del.]

in AMNH 30551 and it covers about a third of the entoplastron. The gular scale is larger, extending onto the entoplastron, and is much wider than the intergular, a unique-condition among bothremydids. In AMNH 30550, the intergular is wide, larger than the gular scales, which do not extend onto the entoplastron. In both, the humeropectoral sulcus is entirely posterior to the epihyoplastral suture and just behind the entoplastron, as in *Cearachelys*. The pectoroabdominal sulcus crosses the mesoplastron in both shells, as in *Cearachelys* and *Euraxemys*.

Three genera of turtles have been collected in the Cenomanian Kem Kem beds: *Galianemys* (Bothremydidae), *Hamadachelys* (Podocnemididae), and *Dirqadim* (Euraxemydidae), all based on isolated skulls. This turtle fauna has a strong affinity with the Early Cretaceous turtle fauna of the Santana Formation. The shells from Kem Kem described above are similar to bothremydids in the shape of the anterior lobe of the plastron. The shells from Kem Kem share with *Cearachelys* the first neural being six-sided with short posterolateral sides contacting the second costal and the four-sided second neural. This character is not known in any other Pelomedusoides. This suggests that the shells may belong to *Galianemys*. The phylogenetic analysis supports this hypothesis by placing these shells in the tribe Cearachelyini. The comparisons between the shells of *Galianemys* and *Cearachelys* are shown in table 22.

There is evidence that the ?*Galianemys* shells are not the same taxon. AMNH 30551 has eight neurals with costal 8 meeting on the midline, and a very narrow intergular scale flanked by large gulars that extend onto the entoplastron. This is in contrast to AMNH 30550 that has six neurals with costals 7 and 8 meeting on the midline, and a wide intergular flanked by smaller gulars that do not extend onto the entoplastron. A fine kettle of fish.

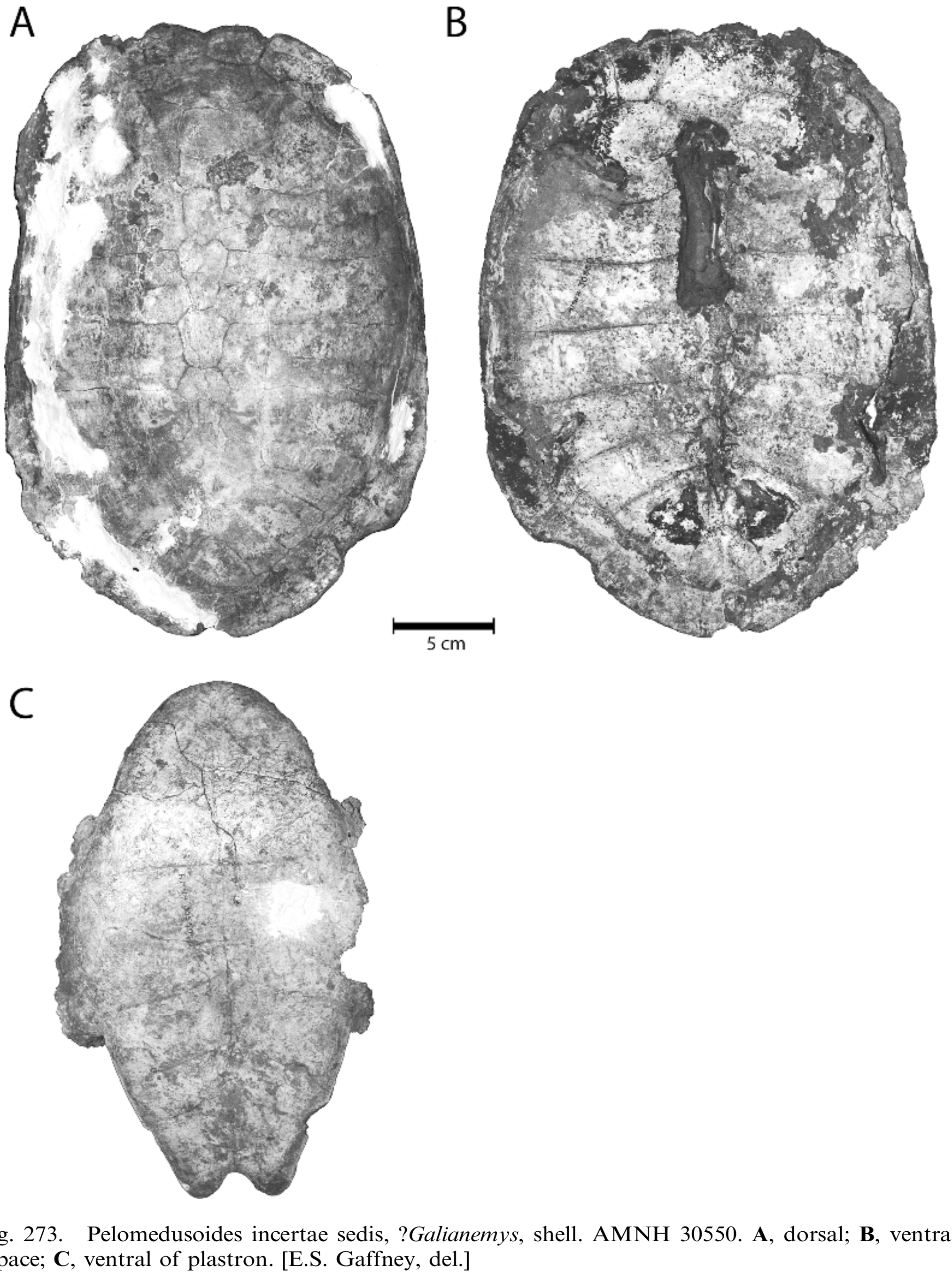

Fig. 273. Pelomedusoides incertae sedis, ?*Galianemys*, shell. AMNH 30550. **A**, dorsal; **B**, ventral of carapace; **C**, ventral of plastron. [E.S. Gaffney, del.]

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Fig. 275. *Bairdemys venezuelensis* (Wood and Díaz de Gamero, 1971). MCZ 9420. Miocene, Venezuela. Ventral view of shell. This species is in the Podocnemididae based on skull characters (Gaffney and Wood, 2002), but the plastron has strong similarities to many bothremydid plastra (see text). [J. Kane, del.]

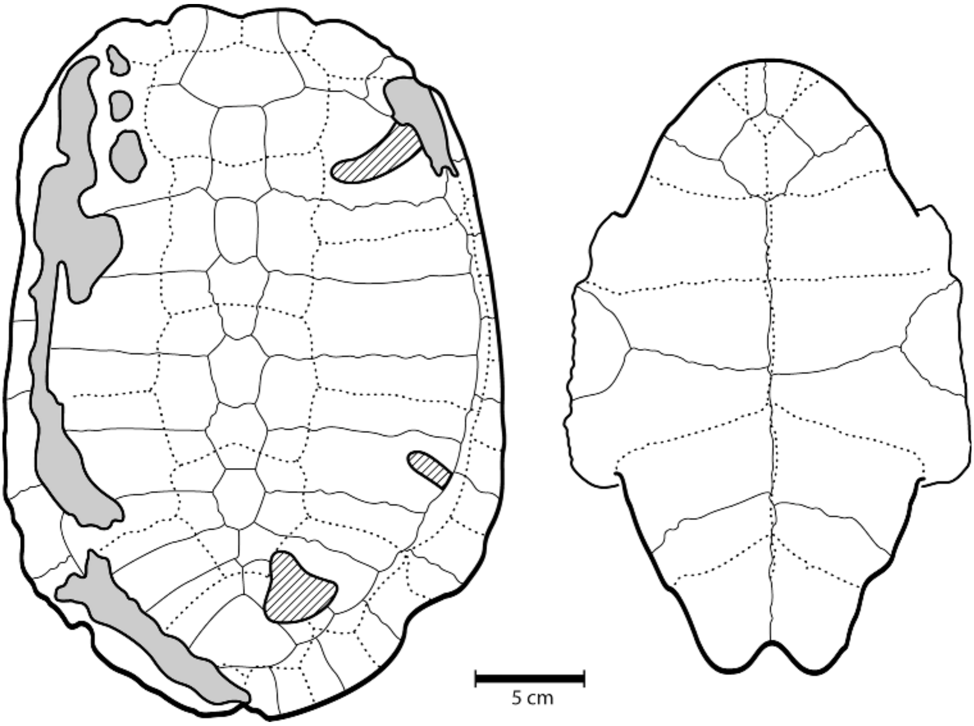
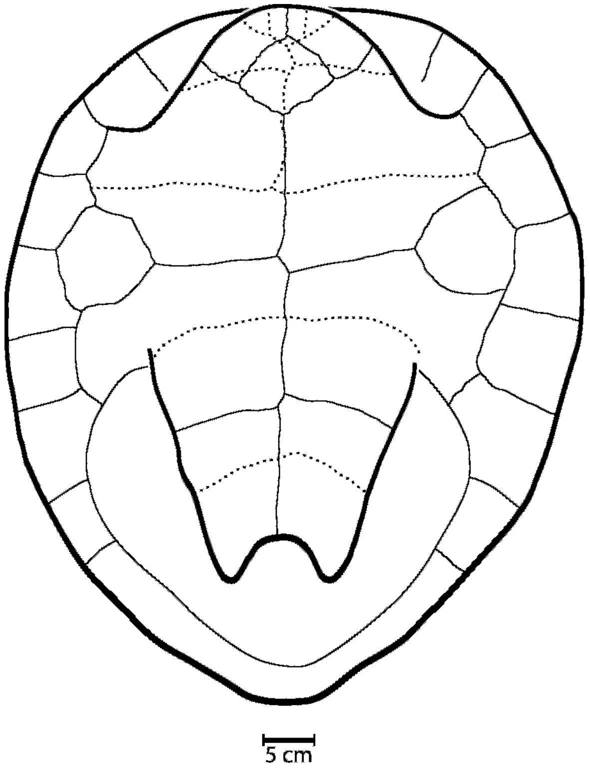


Fig. 274. Pelomedusoides incertae sedis, ?*Galianemys*, shell. AMNH 30550. Dorsal (left), ventral (right). [J. Kane, del.]



PHYLOGENETIC ANALYSIS

METHODOLOGY

The phylogenetic analyses were made with PAUP* version 4.0b10 (Swofford, 2002) using the parsimony algorithm. All characters were run unweighted and unordered, although there is a good argument for ordering at least two characters (characters 20 and 94, see Character Descriptions for discussion). Characters were entered and cladograms examined using MacClade version 4.05 (Maddison and Maddison, 2000). The data matrix (appendix 3) used as the basis of this analysis has 41 taxa and 175 characters (of these, only 171 are parsimony informative for the core analysis, cladogram 1 [fig. 288], due to the presence of some shell characters that vary only in taxa absent in the core analysis; see below). The PAUP analysis of this matrix, using both heuristic and stepwise addition (random), results in one shortest cladogram (fig. 288) of 382 steps with a consistency index of 0.60, a retention index of 0.81, a rescaled consistency index of 0.49, and a homoplasy index of 0.39. Bootstrapping was run using 100 replicates. Bremer decay indices were obtained using TreeRot version 2 (Sorenson, 1999).

One caution in using the dataset provided in appendix 3 is the amount of missing data. Taxa with large numbers of missing characters are a concern because the analytic program supplies the missing characters as most consistent with the shortest cladogram, thus ignoring the likely interference of contradictory characters commonly present. Even so, inclusion of taxa with missing data can produce useful results (Kearney and Clark, 2003). Table 25 lists the amount of missing data for each taxon.

As shown in the decay analysis, there are some groups that lose resolution in the consensus of the 38 cladograms that are one step longer than the MPC. This consensus tree (fig. 289) shows that the Bothremydini loses resolution, with the Foxemydina becoming a multichotomy with the Taphrosphyini and remaining Bothremydini. *Zolhafah* and *Rosasia* form a multichotomy with the remaining Bothremydini. The genus *Bothremys* is paraphyletic with respect to *Chedighaii*. All the other tribes hold up, but the two species of *Galianemys* form a multichotomy with *Cearachelys*. Within the Taphrosphyini, there is a loss of resolution in the basal members, and the species in the genus *Taphrosphys* are paraphyletic with respect to a *Phosphatochelys* + *Ummulisani* + *Rhothonemys* trichotomy. *Araripemys* and the Pelomedusidae form a trichotomy with the remaining Pelomedusoides. All of these alternatives are quite reasonable, as they are held together by few characters. Two particular characters that seem a little more subjective than the others, at least in part, are characters 31 and 110 (see Character Descriptions for discussion). Deleting these characters produces 38 trees with the consensus cladogram seen in figure 290.

The 40 taxa in the core analysis are all represented by good skull material; of these, 21 also have associated shells (fig. 291A) and 20 have associated lower jaws (fig. 291B). The shells are relatively well distributed taxonomically with at least one skull-shell association in each tribe of Bothremydidae (see also fig. 314, character 164). In the dataset skull characters are 70% (122) of the 175 characters, shell characters are 21% (38), and the remaining 9% (14) are other postcranial characters. When all postcranial characters are deleted, the same single cladogram (fig. 288) results, showing the dominance of cranial characters in the dataset and their critical importance to the analysis. The addition of a selected group of eight shell-only taxa to the dataset (indicated by asterisk in fig. 292 and in appendix 3) also results in one cladogram, cladogram 2 (fig. 292). However, these shell-only taxa are not representative of the majority of named shell-only taxa. They have been chosen because they have few missing data and do not generate large numbers of trees. Some shell-only taxa (see section on Dubious Taxa) are represented by very incomplete specimens and have been excluded from this analysis and the resulting cladograms.

The influence of shells on the analysis can be observed by examing the results following the exclusion of all cranial characters. The basic dataset (appendix 3) was modified by

TABLE 25
Missing Data

Taxa with asterisks are shell-only specimens added to the analysis in figure 292. Taxa with two asterisks have high missing data values, are treated in figures 294 and 295, and are discussed in text.

	Taxon	% missing
1	Synapsida/Diapsida	21.7
2	*Proganochelys*	3.4
3	*Australochelys*	72.6
4	*Palaeochersis*	60.6
5	*Kayentachelys*	2.3
6	Selmacryptodira	0.6
7	Chelidae	0.6
8	Pelomedusidae	0.0
9	*Araripemys*	4.0
10	*Euraxemys*	4.0
11	*Dirqadim*	40.0
12	Podocnemididae	0.0
13	*Hamadachelys*	33.7
14	*Brasilemys*	37.7
15	*Cearachelys*	6.9
16	*Galianemys emringeri*	38.3
17	*Galianemys whitei*	37.7
18	*Kurmademys*	12.6
19	*Sankuchemys*	62.9
20	*Foxemys*	6.3
21	*Polysternon*	27.4
22	*Araiochelys*	23.4
23	*Zolhafah*	52.6
24	*Rosasia*	31.4
25	*Bothremys cooki*	65.1
26	*Bothremys maghrebiana*	30.3
27	*Bothremys kellyi*	48.6
28	*Bothremys arabicus*	64.0
29	*Chedighaii hutchisoni*	41.1
30	*Chedighaii barberi*	25.1
31	*Taphrosphys sulcatus*	29.1
32	*Taphrosphys congolensis*	34.9
33	*Taphrosphys ippolitoi*	45.7
34	*Azabbaremys*	38.9
35	CNRST-SUNY 199	43.4
36	*Labrostochelys*	42.3
37	*Phosphatochelys*	40.6
38	*Ummulisani*	36.6
39	*Rhothonemys*	63.4
40	*Nigeremys*	56.6
41	*Arenila*	58.9
42	**Proterochersis*	80.6
43	**Platychelys*	70.9
44	**Notoemys*	69.1
45	**Dortoka*	74.9
46	**Teneremys*	56.6
47	*MNHN GDF 801	76.6
48	**Elochelys perfecta*	83.4
49	**Elochelys convenarum*	77.1
50	**"*Podocnemis*" *parva*	84.0
51	**"*Podocnemis*" *somaliensis*	88.0
52	**AMNH 30550	77.1
53	**AMNH 30551	78.3
54	**"*Taphrosphys*" *olssoni*	84.0
55	**"*Taphrosphys*" *ambiguous*	90.3
56	**"*Platycheloides*" *nyasae*	97.1
57	**"*Eusarkia*" *rotundiformis*	85.7
58	***Bairdemys venezuelensis*	82.9

dropping all cranial characters and all skull-only taxa, with the result seen in figure 293A. This restricted dataset has 28 taxa and 39 characters and produced 2704 trees in a PAUP parsimony analysis with no ordering or weighting. The Pleurodira, Megapleurodira, and Eupleurodira are resolved along with a few lower level bothremydid groups, but most Pelomedusoides form a multichotomy. Admittedly, only 39 characters for 28 taxa are too few to expect complete resolution, but we have used as many shell characters as possible in the analysis. The poor showing of shell characters here seems to be the result of the general conservatism of Pelomedusoides shells. It is possible to find shell characters for alpha-level diagnoses and differentiation in this group. However, even these characters may be questioned because individual variation is so poorly known, and more inclusive comparisons are difficult given our current knowledge of skull-shell associations. Furthermore, most descriptive work on shells emphasize the external suture and scale relations, while many characters can be found in the more complex internal morphology.

In any case, for whatever reason, with the present state of knowledge of this group, the shell alone provides little help in resolving relationships among Pelomedusoides. However, when included with the cranial characters, shell characters do help resolve some groups (see Character Descriptions). In an effort to try squeezing something more out of the shell-only dataset, it has been reanalyzed by weighting using the rescaled consistency index option in PAUP, which is a way of reducing the weight of the more homoplastic characters in favor of the more consistent characters. The resulting consensus of 250 equally parsimonious trees (fig. 293B) is interesting in that it unites almost all bothremydids (shown by asterisks) and excludes the Podocnemididae from the bothremydids.

In order to try to incorporate as much information as possible from the more poorly known shell-only taxa, some have been added singly to the dataset. Most of these are discussed in the Incertae Sedis section following Systematics. Nearly all of these taxa are shells or partial shells, with some lacking as much as 95% of the characters (for effects of missing data and possible solutions, see Wilkinson, 1995, 2003; Strauss et al., 2003; and Wiens, 2003). Some of these may represent shells of named skulls used in the basic list (e.g., *Galianemys* and AMNH 30550, AMNH 30551). Adding these taxa to the basic list one at a time allows some resolution of their phylogenetic position and a determination of a level of incertae sedis within a higher taxon without large numbers of trees obscuring the result.

Basic Taxa Outside Pelomedusoides

Although the Pelomedusoides is the focus of this paper, outgroups are significant in the phylogenetic analysis, and there are taxa that have been identified as pleurodires in the literature that are of questionable status and require discussion.

Synapsida/Diapsida

In order to root the turtle taxa, the main groups of amniotes outside turtles are included as a single taxon. We consider turtles to be the sister group of diapsids, not within diapsids or within pareiasaurs/procolophonids. There are polymorphic codings for some characters, and certain characters that are turtle synapomorphies, like plastral features, are coded "?", so this should not be considered a useful exercise in determining turtle relationships within amniotes. For further literature on these taxa and for other analyses of amniote relationships, see Lee (1997) and Rieppel and Reisz (1999). We are not dealing with the relationships of extinct groups like pareiasaurs and procolophonids to turtles, because to do so would not alter relationships within turtles. We do not consider the hypothesis that turtles are within diapsids (e.g., Braga and Rieppel, 1997) to have merit, but even accepting this would not alter relationships within turtles as analyzed here. *Proganochelys* still comes out as the sister group to cryptodires plus pleurodires.

Proganochelys

The principal work on this taxon is Gaffney (1990). There is abundant support that *Proganochelys* is the sister taxon to all other turtles.

Kordikova (2002) has published new line drawings of the skull of *Proganochelys* showing sutures different from those in Gaffney (1990). In the opinion of the senior author, Kordikova has inadvertently mistaken cracks for sutures. Lucas et al. (2000) have identified a partial dermal ossicle from the Upper Triassic of New Mexico as a probable turtle, very close to *Proganochelys*. Although it is not clear what this fragment belongs to, the senior author thinks its identification as a turtle lacks credibility, and this potential range extension should be ignored.

Australochelys

Gaffney and Kitching (1994 and 1995) described this form.

Palaeochersis

This form is described in Rougier et al. (1995). However, the senior author has studied this material and some undescribed specimens (kindly made available by Andrea Arcucci) and has made corrections to the character matrix used by them (Rougier et al., 1995). In particular, the possible suturing of the pelvis described by Rougier et al. (1995) is incorrect. In the opinion of the senior author, the pelvis of *Palaeochersis* is not sutured to the shell; rather, the appearance of this is due to dorsoventral crushing and deformation. The pelvis articulation in *Palaeochersis* is the same as in *Proganochelys*. The basicranium in *Palaeochersis* is fused, not an open articulation as in *Proganochelys*, and the cavum tympani is advanced over *Proganochelys*, all as described by Rougier et al. (1995).

Kayentachelys

This taxon is described in Gaffney et al. (1987), with some additions in Gaffney (1990) and Gaffney and Kitching (1995).

Selmacryptodira

This taxon consists of all cryptodires except *Kayentachelys*, and it was diagnosed in Gaffney and Meylan (1988).

Proterochersis

This genus is described by Fraas (1913), with additions and a new shell reconstruction in Gaffney (1990). Although only known from the shell, the 20 or so specimens representing this species provide important information on the earliest pleurodires.

Karl and Tichy (2000) have named a new taxon, "*Murrhardtia staeschei*", from the Late Triassic of Germany. This taxon is a junior synonym of *Proterochersis robusta* Fraas, 1913. Karl and Tichy mistakenly used Fraas' reconstruction of the type, SMNS 12777 (Fraas, 1913: figs. 1, 2), as a figure of the actual type specimen for comparison, and they named a more complete specimen of *Proterochersis robusta* (unnumbered shell in the Carl Schweizer Museum, Murhardt, Germany) as a new taxon. SMNS 12777 has only the internal mold of the carapace, plus a partial plastron, while the Karl and Tichy shell is nearly complete. However, two of us (E.S.G., P.A.M.) have studied these specimens, as well as nearly two dozen other *Proterochersis* shells, and have concluded that they belong to a single species. The areas of overlap of the *Proterochersis robusta* type specimen and the type specimen of "*Murrhardtia staeschei*" are nearly identical.

Platychelys

Platychelys has been described by Lang and Rütimeyer (1866), Rütimeyer (1873), Zittel (1877), Bräm (1965), and Lapparent de Broin (2001). As another shell-only taxon, *Platychelys* is missing the cranial characters.

Notoemys

Notoemys laticentralis has been described by Cattoi and Freiburg (1961), Fuente and Fernandez (1989), and Fernandez and Fuente (1994). Rueda and Gaffney (2005) have described another species, *N. zapatocaensis*, and have argued that "*Caribemys*" *oxfordiensis* belongs in *Notoemys*, a conclusion we accept. *Notoemys laticentralis* is known from the shell, some vertebrae, some appendicular elements, and a partial skull. Although we have been unable to examine the partial skull, we suspect that the bone anterolateral to the basisphenoid in Fernandez and Fuente (1994: fig. 2B) is the pterygoid rather than the quadrate, as in chelids and pelomedusids. Although a partial skull is known for *Notoemys*, we have been able to code only a few characters for it, and, at least for the present, recognize *Notoemys* as another shell-only taxon.

Dortoka

This shell taxon was described by Lapparent de Broin and Murelaga (1999).

Chelidae

Monophyly of the Chelidae is well corroborated. Within-group relationships based on morphology (Gaffney, 1977b; Gaffney and Meylan, 1988) and molecules (Shaffer et al., 1997; Seddon et al., 1997; Georges et al., 1998; Krenz et al., 2005; Near et al., 2005) differ significantly, and the molecular phylogenies seem to be well supported. The molecular analyses tend to recognize separate Australian and South American clades, but these relationships become less certain when all chelid genera are represented in the dataset (Georges et al., 1998). We have not adopted a within-group cladogram for chelids, and we have therefore coded some characters as variable. Note that recent discoveries of Cretaceous chelids (Fuente et al., 2001; Lapparent de Broin and Fuente, 2001; Fuente, 2003; Bona and Fuente, 2005) support the morphology-based analyses.

Character Descriptions

The characters chosen here include ones not only relevant for bothremydids but for all pleurodires, outside podocnemidids, and chelids. Although characters primarily resolving *Proganochelys* and all other turtles are included in the analysis, they are only referenced and briefly described, having been discussed elsewhere. The same format of headings used in Gaffney (1996) is used here. The history of use of particular characters in the literature is primarily taken from papers with actual datasets (i.e., Meylan, 1996; Tong et al., 1998; Lapparent de Broin and Murelaga, 1999; Fuente and Iturralde-Vinent, 2001) which explicitly show taxon distribution, although reference is also made to

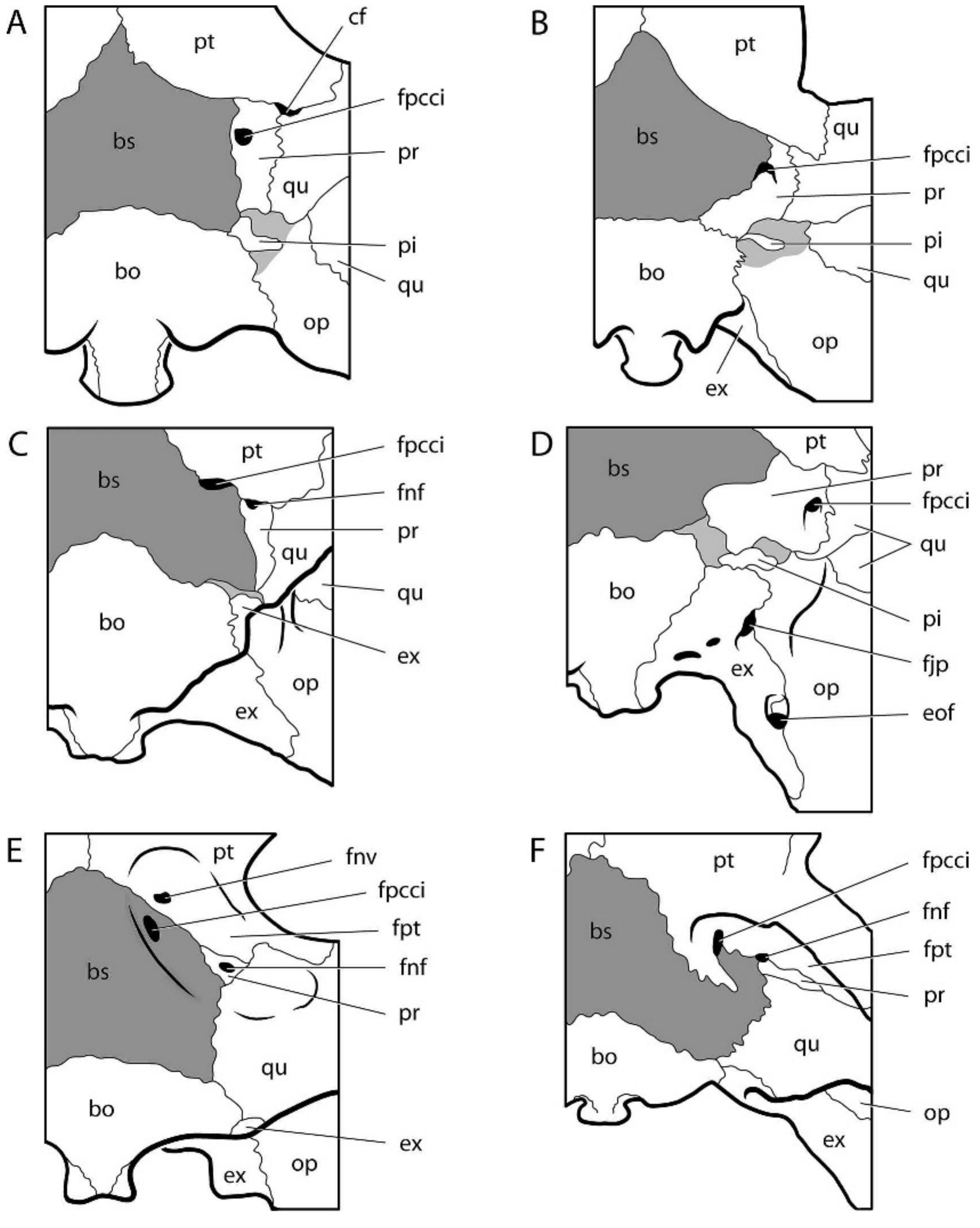


Fig. 276. Comparative views of the left posterior basicranium in ventral view. Basisphenoid is dark gray for a landmark. **A**, *Emydura macquarri*, AMNH 110486 (Chelidae); **B**, *Pelusios sinuatus*, USNM (Herp) 42144 (Pelomedusidae); **C**, *Euraxemys essweini*, FR 4922 (Euraxemydidae); **D**, *Araripemys barretoi*, AMNH 24454 (Araripemydidae); **E**, *Kurmademys kallamedensis*, ISI R152 (Bothremydidae, tribe Kurmademydini); **F**, *Cearachelys placidoi*, BSP 1976 I 160 (Bothremydidae, tribe Cearachelyini). [A. Venjara, del.]

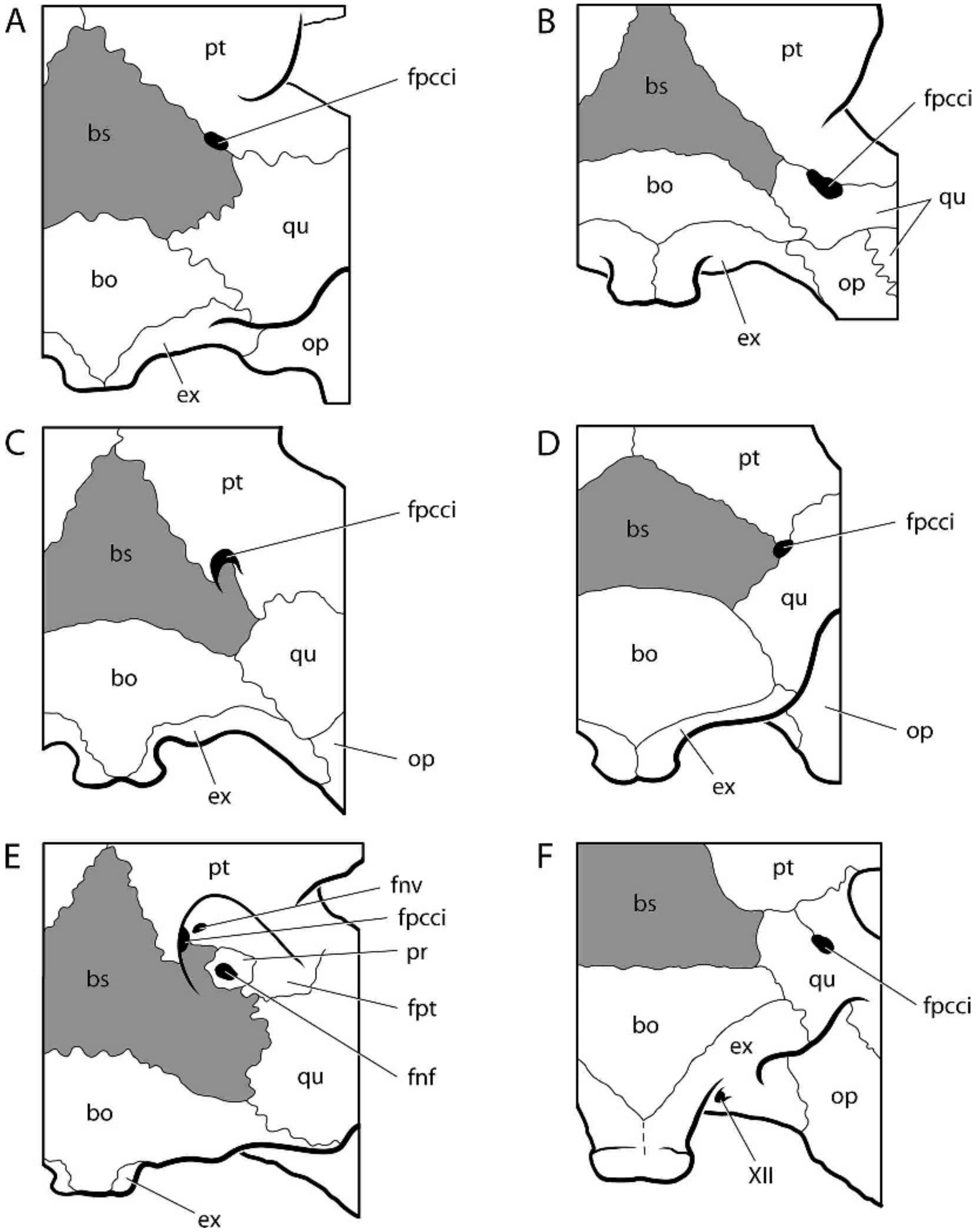


Fig. 277. Comparative views of the left posterior basicranium in ventral view. Basisphenoid is dark gray for a landmark. All are in the family Bothremydidae. **A**, *Cearachelys placidoi*, THUg 1798 (partially restored) (tribe Cearachelyini); **B**, *Bothremys maghrebiana*, n. sp., AMNH 30041 (reversed) (tribe Bothremydini); **C**, *Galianemys whitei*, AMNH 29987 (tribe Cearachelyini); **D**, *Taphrosphys ippolitoi*, n. sp., AMNH 30042 (tribe Taphrosphyini); **E**, *Galianemys emringeri*, AMNH 29985 (tribe Cearachelyini); **F**, *Labrostochelys galkini*, n. gen. et sp., AMNH 30043 (tribe Taphrosphyini). [A. Venjara, del.]

literature with more extensive character descriptions (i.e., Antunes and Broin, 1988; Lapparent de Broin and Werner, 1998; Lapparent de Broin, 2000a), even though they lack character matrices.

These descriptions are also shown in the Character List (appendix 2) and their distributions are shown in the Data Matrix (appendix 3). In the Character List, the senior author has attempted to organize the characters by bone in the same order as in the Cranial Morphology sections. In order to keep track of which bone is involved, in the Character List each character is preceded by the abbreviation of the bone followed by the character name. However, AMNH editorial policy requires that when used as text these abbreviations must be spelled out. Therefore instead of "NA, nasal bones" the discussion below identifies the character as the more cumbersome "Nasal, nasal bones." And so on.

1. Nasal, nasal bones: present (*Emydura*) = 0; absent (*Pelusios*) = 1.

Morphology: When present (fig. 6A), nasals make up the anteriormost part of the skull roof anterior to the orbits. Skull figures showing the morphology of nasal bones in the turtles in which they occur are in Gaffney (1979a). The absent condition is seen in figures 6B and 21A. See discussion of this character in cryptodires in Gaffney (1996).

Primitive condition: Paired nasals are present throughout amniotes and are present in *Proganochelys*, most chelids, and primitive cryptodires.

Homoplasy: There is good evidence that nasals have been lost independently within the Pleurodira and Cryptodira. Within the Pleurodira they are absent in all Pelomedusoides for which this portion of the skull is known. Among chelids they are absent or fused to the frontals only in the genus *Chelus* (Gaffney, 1979a: fig. 144).

Discussion: The absence of nasal bones is a synapomorphy for Pelomedusoides. This character is used in Antunes and Broin (1988), Gaffney and Meylan (1988), Gaffney et al. (1991), Meylan (1996), and Lapparent de Broin and Werner (1998).

2. Lacrimal, lacrimal bone: present (*Proganochelys*) = 0; absent (*Emydura*) = 1.

See Gaffney (1990) and Gaffney et al. (1991) (also used in Gaffney and Meylan, 1988; and Rougier et al., 1995).

3. Lacrimal, lacrimal foramen: present (*Proganochelys*) = 0; absent (*Pelusios*) = 1.

See Gaffney (1990), Gaffney et al. (1991), and Gaffney and Kitching (1995) (also used in Gaffney and Meylan, 1988; and Rougier et al., 1995).

4. Prefrontal, prefrontals meet on midline in dorsal view: no (*Proganochelys*) = 0; yes (*Pelusios*) = 1.

Morphology: When nasals are present, nasal-frontal contact typically excludes midline contact of the prefrontals (fig. 6A). However, prefrontals are not always in contact when nasals are absent (e.g., *Chelus*, Gaffney, 1979a: fig. 144), and on occasion prefrontals may be in midline contact although nasals are present (e.g., *Hydromedusa*, Gaffney, 1979a: fig. 146). State 1 is seen in figure 6B–J.

Primitive condition: The nasal-frontal contact to the exclusion of prefrontal midline contact in *Proganochelys*, most chelids, and primitive cryptodires suggests that prefrontals meeting on the midline represents a derived condition.

Homoplasy: Except for *Hydromedusa* (Gaffney, 1979a, 1979c), none is known within pleurodires.

Discussion: Prefrontals meeting on the midline is a synapomorphy for the Pelomedusoides. This character is used in Gaffney and Meylan (1988) and Gaffney et al. (1991).

5. Prefrontal, preorbital skull broad: narrow (*Galianemys*) = 0; very broad (*Bothremys*) = 1.

Morphology: The snout or preorbital region of turtles generally forms a wide angle of about 70–90°. However, in some species the snout is greatly widened anteriorly, giving the skull a very broad outline in dorsal view (figs. 7, 136, 146). Many bones make up this region; we have arbitrarily chosen to treat this character under the prefrontal.

Primitive condition: The snout of *Proganochelys* forms an angle of about 80° and those of primitive cryptodires and chelids are similarly uninflated, and this is presumed to be the primitive condition.

Homoplasy: Araiochelys lies within the Bothremydini and it is much narrower than

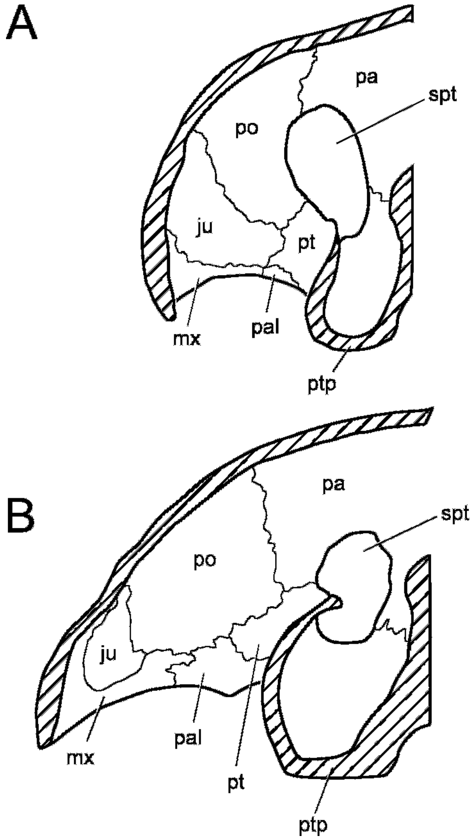


Fig. 278. Comparative views of the left septum orbitotemporale in posterior view. **A**, *Galianemys emringeri*, AMNH 29985; **B**, *Bothremys maghrebiana*, n. sp., AMNH 30041. [A.M. Phillips, del.]

other Bothremydini (fig. 7E) and is a reversal from the very broad condition seen in other Bothremydini.

Discussion: A wide snout, in excess of 80°, is a synapomorphy for the Bothremydini.

6. Prefrontal, anterior margin: straight, broadly convex margin in dorsal view (*Pelomedusa*) = 0; narrow midline process, at least partially dividing nares (*Bothremys*) = 1.

Morphology: The dorsal margin of the apertura narium externa forms an anterior process on the midline, partially dividing the apertura (fig. 7G, H). In some bothremydids, such as *Araiochelys* (fig. 125D), the process almost completely divides the apertura.

Primitive condition: Although the anterior margin is broadly convex in pelomedusids, it is relatively straight in chelids and euraxemydids.

Homoplasy: This character has a CI of 0.33 for this dataset and has originated or been lost multiple times elsewhere within the Pleurodira.

Discussion: The protrusion is present in *Araiochelys* and *Bothremys* within the Bothremydini. It is present only in *Labrostochelys* and *Ummulisani*, among the Taphrosphyini, suggesting that it appeared twice within the family. It helps to define the group *Araiochelys, Bothremys*, and *Chedighaii* within the Bothremydina. There is some ambiguity in identifying the degrees of protrusion. Comparing *Bothremys cooki* and some *Galianemys* specimens shows only a slight difference. As coded, it supports the (*Araiochelys, Bothremys, Chedighaii*) group.

7. Prefrontal, prefrontal-palatine contact: widely separated (*Galianemys*) = 0; closely spaced or in contact (*Bothremys*) = 1.

Morphology: Cryptodires generally have a large ventral process of the prefrontal that contacts the palatine posteriorly (Gaffney, 1979a: 73). However, in most pleurodires the descending process of the prefrontal is smaller and usually not in contact with the vomer or palatine. State 1 is seen through the orbit in *Labrostochelys* (fig. 193). In the taxa in which the bones are close but not in contact (e.g. *Bothremys cooki*, fig. 130A), there is no overlap in morphology with those taxa that have these bones widely separated.

Primitive condition: Gaffney (1990: 37) reported a wide prefrontal-palatine contact in *Proganochelys*, so this contact appears to be primitive for turtles. However, the contact is absent in chelids other than an occasional *Emydura* (Gaffney ,1979a: 73) and it is absent in pelomedusids, except for an occasional *Pelusios* (Gaffney, 1979a: 73), *Araripemys*, euraxemydids, *Hamadachelys*, and members of the Podocnemididae. This distribution suggests that the absence of this contact is primitive for the Bothremydidae.

Homoplasy: Among the Pleurodira this contact occurs as a variant in some individuals of *Pelusios* and *Emydura* (Gaffney, 1979a: 73). These appearances occur independently of those within the Bothremydidae. The character occurs independently in the Bothremydini (*Araiochelys, Bothremys*, and *Chedighaii*) and in the Taphrosphyini (*Labrostochelys*).

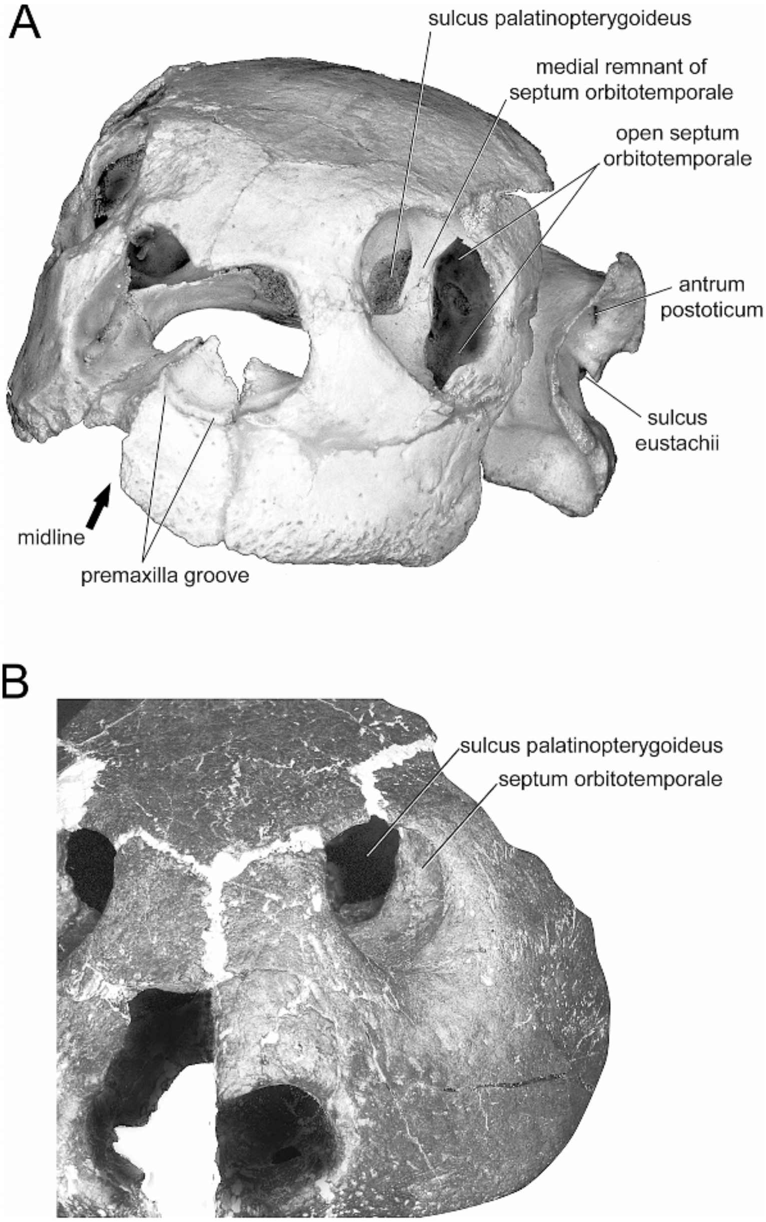


Fig. 279. Comparative views of the left septum orbitotemporale and associated structures in anterior view. **A**, *Phosphatochelys tedfordi*, AMNH 30008 holotype; **B**, *Bothremys cooki*, AMNH 2521 holotype (right side, reversed). [E.S. Gaffney, del.]

Discussion: In spite of homoplasy, this character helps resolve relationships within Bothremydini.

8. Prefrontal, prefrontal-vomer contact: absent (*Proganochelys*) = 0; present (*Pelusios*) = 1.

This character is used by Gaffney and Meylan (1988), Gaffney (1990), Gaffney et al. (1991), and Rougier et al. (1995).

9. Prefrontal, fissura ethmoidalis: very wide (*Proganochelys*) = 0; narrower (*Pelusios*) = 1.

See Gaffney (1990).

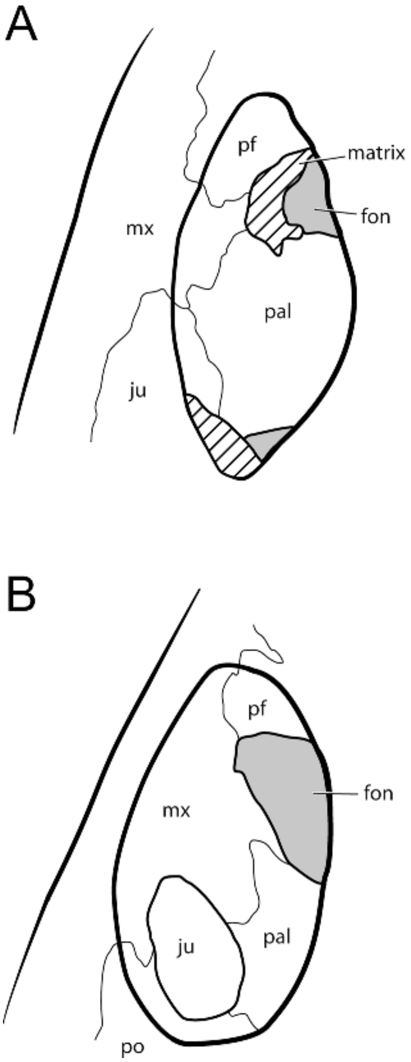


Fig. 280. Comparative views of left orbital floor in dorsal view. Upper, *Azabbaremys moragjonesi*, BMNH R 16370 holotype; lower, *Galianemys whitei*, AMNH 30036. [A.M. Phillips, del.]

10. Prefrontal, prefrontal-parietal contact: absent (*Galianemys*) = 0; present (*Phosphatochelys*) = 1.

Morphology: In most turtles the skull roof is formed by paired prefrontals, frontals, and parietals, with the frontals normally intervening between the other pairs. Prefrontal-parietal contact occurs when the frontals are reduced (fig. 196) or absent (fig. 204).

Primitive condition: In the skull roof of *Proganochelys* and other outgroups this contact is absent (Gaffney, 1990: figs. 16, 114), as is the case in all cryptodires, chelids, pelomedusids, and podocnemidids. Absence of this contact is clearly primitive.

Homoplasy: We are not aware of any homoplasy in this character. When the frontals are greatly reduced in cryptodires (i.e., *Platysternon*), the postorbitals intervene between the prefrontals and parietals (Gaffney, 1979a: 221).

Discussion: This unique feature is a synapomorphy for the two genera *Ummulisani* and *Phosphatochelys*.

11. Frontal, orbits facing upward: orbits facing more laterally (*Galianemys*) = 0; orbits facing more dorsally (*Bothremys*) = 1.

Morphology: In most turtles the skull roof forms a horizontal table, with the maxillae forming nearly vertical walls and the orbits open laterally in a vertically oriented face. In *Bothremys* and *Chedighaii* (figs. 7, 127) there is very little change in slope from the roof and the face of the skull so that the orbits face dorsally and only slightly laterally.

Primitive condition: The orbits of *Proganochelys* are quite vertically oriented (Gaffney, 1990: figs. 16, 114). In primitive cryptodires, chelids, pelomedusids, and podocnemidids, orientation is variable but generally more vertical than horizontal. Thus, the more vertical orientation is considered primitive.

As coded here, the primitive condition includes a wide variety of orbital orientations. However, efforts to specify states, such as nearly vertical, laterally facing orbits as found in *Phosphatochelys* and *Azabbaremys*, were abandoned due to the difficulty of distinguishing gradational conditions in other Taphrosphyini and Cearachelyini.

Homoplasy: Within the Bothremydidae no forms other than *Bothremys* and *Chedighaii* have dorsally facing orbital openings. However, *Araripemys* has the closest approach to this condition, and within chelids the tribe Chelini of Gaffney (1977b) has dorsally facing orbits.

Discussion: The horizontal orbits of *Bothremys* and its friends are presumably related to the great anterior expansion and flattened shape of the skull. This character is a synapomorphy for *Bothremys* + *Chedighaii*.

12. Frontal, foramen interorbitale: high (*Galianemys*) = 0; low (*Bothremys*) = 1.

Morphology: The foramen interorbitale is the opening medial to the orbit defined by the sulcus olfactorius dorsally, the descending process of the parietal posteriorly, and the vomer and dorsal surface of the palatal elements ventrally (fig. 21). In most turtles this opening is round or oval in shape (Gaffney, 1979a). In the Bothremydini the foramen interorbitale is low and reduced in height by a high palate and low sulcus olfactorius (fig. 144).

Primitive condition: The foramen interorbitale is quite tall and rounded in *Proganochelys* (Gaffney, 1990). It is generally broadly rounded in cryptodires and all pleurodires other than *Chelus* and members of the Bothremydini.

Homoplasy: Independent acquisition of this character has occurred in *Chelus*; it has no homoplasy within Pelomedusoides.

Discussion: Although the low foramen interorbitale is diagnostic of the Bothremydini, the character is indeterminable in some Bothremydini (*Polysternon*, *Zolhafah*, *Bothremys arabicus*, and *Chedighaii barberi*). Examination of the endocast (YPM PU 12951) of a presumed *C. barberi* shows that it was low.

13. Parietal, quadratojugal-parietal contact: absent (*Proganochelys*) = 0; present, quadratojugal large and anterior to quadrate (*Euraxemys*) = 1; present, quadratojugal small and dorsal to quadrate (*Phosphatochelys*) = 2.

Morphology: In the skull roof of turtles, the parietal is normally separated from the jugal and quadratojugal by an elongate postorbital that reaches the temporal margin of the skull. In some forms, contact of the quadratojugal and parietal prevents posterior exposure of the postorbital on the temporal margin. This can occur due to a very large quadratojugal that reaches the cheek emargination and extends posteromedially over the quadrate and meets the parietal medially (state 1, figs. 42, 47), or by a laterally enlarged parietal that meets a small quadratojugal that lies dorsal to the quadrate and does not reach the cheek emargination (state 2, figs. 178, 183, 185). We treat these two morphologies as independent states of the same character.

Primitive condition: It is clear that the primitive condition for the turtle skull roof is to have the postorbital separating the parietal and quadratojugal. The postorbital either reaches the squamosal (*Proganochelys*, *Kayentachelys*, *Pleurosternon*, and other primitive cryptodires; Gaffney, 1990) or the temporal margin of the skull (Polycryptodira, Pelomedusidae, *Araripemys*). A parietal-quadratojugal contact is clearly a derived condition.

Homoplasy: The presence of a quadratojugal-parietal contact with a large quadratojugal (state 1) occurs in *Euraxemydidae* and Podocnemididae + *Hamadachelys*. The most parsimonious cladogram shows these as independent acquisitions.

Discussion: State 1 supports Euraxemydidae and, independently, Podocnemididae + *Hamadachelys*. State 2, quadratojugal-parietal contact with a large parietal and small quadratojugal, occurs in *Taphrosphys*, *Ummulisani*, *Labrostochelys*, and *Phosphatochelys* and is without homoplasy in the subgroup of Taphrosphyini that it defines.

This character is used in Gaffney and Meylan (1988) and Lapparent de Broin (2000a).

14. Parietal, temporal emargination: absent, slight (*Proganochelys*) = 0; extreme (*Kurmademys*) = 1; intermediate (*Galianemys*) = 2.

Morphology: The fossa temporalis superior of turtles contains the adductor mandibulae and is primitively roofed over by the skull roof elements, particularly the parietal, squamosal, postorbital, and quadratojugal. Emargination of this skull roof both posteriorly (temporal emargination) and laterally (cheek emargination) is a common theme in turtle evolution (Gaffney, 1979a: 83–86).

In Pelomedusoides the temporal emargination varies a great deal, and dividing this variation into a suite of characters that have a good chance of being homologous is difficult due to the simple morphology involved. We have chosen to identify three conditions in order to obtain some information from this morphologic area. The most extreme emargination, state 1, is relatively easy to recognize. In state 1 only a narrow bridge of bone is present between the orbit and the temporal margin, as found in pelomedusids, *Araripemys* (fig. 26), and the tribe Kurmademydini (figs. 5, 54, 65). Although it is somewhat subjective, the degree of emargination seen in the tribe Cearachelyini (fig. 81), state 2, is defined as intermediate between state 1 and the remaining bothremydids. In state 2 the otic chamber is fully exposed and the bone (postorbital) between the temporal margin and orbit is at least twice as long as in state 1. The principal ambiguity is differentiating state 0 from state 2 in some Bothremydini (such as *Bothremys maghrebiana* and *Chedighaii*, which have most but not all of the otic chamber exposed), and the degree is partially dependent on how the skull is oriented.

Primitive condition: Proganochelys (Gaffney, 1990) has a complete skull roof with no emargination. In the Chelidae (Gaffney, 1979c) temporal emargination is slight or absent except in those cases where cheek emargination appears to have joined with temporal emargination. In other outgroups to the Bothremydidae, temporal emargination is extreme (Pelomedusidae, *Araripemys*), moderate (*Hamadachelys*), or variable (Podocnemididae). The extensive skull roof of the Bothremydini and the Taphrosphyini is interpreted as a reversal.

Homoplasy: This is a character in which there is a great deal of homoplasy within cryptodires, both in the form of independent acquisition of states and as reversals. The presence of extensive skull roofs in primitive cryptodires such as *Kayentachelys*, *Pleurosternon, Glyptops*, and most baenids (Gaffney, 1979b) also suggests that well-developed emargination has occurred independently in pleurodires and cryptodires. Similarly, the presence of well-roofed forms in the Meiolaniidae, Chelonioidea, Chelydridae, Podocnemididae, and Bothremydidae suggests that secondary redevelopment of the skull roof has occurred on multiple occasions.

The emargination states as scored here show homoplasy in state 1, but none in state 2. The extreme temporal emargination of state 1 has arisen three times in the MPC. The conditions in *Kurmademys* and *Sankuchemys* are very similar, but the skulls of *Araripemys* and pelomedusids are not, and the emargination is not identical.

State 2, intermediate or moderate emargination, is not as subjective as it sounds and is recognizable within the Pelomedusoides. The degree of emargination is very similar in *Cearachelys* and *Galianemys*, supporting the monophyly of the Cearachelyini.

Discussion: The principal difficulty with this character is the primitive condition, state 0, a well-roofed skull. The morphology of *Proganochelys* and the Taphrosphyini, for example, is not even similar and is questionably homologous on morphological grounds alone. Yet the well-roofed skulls of the Taphrosphyini and the Bothremydini are similar and probably homologous considering that the two immediate outgroups, the tribes Cearachelyini and Kurmademydini, have distinctly greater degrees of temporal emargination.

This character is used in many papers (see Gaffney and Meylan, 1988; Lapparent de Broin and Werner, 1998; Lapparent de Broin and Murelaga, 1999; Lapparent de Broin, 2000a).

15. Parietal, parietal-squamosal contact: present (*Proganochelys*) = 0; absent (*Pelusios*) = 1.

Morphology: This condition (state 1) is related to the degree of posterior skull roof (temporal) emargination, and it is seen in most Pelomedusoides (figs. 6–8).

Primitive condition: The contact is present (state 0) in *Proganochelys*, *Kayentachelys* and other primitive cryptodires, and chelids and is considered the primitive condition.

Homoplasy: Skull roof emargination is homoplastic in this analysis (see character 14), but the widespread loss of the squamosal-parietal contact in Pelomedusoides suggests that at least the development of temporal emargination to the point of parietal-squamosal separation is synapomorphic for the group. *Dirqadim* is the only reversal.

Discussion: It is possible to put this character as a state in character 14, temporal emargination. However, that character seeks to identify the most emarginate extremes, while this one deals with the other end of the spectrum, the most minimal emargination.

This character is used in Gaffney et al. (1991).

16. Parietal, parietal contacts pterygoid at base of processus trochlearis pterygoidei: absent (*Pelusios*) = 0; ventral process of parietal reaches pterygoid on lateral side of sulcus palatinopterygoideus (*Bothremys*) = 1.

Morphology: A ventral process of the parietal contacts the pterygoid lateral to the sulcus palatinopterygoideus near the base of the processus trochlearis pterygoidei (fig. 62).

Primitive condition: In *Proganochelys* and in all of the pleurodiran outgroups to the Bothremydidae, parietal-pterygoid contact is restricted to the processus inferior parietalis.

Homoplasy: This contact is not known to occur outside of the Bothremydidae. However, within the Bothremydidae it has arisen three times in the MPC. There is no indication of different morphologies for the separate occurrences.

Discussion: Unfortunately this character requires a well-preserved and well-prepared skull for its determination, and the inadequate preservation among the Taphrosphyini in particular limits its use. As known, however, it supports *Bothremys* + *Chedighaii*.

17. Parietal, sulcus palatinopterygoideus: absent (*Proganochelys*) = 0; present and high (*Galianemys*) = 1; present and low due to thick parietal and postorbital roof (*Bothremys*) = 2.

Morphology: The sulcus palatinopterygoideus (figs. 23, 25, 62, 78) is the space found only in pleurodires between the fossa orbitalis and the fossa temporalis, with its medial wall formed by the processus inferior parietalis plus crista pterygoidea and its lateral wall formed by the processus trochlearis pterygoidei. We adopt the term "sulcus palatinopterygoideus" following Antunes and Broin (1988: figs. 3, 4, 8). However, they also used a synonym "gouttière ptérgoidienne". In Lapparent de Broin and Werner (1998) they used "pterygoid sulcus" as well as "sulcus palatinopterygoideus". Schumacher (1954: fig. 25; 1955a: figs. 1, 3) used the broader term "orbitale Pterygoideusrinne" or "orbitaler Pterygoideuskanalrinne" for this space in pleurodires. However, he also used the term for the dorsal surface of the pterygoid in cryptodires (Schumacher, 1955a: fig. 6), so it is clearly not the restricted usage we employ here. The sulcus palatinopterygoideus is defined laterally by the processus trochlearis pterygoidei and is therefore found only in taxa with this structure, that is, pleurodires.

The two conditions of the sulcus recognized here are the more common: the relatively high sulcus (state 1, fig. 78) and the more restricted, relatively low condition (state 2, figs. 130, 279), formed by a thicker and lower parietal, with some participation of postorbital, as seen in *Bothremys* and *Chedighaii hutchisoni*.

Primitive condition: For turtles, the absence of this structure is primitive. Within the Pleurodira, the higher condition of the sulcus palatinopterygoideus is present in chelids, pelomedusids, and euraxemydids and can be considered primitive.

Homoplasy: There is no homoplasy in the analysis for the presence of the sulcus palatinopterygoideus, which is a pleurodiran synapomorphy (fig. 297). However, a low sulcus palatinopterygoideus also occurs in some Podocnemididae as well as within the Bothremydini (fig. 297). The conditions do not appear to be distinguishable morphologically.

Discussion: This character is not the same as simply having a low skull. *Araripemys* and *Labrostochelys* have very low skulls, but they have a relatively high sulci palatinopterygoideus. The degree of dorsal restriction of the sulcus is not clear. *Rosasia* could be interpreted as having a lower sulcus than that in Cearachelyini but higher than that in *Bothremys*. We have chosen to recognize only the more clearly identifiable extreme condition. Several key taxa, *Araiochelys* and *Zolhafah*, among Bothremydini, are not well enough preserved to code this character and that limits its usefulness.

18. Parietal, enters orbital margin: no (*Galianemys*) = 0; yes (*Phosphatochelys*) = 1.

Morphology: The dorsal plate of the parietal enters the posteromedial margin of the orbit in *Rhothonemys, Ummulisani*, and *Phosphatochelys* (figs. 196, 204, 208). In ventral view, the parietal forms part of the fossa nasalis roof.

Primitive condition: In all outgroups and in Euraxemydidae and Cearachelyini, the parietal does not enter the orbital margin.

Homoplasy: No homoplasy seen in the MPC.

Discussion: This character occurs only in three taxa in Pelomedusoides: *Rhothonemys, Ummulisani*, and *Phosphatochelys*. The shape of the parietal itself is very similar in the three taxa, but some of the surrounding elements differ. In *Phosphatochelys* and *Ummulisani* the frontal is very small (or absent) and does not enter the orbital margin due to a prefrontal-parietal contact. In *Rhothonemys* the frontal is larger, widely enters the orbital margin, and there is no prefrontal-parietal contact. However, the parietals of all three taxa also agree in being relatively farther forward in the skull roof than in any other Pelomedusoides, so that they form a significant part of the fossa orbitalis roof, also in contrast to other Pelomedusoides.

19. Supratemporal, supratemporal bone: present (*Proganochelys*) = 0; absent (*Pelusios*) = 1.

See Gaffney (1990), Gaffney et al. (1991), and Rougier et al. (1995).

20. Jugal, jugal retracted from orbital margin: jugal enters orbit (*Pelusios*) = 0; jugal slightly retracted (*Cearachelys*) = 1; jugal widely retracted (*Galianemys*) = 2.

Morphology: In *Cearachelys* (figs. 71E, 78) the postorbital has a long ventral process extending along the orbital margin that nearly meets the maxilla (*Cearachelys*, Postorbital). There is some variation in degree and preservation, but this condition (state 1) occurs in all three *Cearachelys* skulls. In the two species of *Galianemys* (figs. 81, 89), the postorbital and maxilla widely meet, completely separating the jugal from the orbital margin (state 2).

Primitive condition: Substantial jugal exposure in the orbital margin is clearly the primitive condition, as seen in *Proganochelys* (Gaffney, 1990: fig. 16) and nearly all pleurodires.

Homoplasy: This feature appears to have occurred independently in several lineages of cryptodires, but there is no indication of homoplasy within the Pleurodira (fig. 298).

Discussion: This character is run ordered in the preferred analysis, with state 1, partial retraction, the primitive state relative to state 2, complete retraction. The additive nature of this character could also be expressed as two states only: no retraction, and at least partial jugal retraction present. When the analysis is run with the three states ordered, the character unites the Cearachelyini (with the partial condition) and the genus *Galianemys* (with full retraction). When the character is run unordered, the same MPC results (fig. 298).

21. Jugal, jugal narrow dorsoventrally: absent (*Bothremys*) = 0; present (*Taphrosphys, Labrostochelys*) = 1.

Morphology: In *Taphrosphys* and *Labrostochelys* (figs. 178, 185, 190) the lateral exposure of the jugal is long horizontally and short vertically. Although there is a contribution to the orbital margin, the height of the bone is significantly less than in other Taphrosphyini and in turtles in general.

Primitive condition: The jugal in *Proganochelys*, most chelids, pelomedusids, *Araripemys*, euraxemydids, and podocnemidids has a large exposure on the cheek.

Homoplasy: Reduced jugal exposure on the cheek also occurs in some chelids with well-developed cheek emargination, such as *Hydromedusa* and *Platemys*, and in some testudinoids (*Cuora*, *Melanochelys*, *Rhinoclemmys*, *Terrapene*, *Gopherus*, *Kinixys*, and *Psammobates*). Within the Pelomedusoides, there is no evidence of homoplasy. In the MPC, the character occurs independently in *Labrostochelys* and *Taphrosphys*.

Discussion: The character occurs only in members of the Taphrosphyini. It unites two species of *Taphrosphys, T. ippolitoi* and *T. congolensis*; it is not known in *T. sulcatus*.

22. Jugal, jugal-quadrate contact: absent (*Bothremys*) = 0; present (*Azabbaremys*) = 1.

Morphology: In the Taphrosphyini the cheek is relatively short with a dorsally retracted quadratojugal, allowing the jugal to contact the large quadrate (figs. 178, 185, 196).

Primitive condition: Although the sutures in this area are not definite in *Proganochelys*, contacts observed in most Casichelydia, including primitive cryptodires and pleurodires, show that separation of these elements by the quadratojugal is the primitive condition for Pleurodira.

Homoplasy: Although there is no homoplasy in the Bothremydidae, this feature occurs within the Podocnemididae in *Peltocephalus* and *Erymnochelys*. It occurs with a large jugal crossing the area where cheek emargination normally occurs; the quadratojugal is not reduced in size. In the Taphrosphyini with this contact, the quadratojugal is small and dorsally located. Jugal-quadrate contact also occurs in the cryptodire *Archelon*.

Discussion: The jugal-quadrate contact is a diagnostic character of the Taphrosphyini in the MPC, but the character is determinable with certainty in only 5 of 11 taxa, although *Labrostochelys* probably has it. The contact also differs among the known taxa. In *Azabbaremys* it is a wide contact with both bones relatively thick. In *Phosphatochelys* the bones are very thin and the contact could almost be kinetic.

23. Jugal, exposure on triturating surface: none (*Pelusios*) = 0; large exposure visible in ventral view (*Bothremys*) = 1.

Morphology: The upper triturating surface in turtles is made up mostly by the maxilla with an anterior contribution by the premaxilla. In many forms there is also some contribution posteriorly or posteromedially from the palatine. However, contribution by the jugals to the triturating surface is rare. Character state 1 is the ventral exposure of the jugal on the triturating surface in palatal view (figs. 10, 130). A small amount of jugal may be exposed, as in *Cearachelys* (fig. 77), but this is not the character as delimited here.

Primitive condition: In *Proganochelys*, all primitive cryptodires, chelids, pelomedusids, euraxemydids, and podocnemidids the jugals are excluded from the triturating surface.

Homoplasy: The MPC shows this character as a synapomorphy of the Bothremydina, with a reversal in *Chedighaii*. The character also occurs independently in the Taphrosphyini in CNRST-SUNY 199, an undescribed form from Mali.

The only taxon outside of the Bothremydidae in which jugal participation in the triturating surface is known is *Sandownia* (Meylan et al., 2000) and a probably related undescribed form from the Paleocene of Morocco. In *Sandownia* jugal participation is long and narrow and lateral to the maxilla and pterygoid. There is no jugal-palatine contact on the triturating surface as in bothremydids.

Discussion: Within the Cearachelyini, a slightly exposed jugal occurs in *Cearachelys* and one species of *Galianemys*, *G. whitei*, but not in the other species, *G. emringeri*. The three skulls of *Cearachelys* (fig. 77) show some variation in the degree of jugal exposure, suggesting that this character is one of degree rather than the all or none used in the character coding. Nonetheless, we have coded the small exposure as "0" and only recognized the more extreme condition as the character.

This character is used in Meylan (1996), Lapparent de Broin and Werner (1998), and Tong et al. (1998).

24. Squamosal, posterior projection: absent (*Galianemys*) = 0; present, projecting posteriorly, forming distinct process (*Bothremys*) = 1.

Morphology: In the Bothremydini and some Taphrosphyini, the squamosal forms a posterior process that extends well posterior to the opisthotic (figs. 7, 101, 102, 122, 123).

Primitive condition: In the outgroups, either there is no projection (*Proganochelys*, euraxemydids) or the opisthotic projects no farther than the squamosal (chelids, pelomedusids). In most Bothremydidae (except Bothremydini and *Labrostochelys* and CNRST-SUNY 199), the squamosal is even with or projects only a short distance beyond the opisthotic.

Homoplasy: This character occurs in *Labrostochelys* and CNRST-SUNY 199 outside the Bothremydini, although it is longer and deeper in *Labrostochelys*, consistent with the hypothesis that it is nonhomologous.

Discussion: The character is a synapomorphy for the Bothremydini but remains uncertain in several taxa for which this part of the skull is poorly known.

Another character, character 102, processus paroccipitalis not projecting beyond squamosal, is distinct from this one. In the opisthotic character, the processus paroccipitalis is very similar in all Bothremydidae; it is relatively small compared to those in outgroups like pelomedusids. The squamosal projection is present with a small opisthotic.

25. Squamosal, posteroventral vertical flange: absent (*Galianemys*) = 0; present (*Labrostochelys*) = 1.

Morphology: The squamosal forms the posterolateral corner of the skull posterior to the quadrate. It is generally a cone-shaped bone with the hollow of the cone contributing to the antrum postoticum if one is present. In *Proganochelys* the antrum postoticum is absent and the squamosal is a simple curved plate with a nearly flat ventral surface. When the character is present, the flange (figs. 168, 169, 172, 177–209, 287) is a thin sheet of bone running anteroposteriorly on the ventral surface of the squamosal. It appears to be related to the attachment of the depressor mandibulae musculature.

Primitive condition: The squamosal flange is absent in *Proganochelys* and all outgroups.

Homoplasy: None observed (fig. 299).

Discussion: The ventral flange developed as a vertical plate on the squamosal is unique to a monophyletic group (fig. 299) within the subtribe Taphrosphyina: *Taphrosphys*, *Labrostochelys, Ummulisani*, *Rhothonemys*, and *Phosphatochelys*.

26. Squamosal, lateral tubercle: absent (*Galianemys*) = 0; present (*Labrostochelys*) = 1.

Morphology: At the posterodorsal edge of the cavum tympani in *Taphrosphys*, *Labrostochelys, Ummulisani*, and *Phosphatochelys* is a small tubercle produced by the squamosal that is directed laterally and ventrally along the suture with the quadrate (fig. 287). The tubercle may be at the posterior edge of the scale covering the cavum tympani. Posterior and ventral to the tubercle, the bone trends medially and was presumably covered by some part of the depressor mandibulae.

Primitive condition: The tubercle is absent in all outgroups.

Homoplasy: None apparent.

Discussion: The function of this peculiar structure is unknown. It appears to mark the division between the scaled surface and the muscular covering.

27. Postorbital, fossa orbitalis posterior enlargement: absent (*Galianemys*) = 0; present (*Bothremys*) = 1.

Morphology: The fossa orbitalis of bothremydids is well defined by bone: the postorbital and jugal posteriorly, the postorbital and parietal dorsally, and the maxilla and palatine ventrally. In many bothremydids, the internal fossa is much larger than the orbital rim, and some of the bones form pockets or concavities that seem to be significantly larger than a spherical eyeball would require (fig. 144). Although there is some variation in the extent of this enlargement and which bones form it, we use a single character state to treat it. All of the taxa that have the character have a postorbital forming the septum orbitotemporale distinctly posterior to the orbital rim (figs. 211, 278), and some have a more pronounced ventral concavity formed by the maxilla (fig. 211) as well. Even those Taphrosphyini that have a small or mostly absent septum orbitotemporale have ridges on the parietal (fig. 211), which indicate the position of the posterior limits of the fossa orbitalis.

Primitive condition: The pelomedusids (fig. 25) and chelids (Gaffney, 1979a: fig. 55) show the primitive condition of a fossa orbitalis close to the size of the orbital rim.

Homoplasy: The condition may be a synapomorphy for the Bothremydidae with loss in *Cearachelys*, and within the Taphrosphyini in the MPC.

Discussion: The identification of this character in *Chedighaii barberi* is based on the whole skull endocast YPM PU 12951 (figs. 166, 167), also described by Gaffney (1977b).

The principal difficulty with this character is that it may be related to relative skull/orbit size. Skulls with relatively small orbital openings (e.g., *Bothremys*) may have a larger fossa orbitalis than skulls with relatively large orbits (e.g., *Phosphatochelys*). Nonetheless, identification of the character is based on the position of the ridges, particularly parietal and postorbital. Therefore, both *Phosphatochelys* and *Bothremys* are identified as having this character.

28. Postorbital, septum orbitotemporale: absent (*Proganochelys*) = 0; postorbital wall present (*Galianemys*) = 1; postorbital wall at least partially open (*Phosphatochelys*) = 2.

Morphology: In pleurodires the posterior wall of the fossa orbitalis formed mostly by the jugal, palatine, and postorbital is a distinct structure (state 1), the septum orbitotemporale (figs. 23, 25, 43, 78). *Proganochelys* and cryptodires lack this wall (state 0). In some Taphrosphyini (*T. congolensis*, *Phosphatochelys*, *Azabbaremys*) this wall is reduced and mostly open (state 2; fig. 300). In this state (fig. 279), the ventral part of the postorbital is missing, lacking the palatine contact, and much of the jugal vertical component is reduced. The sulcus palatinopterygoideus is not defined laterally except for the pterygoid portion of the processus trochlearis pterygoidei. The partially open condition of this wall in the Taphrosphyini is a different condition from that in *Proganochelys* and cryptodires, as a portion of the postorbital wall and the sulcus palatinopterygoideus is still determinable in every pleurodire.

Primitive condition: For pleurodires, a well-developed septum orbitotemporale is primitive (fig. 300). The septum orbitotemporale is part of the complex forming the processus trochlearis pterygoidei and the sulcus palatinopterygoideus (figs. 23, 25), all pleurodiran synapomorphies.

Homoplasy: None known. Some cryptodires (e.g., trionychids; Gaffney, 1979a: fig. 144) may develop a partial wall along the posterior orbital rim, but it is clearly morphologically distinct from the pleurodiran condition.

29. Postorbital, size: relatively short (*Euraxemys*) = 0; relatively long (*Galianemys*) = 1.

Morphology: Considering the simple nature of the character definitions and the relatively large amount of variation in pleurodire skull roofs, this character may seem at first to be useless. However, there is an objective kernel in all this corn. The short postorbital, either entering the temporal margin (fig. 6B, F) or being bordered by the quadratojugal-parietal contact (fig. 6D, E), appears qualitatively distinguishable from the long, narrow postorbital of the Cearachelyini, Bothremydini, and *Azabbaremys* (figs. 6H–J, 7A, B, E, H–J, 8J).

Primitive condition: The short postorbital occurs in the outgroups *Proganochelys*, chelids, pelomedusids, and *Araripemys*. Primitively, the postorbital was both short and not exposed by emargination. Exposure due to temporal emargination is treated elsewhere.

Homoplasy: The longer than wide postorbital (state 1) appears only once within the Bothremydidae, but it is reversed within the Taphrosphyini for the *Taphrosphys-Labrostochelys-Ummulisani-Phosphatochelys* group. However, it also occurs in the Cryptodira.

Discussion: Interestingly, the long, narrow postorbital within Bothremydidae occurs along with a well-roofed skull lacking an extensive temporal emargination. The Kurmademydini have a short postorbital, because they are extensively emarginated. One might speculate that this was the primitive Bothremydidae condition and that the elongate postorbital is correlated with the presumably re-evolved roofed skull found in all other bothremydids.

This character is used in Meylan (1996), Tong et al. (1998), and Lapparent de Broin (2000b).

30. Premaxilla, protrudes anteriorly beyond labial ridge: no, or slightly (*Galianemys*) = 0; yes, in ventral view projects anteriorly (*Bothremys*) = 1

Morphology: The premaxilla, seen in ventral view, projects anteriorly beyond the labial ridge (figs. 10E, G–I, 11F, G, J).

Primitive condition: A vertical or slightly inclined wall of the premaxilla between the labial ridge and the apertura narium externa is present in *Proganochelys* (Gaffney, 1990: fig. 27) and nearly all turtles and represents the primitive condition.

Homoplasy: This character has a CI of 0.20, showing that it has a lot of homoplasy. However, there are three independent origins within the Taphrosphyini alone and only one in the Bothremydini. In the Bothremydini the premaxilla and maxillae have similar anterior protrusions beyond the labial ridge of the triturating surface. In *Labrostochelys* there is a long triangular projection of the premaxilla that is unlike any morphology known in any fossil or living turtle. Other Taphrosphyini have thick premaxillae, different from those in the Bothremydini. What is treated as one character could be argued to be different character states rather than one.

Discussion: Although *Chedighaii hutchisoni* completely lacks the premaxillae, the receded prefrontals and inclined maxillae strongly suggest that the premaxilla was protruding. We have coded this taxon as "?" anyway, but it is nice to see that the MPC has decided *Chedighaii* should have a protruded premaxilla.

31. Premaxilla, midline depression: absent, shallow, or indistinct (*Euraxemys*) = 0;

distinct and wide (*Bothremys kellyi*) = 1; distinct and narrow (*Rosasia*) = 2.

Morphology: When the lingual ridge of the triturating surface is well defined and extends onto the premaxillae, a midline depression or concavity between the pair of ridges is sometimes formed on the triturating surface of the premaxilla. In Bothremydidae this depression is usually deep and well defined. It may be very broad, widening posteriorly as in *Kurmademys, Zolhafah, Bothremys kellyi*, and *B. arabicus* (state 1, figs. 9F, 10C, F, I) or it may be narrow, with essentially parallel sides as in *Bothremys cooki, B. maghrebiana, Rosasia*, and *Araiochelys* (state 2, fig. 10D, E, G, H).

Primitive condition: In *Proganochelys* the lingual ridge does not extend up onto the triturating surface of the premaxilla. This is also the case in many pleurodires, including chelids, pelomedusids, *Araripemys*, euraxemydids, and most podocnemidids (a lingual ridge is present in *Erymnochelys* and *Peltocephalus*). These premaxillary depressions are generally absent in cryptodires. Similar depressions are seen only in cryptodires with multiple ridges on the triturating surface (e.g., *Meiolania*, *Geochelone*, *Kachuga*) in which they are formed at least in part by lateral accessory ridges of the triturating surface.

Homoplasy: In the MPC the deep, wide midline concavity (state 1) occurs as a synapomorphy for Bothremydidae, but there are a number of reversals. State 1 is lost within the Bothremydini, but re-evolves in *Chedighaii* and in *Bothremys arabicus* and *B. kellyi.* There is also a reversal of the wide condition within Taphrosphyini where *Azabbaremys* loses the concavity (state 0) and *Labrostochelys* acquires a narrow one (state 2).

Discussion: The extremes of this character, states 1 and 2, are easily recognized, but because it is a gradational character, intermediate stages are a problem. As with a number of these more subjective, gradational characters, the senior author has chosen to try recognizing just the most extreme conditions as states and to ignore the variation between them. However, this can be considered too subjective in some cases. Deleting this character from the analysis has a significant effect on the MPC, so this issue is important. When this character is deleted, the result is a loss of resolution for the four species in *Bothremys*, which become a multichotomy with *Chedighaii*, and a loss of resolution for *Zolhafah* and *Rosasia*, which become a multichotomy with the remaining Bothremydina. These are obviously poorly supported nodes and it is worth looking at the character in more detail. The taxa that it resolves in *Bothremys* have the character states clearly recognized. *B. kellyi* and *B. arabicus* have distinctly wide median depressions, and *B. cooki* and *B. maghrebiana* do have distinctly narrow ones. It is outside the Bothremydina that coding the depressions becomes more subjective. Rather than delete the character entirely from the dataset, it seems better to use it in the analysis and present the alternative cladogram (fig. 290).

The midline space between the lateral triturating surfaces seen in state 1 is reduced in state 2, perhaps by increasing durophagy within the clades in which state 2 occurs.

This character is used in Antunes and Broin (1988) and is probably equivalent to the "anterior palatine sulcus" of Lapparent de Broin and Werner (1998).

32. Premaxilla, midline dorsal process: present, meeting nasals (*Proganochelys*) = 0; absent or low (*Galianemys*) = 1; present, at least partially separating nares (*Araiochelys*) = 2.

Morphology: In *Bothremys*, *Araiochelys*, *Rhothonemys*, and *Labrostochelys* the apertura narium externa is at least partially divided by a dorsal process, half formed by each premaxilla, which rises from the lower margin of the apertura (figs. 130, 141, 143). In *Araiochelys* (fig. 125D) this almost completely divides the apertura.

Primitive condition: *Proganochelys* has a dorsal premaxillary process, as in many other amniotes, which completely divides the apertura narium externa. However, chelids, pelomedusids, euraxemydids, *Araripemys*, podocnemidids, Cearachelyini, and Kurmademydini all lack one, and this is the presumed primitive condition for Pleurodira.

Homoplasy: The dorsal premaxillary process is lost once in the MPC, at the Casichelydia node, and reversed twice, within the tribes Bothremydini and within Taphrosphyini.

Discussion: An earlier version of this character was "figure eight shaped apertura narium externa", but this version may be a little more objective. There are many stories in the nose of pleurodires, and this is just one of them.

This character is used in Gaffney and Kitching (1995) and Rougier et al. (1995).

33. Premaxilla, dorsal sulcus: smooth surface (*Bothremys*) = 0; sulcus parallel to margin of apertura narium externa (*Phosphatochelys*) = 1.

Morphology: A narrow, parallel-sided trough occurs along the anterior edge of the apertura narium externa on the dorsal surface of the premaxilla in *Taphrosphys congolensis*, *T. ippolitoi*, and *Phosphatochelys* (fig. 279). The sulcus has a variable number of foramina in its floor that extend ventrally into the premaxilla. The sulcus presumably held an artery or vein.

Primitive condition: Neither *Proganochelys* nor any of the pleurodiran outgroups have this sulcus. The floor of the fossa nasalis in this area in various pleurodires may have a lip and scattered foramina, but not this well-defined sulcus.

Homoplasy: None known.

Discussion: This is a fairly "minor" character that intuitively seems particularly liable to individual variation, but it occurs only once in the MPC and does help define a group within the Taphrosphyina.

34. Maxilla, triturating surfaces: relatively narrow, parallel sides (*Taphrosphys*) = 0; triangular, wider posteriorly than anteriorly (*Galianemys*) = 1: triangular, very wide posteriorly (*Bothremys*) = 2.

Morphology: The bothremydid tribes Cearachelyini, Kurmademydini, and Bothremydini all have wide triturating surfaces formed by maxilla, premaxilla, palatine, and sometimes jugal. They are expanded posteriorly to form a roughly triangular shape in ventral view in which the lingual ridge converges anteriorly toward the labial ridge. In state 1 the triangle is narrow posteriorly (figs. 9F, H–J, 10B, E). In state 2, the triangle is broader and the midline depression (Character 32) is narrower (fig. 10A, C, D, F, G, I, K). Some Taphrosphyini have relatively wide triturating surfaces (*Azabbaremys*, *Nigeremys*), but the lingual and labial ridges are parallel.

Primitive condition: Although there is some variation in triturating surface shape in the outgroups, all are narrower and more parallel-sided in comparison to bothremydids.

Homoplasy: With a CI of 0.33, this character has homoplasy problems. In the MPC (fig. 301), the derived condition of a wide triturating surface of any sort originates once at Bothremydidae and reverses once at Taphrosphyini. Within the Bothremydini, the very wide condition (state 2) is reversed three times or originates twice and is lost twice. Triangular, or at least very wide, triturating surfaces occur within Podocnemididae and in many cryptodire groups.

Discussion: It is possible to subdivide the wide condition into two states, because some Bothremydini have significantly wider palates (*Foxemys*, *Zolhafah*, *Rosasia*, *Bothremys*, and *Chedighaii hutchisoni*) than do other bothremydids. Comparing these widths using the width of posterior triturating surface/skull length as a ratio produces two possible ranges: 16–28 for state 1 and 31–40 for state 2. However, within *Cearachelys* the ratio for two specimens shows a fairly wide range of 21–28, suggesting that the role of individual variation could be considerable. The range of variation in recent broad-jawed taxa (some chelids show a wide range within one species) supports the suggestion that without a larger sample, subtle differences in triturating surface width would best be ignored. We thereforeadopt a fairly simplistic view of what is undoubtedly a more complex character (see also discussion under *Araiochelys* in the Systematics section for maxilla width in *Araiochelys* compared with *Bothremys maghrebiana*). It might also be argued that these states should be ordered, and the MPC is consistent with this, given a few not unreasonable reversals (fig. 301). If ordered, the same MPC results.

This character, or a similar version of it, is used by Antunes and Broin (1988), Lapparent de Broin and Werner (1998), and Tong et al. (1998).

35. Maxilla, triturating surface pits: absent (*Kurmademys*) = 0; present (*Bothremys*) = 1.

Morphology: The paired conical depressions in the triturating surface are known in *Bothremys, Zolhafah, Rosasia*, and *Araiochelys* (figs.123, 128, 133, 137; see also text under Maxilla and Jugal for these taxa). The pit is formed mostly by the maxilla with a widely varying contribution from the jugal.

Primitive condition: The absence of triturating pits is primitive, as all pleurodires outside bothremydids lack them.

Homoplasy: A shallow pit is present in CNRST-SUNY 199 (fig. 302), an undescribed Taphrosphyini skull. Its morphology, however, is different from the pits in Bothremydini. Some *Cearachelys* have a shallow pit.

Outside pleurodires, a very similar paired set of triturating pits occurs in an undescribed cryptodire from the Paleocene of Morocco, represented by a series of skulls: AMNH 30001, AMNH 30558, and AMNH 30554.

Discussion: This character (fig. 302) is a synapomorphy for the subfamily Bothremydini, being absent in *Chedighaii*. Character 23 (jugal exposed in triturating surface) overlaps with this character in that the formation of the pit exposes the jugal overlying the maxilla in the cheek. This exposure, however, varies widely in extent. The overlap is incomplete in that *Cearachelys* has some jugal exposure but no deep pit. In any case, deleting this character results in the same MPC.

36. Maxilla, accessory ridge on triturating surface: absent (*Galianemys*) = 0; present (*Euraxemys*) = 1.

Morphology: A ridge on the triturating surface between the lingual and labial ridges can be seen in the Euraxemydidae (figs. 42, 47). It also occurs in *Sankuchemys* (fig. 65). The ridge lies parallel to the lingual and labial ridges.

Primitive condition: *Proganochelys*, basal cryptodires, and most chelids and pelomedusids lack accessory ridges. Within chelids and pelomedusids, accessory ridges do pop up so to speak, but it is unlikely that this is primitive for these groups.

Homoplasy: Accessory ridges are frequent within the Podocnemididae (especially *Podocnemis*), chelids, and pelomedusids, and they are also common within several groups of cryptodires. However, in the MPC accessory ridges are a synapomorphy for the Euraxemydidae. Within the Bothremydidae only *Sankuchemys*, one *Foxemys*, and the undescribed CNRST-SUNY 199 have one.

Discussion: The triturating surface of turtles has produced accessory ridges on multiple occasions within turtles. However, within the Pelomedusoides, distribution of this character proves useful and it is included in the dataset.

37. Maxilla, labial ridge depth below orbit: relatively shallow (roughly equal to or less than orbital diameter) (*Galianemys*) = 0; very deep (greater than orbital diameter) (*Bothremys*) = 1.

Morphology: In *Bothremys* and *Chedighaii hutchisoni* the maxilla ventral to the orbit is very deep (figs. 127, 130, 136, 146, 149) compared to Kurmademydini, Cearachelyini, and other Bothremydini.

Primitive condition: All outgroups have a relatively shallow labial ridge.

Homoplasy: In the MPC, this character has evolved independently within the Bothremydini and the Taphrosphyini. There is morphologic support for this in that the Taphrosphyini maxilla is a very thin sheet of maxilla in contrast to the thick, wedge-shaped maxilla of the Bothremydini.

Discussion: Chedighaii barberi is scored as "?" because the orbit is broken along most of the edges in Alabama 2001.2; however, the endocast YPM PU 12951 shows that the orbits were small, as in *C. hutchisoni*. The labial ridge in *C. barberi* is shallower than in *C. hutchisoni*, but it is still deep compared to other Bothremydini.

38. Maxilla, maxilla-quadratojugal contact: absent (quadratojugal present) (*Euraxemys*) = 0; present (*Galianemys*) = 1; absent (quadratojugal absent, chelids only) (*Emydura*) = 2.

Morphology: The lateral face of the turtle skull is made up by the maxilla anteriorly, the jugal and postorbital posterior to the orbit, and the quadratojugal, quadrate, and squamosal posteriorly. In most turtles the jugal is positioned posteroventrally to the orbit and reaches the cheek margin (Gaffney, 1990: fig. 16). In this position it prevents maxilla-quadratojugal contact. If the jugal is retracted from the cheek margin, the quadratojugal may meet the maxilla ventral to the jugal. This is the condition seen in the tribes Kurmademydini, Cearachelyini, and Bothremydini (figs. 3, 4). In the Taphrosphyini the quadratojugal is small and dorsal (fig. 5).

Primitive condition: Separation of the maxilla and quadratojugal by the jugal occurs in all the relevant outgroups (fig. 3).

Homoplasy: Maxilla-quadratojugal contact occurs in some cryptodires independently. Within the Bothremydidae the absence of a maxilla-quadratojugal contact is a Taphrosphyini synapomorphy. In this tribe the quadratojugal is retracted dorsally and lacks the ventral portion (see character 13), typically present in other Pelomedusoides. Therefore, there is morphological support for the nonhomology of the primitive condition in Taphrosphyini versus the pleurodiran outgroups outside Bothremydidae.

Discussion: Although the character is not determinable in a number of bothremydids, its distribution in the MPC shows it as a synapomorphy for Bothremydidae and its reversal as a synapomorphy for Taphrosphyini.

39. Maxilla, maxilla-quadrate contact, cheek emargination: absent, little or no emargination (*Galianemys*) = 0; present, no emargination (*Azabbaremys*) = 1; absent, barely separated by narrow fissure (*Phosphatochelys*) = 2; absent, deep emargination, quadratojugal present (*Euraxemys*) = 3; absent, deep emargination, quadratojugal absent (*Emydura*) = 4.

Morphology: The lateral surface of the turtle skull is made up of the maxilla anteriorly, the jugal and postorbital posterior to the orbit, and the quadratojugal, quadrate, and squamosal posteriorly (Gaffney, 1979a). In most turtles both the jugal and the quadratojugal reach the cheek margin (Gaffney, 1990: fig. 16). In this position they prevent maxilla-quadrate contact. If both the jugal and quadratojugal are placed dorsally from the cheek margin, then the maxilla may contact the quadrate, and this is state 1 (fig. 4D, H). Within the Bothremydidae, an anteriorly elongate quadrate and an elongate maxilla meet to prevent jugal and quadratojugal exposure on the cheek margin. This contact is present in most Taphrosphyini, but there is some variation in form. In *Azabbaremys* (figs. 5J, 215) the contact results from a broad, posterior process of the maxilla. In *Labrostochelys* and *Taphrosphys* there is a narrow quadrate-maxilla contact, with an anterior process of the quadrate not seen in *Azabbaremys* or *Phosphatochelys*. Within the Bothremydini, *Rosasia*, *Araiochelys*, and *Bothremys* have a broad quadrate-maxilla contact.

State 2 (fig. 5D) is the narrow fissure present in *Phosphatochelys* and *Ummulisani*, which separates the quadrate and maxilla. This does not seem to be homologous with the deep emargination condition with the quadratojugal present, state 3 (fig. 3D). State 4 (fig. 3A) is the condition of a deep emargination with the quadratojugal entirely missing, known only in chelids.

Primitive condition: Intervention of the jugal and quadratojugal between the maxilla and quadrate occurs in all outgroups.

Homoplasy: We are unaware of any turtles outside of the Bothremydidae in which contact between the maxilla and quadrate occurs. The MPC shows the quadrate-maxilla contact occurring within the Taphrosphyini and within the Bothremydini (fig. 296A). *Foxemys* and *Polysternon* lack the contact and have the primitive condition for the quadratojugal, so it can be interpreted that the presence of the quadrate-maxilla contact is not primitive for Bothremydini. However, a large quadratojugal is present in *Chedighaii hutchisoni*, although not well preserved (and not determinable in *C. barberi*), so presence of a maxilla-quadrate contact in the other Bothremydini is equivocal. The MPC is still consistent with a single origin of a maxilla-quadrate contact for the Bothremydodda (Taphrosphyini + Bothremydini) with reversals in the Foxemydina and Nigeremydina (see below).

Discussion: Character state 1 may not be homologous between the Taphrosphyini and the Bothremydini, due to different morphologies as well as ambiguity in the MPC (fig. 296A). Alternatively, it may be a synapomorphy for the tribes Bothremydini + Taphrosphyini and may be reversed in *Foxemys*, *Polysternon*, and *Chedighaii*. Character state 3 is a synapomorphy for Pelomedusoides and is lost in the subfamily Bothremydinae (tribes Cearchelyini + Bothremydini + Taphrosphyini).

This character or a version of it is used in Antunes and Broin (1988).

40. Maxilla, orbitonarial bar width: roughly equal to or slightly less than diameter of orbit (*Galianemys*) = 0; wider than orbit (*Bothremys*) = 1; more than twice orbital diameter (*Labrostochelys*) = 2; very narrow, much less than diameter of orbit (*Phosphatochelys*) = 3.

Morphology: The bone between the orbit and the lateral margin of the apertura narium externa, the orbitonarial bar, is formed by the maxilla and prefrontal, but usually the maxilla forms most of it. The width of this bar varies, and this character is an attempt to use the extremes of this variation. The extremely narrow orbitonarial bar (state 3, fig. 5D) present in *Phosphatochelys, Ummulisani*, and *Rhothonemys* is unique in pleurodires. The Bothremydini have a wider bar than in most pleurodires, and *Bothremys* is the widest (state 1, fig. 4H). The *Bothremys arabicus* condition is unknown, however. *Labrostochelys* is unique among pleurodires in its extremely long snout and very wide orbitonarial bar (state 2, fig. 5G).

Primitive condition: The intermediate state (state 0) is fairly consistent among the outgroups, *Proganochelys*, chelids, and pelomedusids, but it is unlikely that all the intermediate states identified here are actually homologous.

Homoplasy: As restricted here, the states are not homoplastic in the MPC, but variation of the orbitonarial width is considerable throughout turtles.

Discussion: Although this character is not defined with precision, it seems to be the best way to obtain information from this morphology. Measuring some parameters might enhance the use of the character and allow more states to be distinguished, but there is a great deal of variation of this character in turtles and a very restricted usage seems best. Nonetheless, this is a relatively subjective character set and must be used with caution.

41. Maxilla, dorsal process onto skull roof: maxilla more lateral and ventral (*Galianemys*) = 0; maxilla extending dorsomedially onto skull roof, restricting lateral extent of prefrontal (*Bothremys cooki*) = 1.

Morphology: The dorsal process of the maxilla extends onto the skull roof in two *Bothremys* species, *B. maghrebiana* and *B. cooki*, restricting the prefrontal exposure in dorsal view (fig. 7G, H). The maxilla is more extensive medially in *B. cooki* than in *B. maghrebiana*, and in both species the prefrontal is more L-shaped in contrast to the more rectangular prefrontal of other pleurodires.

Primitive condition: Rectangular prefrontals and no dorsal extension of the maxilla are found throughout all outgroups.

Homoplasy: None apparent.

Discussion: Presumably the wide orbitonarial bar and very short snout in *Bothremys* are related to the dorsal extent of the maxilla.

42. Maxilla, ventral rim of orbit: rim with distinct margin (*Galianemys*) = 0; rim absent, continuous slope (*Bothremys*) = 1.

Morphology: In most turtles, the floor of the fossa orbitalis is nearly horizontal and the lateral surface of the maxilla is nearly vertical, with the two surfaces meeting at a distinct edge, often forming a ridge. In *Bothremys cooki* and *B. maghrebiana* the two surfaces are continuous without a distinct edge or break in slope, state 1 (figs. 129, 138).

Primitive condition: The outgroups, *Proganochelys*, chelids, pelomedusids, euraxemydids, and Cearachelyini, all have a low ridge marking the change in slope between the fossa orbitalis floor and the external surface of the maxilla.

Homoplasy: The absent rim of *Bothremys cooki* and *B. maghrebiana* is closely approached by *Foxemys*, which is coded as having this character. However, *Foxemys* does have more of a rim than does *Bothremys*, although the distinction is somewhat subjective. One specimen of *B. maghrebiana*, MHNL 20-268370, has a low rim (see discussion under Systematics, *B. maghrebiana*), showing that there is some intraspecific variation of this character.

Discussion: Although it would seem likely that this character should be related to size of the fossa orbitalis, all *Bothremys* have a large fossa and only two of the species lack the rim.

43. Maxilla, exposure in orbital floor: maxilla broadly exposed (*Galianemys*) = 0; maxilla narrowly or not exposed (*Azabbaremys*) = 1.

Morphology: In most turtles the maxilla forms the major part of the floor of the fossa orbitalis. In *Taphrosphys ippolitoi*, *Labrosto-*

chelys, CNRST-SUNY 199, and *Azabbaremys* the maxilla does not have an extensive medial process as in other turtles (fig. 280). The orbital floor in these forms is formed mostly by the palatine.

Primitive condition: The wide occurrence of a medial maxillary process in the outgroups shows it to be primitive for pleurodires.

Homoplasy: The character must be lost in *Phosphatochelys, Arenila*, and *Ummulisani.*

Discussion: As the character is only determinable in one of three *Taphrosphys* species, a new discovery could alter this distribution; as it is, this character is a subtribe Taphrosphyina synapomorphy.

44. Vomer, maxilla-vomer contact: present (*Proganochelys*) = 0; absent (*Azabbaremys*) = 1.

Morphology: The vomer is restricted to the premaxilla and allows premaxilla exposure on the apertura narium interna (fig. 215B). The premaxilla may be exposed on the apertura narium interna if there is no vomer-maxilla contact (figs. 65, 155) or if the vomer is simply absent (fig. 21). The character could be coded with a third state for this latter condition. This also has the effect of counting the vomer absent condition (character 45) twice. We have combined both conditions as one state.

Primitive condition: A vomer with a narrow anterolateral maxillary contact is present in *Proganochelys*, early cryptodires, and chelids, and it is presumed to be primitive for pleurodires. The absence of a contact would then be the derived state.

Homoplasy: This is a highly variable character with a CI of 0.16. Keeping this character demonstrates the complete objectivity of this work, and any decent amount of cooking would remove it. The loss and subsequent reappearance of the vomer is suspected within the Podocnemididae.

Discussion: The Kurmademydini and podocnemidids have this character, so it may be primitive at the level of the superfamily Podocnemidoidea within Pelomedusoides, although with multiple reversals. It also unites *Azabbaremys* and CNRST-SUNY 199. Due to the fragile nature of the vomer area, there are many missing data for taxa that otherwise have well-preserved skulls. Better material may eventually clarify the distribution of this character.

45. Vomer: present, paired (*Proganochelys*) = 0; present, single (*Galianemys*) = 1; absent (*Pelusios*) = 2.

Morphology: The living Pelomedusoides are unusual among living turtles for lacking a vomer (its apparent presence in some living podocnemidids is interpreted here as a neomorph). However, the fossil record shows that the vomer was widely present in extinct Pelomedusoides. *Pelusios* and *Pelomedusa* lack a vomer but the condition in *Araripemys* is indeterminate, although it probably lacked a large, "normal" vomer. *Hamadachelys*, based on two specimens, has a vomer, and some extinct podocnemidids have well-developed vomers. Where determinable, all bothremydids have vomers.

Primitive condition: A vomer is primitive for pleurodires.

Homoplasy: Within Podocnemididae the vomer may be lost twice. It is lost independently in Pelomedusidae.

Discussion: In the MPC, the vomer loss does not define any groups, other than Pelomedusidae. It is very easy for the small, loosely attached vomer to be missing in fossil skulls and to fall out of recent ones. Nonetheless, representation within the Bothremydidae is good, and there is no indication of loss within the group.

This character is used in Gaffney et al. (1991), Lapparent de Broin and Werner (1998), Meylan (1996), and Rougier et al. (1995).

46. Vomer, vomerine teeth: present (*Proganochelys*) = 0; absent (*Pelusios*) = 1.

See Gaffney (1990), Gaffney et al. (1991), Gaffney and Kitching (1995), and Rougier et al. (1995).

47. Vomer, central bar: thin, sutured at both ends (*Proganochelys*) = 0; thin, attached anteriorly only (*Azabbaremys*) = 1; vomer absent (*Emydura*) = 2.

Morphology: In *Azabbaremys* and CNRST-SUNY 199 the vomer tapers posteriorly and ends before reaching the palatine attachment (fig. 216).

Primitive condition: A narrow vomer, attached at both ends, occurs in the outgroups (fig. 9).

Homoplasy: None known.

Discussion: When first seen in *Azabbaremys*, the senior author thought this was due to preservational damage, but there is no indication of that, and CNRST-SUNY 199 has a very similar morphology with a clearly well-preserved vomer that is sutured anteriorly only.

48. Palatine, foramen palatinum posterius: in floor of orbit (*Chelydra*) = 0; behind orbit, in floor of sulcus palatinopterygoideus (*Pelusios*) = 1.

Morphology: The foramen palatinum posterius is described and figured in Gaffney (1979a: figs. 53–65) for a number of turtles. In cryptodires, the foramen lies in the floor of the fossa orbitalis, but in pleurodires it is separated from the fossa due to the presence of the septum orbitotemporale and the sulcus palatinopterygoideus (figs. 23. 24). The foramen is usually in the floor of the sulcus palatinopterygoideus.

Primitive condition: *Proganochelys* and cryptodires lack this character.

Homoplasy: None known.

Discussion: This character is synapomorphic at least for Eupleurodira, being unknown for shell-only taxa. A decently preserved skull is necessary for determining the character. The orbit or sulcus palatinopterygoideus needs to be visible; a ventral view of the foramen palatinum posterius is insufficient.

This character is used by Gaffney and Meylan (1988), Gaffney et al. (1991), and Fuente and Iturralde-Vinent (2001).

49. Palatine, dorsally arched palate: absent (*Galianemys*) = 0; present (*Azabbaremys*) = 1.

Morphology: The area between the lingual ridges of the triturating surfaces forms the roof of the mouth and the choanal passages. In *Azabbaremys*, CNRST-SUNY 199, *Nigeremys*, *Phosphatochelys*, and probably *Rhothonemys*, this area, particularly the part formed by the palatines posterior to the apertura narium interna, is an anterodorsally sloping surface that rises well above the level of the maxillary triturating surfaces (fig. 215C). The anterolateral margins of the apertura narium interna are relatively low, so the result is an apertura that is deeper than in other bothremydids.

Primitive condition: Although the outgroups and other pleurodires have many different shapes to the central palatal surface, all are shallower than in these taxa. A relatively flat palate is found in most relevant outgroups.

Homoplasy: There is a reversal in *Labrostochelys*; otherwise, all Taphrosphyini that can be determined (only 5 out of 11) have the character present.

Discussion: *Arenila* is scored as "?" because the area is damaged, but the MPC suggests that it should have the deep choanal passage/arched palate, based on the morphology that is present. The best skull of *Taphrosphys*, the type of *T. ippolitoi*, is damaged in this region, but the palatines as preserved have an anterodorsal slope, suggesting that it also has an arched palate. If this proves to be the case, this character will be a Taphrosphyini synapomorphy with one reversal.

50. Palatine, palatine contribution to triturating surface: little or none (*Euraxemys*) = 0; moderate to extensive (*Bothremys*) = 1.

Morphology: The upper triturating surface of turtles is usually made up mostly by the maxilla with a smaller contribution by the premaxilla anteromedially. The palatine is typically present just medial to the triturating surface and may also provide a small contribution. In many bothremydids, the palatine forms a significant part of the posteromedial part of the triturating surface (figs. 9F, 10H), and the maxilla-palatine suture is more anterolateral than in the primitive condition.

Primitive condition: The outgroups have little or no palatine contribution to the triturating surface.

Homoplasy: The character is a Bothremydidae synapomorphy, lost in the Taphrosphyini. The occurrence in *Araripemys* is probably independent on morphological grounds, as the triturating surface is narrow. The character is unclear in *Sankuchemys*; it may be present but the specimen is ambiguous and has been coded "?".

Discussion: Although there is a gradational aspect to this character, we have tried to restrict it to the most extreme condition, particularly as seen in the Bothremydini. Nonetheless, some decisions about scoring are subjective. This character is generally correlated with the wide triturating surface in many bothremydids, but it is not a consistent correlation (*Araiochelys* and *Araripemys* are exceptions).

This character is used in Meylan (1996) and Tong et al. (1998).

51. Quadrate, antrum postoticum: absent, open incisura columellae auris (*Proganochelys*) = 0; small (*Bothremys*) = 1; absent, closed incisura columellae auris (*Azabbaremys*) = 2; moderate to large (*Galianemys*) = 3.

Morphology: The antrum postoticum shows a wide range of variation in Pelomedusoides (figs. 176, 281–286). The antrum postoticum is smaller in many bothremydids than it is in other pleurodires. In *Azabbaremys, Nigeremys, Ummulisani*, and *Arenila*, it is completely filled with bone and no indication of the antrum is present in the cavum tympani (state 2, fig. 281C). This condition is clearly identifiable. The remaining taxa have a varying size for the antrum postoticum, and we have identified the small extreme (state 1, fig. 286D) and the moderate to large (state 3, fig. 281A, 282, 284) as character states. It is useful to compare figure 284C with figure 286D; both are broken, exposing the internal shape of the antrum postoticum.

The small condition, state 1, is found in *Labrostochelys*, *Araiochelys*, *Bothremys maghrebiana*, and *Chedighaii barberi* (it is indeterminate for the other species of *Bothremys* and *Chedighaii*). However, within state 3 (moderate to large), *Taphrosphys* (fig. 176), for example, has an antrum that is larger than that in *Labrostochelys* but smaller than those in the Kurmademydini and Cearachelyini (figs. 283, 284). We have been unable to distinguish this degree of gradation because it seems to be too subjective.

Primitive condition: *Proganochelys* lacks an antrum postoticum, but a large antrum is apparently primitive for pleurodires as it occurs in chelids, pelomedusids (fig. 282A), and *Araripemys* (fig. 282C). However, euraxemydids and podocnemidids have a smaller antrum, as do the Kurmademydini and Cearachelyini. All these are coded within the "moderate to large" character state 3.

Homoplasy: Although the CI is a respectable 0.5, there is actually more homoplasy within bothremydids, which is hidden by the lumping of a lot of size variation into the "moderate to large" character state 3. It is difficult to divide this continuous variation objectively (except for absence) and is therefore hard to identify independent acquisitions morphologically. As defined here, the small condition (state 1) is acquired twice, once for *Araiochelys* + *Bothremys* + *Chedighaii* within the Bothremydini and once in the Taphrosphyini in *Labrostochelys*. The absent condition, state 2, appears independently three times, in *Ummulisani, Azabbaremys*, and *Nigeremys*.

Discussion: Although the size of the antrum postoticum varies widely in pleurodires, from very large to completely absent, it has been difficult to objectively divide this variation into discrete character states. The difference between "moderate" and "small" is subjective and based on what we perceive as a gap in antrum size. More specimens may alter this division. Attempts to measure the variation have been unsatisfactory but could be worth future efforts.

This character is used in Gaffney and Meylan (1988), Meylan (1996), and Tong et al. (1998).

52. Quadrate, incisura columellae auris: no posterior bony restrictions (*Euraxemys*) = 0; eustachian tube and stapes separated by bone or a narrow fissure (*Foxemys*) = 1; eustachian tube and stapes enclosed together by bone (*Podocnemis*) = 2.

Morphology: The incisura columellae auris can be open to a varying degree (state 0, fig. f281A) or it can be closed by a meeting or near meeting of dorsal and ventral processes of the quadrate. In state 1, the incisura is closed, or nearly closed, separating the stapes and eustachian tube (fig. f281B, C). In state 2, the dorsal and ventral processes meet or nearly meet, posterior to the eustachian tube, enclosing both stapes and eustachian tube in the same oval opening (Gaffney, 1979a: figs. 134, 140).

Primitive condition: The open incisura columellae auris of euraxemydids, early cryptodires, and *Proganochelys* is the presumed primitive condition for pleurodires. However, the apparently independent occurrence of state 2 in chelids and pelomedusids, as well as podocnemidids in the MPC (fig. 303), suggests an alternative that the

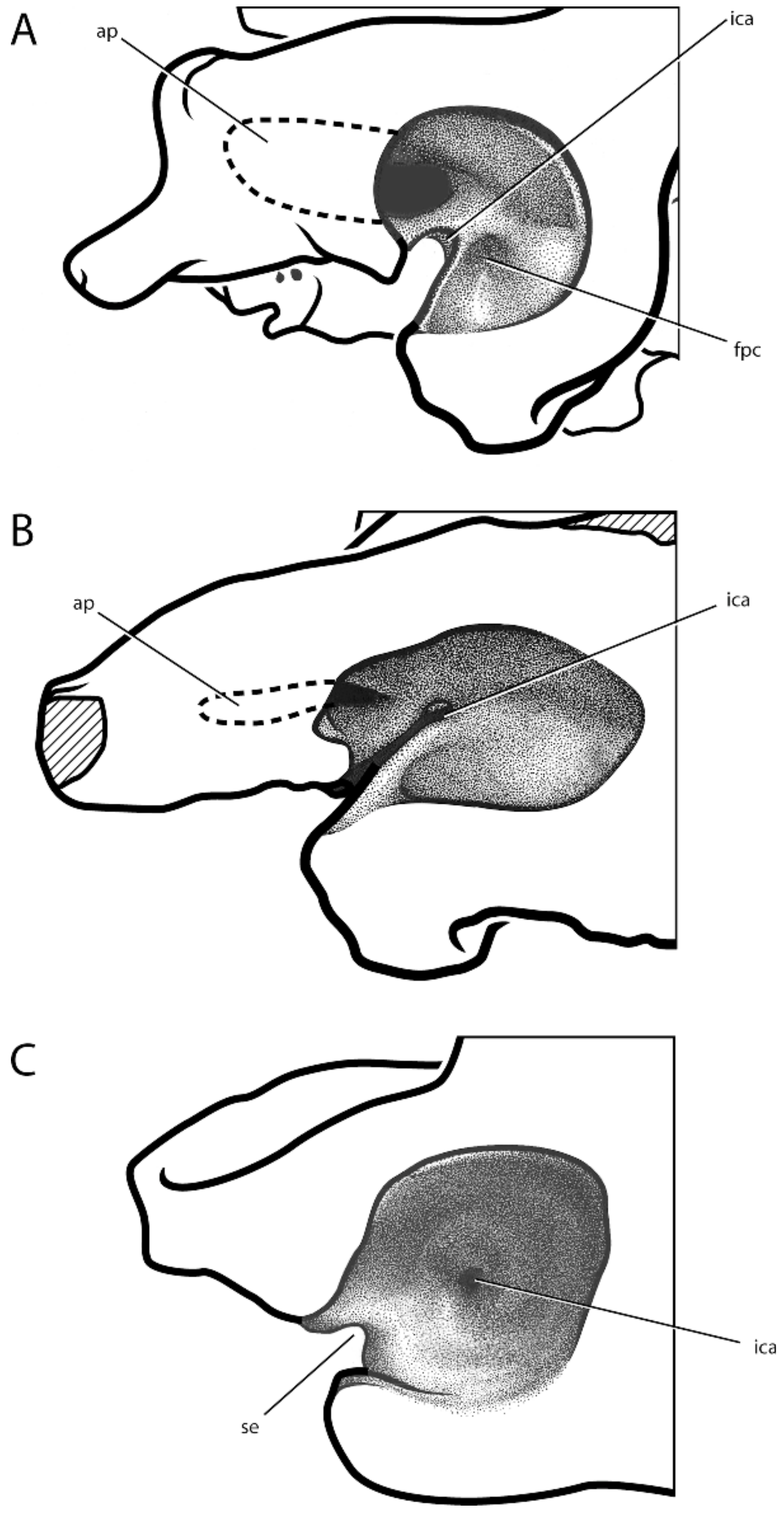


Fig. 281. Right quadrate and cavum tympani in lateral views. **A**, *Euraxemys essweini*, FR 4922 holotype; **B**, *Foxemys mechinorum*, PAM 511A; **C**, *Azabbaremys moragjonesi*, BMNH R 16370 holotype. [F. Ippolito and A.M. Phillips, del.]

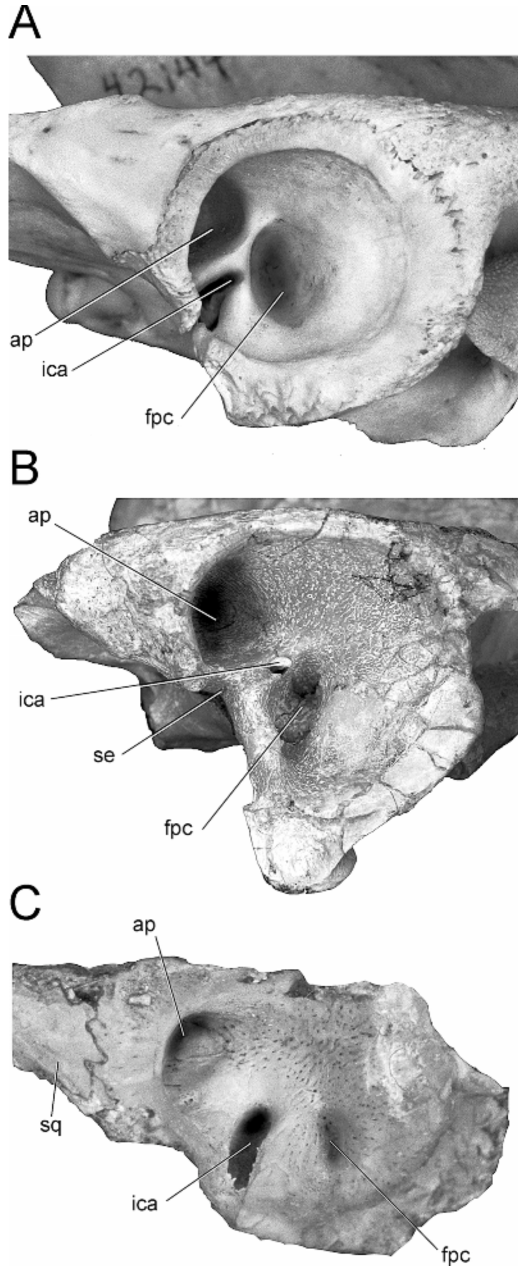


Fig. 282. Right quadrate and cavum tympani in lateral views. **A**, *Pelusios sinuatus*, USNM (Herp) 42144; **B**, *Kurmademys kallamedensis*, ISI R152 holotype; **C**, *Araripemys barretoi*, AMNH 24454. [E.S. Gaffney, del.]

enclosure of stapes and eustachian tube may be primitive for eupleurodires and lost in euraxemydids, *Brasilemys, Araripemys*, and *Teneremys*.

Homoplasy: None for state 1, but state 2 occurs three times independently (see above) in the MPC (fig. 303).

Discussion: The main objection to this character is that state 1 might be interpreted as redundant with character 53, incisura columellae auris completely closed to form a canal containing the stapes. The decision to make two characters using different morphologic criteria in this area is based on the open, but slitlike condition of the incisura in a few bothremydids, *Cearachelys* (fig. 283), *Foxemys* (fig. 281B), and *Polysternon*. Therefore, the two characters are not strictly redundant, and we use state 1 to try to reflect another aspect of the cavum tympani morphology.

The position of the eustachian tube in a fossil turtle is not, strictly speaking, determinable. The position of this soft tissue structure may not be indicated in bone. However, examination of thin sections and dissections of recent turtles by the senior author shows that its position and structure are relatively consistent in all turtles, particularly pleurodires. Although the eustachian tube in recent pleurodires does tend to take the shape of surrounding bones, it is unlikely that it would be thin and narrow enough to fit into the fissure or slitlike incisura columellae auris found in *Cearachelys*, *Foxemys*, and *Polysternon*. Its position in forms like the Euraxemydidae, with a wide incisura, is not determinable, but a distinct groove (the sulcus eustachii) showing its position is present on the posterior surface of the quadrate in bothremydids. Therefore, it is possible to argue that in bothremydids, the stapes and eustachian tube were separated by bone, either completely by bone or with a narrow fissure in the bone remaining, in contrast to all other pleurodires.

Although *Araripemys* is open posteriorly and we have coded it as "0", there is a small dorsal and ventral process (fig. 282) that almost completely closes the incisura. In euraxemydids the incisura is more open than in *Araripemys*: however, there is a partial restriction with small dorsal and ventral processes. Thus, euraxemydids (also coded as "0") could be coded separately from *Araripemys* as a different state, or *Araripemys* could be coded as "2". Using this approach, however, does not change the MPC.

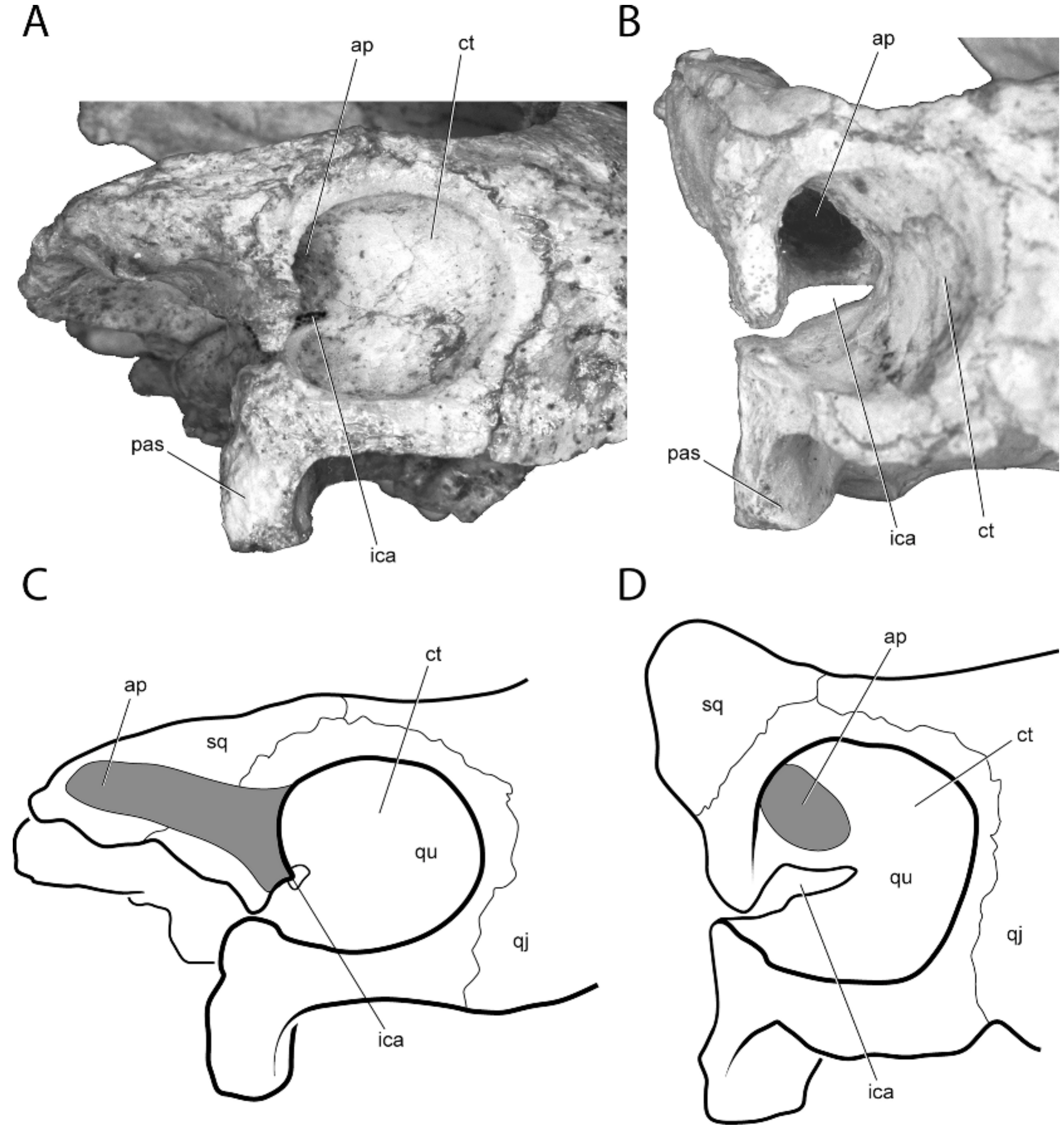


Fig. 283. *Cearachelys placidoi*, MPSC uncatalogued type specimen. **A**, **C**, quadrate and cavum tympani in lateral view; **B**, **D**, quadrate and cavum tympani in anterolateral view. Figures are of left side reversed. Gray indicates extent of antrum postoticum. [A.M. Phillips and E.S. Gaffney, del.]

A version of this character is used in Antunes and Broin (1988), Meylan (1996), Lapparent de Broin and Werner (1998), and Tong et al. (1998).

53. Quadrate, stapes contained in bony canal: stapes not completely contained in bone (*Euraxemys*) = 0; stapes completely enclosed by bony incisura columellae auris (*Bothremys*) = 1.

Morphology: The quadrate of most bothremydids completely surrounds the stapes, causing the incisura columellae auris to be a bony canal. This character is easily determined; that is, there are no cases of ambiguity. As can be seen in figures 176, 281, and 286, the canal is encased by bone on all sides, even in the Kurmademydini (fig. 282B) and *Galianemys* (fig. 284), which

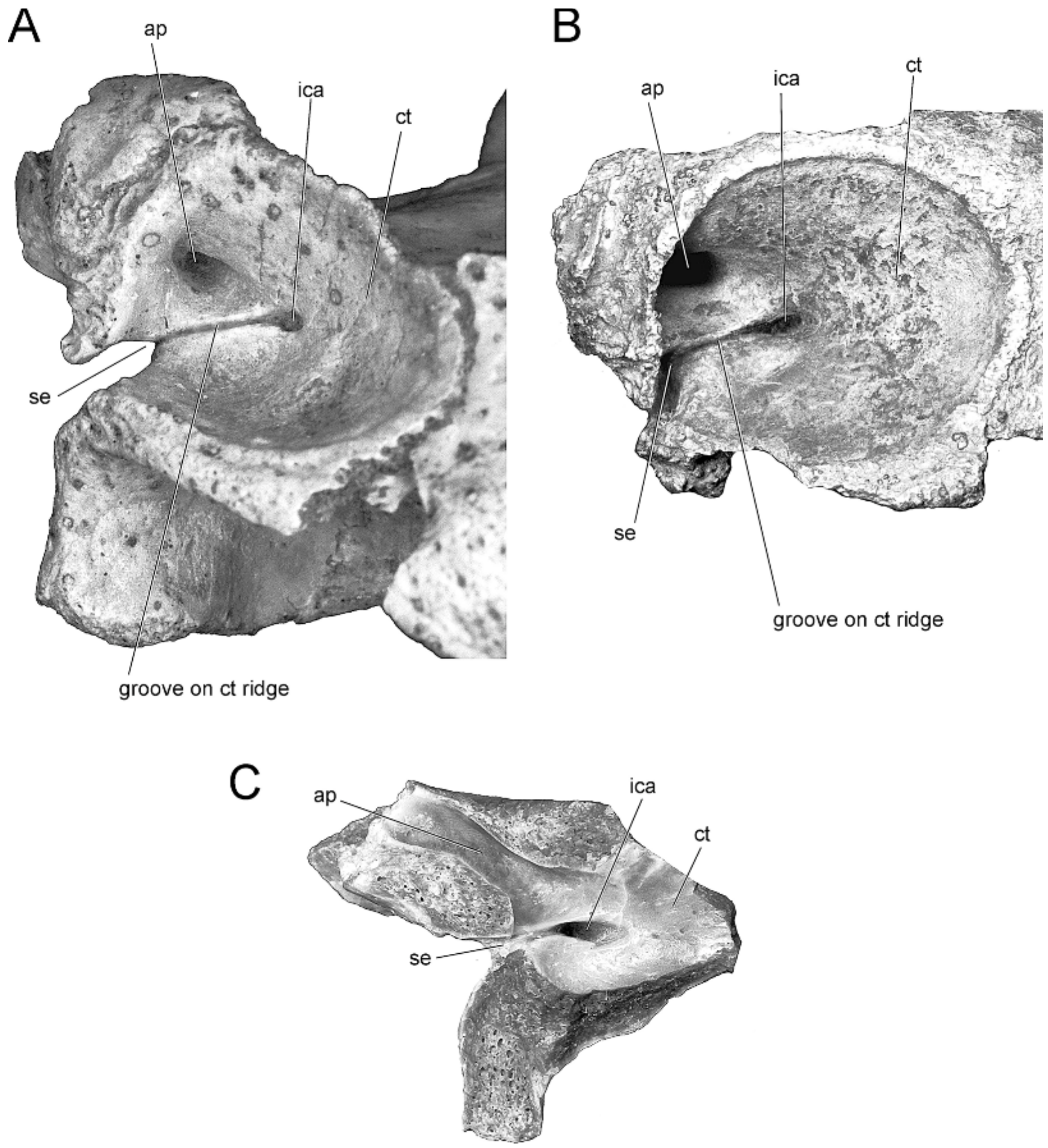


Fig. 284. Right quadrate and cavum tympani in lateral view. **A**, *Galianemys whitei*, AMNH 29987 holotype; **B**, *Galianemys emringeri*, AMNH 30035; **C**, *Galianemys whitei*, AMNH 30027. [E.S. Gaffney, del.]

are more generalized in most characters than in other bothremydids. The narrow fissure condition seen in *Foxemys* (fig. 281B), *Polysternon*, and *Cearachelys* (fig. 283) is excluded from this character.

Primitive condition: An open quadrate, with the incisura columellae auris only partially surrounding the stapes and not forming a canal, is found in all the relevant outgroups (fig. 282).

Homoplasy: Two reversals of this character occur in *Cearachelys* and the Foxemydina (fig. 304). The reversal is a synapomorphy for *Foxemys* + *Polysternon*. The morphology of the open incisura columellae auris in these bothremydids does differ from the open

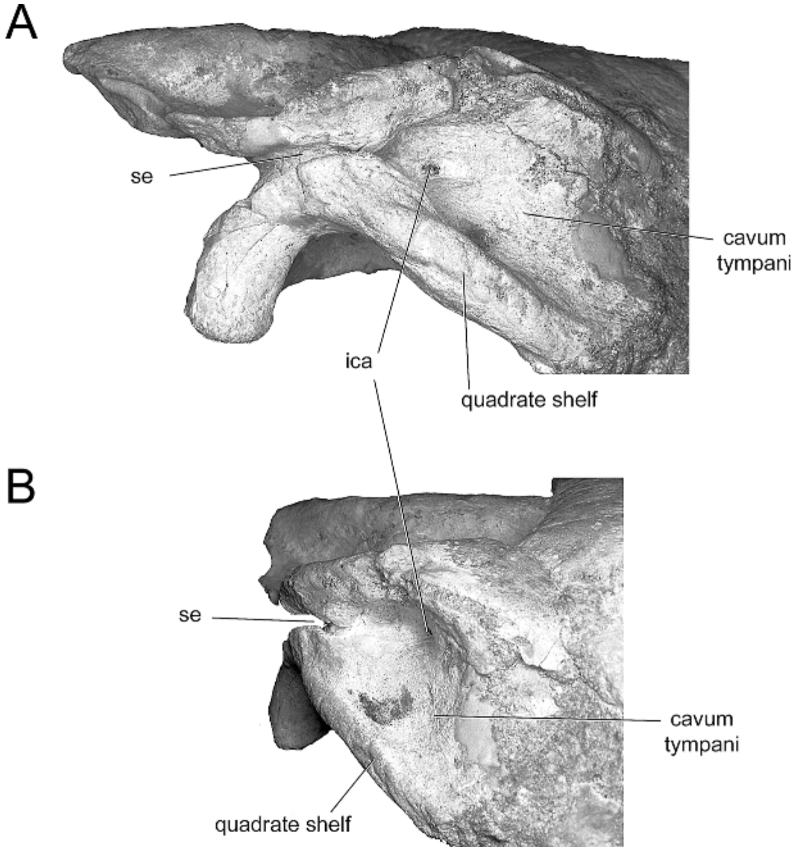


Fig. 285. *Bothremys kellyi*, n. sp., AMNH 30553 holotype. Right quadrate and cavum tympani. **A**, lateral; **B**, anterolateral. [E.S. Gaffney, del.]

condition in outgroups like podocnemidids, pelomedusids, euraxemydids, and chelids (see character 52 for discussion). Lapparent de Broin (2000b) considered the *Polysternon-Foxemys* condition a reversal as well. A number of cryptodires have a completely closed incisura columellae auris (Gaffney, 1979a, 1996), but they do not develop the bony canal as seen in bothremydids.

Discussion: The bony canal for the stapes in bothremydids is an unusual feature, synapomorphic at the level of Bothremydidae (fig. 304), and it is not found in any other pleurodires.

This character is used in Gaffney and Meylan (1988), Lapparent de Broin and Werner (1998), Tong et al. (1998), and Lapparent de Broin (2000b).

54. Quadrate, sulcus eustachii: without ventral process (*Bothremys*) = 0; with ventral process overhanging dorsal margin (*Labrostochelys*) = 1.

Morphology: The groove on the posterior surface of the quadrate, presumably marking the position of the eustachian tube (the sulcus eustachii), forms an indentation on the posterior margin of the cavum tympani. In *Taphrosphys, Labrostochelys*, and *Phosphatochelys*, the anterodorsal margin of the notch has a small, ventrally dependent process. In *Labrostochelys* (fig. 287) the process is narrow, but in *Phosphatochelys* (fig. 199) and *Taphrosphys* it is wider, forming a small, anteroposteriorly broad flange.

Primitive condition: All outgroups and other pleurodire taxa lack this process.

Homoplasy: None known. We know of no other turtle with this process.

Discussion: The small ventral process at the posterior edge of the cavum tympani,

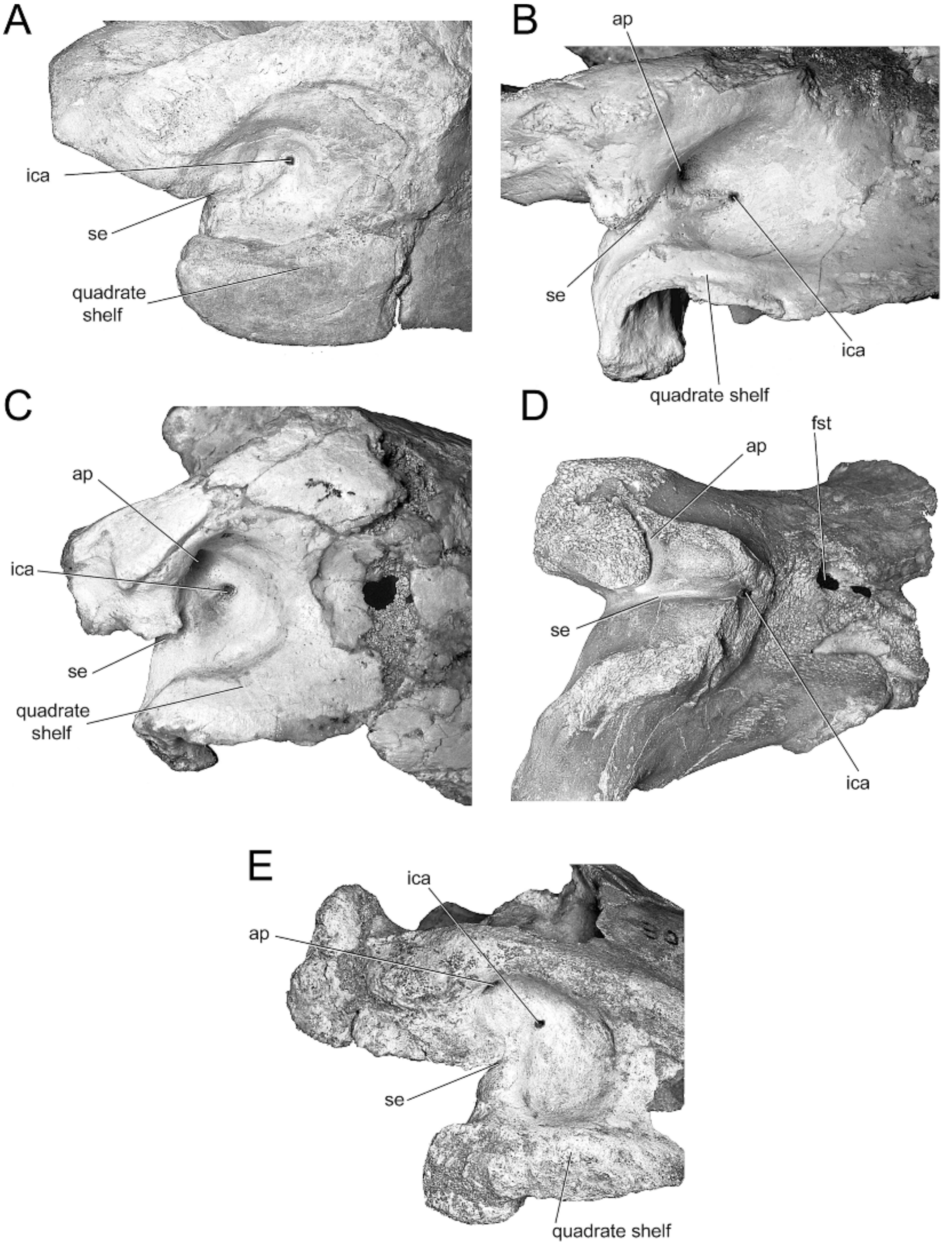


Fig. 286. Right quadrate and cavum tympani in lateral view. **A**, *Azabbaremys moragjonesi*, BMNH R 16370; **B**, *Bothremys maghrebiana*, n. sp., AMNH 30522; **C**, *Phosphatochelys tedfordi*, AMNH 30008 holotype; **D**, ?*Chedighaii barberi*, n. gen., NCSM 12766; **E**, *Taphrosphys ippolitoi*, n. sp., AMNH 30500. [E.S. Gaffney, del.]

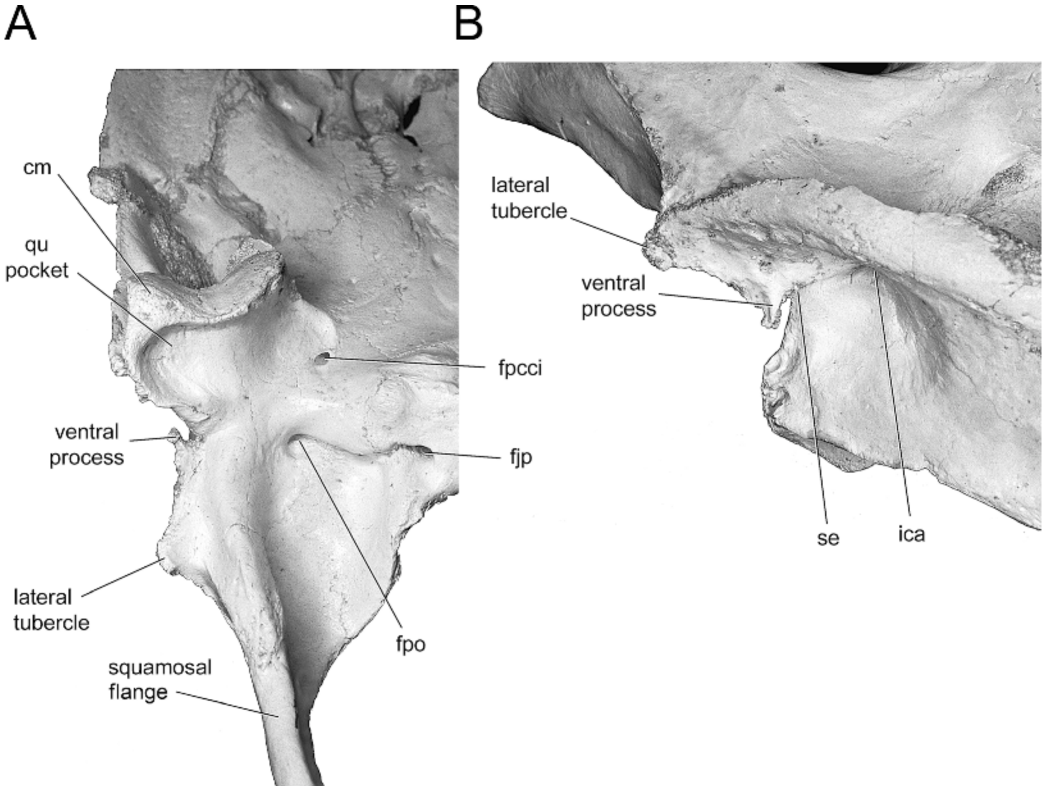


Fig. 287. *Labrostochelys galkini*, n. gen. et sp., AMNH 30043 holotype. **A**, posteroventral view of right quadrate and squamosal, anterior is at top of page; **B**, anterodorsolateral view of right quadrate and cavum tympani, anterior is bottom right of page. [E.S. Gaffney, del.]

above the sulcus eustachii, seems to be related to some soft structure, probably the attachment of the eustachian tube, which enters the cavum tympani at this edge. The process is broken off in the *Taphrosphys* specimens, but its presence is determinable from the broken base.

55. Quadrate, trough on incisura columellae auris ridge: absent (*Bothremys*) = 0; present (*Galianemys*) = 1.

Morphology: When the incisura columellae auris is completely closed by bone, as in most bothremydids, there may be a ridge in the position across the surface of the cavum tympani, extending from the remnant of the incisura (the bony stapedial canal) to the sulcus eustachii. In *Kurmademys* (fig. 282B) and *Galianemys* (fig. 284) this ridge has a shallow groove along its lateral surface. This is thought to be a suture in Lapparent de Broin (2000b), but it is only a surface feature.

Primitive condition: A closed incisura columellae auris is absent in all the pleurodire outgroups, so none has a ridge or a trough. In the other bothremydids, there may be a low, poorly defined trough (*Labrostochelys*) but no distinct ridge.

Homoplasy: In the MPC, the character evolves once in *Kurmademys* and independently in *Galianemys*. However, the incisura is open in *Cearachelys*, and the character may be primitive for Bothremydidae and lost in *Cearachelys* and in the infrafamily Bothremydodda (the tribes Bothremydini + Taphrosphyini).

Discussion: This character is a distinctive one for *Galianemys*. Although similar to the condition in *Kurmademys*, *Galianemys* has the distal ends of the groove separating, making it different from *Kurmademys*.

56. Quadrate, fossa precolumellaris: very small to absent (*Galianemys*) = 0; present but shallow (*Euraxemys*) = 1; deep and well defined (*Pelusios*) = 2.

Morphology: Just anterior to the incisura columellae auris, where the quadrate forms the medial wall of the cavum tympani, many pleurodires have a depression, the fossa precolumellaris. Described and figured by Williams (1954b) in Podocnemididae (also in Gaffney, 1979a) as the precolumellar fossa, we have formalized it as the fossa precolumellaris. The distinction between shallow (state 1, fig. 281A) and deep (state 2, fig. 282A, B) is not as arbitrary as it might seem. The euraxemydid condition (state 1) shows a small dimple, which we think should be differentiated from the deep condition (state 2) seen in pelomedusids, chelids, *Araripemys*, and *Hamadachelys*.

Within Podocnemididae, the fossa varies in size, as described by Williams (1954b). All bothremydids except *Kurmademys* (it is indeterminate for *Sankuchemys*) lack a fossa precolumellaris, so that the cavum tympani anterior to the incisura columellae auris is smooth (fig. 281B, C).

Primitive condition: The fossa precolumellaris is absent in *Proganochelys* and cryptodires, but a deep one is present in chelids and pelomedusids, the presumed primitive condition for pleurodires (a variable one is present in podocnemidids).

Homoplasy: Most bothremydids lack a fossa precolumellaris, and this is the primitive condition for turtles; however, this is a reversal and must have originated independently within bothremydids, as pleurodiran outgroups have a deep fossa.

Discussion: *Kurmademys* has a deep fossa precolumellaris, as in pleurodire outgroups Pelomedusidae and Chelidae. All other bothremydids lack the fossa, which is a synapomorphy for the subfamily Bothremydinae (the tribes Taphrosphyini + Bothremydini + Cearachelyini).

This character, or one like it, is used by Meylan (1996), Lapparent de Broin and Werner (1998), Tong et al. (1998), and Lapparent de Broin (2000b).

57. Quadrate, shelf below cavum tympani: absent (*Galianemys*) = 0; present, lower portion of cavum tympani unusually deep (*Bothremys*) = 1.

Morphology: In the bothremydid tribes Bothremydini and Taphrosphyini the cavum tympani is recessed deeply into the quadrate, and its lower edge is deep, forming a sloping shelf along the ventral margin of the cavum (figs. 285, 286). In *Labrostochelys* and *Phosphatochelys* the cavum is not recessed, but the shelf persists as a ventrally sloping surface.

Primitive condition: All outgroups lack a ventral shelf on the quadrate.

Homoplasy: None known.

Discussion: The principal problem with this character is variation in the slope of the shelf within the tribe Taphrosphyini; however, scoring *Labrostochelys* and *Phosphatochelys* as absent produces the same MPC.

58. Quadrate, medial process contacting braincase elements and underlying cranioquadrate space: absent (*Chelydra*) = 0; present (*Pelusios*) = 1.

Morphology: This character is figured and described in Gaffney (1975b, 1979a). The quadrate of pleurodires has a medial process that contacts the prootic and basisphenoid, although on the ventrally exposed surface, these contacts are not always exposed. The basisphenoid itself may cover the prootic or the prootic may contact the pterygoid. The medial process underlies the cranioquadrate space, which in the adult is the canalis cavernosus.

Primitive condition: The character is absent in *Proganochelys* and Cryptodira.

Homoplasy: None known.

Discussion: This character is a synapomorphy for Pleurodira. This character is used in Gaffney and Meylan (1988), Gaffney et al. (1991), and Fuente and Iturralde-Vinent (2001).

59. Quadrate, quadrate-basioccipital contact: absent (*Euraxemys*) = 0; present (*Galianemys*) = 1.

Morphology: The medial process of the quadrate in the Podocnemididae and Bothremydidae is larger and more extensive posteromedially than in other pleurodires (fig. 9H–J). The shape of the basioccipital is not very different in pleurodires with respect to this character; it is primarily a difference in quadrate shape that causes the contact. The quadrate covers the processus interfenestralis of the opisthotic and the prootic ventrally, resulting in a significant difference in the basicranium between podocnemidoids (podocnemidids + bothremydids) and all other pleurodires.

Primitive condition: *Proganochelys* and cryptodires completely lack the medial process of the quadrate (Gaffney, 1975b, 1979a). Within pleurodires, a smaller medial quadrate process is present in chelids, pelomedusids, and *Araripemys*; as they lack a basioccipital-quadrate contact, the prootic is exposed. This appears to be the primitive condition for pleurodires.

Homoplasy: None known.

Discussion: This character supports the monophyly of the families Podocnemididae + Bothremydidae as the superfamily Podocnemidoidea and represents a major difference between their basicrania and those in all other pleurodires.

This character is in Antunes and Broin (1988), Meylan (1996), Lapparent de Broin and Werner (1998), and Tong et al. (1998).

60. Quadrate, condylus mandibularis position: near or in line with the basioccipital-basisphenoid suture (*Galianemys*) = 0; distinctly anterior to plane of basioccipital-basisphenoid suture (*Pelusios*) = 1; distinctly posterior to condylus occipitalis (*Nigeremys*) = 2.

Morphology: This character is an attempt to use the variation in position of the condylus mandibularis relative to the elements of the basicranium. Although this variation is somewhat continuous, it is apparent that most bothremydids, compared to other pleurodires, have the condylus mandibularis far posterior, relative to the condylus occipitalis. This may also be described as a shortened or telescoped basicranial and otic region (Lapparent de Broin and Werner, 1998). The character has been determined by drawing a line between each condylus mandibularis and seeing where the basioccipital-basisphenoid suture falls with respect to this line. If the line falls slightly behind, on, or slightly anterior to the suture, it is character state "0" (fig. 9H). If the line is well anterior to the basioccipital-basisphenoid suture, that is, well onto or anterior to the basisphenoid, it is character state "1" (fig. 9B). In *Nigeremys* and *Arenila* the line across the condylus mandibularis falls so far behind the basioccipital-basisphenoid suture that it is posterior to the condylus occipitalis, and this is character state "2" (fig. 11H, I).

Primitive condition: *Proganochelys* and early cryptodires have state "0", the primitive state at the level of all turtles. However, as all the pleurodire outgroups have state "1", this seems to be primitive for pleurodires.

Homoplasy: This character has a CI of 0.33, showing that there is a lot of homoplasy. Bothremydids are characterized by a reversal to state "0" at the level of the subfamily Bothremydinae (consisting of the tribes Cearachelyini, Bothremydini, and Taphrosphyini). Within this group a number of the Taphrosphyini have a reversal to state "1" independently of *Polysternon*, which is also coded "1". However, this character is a relatively simplified summary of a lot of complex morphology, making more detailed comparisons to test homoplasy inconclusive.

Discussion: The difficulty with this character is scoring intermediate taxa (e.g., *Azabbaremys* and *Labrostochelys*) that have a condylus mandibularis just anterior to the basioccipital-basisphenoid suture. We have scored both as "0" because the condylus mandibularis line falls close to the suture, although they could be scored "1" because the line is just anterior to the suture. We have run the dataset both ways with the same MPC resulting.

A similar character is used in Lapparent de Broin and Werner (1998).

61. Quadrate, fully formed cavum tympani: no (*Proganochelys*) = 0; yes (*Pelusios*) = 1.

See Gaffney (1990), Gaffney and Kitching (1995), and Rougier et al. (1995).

62. Quadrate, cavum tympani with acute posterior edge: no (*Proganochelys*) = 0; acute edge, also enclosing stapes (*Pelusios*) = 1.

See Gaffney (1990), Gaffney and Kitching (1995), and Rougier et al. (1995).

63. Quadrate, middle ear with complete lateral wall: no (*Proganochelys*) = 0; yes (*Pelusios*) = 1.

See Gaffney (1990), Gaffney et al. (1991), Gaffney and Kitching (1995), and Rougier et al. (1995).

64. Quadrate, cavum tympani curved dorsally: no (*Proganochelys*) = 0; yes (*Palaeochersis*) = 1.

See Gaffney (1990), Gaffney and Kitching (1995), and Rougier et al. (1995).

65. Quadrate, covers opisthotic laterally: no (*Proganochelys*) = 0; yes (*Australochelys*) = 1.

See Gaffney (1990), Gaffney et al. (1991), Gaffney and Kitching (1995), and Rougier et al. (1995).

66. Quadrate, pocket for stapes articulation: present (*Proganochelys*) = 0; absent (*Australochelys*) = 1.

See Gaffney (1990), Gaffney and Kitching (1995), and Rougier et al. (1995).

67. Quadrate, cranioquadrate space: relatively open (*Proganochelys*) = 0; well-defined canal (*Australochelys*) = 1.

See Gaffney (1990), Gaffney and Kitching (1995), and Rougier et al. (1995).

68. Pterygoid, fossa pterygoidea: absent or small (*Pelusios*) = 0; moderate (*Galianemys whitei*) = 1; deep and narrow (*Foxemys*) = 2.

Morphology: The fossa pterygoidea in bothremydids is an anteromedial–posterolaterally elongate depression formed by the pterygoid, quadrate, and basisphenoid (figs. 101, 102). The foramen posterius canalis carotici interni, the foramen nervi facialis, and the foramen nervi vidiani may open within this depression. The prootic may be exposed in the deepest part of the depression in some forms (*Kurmademys*, fig. 276E; *Galianemys emringeri*, fig. 277E).

The distinction between the two states of fossa development is not arbitrary because there is a gap in the size variation. *Kurmademys* (fig. 55), *Cearachelys* (two of three specimens) (fig. 74), *Galianemys emringeri* (fig. 82), and *Rosasia* (fig. 119) have a fossa pterygoidea that is not as deep as it is wide. The margin is recessed and the center is relatively shallow (state 1). In *Foxemys* (fig. 102), *Polysternon* (fig. 109), *Nigeremys*, and *Arenila* (fig. 225), the fossa pterygoidea is about as deep as it is wide, particularly at its center (state 2).

Lapparent de Broin and Werner (1998) and Lapparent de Broin (2000b) treated this structure as homologous to what we call the cavum pterygoidei (here restricted to the epifamily Podocnemidinura, which is the Podocnemididae + *Hamadachelys* + *Brasilemys*) and referred to this depression as the "podocnemidid fossa". They asserted that it becomes enlarged to form "the true enlarged carotid canal of the Podocnemididae" (Lapparent de Broin, 2000b: 69). However, unlike the cavum pterygoidei of podocnemidids, there is no bony covering beneath the fossa pterygoidea and it never ends anteriorly in a single large opening, both features of the cavum pterygoidei. Thus, we treat the fossa pterygoidea as an independent structure from the cavum pterygoidei. Furthermore, the cladogram shows no homologous relationship between these concavities; they are both derived independently.

Primitive condition: Depressions of this kind are absent in the pterygoids of chelids, pelomedusids, *Araripemys* and euraxemydids. The absence of a fossa pterygoidea is the primitive condition.

Homoplasy: Lapparent de Broin (2000b) argued that the cavum pterygoidei of podocnemidids is homologous to the fossa pterygoidea of bothremydids and that the two are derived from the "podocnemidoid fossa" of *Brasilemys*. If this is correct, then the depression has occurred one time in the Pelomedusoides and been enlarged in the Podocnemididae and reduced and lost within most of the Bothremydidae. However, the distribution of the fossa in the MPC (fig. 305) shows that the fossa has originated five times within the Bothremydidae, all independently of the Podocnemididae. A similar but groovelike fossa occurs on the pterygoid of cheloniids (Gaffney, 1979a: fig. 210).

The CI of this character in the MPC is 0.33, reflecting the high degree of homoplasy present in this character. A moderately developed fossa pterygoidea (state 1) originated three times and the deep fossa (state 2) three times within the Bothremydidae. There is no evidence from the cladogram (fig. 305) that the two states should be treated as additive, even though this might be expected from the morphology, that is, moderate (state 1) and deep (state 2).

Discussion: Although the fossa pterygoidea is a prominent feature of the palate, it is too sporadic in distribution to be of much phylogenetic significance. The deep fossa unites (*Foxemys*, *Polysternon*) with (*Nigeremys*, *Arenila*), but the moderate condition seems to have arisen independently in each case. The fossa seems to be the attachment site of a portion of the pterygoideus muscle.

A form of this character is used in Antunes and Broin (1988), Meylan (1996), Lapparent de Broin and Werner (1998), Tong et al. (1998), and Lapparent de Broin (2000b).

69. Pterygoid, cavum pterygoidei: absent (*Pelusios*) = 0; present (*Podocnemis*) = 1.

Morphology: Used by many previous authors, the cavum pterygoidei is a more formalized name for the "pterygoideus muscle chamber" or "enlarged carotid channel" of Gaffney (1979a: fig. 86). This is a relatively large opening from the palate into the braincase located at the posterior end of the pterygoid that contains a subdivision of the pterygoideus muscle (Schumacher, 1954, 1955a, 1955b, 1973). It is differentiated from the fossa pterygoidea, character 68, by having at least a partial covering ventrally and an anteromedial opening into the braincase.

Primitive condition: All outgroups lack this character.

Homoplasy: None known, but see Quadrate, fossa pterygoidea (character 68).

Discussion: The two sister groups of the Podocnemididae, *Brasilemys* (Lapparent de Broin, 2000b) and *Hamadachelys* (Tong and Buffetaut, 1996), have a cavum pterygoidei that is hidden anteromedially by the underlapping basisphenoid medially and the pterygoid laterally. In these taxa the cavum is not as deep as in all other Podocnemididae, but the cavum pterygoidei is interpreted here as homologous in *Hamadachelys, Brasilemys*, and Podocnemididae.

This character is used by Gaffney and Meylan (1988), Meylan (1996), Lapparent de Broin and Werner (1998), and Lapparent de Broin (2000b).

70. Pterygoid, processus trochlearis pterygoidei: absent (*Proganochelys*) = 0; present (*Pelusios*) = 1.

Morphology: The processus trochlearis pterygoidei (figs. 23, 24) is an important pleurodire synapomorphy described in Schumacher (1954, 1955a, 1955b, 1956) and Gaffney (1975b, 1979a).

Primitive condition: All turtles outside Pleurodira lack the processus entirely.

Homoplasy: None known.

Discussion: This is a synapomorphy for Pleurodira.

This character is used in Gaffney and Meylan (1988), Gaffney et al. (1991), Rougier et al. (1995), Lapparent de Broin and Werner (1998), and Fuente and Iturralde-Vinent (2001).

71. Pterygoid, posteroventral flange along lateral edge, medial to processus trochlearis pterygoidei: absent (*Chelydra*) = 0; present (*Pelusios*) = 1.

Morphology: In pleurodires, the pterygoid forms a very thin sheet of bone, just medial to the processus trochlearis pterygoidei, which extends ventrally below the level of the rest of the pterygoid. These are figured in Gaffney (1979a: figs. 134, 142) and in figure 136B. Antunes and Broin (1988) Lapparent de Broin and Werner (1998) referred to this flange as a "pterygoid wing".

Primitive condition: *Proganochelys* and cryptodires lack these.

Homoplasy: None known.

Discussion: Lapparent de Broin and Werner (1998) argued that the flange or wing is found in most pleurodires, but that bothremydids and *Araripemys* lack them. We have concluded, however, that the flange is present in all pleurodires and that its supposed absence in some is a consequence of preservation. The flange or wing is very thin and fragile, often being damaged or broken off entirely in recent pleurodire specimens. The flange does occur in better preserved specimens of *Araripemys* (THUg 1907, fig. 33B) and in a number of bothremydids: *Bothremys maghrebiana* (fig. 141B), *Labrostochelys* (fig. 193B), and *Cearachelys* (fig. 71B).

72. Pterygoid, processus pterygoideus externus: without vertical plate (*Pelusios*) = 0; with vertical plate (*Chelydra*) = 1.

See Gaffney et al. (1987), Gaffney et al. (1991), Rougier et al. (1995), and Gaffney (1996).

73. Pterygoid, trigeminal ridge: absent (*Galianemys*) = 0; ridge extending posteroventrally from foramen nervi trigemini to condylus mandibularis (*Phosphatochelys*) = 1.

Morphology: In *Taphrosphys*, *Ummulisani*, and *Phosphatochelys* a thin ridge extends from the ventral margin of the foramen nervi trigemini posteroventrally along the quadrate process of the pterygoid, to the vicinity of the condylus mandibularis (fig. 202). This ridge may be an attachment area for a part of the pterygoideus muscle.

Primitive condition: All outgroups lack this character.

Homoplasy: This character occurs only in *Taphrosphys* and *Phosphatochelys*.

Discussion: This character supports the subgroup of Taphrosphyina consisting of *Taphrosphys, Ummulisani*, and *Phosphatochelys*.

74. Pterygoid, position of the foramen posterius canalis carotici interni: in ventral surface of basisphenoid (*Proganochelys*) = 0; in pterygoid-quadrate suture (*Araiochelys*) = 1; in medial wall of basisphenoid (*Kurmademys*) = 2; in prootic (*Pelusios*) = 3; in pterygoid-basisphenoid (also prootic in some cases) suture (*Euraxemys*) = 4; in pterygoid-basisphenoid-quadrate suture (*Taphrosphys*) = 5; in quadrate only (*Labrostochelys*) = 6.

Morphology: The internal carotid artery of turtles enters the skull through the foramen posterius canalis carotici interni (Albrecht, 1967, 1976; Gaffney, 1979a), which may be located in the basisphenoid, adjacent palatoquadrate elements, or in sutures between these elements. In *Proganochelys* and *Kayentachelys*, the internal carotid enters the skull via the ventral surface of the basisphenoid (state 0; Gaffney, 1990: fig. 20). Pleurodires modify this direct entry by interposing other elements (see figs. 276 and 277 for all states of the foramen posterius canalis carotici interni in pleurodires). Phylogenetically, based on the MPC (fig. 296B), the first element to contain the foramen was the prootic. In chelids, pelomedusids, and *Araripemys*, the carotid enters the prootic before entering the basisphenoid so that the foramen posterius canalis carotici interni is formed in the prootic (state 3). This character is synapomorphic for Pleurodira in the MPC; of course it is not known in the shell-only taxa. In all pleurodires (except possibly *Kurmademys*), the carotid goes through the prootic, even though this may be covered ventrally by other bones.

The formation of the foramen posterius canalis carotici interni by the basisphenoid and pterygoid (fig. 277A, state 4) occurs in Euraxemydidae, Podocnemididae, *Sankuchemys*, Cearachelyini, *Arenila*, and some Bothremydini, so that in the MPC this condition is primitive for Bothremydidae and a synapomorphy for the magnafamily Podocnemidera (fig. 296B). This makes morphologic sense as well because the large medial process of the quadrate seen in many Bothremydini and Taphrosphyini may be interpreted as a modification of state 4, with the quadrate covering some of the basisphenoid to produce a foramen posterius canalis carotici interni formed by the quadrate and pterygoid, recognized here as a different condition, state 1 (fig. 277B).

In podocnemidids (Gaffney, 1979a: fig.86), *Hamadachelys*, and *Brasilemys*, the carotid enters the skull at the anterior margin of the cavum pterygoidei. The foramen posterius canalis carotici interni is formed mostly by the basisphenoid, but the pterygoid and prootic are close. This character could be interpreted as unique to this group, but we have included it in state 4 because the bones involved in it are the same as in other taxa with state 4.

The three species of *Taphrosphys*, *Bothremys kellyi*, and *Zolhafah* have the foramen posterius canalis carotici interni formed at the junction of three bones: pterygoid, quadrate, and basisphenoid (fig. 277D, state 5).

Kurmademys is unique in having the carotid enter the basisphenoid on a laterally facing surface that forms the anteromedial edge of a moderate fossa pterygoidea (state 2, fig. 63). This is morphologically distinct from the primitive chelonian condition (state 0) in being more laterally placed on a much wider basisphenoid. Scoring it as state 0, however, does not change the MPC.

Labrostochelys (fig. 277F) (and one specimen of *Ummulisani*) is unique in having only the quadrate form the foramen posterius canalis carotici interni. Nonetheless, it is not very different morphologically from state 1, formation by pterygoid and quadrate, as the pterygoid is not far from the foramen in *Labrostochelys*. The quadrate has a suture extending from the foramen posterius canalis carotici interni to the pterygoid, suggesting that the canal is only barely covered by quadrate. A separate state, state 6, is created for the quadrate only. However, the condition in *Labrostochelys* is morphologically so similar to state 1, pterygoid plus quadrate, that *Labrostochelys* is scored as polymorphic. This decision does make a difference in the cladogram, however. Scoring both *Labrostochelys* and *Ummulisani* as state 6 makes the three species of *Taphrosphys* a multichotomy with the *Ummulisani-Rhothonemys-Labrostochelys* clade, reflecting the low support for the species of *Taphrosphys*.

Teneremys (Broin, 1980: pl. 2) seems to have a foramen posterius canalis carotici interni formed by both basisphenoid and pterygoid (although this has not been substantiated), but it is unique in having the foramen at the anterior end of the basisphenoid.

Primitive condition: The formation of the foramen posterius canalis carotici interni by a narrow basisphenoid as described in Gaffney (1990) is presumed to be primitive for turtles. Within Pleurodira, state 3, formation of the foramen by the prootic, is interpreted as primitive within this group.

Homoplasy: Although this is a complex character (fig. 296B) with seven states, its CI is a respectable 0.5. None of the states reverses back to state 0. States 0 and 3 do not reverse at all, although they are each lost once. The more general state 4 is lost four times, possibly more. State 1 arises independently within Bothremydini and Taphrosphyini. State 5 arises three times. State 6 occurs in only *Labrostochelys* and one of three specimens of *Ummulisani*.

Discussion: The formation of the internal carotid entry and its canal is more complex in pleurodires than in cryptodires (Gaffney, 1979a, 1996), and this character is only one way of coding this variation. The formation of a fossa pterygoidea or a cavum pterygoidei alters the bones around the foramen posterius canalis carotici interni, obscuring a more general similarity. Combining the quadrate plus pterygoid with prootic plus quadrate plus pterygoid condition into one state was done because the prootic is exposed when the fossa pterygoidea is present (see character 68, fossa pterygoidea).

Some aspect of this character is used in Meylan (1996), Lapparent de Broin and Werner (1998), Tong et al. (1998), and Lapparent de Broin (2000b).

75. Pterygoid, posterior margin of pterygoid forms part of foramen posterius canalis carotici interni: no, pterygoid does not enter foramen (*Pelusios*) = 0; yes, pterygoid enters anterior margin of foramen (*Galianemys*) = 1.

Morphology: The pterygoid enters the anterior margin of the foramen posterius canalis carotici interni, apparently correlated with a posterior extension of the pterygoid (figs. 276, 277). Even in podocnemidids (Gaffney, 1979a: fig.86), the pterygoid enters into the formation of the foramen.

Primitive condition: In chelids, pelomedusids, and *Araripemys*, the foramen posterius canalis carotici interni lies almost entirely within the prootic, sometimes with the basisphenoid entering it. In nearly all bothremydids the pterygoid is slightly more posterior and covers part of the foramen posterius canalis carotici interni. The more anterior position of the pterygoid posterior edge is primitive based on comparisons with *Proganochelys*.

Homoplasy: *Kurmademys* and *Labrostochelys* have unique conditions of the foramen posterius canalis carotici interni and lack a pterygoid contribution.

Discussion: In this analysis, this character is considered distinct from the preceding character 74, which also deals with the formation of the foramen posterius canalis carotici interni, because there are multiple patterns involving the foramen that are not expressed with only one character, even with multiple states. This character seeks to use the pattern that occurs in Euraxemydidae, Podocnemididae, and most Bothremydidae (fig. 306), that is, a slight posterior extension of the pterygoid reaching the foramen posterius canalis carotici interni. This condition seems to be a more general one (fig. 306) than the states identified in character 74 (fig. 296B); the other attempts to codify carotid variation. There are many carotid stories, and this is only one of them.

76. Pterygoid, foramen caroticum laterale: present (*Emydura*) = 0; absent (*Pelusios*) = 1.

Morphology: The foramen caroticum laterale is the anterior opening of the canalis caroticus lateralis (a lateral branch of the canalis caroticus internus) into the sulcus cavernosus that is usually just lateral to the foramen anterius canalis carotici interni and just medial to the foramen cavernosum (Gaffney, 1979a: 101; see also Albrecht, 1967, 1976). It is an opening in the dorsal surface of the pterygoid adjacent to the basisphenoid. This opening usually transmits the palatine artery. Its presence seems to be primitive for Pelomedusoides, as it is found in chelids and *Araripemys* (fig. 34); however, this is not well supported because of its absence in pelomedusids.

Primitive condition: *Proganochelys* has a partially open cranioquadrate space, so the foramen caroticum laterale is not defined by bone (Gaffney, 1990). It is present in many casichelydians (Gaffney, 1979a: 101, figs. 54–65). Among pleurodires, it has been identified in *Podocnemis*, *Peltocephalus*, *Erymnochelys*, and all chelids except *Chelus*. It is considered to be absent in *Pelusios* and *Pelomedusa* (Albrecht, 1976).

Homoplasy: The foramen caroticum laterale appears to have been lost at least three times within the Pleurodira: once in the genus *Chelus*, once in the Pelomedusidae, and at least once for the Bothremydidae.

Discussion: This character can be scored only in specimens in which the braincase is very well preserved and has been prepared in detail. Thus, although the foramen caroticum laterale has yet to be found in bothremydids, its absence can be confirmed in only six species. Nonetheless, these six (*Kurmademys*, *Cearachelys*, *Galianemys*, *Bothremys cooki*, *B. maghrebiana*, and *Taphrosphys sulcatus*) include taxa in each tribe and are well distributed taxonomically.

77. Pterygoid, midline contact: midline contact of pterygoids relatively long (*Galianemys*) = 0; midline contact very short (*Dirqadim*) = 1.

Morphology: The pterygoids meet on the midline at their anterior end, anterior to the basisphenoid. In some taxa, the contact is very short (*Labrostochelys*, fig. 11G) and the basisphenoid is close to the palatines.

Primitive condition: Most outgroups have a longer midline contact.

Homoplasy: Rampant, with a CI of 0.14. Within pleurodires, the character arises independently six times in the MPC.

Discussion: The only group this noisy feature supports is *Nigeremys* + *Arenila*.

This character is used in Meylan (1996) and Lapparent de Broin (2000b).

78. Epipterygoid, absent: present (*Chelydra*) = 0; absent (*Pelusios*) = 1.

Morphology: Described and figured by Gaffney (1975a, 1975b, 1979a, 1979b), this bone is absent in pleurodires and some cryptodires.

Primitive condition: The bone is present in *Proganochelys*.

Homoplasy: Epipterygoid loss or fusion occurs within cryptodires in baenids and *Dermochelys*, but apparently only once in pleurodires.

Discussion: This character is a Pleurodira synapomorphy, but it is known only for taxa with good skulls, so it could be present from Pleurodira to Eupleurodira.

This character is used by Gaffney and Meylan (1988) and Gaffney et al. (1991).

79. Supraoccipital, supraoccipital-quadrate contact: absent (*Pelusios*) = 0; present on dorsal surface of otic chamber (*Bothremys*) = 1.

Morphology: The otic region of turtles in dorsal view can be seen to be made up of contributions of four elements: the quadrate laterally, the prootic anteriorly, the supraoccipital medially, and the opisthotic posteriorly. Although there is variation in the contributions made by these elements, in nearly all turtles the prootic and opisthotic make contact and thus intervene between the supraoccipital and quadrate. In most bothremydids (fig. 143A) the supraoccipital and quadrate meet on the dorsal surface of the otic region, preventing contact of the prootic and opisthotic.

The contacts of the otic chamber bones as seen on the dorsal surface do not necessarily reflect underlying contacts. As might be expected, the prootic-opisthotic contact is still present in some broken specimens, beneath the supraoccipital-quadrate contact.

Primitive condition: Prootic-opisthotic contact occurs in *Proganochelys* and all relevant outgroups.

Homoplasy: Although this is an important character in Bothremydidae (fig. 307), it has a low CI of 0.25. All bothremydids have a supraoccipital-quadrate contact except for *Zolhafah* and the Taphrosphyini, which represent reversals. Within the tribe Taphrosphyini, the undescribed skull CNRST-SUNY 199 is reversed to acquire the supraoccipital contact. No other pleurodires have the contact. However, some baenids (Gaffney, 1979a: fig. 56) have a supraoccipital-quadrate contact.

Discussion: This character is a synapomorphy for the Bothremydidae, and its reversal is a synapomorphy for the Taphrosphyini (fig. 307).

This character is used in Tong et al. (1998).

80. Supraoccipital, crista supraoccipitalis: low to absent (*Proganochelys*) = 0; a distinct sagittally oriented plate (*Pelusios*) = 1.

See Gaffney (1990), Gaffney and Kitching (1995), and Rougier et al. (1995).

81. Supraoccipital, wide occipital plate: wide occipital plate with posteriorly concave depression (*Proganochelys*) = 0; narrower occiput (*Pelusios*) = 1.

See Gaffney (1990), Gaffney and Kitching (1995), and Rougier et al. (1995).

82. Exoccipital, foramen jugulare posterius: not formed in bone (*Proganochelys*) = 0; formed by bone and open or partially closed (*Galianemys*) = 1; completely closed by bone (*Azabbaremys*) = 2.

Morphology: The foramen jugulare posterius is an opening surrounded mostly by the exoccipital that leads into the recessus scalae tympani. When completely closed (state 2, fig. 195), the lateral margin of this foramen is usually formed by the exoccipital but sometimes by the opisthotic (fig. 203). The foramen may be open laterally and continuous with the fenestra postotica (figs. 46, 98).

Primitive condition: The foramen jugulare posterius does not exist in bone in *Proganochelys* (Gaffney, 1990: 80). In most cryptodires it is enclosed by the exoccipital alone or by the exoccipital in combination with the opisthotic or pterygoid; in other cryptodires, it is continuous laterally with the fenestra postotica. Among living pleurodires it is closed laterally in *Pelusios*, *Podocnemis*, and in chelids other than *Pseudemydura* (Gaffney, 1979a). In *Araripemys* it is both open (fig. 36) and closed (fig. 37). In *Euraxemys* (fig. 46), it is open laterally. The fact that this opening is not defined by bone in *Proganochelys* has led us to score the open condition as primitive for turtles, but the closed condition seems to be primitive for pleurodires.

Homoplasy: This is a variable character with a CI of 0.33, and it has undoubtedly undergone multiple reversals and/or multiple acquisitions. Morphologically, it would be expected that the open or less complete condition would be primitive to the closed, more ossified condition, and this seems to be the case for Cryptodira (Gaffney, 1996). However, the closed condition in chelids and pelomedusids, as well as in podocnemidids, *Kurmademys*, and some *Araripemys*, suggests that the reverse is true. The open condition occurs independently three times in Pleurodira: Euraxemydidae, Cearachelyini, and Foxemydina.

Discussion: The open or reversed condition supports three groups in pleurodires (see above).

This character is used in Lapparent de Broin and Werner (1998) and Lapparent de Broin (2000b).

83. Exoccipital, recessus scalae tympani: not formed in bone (*Proganochelys*) = 0; formed by bone, also forming fenestra perilymphatica (*Pelusios*) = 1.

See Gaffney (1990), Gaffney and Kitching (1995), and Rougier et al. (1995).

84. Exoccipital, condylus occipitalis: basioccipital plus both exoccipitals (*Euraxemys*) = 0; exoccipitals only (*Pelusios*) = 1.

Morphology: The occipital condyle in the tribes Taphrosphyini and Bothremydini is unusual in being made up of only the two exoccipitals (fig. 203) rather than the three bones in nearly all cryptodires (except *Carettochelys*) and most other pleurodires (except pelomedusids and *Cearachelys*). The bothremydid condyle often has a vertical cleft down its center marking the suture.

Primitive condition: The outgroups Cryptodira, Chelidae, *Araripemys*, Euraxemydidae, Podocnemididae, and *Kurmademys* have three bones in the condylus occipitalis, the presumed primitive condition.

Homoplasy: The CI of this character is 0.33. The complete exclusion of the basioccipital from the condylus occipitalis neck must originate three times in the MPC: in the Pelomedusidae, *Cearachelys*, and the infrafamily Bothremydodda (the tribes Taphrosphyini and Bothremydini). *Galianemys* has a wedge-shaped part of the basioccipital extending into the neck of the condylus occipitalis, almost to the articulating surface.

Discussion: This character is used in Gaffney and Meylan (1988), Meylan (1996), and Tong et al. (1998), Lapparent de Broin and Murelaga (1999), and Lapparent de Broin (2000b).

85. Exoccipital, exoccipital-quadrate contact: absent (*Pelusios*) = 0; extensive, prootic absent (*Galianemys*) = 1; narrow, prootic present (*Euraxemys*) = 2; narrow, prootic absent (*Brasilemys*) = 3.

Morphology: In most pleurodires the quadrate does not extend all the way to the occipital region so that the prootic and opisthotic prevent contact between the quadrate and exoccipital. In bothremydids the quadrate does extend medially to reach the occipital elements and has broad contact with the basioccipital (character 59) and the exoccipital (state 1, fig. 88). There is also contact between the quadrate and exoccipital in Euraxemydidae (state 2, figs. 44, 53), but the morphology differs from that in bothremydids in that the prootic is exposed ventrally, the exoccipital has a unique ventral process (see character 86), and the quadrate-exoccipital contact is very narrow. *Brasilemys* has a third condition (state 3) in which the contact is narrow and the prootic is absent (Lapparent de Broin, 2000b).

Primitive condition: Quadrate-exoccipital contact is absent in *Proganochelys* (Gaffney, 1990) and relevant outgroups, and thus this contact between these elements is considered derived.

Homoplasy: If the state for Euraxemydidae is considered distinct from that in the bothremydids, there is no known homoplasy for the states in this character (fig. 308).

Discussion: State 2 is synapomorphic for the Euraxemydidae and state 1 is synapomorphic for the Bothremydidae (fig. 308). Even though both states have “exoccipital-quadrate contact present”, the differing morphologies suggest that these should not be ordered because the contact alone does not seem to be homologous.

A version of this character is used in Lapparent de Broin (2000b).

86. Exoccipital, ventral process: absent (*Pelusios*) = 0; present (*Euraxemys*) = 1.

Morphology: In most turtles the exoccipital forms the lateral margins of the foramen magnum, the dorsolateral part of the occipital condyle, and the posteroventral part of the cavum cranii. It does not normally form part of the ventral surface of the skull. In *Euraxemys* and *Dirqadim* there is a unique condition in which a process of the exoccipital extends ventrally between the opisthotic and basioccipital and is exposed on the ventral surface lateral to the basioccipital (figs. 44, 46, 53).

Primitive condition: The exoccipital of *Proganochelys* is excluded from participation in the ventral surface of the skull by prootic–opisthotic contact ventral to the exoccipital. In most cryptodires, the basioccipital or pterygoid excludes the exoccipital from ventral exposure (but see *Baena arenosa*, Gaffney, 1979a: fig. 153), and in pleurodires some combination of contacts between the quadrate, basioccipital, prootic, and opisthotic prevents contribution of the exoccipital to the ventral surface. Thus, exclusion of the exoccipital from the ventral surface is clearly the primitive condition.

Homoplasy: Some baenids (Gaffney, 1972a, 1979a) have a ventral exposure of the exoccipital, but its position and shape differ from euraxemydids. *Brasilemys* (Lapparent de Broin, 2000b) has apparently independently acquired this character. It also occurs as a variation in some chelids (*Phrynops gibba* PAM 2051, FMNH 45669 in fig. 147; Gaffney, 1979c). *Araripemys* (fig. 26) has a widely exposed exoccipital on the ventral surface correlated with a very narrow basioccipital.

Discussion: This feature is a synapomorphy for Euraxemydidae.

87. Basioccipital, basioccipital short: long, length/width of 0.60 or higher (*Pelusios*) = 0; short, length/width of 0.59 or lower (*Bothremys*) = 1.

Morphology: The basioccipital of turtles is variable in shape but always makes up the posteriormost part of the ventral surface of the braincase. In most turtles it is approximately as long as wide. In bothremydids the basioccipital is comparatively short relative to its width (figs. 9–11), a clear difference from chelids, for example. However, this character could be judged as continuously variable with the distinction between "long" and "short" being subjective and perhaps arbitrary. A ratio of basioccipital length over width reveals a short gap so that "long" could be considered 0.60 and higher, with "short" being 0.59 and lower. Using this slight gap to differentiate the two states, podocnemidids and bothremydids are long. With one exception (*Taphrosphys sulcatus*), the Bothremydidae ratio varies from 0.31 (*Chedighaii*) to 0.57 (*Cearachelys*, *Phosphatochelys*). Podocnemidids (including *Hamadachelys*) are 0.59 or lower. The chelids,which are variable (we have chosen *Emydura*), are 0.64, but pelomedusids are higher at 0.70–0.78. Euraxemydids are 0.73–0.77 and *Araripemys* is the highest at 1.2. Therefore, the closest ratios for the two states are podocnemidids at 0.59 and chelids at 0.64.

Primitive condition: The pleurodiran outgroups are long in the basioccipital.

Homoplasy: A simple character like this is difficult to test for homology, but the only reversal in the MPC is the relatively long basioccipital of *Taphrosphys sulcatus* at 0.68. Interestingly, the other two *Taphrosphys* species are 0.47 (*T. congolensis*) and 0.57 (*T. ippolitoi*), suggesting that this condition evolved within this genus.

Discussion: Although a continuous character like this one could be divided into a number of states, we have chosen only two to try to reflect the short basioccipital of bothremydids. As a result, it seems that this feature is shared with podocnemidids, although choosing another division point could change that.

This character or a version of it ("telescoped occiput") is used in Antunes and Broin (1988), Lapparent de Broin and Werner (1998), and Lapparent de Broin (2000b).

88. Basioccipital, basioccipital thick: basioccipital and basisphenoid relatively thick in cross section (*Proganochelys*) = 0; thinner (*Pelusios*) = 1.

See Gaffney (1990) and Gaffney and Kitching (1995).

89. Basioccipital, basioccipital-opisthotic contact: absent (*Galianemys*) = 0; present (*Pelomedusa*) = 1.

Morphology: In most casichelydians, the opisthotic is excluded from contact with the basioccipital except in cases where the processus interfenestralis is well ossified ventrally (Gaffney, 1979a: 135–136). In certain pleurodires, there is a ventral process of the opisthotic that is posterior to the processus interfenestralis that makes a strong, sutured contact with the basioccipital between the foramen jugulare posterius and the fenestra postotica (Gaffney, 1979a: figs. 85, 86). Among pleurodires, this contact is present in most but not all Chelidae (Gaffney, 1979a: fig. 88), but not in *Phrynops gibba* PAM 2051 or in *Chelodina* (Gaffney, 1979a: 136) in which the exoccipital intervenes. It is present in the Pelomedusidae (fig. 21) and Podocnemididae as well as *Hamadachelys*. The contact is absent in all Bothremydidae.

Primitive condition: In *Proganochelys* the opisthotic makes a ventromedial contact with the basioccipital. Although the exact position of the suture is unclear (Gaffney, 1990: 86), it is posterior to the processus interfenestralis and may be homologous to the contact seen in several pleurodiran groups. Whether the condition in *Proganochelys* is homologous (we have scored it as questionable), this sutured posterior contact in members of the Chelidae, Pelomedusidae, and Podocnemididae (plus *Hamadachelys*) suggests that the presence of this contact may be primitive for pleurodires, although this is equivocal.

Homoplasy: Opisthotic–basioccipital contact between the foramen jugulare posterius and the fenestra postotica occurs in some cryptodires. It has arisen independently in podocnemidids. The CI is 0.5.

Discussion: The distribution of this character among the Pleurodira suggests that it has been gained twice or lost three times. In either case, it is uniformly absent in the Bothremydidae although it is present in the sister group, the Podocnemidinura.

A version of this character is used in Lapparent de Broin (2000b).

90. Prootic, hyomandibular branch of facial nerve lies in its own canal: no (*Chelydra*) = 0; yes (*Podocnemis*) = 1.

Morphology: Described and figured in Gaffney (1975b, 1979a), determining this character requires access to the canalis cavernosus and the internal morphology of the prootic. A short canal contains the hyomandibular nerve, separating it from the canalis cavernosus.

Primitive condition: The absence of a canal is the condition in *Proganochelys* and Cryptodira.

Homoplasy: None known.

Discussion: This character is a synapomorphy for the Pleurodira. Despite the fact that it can only be seen in well-preserved and partially disarticulated skulls, it is included. It is determinable in some fossils; *Galianemys* and *Dirqadim* are known from CT scans.

This character is used by Gaffney and Meylan (1988) and Gaffney et al. (1991).

91. Prootic, foramen stapedio-temporale: not a canal (*Proganochelys*) = 0; a distinct foramen and canal (*Pelusios*) = 1.

See Gaffney et al. (1987), Gaffney et al. (1991), and Gaffney (1996).

92. Prootic, foramen stapedio-temporale opens anteriorly: no (*Pelusios*) = 0; yes (*Galianemys*) = 1.

Morphology: The foramen stapedio-temporale lies on the anterior surface of the otic chamber in most bothremydids. Compared with the outgroups, the foramen is placed more anteroventrally in the prootic-quadrate suture. When the skull is seen in dorsal view, there is either no sign of the foramen or only a narrow part of the margin (figs. 7,8). This depends to a certain extent on how the skull is oriented, but unless the skull is strongly tilted, the foramen margins usually cannot be seen. If an extensive skull roof covers the otic chamber, some rotation of the skull must be done to see the position of the foramen stapedio-temporale.

Primitive condition: In the pleurodire outgroups Chelidae, Pelomedusidae (fig. 21A), Euraxemydidae (fig. 45), and Podocnemididae, the foramen stapedio-temporale is visible in dorsal view because it is in a more posterodorsal position than in the Bothremydidae.

Homoplasy: The subfamily Bothremydinae (consisting of the tribes Cearachelyini, Taphrosphyini, and Bothremydini) has this character (fig. 309). *Kurmademys* has the primitive condition, but *Sankuchemys* may have the derived condition. Unfortunately, *Sankuchemys* is badly crushed and the presence or absence of the foramen is ambiguous. However, the otic chamber is crushed directly dorsoventrally, and there is no sign of the foramen stapedio-temporale on either side. In the character set *Sankuchemys* is coded as missing for this character.

Discussion: Despite the ambiguity in Kurmademydini, this character is definitely found only in the subfamily Bothremydinae (fig. 309) and is a synapomorphy for it.

This character is used in Meylan (1996) and Tong et al. (1998).

93. Prootic, foramen stapedio-temporale and foramen nervi trigemini: separated by most of prootic (*Pelusios*) = 0; separated by narrow bar of prootic (*Bothremys*) = 1.

Morphology: In the bothremydid tribes of Bothremydini and Taphrosphyini, the foramen stapedio-temporale lies on the anterior surface of the otic chamber, separated from the foramen nervi trigemini by a thin bar of prootic (fig. 132F). In these taxa, the foramen stapedio-temporale is mostly formed by the prootic, with a narrow part of quadrate entering the margin. The foramen itself is usually close to the center of the prootic along its ventral edge. In many specimens the prootic bar is broken away, but the position of the foramen is still determinable.

Primitive condition: The pleurodiran outgroups show a foramen stapedio-temporale and foramen nervi trigemini separated by most of the prootic to be the primitive condition.

Homoplasy: None known.

Discussion: As this character requires the foramen stapedio-temporale to be on the anterior surface of the otic chamber, it could be coded as a third state in the preceding character: foramen stapedio-temporale not visible in dorsal view. When the character states are ordered, it produces the same MPC.

94. Prootic, ventral exposure: most of prootic exposed ventrally (*Emydura*) = 0; prootic about half covered by quadrate and basisphenoid (*Euraxemys*) = 1; nearly all of prootic covered by quadrate, basisphenoid, and pterygoid (*Taphrosphys*) = 2.

Morphology: In euraxemydids the basisphenoid and quadrate cover most of the prootic, leaving only a narrow exposure of prootic (state 1, fig. 44). In podocnemidids and bothremydids the prootic is completely covered (except for a small exposure described as another character, Prootic, ventral exposure 2). This is state 2 (fig. 277).

Primitive condition: *Proganochelys* has a completely exposed prootic (Gaffney, 1990). Chelids and pelomedusids (figs. 21, 276) also have this condition, although other bones encroach on the prootic.

Homoplasy: None. Cryptodires also cover the prootic ventrally, but it is done entirely by the pterygoid and appears to be nonhomologous (Gaffney, 1975b, 1979a).

Discussion: The partial covering of the prootic in euraxemydids is very similar to the complete covering in other pleurodires, as it involves a lateral extension of the basisphenoid and a medial extension of the quadrate. This character could be run ordered because state 1 is additive with respect to state 2 (fig. 310). All taxa that have state 2 also have state 1, so to run them as separate characters would lose this information. However, running this character unordered results in the same MPC (fig. 310).

This character is used in Antunes and Broin (1988), Meylan (1996), Lapparent de Broin and Werner (1998), and Tong et al. (1998).

95. Prootic, quadrate-pterygoid-basisphenoid exposure: complete exposure of prootic or no exposure of prootic (*Pelusios*) = 0; exposure of prootic small, surrounded by pterygoid, basisphenoid, and quadrate, with foramen nervi facialis exposed (*Kurmademys*) = 1.

Morphology: In the bothremydids *Kurmademys*, *Sankuchemys*, *Cearachelys* (not all specimens, see *Cearachelys*), and *Galianemys emringeri*, there is a small, irregular exposure of the prootic at or near the junction of the pterygoid, basisphenoid, and quadrate (fig. 277E). This exposure surrounds or nearly surrounds the foramen nervi facialis, which is therefore visible in ventral view in these forms, in contrast to other bothremydids.

Primitive condition: The primitive condition for prootic exposure is widely exposed, as in chelids and pelomedusids, but in this character we identify as primitive all other prootic conditions that lack the character as specified.

Homoplasy: In the MPC (fig. 311), this character appears at least three and possibly four times independently, and it has a CI of 0.33. Elsewhere (character 68, fossa pterygoidea, fig. 305) we argue that at least in some cases the exposure of the prootic is the result of a deep fossa pterygoidea that has eroded the basisphenoid, pterygoid, and quadrate, exposing the underlying prootic.

Discussion: The high degree of homoplasy and the frequent (but not exclusive) association of the prootic exposure with a deep fossa pterygoidea suggest it may not be homologous everywhere it appears. However, *Kurmademys* has a moderate fossa and a prootic exposure, and *Sankuchemys* has the exposure but no evidence of a fossa (although the only known skull is crushed). In the MPC the small exposure is a synapomorphy for the tribe Kurmademydini (fig. 311).

96. Prootic, processus trochlearis oticum: absent (*Proganochelys*) = 0; present (*Chelydra*) = 1.

See Gaffney et al. (1987), Gaffney et al. (1991), Gaffney (1996), and Rougier et al. (1995).

97. Prootic, plane of fenestra ovalis: inclined from the vertical (*Proganochelys*) = 0; very close to vertical (*Chelydra*) = 1.

See Gaffney (1990), Gaffney and Kitching (1995), and Rougier et al. (1995).

98. Opisthotic, processus interfenestralis expanded ventrally: narrow ventrally (*Proganochelys*) = 0; expanded ventrally (*Pelusios*) = 1.

See Gaffney (1990).

99. Opisthotic, processus interfenestralis covered in ventral view: exposed ventrally (*Emydura*) = 0; covered by bone (*Bothremys*) = 1.

Morphology: The processus interfenestralis (Gaffney, 1972b, 1979a) of the opisthotic is visible in ventral view in chelids, pelomedusids, and *Araripemys* (fig. 276). This is correlated with portions of the cavum labyrinthicum, fenestra ovalis, and recessus scalae tympani also being open ventrally. In life, this area is filled with cartilage in chelids and pelomedusids (Gaffney, 1979a). In euraxemydids, podocnemidids, and bothremydids, a medially large quadrate and posterolaterally large basisphenoid cover this area with bony ossification (figs. 276, 277).

Primitive condition: The exposed condition of chelids and pelomedusids is closest to the completely open condition in *Proganochelys* and is presumed to be primitive for pleurodires.

Homoplasy: None known, except for within Selmacryptodira.

Discussion: It might be possible to break the derived state into two states, including one for euraxemydids, which can be interpreted as having a smaller medial quadrate process than do podocnemidids and bothremydids. If ordered, no information would be lost. However, judging the difference in size of the medial quadrate process seems too subjective, even for me.

This character is used in Lapparent de Broin and Werner (1998), Lapparent de Broin and Murelaga (1999), and Lapparent de Broin (2000b).

100. Opisthotic, fenestra postotica closed medially: open medially (*Euraxemys*) = 0; closed medially by opisthotic-quadrate contact (*Taphrosphys*) = 1.

Morphology: The fenestra postotica (Gaffney, 1972b, 1979a) is limited laterally and ventrally by the quadrate and dorsally by the opisthotic. When the opisthotic and quadrate meet medial to the fenestra postotica, it is closed (figs. 132D, 218). Only the Cearachelyini (figs. 87, 88, 98–100) among bothremydids have a medially open fenestra postotica.

Primitive condition: All the pleurodiran outgroups have a medially open fenestra postotica.

Homoplasy: In the MPC, the closed condition evolved twice, once in *Kurmademys* (*Sankuchemys* is unknown) and once in the infrafamily Bothremydodda (the tribes Taphrosphyini and Bothremydini), or it was lost once in the tribe Cearachelyini.

Discussion: This character is independent of a laterally closed foramen jugulare posterius. Chelids and pelomedusids have a laterally closed foramen jugulare posterius with an open fenestra postotica.

This character or a version of it was used in Lapparent de Broin and Werner (1998) and Lapparent de Broin (2000b).

101. Opisthotic, fenestra postotica short horizontal slit: more open dorsoventrally (*Euraxemys*) = 0; short slit (*Galianemys*) = 1.

Morphology: The Cearachelyini have a uniquely shaped fenestra postotica. The fenestra postotica is open medially, and it is dorsoventrally compressed in comparison to other pleurodires. The result appears as a short slit (figs. 87, 88, 98–100), in contrast to the round or oval opening of other bothremydids.

Primitive condition: A more open condition is in all relevant outgroups and is presumed primitive.

Homoplasy: None known.

Discussion: This character is a synapomorphy for the tribe Cearachelyini. This character could be a state within the closed fenestra postotica character, but it would be confusing, at least to me.

102. Opisthotic, processus paroccipitalis: projects posteriorly beyond squamosal (*Euraxemys*) = 0; smaller, does not project beyond squamosal (*Galianemys*) = 1.

Morphology: The variation in shape of the opisthotic-squamosal area of the occiput in pleurodires is a source of characters, but some are hard to define. This character is an attempt to reflect the small size of the processus paroccipitalis (Gaffney, 1972b, 1979a) in bothremydids as a character. It is compared to the size of the squamosal, although this is not entirely satisfactory as some taxa (e.g., *Labrostochelys*) have very long squamosals. The character is best seen in figures 9–11.

Primitive condition: The condition in *Proganochelys* (Gaffney, 1990) is presumed to be primitive, with the processus paroccipitalis projecting posteriorly. However, *Proganochelys* has a unique morphology (among turtles), and the squamosal is very small. Cryptodires and chelids have a larger squamosal with a smaller processus paroccipitalis, and this may be primitive for pleurodires. Nonetheless, pelomedusids, *Araripemys*, euraxemydids, and podocnemidids have a long, projecting processus paroccipitalis, and it is possible that this is the primitive condition.

Homoplasy: The small processus paroccipitalis has originated twice in the MPC, once (possibly twice) within cryptodires and in chelids and once in bothremydids, being reversed in all other pleurodires. However, the reversed condition in pleurodires is morphologically distinct from the *Proganochelys* condition.

Discussion: Although it gets a little fuzzy around cryptodires, chelids, and *Proganochelys*, this character is a bothremydid synapomorphy.

103. Opisthotic, thin horizontal flange: absent (*Galianemys*) = 0; thin horizontal flange present on posterior edge of opisthotic just dorsal to fenestra postotica (*Chedighaii hutchisoni*) = 1.

Morphology: Best seen in *Chedighaii hutchisoni* (fig. 159), KUVP 14765, this thin flange lies ventral to the distinct curve or "step" as the opisthotic curves from a horizontal surface ventrally to a vertical surface. The flange is so distinct in *Chedighaii* that it has a shallow, horizontal groove above it. Below the flange is the fenestra postotica. In *C. barberi*, Alabama 2001.2, the flange is broken off on both sides but its base is clear and is nearly identical to that in KUVP 14765.

Primitive condition: All other pleurodires and *Proganochelys* lack this flange.

Homoplasy: None known, except that among the five skulls of *Bothremys maghrebiana* the flange is variable.

Discussion: Chelids and pelomedusids may have a narrow posterior margin to the processus paroccipitalis of the opisthotic, but this condition is distinct from the *Chedighaii*/*Bothremys* condition.

104. Basisphenoid, basisphenoid-quadrate contact: absent = 0; present and wide, as in *Galianemys* = 1; present and narrow, as in *Azabbaremys* = 2.

Morphology: The basisphenoid-quadrate contact is a Podocnemidoidea (Podocnemididae + Bothremydidae) synapomorphy, known for some time (Lapparent de Broin and Werner, 1998; Lapparent de Broin, 2000b). Examination of its distribution in the Bothremydidae (figs. 9–11) suggests that two states can be distinguished, a broader contact (as in *Galianemys*, fig. 81B) and a narrower contact (as in *Azabbaremys*, fig. 212B). As in all of these more subjective states, there is an arbitrary element to determining which state is present.

Primitive condition: The absence of a contact in nearly all of the relevant outgroups indicates that this is the primitive state. Some *Pelusios* may have the contact as an individual variation.

Homoplasy: None known for the presence of a contact (except some *Pelusios*). However, the two states in the MPC (fig. 312) show two origins and a loss for state 2, the narrow contact, once in *Bothremys* + *Chedighaii* and once for Taphrosphyini, with a reversal in *Taphrosphys* + *Ummulisani* + *Phosphatochelys*. However, *Phosphatochelys* shows variation in this feature and it has been coded with both states. The CI is 0.5.

Discussion: There may be some ambiguity in discriminating a few taxa, such as *Phosphatochelys*, regarding the two derived states, but it still seems worthwhile to extract this information and reflect it in the datasets. The character can also be run as a simple presence or absence of the contact; this is a synapomorphy for Bothremydidae (fig. 312).

This character is used in Lapparent de Broin and Werner (1998) and Lapparent de Broin (2000b).

105. Basisphenoid, interpterygoid vacuity: large and open (*Proganochelys*) = 0; small or absent (*Pelusios*) = 1.

See Gaffney (1990), Gaffney et al. (1991), Gaffney and Kitching (1995), and Rougier et al. (1995).

106. Basisphenoid, ventral outline: elongate, basisphenoid not sutured to pterygoids (*Proganochelys*) = 0; more triangular (baenids) = 1; more pentagonal (*Taphrosphys*) = 2; very elongate (*Araripemys*) = 3; V-shaped pointing anteriorly (*Arenila*) = 4.

Morphology: The shape of the basisphenoid as seen in ventral view varies, and this character set is an attempt to identify some of this variation. In most bothremydids (figs. 9–11) the basisphenoid is triangular, with the base and the anterolateral contacts with the pterygoid being dominant (state 1, 9H). The shape can also be more pentagonal (state 2, fig. 11B), with the quadrate contact being much longer and the pterygoid contact shorter. The pentagonal (state 2) occurs in chelids, pelomedusids, podocnemidids, the Kurmademydini, *Foxemys* + *Polysternon*, and *Taphrosphys*. *Araripemys* is unique in having a very elongate basisphenoid (state 3, fig. 9C). In *Nigeremys* and *Arenila*, the basisphenoid is V-shaped or arrow-shaped (state

4, fig. 11I), with its posterior margin embayed, concave posteriorly.

Primitive condition: Although not exactly comparable to casichelydians due to the absence of a sutured pterygoid, *Proganochelys* has a roughly triangular shape, but it lacks the flat ventral surface and contacts of other turtles and is coded as a separate state. Cryptodires are scored triangular, and this is the outgroup for the pleurodires. However, the pentagonal shape (state 2) is in chelids and pelomedusids.

Homoplasy: The CI is 0.44 and there is a fair amount of homoplasy within bothremydids.

The V-shaped state 4 is unique to *Nigeremys* + *Arenila*, and state 3 is unique to *Araripemys*. The pentagonal state 1, however, is more complex. In the MPC, it is primitive for pleurodires and lost or reversed in *Araripemys*, euraxemydids, and Cearachelyini +Bothremydini + Taphrosphyini. It appears independently in *Foxemys* + *Polysternon* and the genus *Taphrosphys*.

Discussion: The pentagonal basisphenoid is a way of wresting information from the extent of quadrate-basisphenoid contact. Such a simple character is hard to homologize and is somewhat subjective. *Phosphatochelys* has a more irregularly shaped basisphenoid that could be considered pentagonal, but we have scored it triangular. Thus, there are some ambiguities in this state. The V-shaped basisphenoid of *Arenila* and *Nigeremys* is quite different from other taxa.

107. Basisphenoid, processus clinoideus: present, with abducens canal (*Pelusios*) = 0; processus clinoideus absent, canal is a groove (*Bothremys*) = 1.

Morphology: In *Bothremys* and *Chedighaii barberi* the small, spurlike processus clinoideus (Gaffney, 1972b, 1979a) is not ossified and the rim of the sella turcica and the dorsum sellae is a smooth edge (fig. 134). Just lateral to the dorsum sellae is a shallow groove that seems to be for the abducens nerve. This condition is visible in *Bothremys cooki*, AMNH 2521; *B. maghrebiana*, AMNH 30041; and in the endocast of a presumed *Chedighaii barberi*, YPM PU 12951.

Primitive condition: The processus clinoideus and foramen nervi abducentis are found in all other pleurodires and *Proganochelys*.

Homoplasy: None known at present, given the current MPC. However, the dorsal surface of the basisphenoid is determinable only in eight other bothremydid species.

Discussion: The dorsal surface of the basisphenoid is not visible in *Bothremys arabicus*, *Chedighaii hutchisoni*, and *Araiochelys*, which makes this character known in only about half of the important taxa, so there are many missing data.

108. Basisphenoid, skull akinetic: no, basipterygoid articulation present (*Proganochelys*) = 0; yes, basipterygoid articulation sutured (*Australochelys*) = 1.

See Gaffney (1990), Gaffney et al. (1991), Gaffney and Kitching (1995), and Rougier et al. (1995).

109. Basisphenoid, cultriform process: rodlike, thin (*Proganochelys*) = 0; broad, flat, covered ventrally (*Australochelys*) = 1.

See Gaffney (1990) and Gaffney and Kitching (1995).

110. Basisphenoid, sella turcica/dorsum sellae: deep, well-defined margins (*Bothremys*) = 0; very shallow, low margins (*Taphrosphys sulcatus*) = 1.

Morphology: Nearly all pleurodires have a well-defined and relatively deep sella turcica concavity with a distinct dorsum sellae at its posterior margin (Gaffney, 1979a). In two species of *Taphrosphys, T. sulcatus* and *T. ippolitoi*, the sella is very low, being barely recognizable, and the dorsum sellae is not significantly above the floor of the sella turcica (fig. 174).

Primitive condition: The deep, well-defined sella turcica occurs in chelids, pelomedusids, and other outgroups and is the presumed primitive condition.

Homoplasy: None known.

Discussion: Although this character resolves the three species of *Taphrosphys*, the few bothremydid taxa for which it is known, particularly among the other Taphrosphyini, make its use questionable and it has been deleted in some of the analyses. When deleted, the three species are a multichotomy.

111. Basisphenoid, ventral tubercle: single tubercle formed by basisphenoid and basioccipital (*Proganochelys*) = 0; paired tubercles (*Australochelys*) = 1; no tubercle (*Pelusios*) = 2.

See Gaffney (1990) and Rougier et al. (1995).

112. Columella auris, footplate: footplate absent, stapes thick (*Proganochelys*) = 0; wide footplate present, stapes thin (*Pelusios*) = 1.

See Gaffney (1990) and Gaffney and Kitching (1995).

113. Splenial: present (*Proganochelys*) = 0; absent (*Pelusios*) = 1.

Morphology: The splenial bone (Gaffney, 1979a) lies on the medial surface of the lower jaw, anterior to and slightly separating the prearticular and angular. It is missing in all pleurodires except Chelidae. In these forms, the angular and prearticular tend to extend anteriorly, filling the space occupied by the splenial in chelids (fig. 241).

Primitive condition: A large splenial is present in *Proganochelys* (Gaffney, 1990), the presumed primitive condition.

Homoplasy: None known within pleurodires.

Discussion: Due to lack of lower jaws and the need of a well-preserved specimen to determine the absence of a splenial, the character can be scored in only four bothremydids. Nonetheless, it remains as a Pelomedusoides synapomorphy.

This character is used in Gaffney and Meylan (1988), Meylan (1996), and Lapparent de Broin (2000b).

114. Dentary, high lingual ridge: absent (*Pelusios*) = 0; present (*Bothremys*) = 1.

Morphology: The lingual ridge in bothremydids like *Bothremys*, *Kurmademys*, *Cearachelys*, and *Foxemys* is higher and deeper than the labial ridge (fig. 241). It is about the same height (or even lower) anteriorly, and it rises posteriorly to be wedge-shaped in lateral view.

Primitive condition: All the outgroups have both lingual and labial ridges of equal size or have a higher labial ridge. We have not distinguished these conditions.

Homoplasy: A high lingual ridge is present in the Cearachelyini, Kurmademydini, and Bothremydini, but it is reversed in Taphrosphyini. The living podocnemidids also have a larger lingual ridge, but fossil taxa vary. *Hamadachelys* has a lower jaw with both ridges nearly the same, but the lingual is slightly higher than the labial, an appropriate primitive condition. It is possible that a higher lingual ridge is primitive for Podocnemididae and could be argued as primitive for Podocnemididae + Bothremydidae, but at present, it is more likely to have appeared independently within Podocnemididae and Bothremydidae.

Discussion: The principal difficulty with this character is the few lower jaws available for bothremydids and other pleurodires. Nonetheless, the known jaws are representative of the bothremydid tribes.

115. Dentary, dentary pits: absent (*Euraxemys*) = 0; present (*Bothremys*) = 1.

Morphology: The pitted lower jaws were first described by Leidy (1865) in *Bothremys cooki* (fig. 19), and later by Hay (1908). Gaffney and Zangerl (1968) redescribed *B. cooki* and added the lower jaws of "*Bothremys*" *barberi* (here referred to *Chedighaii barberi*). The conical pits (fig. 239) are concave anteriorly. The pits are known in *Araiochelys*, *B. cooki* (fig. 239), *B. maghrebiana* (fig. 241), and *Chedighaii barberi*.

Primitive condition: The absence of pits is primitive.

Homoplasy: None known.

Discussion: In *Chedighaii barberi*, the lower jaw has pits but the maxilla does not. In the other forms with lower jaw pits, there are also pits in the maxilla. This lack of complete correspondence is the rationale, however dubious, for recognizing separate characters in the lower jaw and the skull.

116. Dentary, U-shaped lingual ridges on symphysis: absent (*Euraxemys*) = 0; present (*Bothremys*) = 1.

Morphology: In bothremydids the lingual ridge of the dentary is higher than the labial ridge and is strongly developed. In some, the pair of lingual ridges join to form a U-shaped ridge on the dentary at the symphysis (figs. 241, 247). The jaw edges are not parallel to the labial ridges. The U-shaped ridge may be excavated medially, as in *Bothremys maghrebiana* and *Araiochelys*, or it may be filled with bone to form a wedge, as in *Bothremys cooki* (see also fig. 247, a Madagascar lower jaw described in Gaffney and Forster, 2003).

Primitive condition: The U-shaped symphyseal ridge is absent in *Proganochelys*, chelids, *Araripemys*, and *Euraxemys*. In the

Podocnemididae there are strong lingual ridges that are taller than the labial ridges. but they form a V-shaped rather than a U-shaped ridge with a pointed apex.

Homoplasy: A U-shaped ridge like that in most bothremydids also occurs in some *Pelusios*. There is a reversal within the Taphrosphyini (see Discussion).

Discussion: A U-shaped ridge on the symphysis appears to be a synapomorphy for the Bothremydidae that is lost within the tribe Taphrosphyini. The distribution of lower jaws in the Taphrosphyini is too poorly known to be certain where this reversal occurs.

117. Dentary, symphysis: fused (*Bothremys*) = 0; sutured (*Euraxemys*) = 1.

Morphology: The symphysis between the two dentaries is normally fused in turtles with no evidence of a suture. In a few members of the Pleurodira the two dentaries are sutured in the midline instead of being fused. The symphysis is sutured in *Araripemys*, *Euraxemys* (figs. 231, 232), *Pelomedusa*, some *Pelusios*, and the chelid genera *Platemys*, *Phrynops*, *Chelus*, *Chelodina*, and *Hydromedusa* (Gaffney, 1979a).

Primitive condition: The fused condition seen in *Proganochelys* and all cryptodires is presumably the primitive condition.

Homoplasy: In the MPC, the character distribution is ambiguous due to polymorphism within chelids and pelomedusids. The CI is 0.5 but the character is reversed within the Chelidae and Pelomedusidae.

Discussion: Sutured rami are found in *Araripemys* and *Euraxemys* and were used by Meylan (1996) to unite them in a family Araripemydidae. However, in the MPC this character is polymorphic in chelids and pelomedusids. The chelid distribution suggests that if Gaffney (1977b) is correct, the fused condition is primitive for chelids. In pelomedusids it is fused only in some *Pelusios*, so the sutured condition may be primitive for this group plus *Araripemys*. If this interpretation is correct, the sutured condition evolved once within chelids and once for all remaining pleurodires, being reversed for the Podocnemidoidea (the families Podocnemididae + Bothremydidae).

This character is used in Meylan (1996) and Lapparent de Broin (2000b).

118. Dentary, triturating surfaces: relatively narrow (*Euraxemys*) = 0; wide posteriorly (*Cearachelys*) = 1.

Morphology: Many bothremydids have a lower jaw with a triangular-shaped surface that is much wider posteriorly than anteriorly (fig. 241).

Primitive condition: Relatively narrow jaws, with labial and lingual ridges that are more nearly parallel to each other, are present in the outgroups.

Homoplasy: Podocnemidids evolve broad lower jaws, but these do not have the same morphology as bothremydids. The CI is 0.33, and the character is reversed in *Araiochelys* and the Taphrosphyini, which have narrower jaws. *Araiochelys*, however, is still very similar to *Bothremys*, just narrower. The Taphrosphyini, though, do have a very narrow triturating surface that is morphologically distinct form other bothremydids to the extent they are known.

Discussion: Although lower jaws are represented by many missing data, they are known for each major group (tribes). The triangular or wide shape is synapomorphic for the Bothremydidae, and the reversed, narrow shape is synapomorphic for the Taphrosphyini.

119. Dentary, widely exposed on lateral surface: yes, widely exposed posteriorly (*Euraxemys*) = 0; no, covered posteriorly by surangular (*Bothremys*) = 1.

Morphology: The surangular and coronoid in the tribes Bothremydini and Taphrosphyini are extensively exposed on the lateral surface of the jaw ramus (fig. 241), so that the dentary exposure is relatively small.

Primitive condition: The outgroups have broad exposure of the dentary posteriorly.

Homoplasy: A widely exposed dentary also occurs in the Podocnemididae (fig. 313) but not in *Hamadachelys* or *Brasilemys*.

Discussion: This character (fig. 313) is a synapomorphy for the infrafamily Bothremydodda (the tribes Bothremydini and Taphrosphyini).

120. Surangular, foramen nervi auriculotemporalis: absent (*Proganochelys*) = 0; present (*Podocnemis*) = 1.

Morphology: The foramen nervi auriculotemporalis (fig. 232C, see also Gaffney, 1979a) lies at the posterolateral end of the lower jaw in the surangular. Its absence results in a smooth lateral surface on the surangular (fig. 241).

Primitive condition: The foramen is widely present in pleurodire outgroups and cryptodires, but it seems to be absent in *Proganochelys*.

Homoplasy: None, other than a reversal for the infrafamily Bothremydodda.

Discussion: The absence of the foramen nervi auriculotemporalis is a synapomorphy for the infrafamily Bothremydodda (Bothremydini + Taphrosphyini).

121. Coronoid, wide lateral exposure: no (*Euraxemys*) = 0; yes (*Bothremys*) = 1.

Morphology: In the Bothremydini, the coronoid is exposed ventrolaterally and anteroventrally on the lateral surface of the jaw (fig. 241C).

Primitive condition: The coronoid is typically not exposed widely on the lateral surface of the jaw (fig. 232C). This condition is in *Proganochelys* and most pleurodire outgroups.

Homoplasy: *Araripemys* independently acquires a wide coronoid in the MPC.

Discussion: Unfortunately, none of the Taphrosphyini lower jaws is well enough preserved to allow determination of this character. It only occurs in the tribe Bothremydini within the Bothremydidae.

122. Prearticular, fossa meckelii open anteriorly: no, closed by long angular-prearticular contact (*Euraxemys*) = 0; yes, short prearticular-angular contact (*Bothremys*) = 1.

Morphology: In the lower jaw of most turtles the sulcus cartilaginis meckelii is closed ventrally by the prearticular and angular, which meet in a long suture medial to the sulcus. In the tribes Bothremydini and Taphrosphyini, much of the fossa meckelii is open anteriorly, and the prearticular-angular contact is short (fig. 241D).

Primitive condition: The condition in *Proganochelys*, in which the prearticular-surangular suture begins below the fossa meckelii, is also found in chelids and baenids and is assumed to be the primitive condition for pleurodires.

Homoplasy: The Podocnemididae acquire the more open fossa meckelii independently of the infrafamily Bothremydodda (Bothremydini + Taphrosphyini).

Discussion: This is a synapomorphy for the infrafamily Bothremydodda (Bothremydini + Taphrosphyini). The problem with this character is the few lower jaws known, particularly for the Taphrosphyini.

123. Articular, processus retroarticularis: long and projecting posteriorly (*Bothremys*) = 0; short or absent (*Pelusios*) = 1; long and projecting posteroventrally (*Podocnemis*) = 2.

Morphology: The lower jaw of bothremydids has a processus retroarticularis that projects straight posteriorly (state 0, fig. 241A). It is not an extremely long processus, as in some cryptodires like trionychids, but it is distinctly longer than in chelids, pelomedusids, and euraxemydids. Unfortunately, it is known for only 7 of 29 taxa of bothremydids. In podocnemidids, *Brasilemys*, and *Hamadachelys*, there is also a distinct processus retroarticularis, but it is directed posteroventrally (state 2) and lies below the axis of the jaw ramus (Gaffney, 1979a: fig. 135).

Primitive condition: *Proganochelys* has a long processus retroarticularis (Gaffney, 1990), but cryptodires generally lack one. It is also short or absent in pelomedusids, chelids, and euraxemydids. Although the presence of a processus seems to be primitive for turtles, its absence is primitive for pleurodires.

Homoplasy: The short or absent state of this character is present in Pelomedusoides primitively, but it is reversed for bothremydids. The *Proganochelys* condition is a process with a dorsally open pocket, not seen in bothremydids, supporting the idea that the bothremydid condition is a nonhomologous reversal.

This character is in Antunes and Broin (1988), Meylan (1996), and Lapparent de Broin (2000b).

124. Vertebrae, cervical ribs: present (*Proganochelys*) = 0; absent (*Pelusios*) = 1.

Morphology: Cervical vertebrae of pleurodires (Williams, 1950; Hoffstetter and Gasc, 1969) lack ribs, even in the Jurassic *Platychelys*.

Primitive condition: The presence of cervical ribs is primitive for turtles as they occur in

Proganochelys (Gaffney, 1990) and primitive cryptodires (Gaffney, 1996).

Homoplasy: None within pleurodires.

125. Vertebrae, cervical postzygapophyses fused: all separate (*Proganochelys*) = 0; some fused (*Podocnemis*) = 1.

Morphology: The postzygapophyses of cervicals in some pleurodires unite to form a combined, single curved surface for the articulation of the prezygapophyses (Meylan, 1996: fig. 9).

Primitive condition: Separate postzygapophyses occur in *Proganochelys* and cryptodires, but within pleurodires the primitive condition is equivocal. The one cervical of *Platychelys* is unfused, as are all cervicals of Pelomedusidae. Within chelids, fusion is variable but absent in *Emydura* and *Elseya*. It is likely that the unfused condition is primitive for Pleurodira.

Homoplasy: A problem with this character is the recognition of the form of variability of postzygapophyseal fusion. All cervicals in *Araripemys* and *Euraxemys* show fusion, but in chelids and podocnemidids some cervicals in the column are fused and some are not, and this even varies among species. These are all treated as one character, but this may be too simplistic as it lumps a variety of morphologies that may not be homologous. However, to recognize more character states at this point will only make a series of autapomorphies.

Discussion: The cervicals of *Euraxemys* and *Araripemys* are known, but within Bothremydidae only a few cervicals of *Taphrosphys sulcatus*, *Chedighaii barberi*, and *Cearachelys* are known. *Taphrosphys* and *Chedighaii* show fused postzygapophyses, but the two probably posterior cervicals of *Cearachelys* do not. Because other cervicals of *Cearachelys* could be fused, it has been coded as "?", but all of the cervicals could lack fused zygapophyses.

This character is used in Meylan (1996) and Lapparent de Broin (2000b).

126. Vertebrae, cervical postzygapophyses elevated: separated and relatively low (*Proganochelys*) = 0; extended posterodorsally on neural spine (*Podocnemis*) = 1.

Morphology: The neural spine of the cervicals of living pleurodires (Williams, 1950; Hoffstetter and Gasc, 1969) is extended posterodorsally and bears the postzygapophyses. This also occurs in bothremydids, *Euraxemys*, *Araripemys*, and *Dortoka* (Lapparent de Broin and Murelaga, 1999), but it is absent in *Notoemys* and *Platychelys*.

Primitive condition: The outgroups lack the extended neural spine.

Homoplasy: None known.

Discussion: Lapparent de Broin and Murelaga (1999) used this character in a dataset and figured a cervical for the skull-less taxon *Dortoka*. This character helps unite *Dortoka* with the Eupleurodira.

127. Vertebrae, cervical centra: amphicoelous, platycoelous (*Proganochelys*) = 0; formed articulation is wider than high (*Platychelys*) = 1; formed articulation is higher than wide (*Podocnemis*) = 2.

Morphology: The wider than high condition (state 1) occurs in *Platychelys* and *Notoemys* (Fernandez and Fuente, 1994: fig. 3). It also occurs within Selmacryptodira, but only within Eucryptodira. Unformed articular surfaces are primitive for Selmacryptodira, so the eucryptodiran condition is not reflected in the coding. Although there are few bothremydid cervicals known, they all have cervical centra that are higher than wide (*Cearachelys*, *Chedighaii*, *Taphrosphys*).

Primitive condition: Unformed central articulations are in *Proganochelys*, *Palaeochersis*, and Cryptodira, and this is the presumed primitive condition.

Homoplasy: None in the MPC, but eucryptodires evolve wide centra independent of *Platychelys* and *Notoemys*. The higher than wide condition only evolves once, and that is within the Pleurodira.

Discussion: State 1 is a synapomorphy for *Notoemys* + *Platychelys*. State 2 is a synapomorphy for *Dortoka* + Eupleurodira.

128. Vertebrae, cervical articulation pattern: amphicoelous, platycoelous (*Proganochelys*) = 0; (2))3))4))5))6))7))8) (*Pelusios*) = 1; (2((3((4((5))6))7((8) (*Emydura*) = 2.

Morphology: The articulation patterns of procoelous, opithocoelous, biconvex, and biconcave cervical vertebrae developed particularly by Williams (1950) are based on the articulation surface of the cervical centrum. These are described in Vaillant (1881), Kasper (1903), Williams (1950), and Hoffstetter and Gasc (1969), who also provide an introduction to the turtle vertebral literature. The use of parentheses follows that of Williams (1950) and most authors describing vertebrae and symbolizes the shape of the central articulation.

Primitive condition: The unformed central surface (Gaffney, 1990, 1996) is primitive for turtles, but Lapparent de Broin and Murelaga (1999) have argued that the chelid condition may be primitive for Pleurodira. According to those authors, *Notoemys*, *Platychelys*, and *Dortoka* all probably have state 2, the chelid articular pattern (see Lapparent de Broin and Murelaga, 1999: 153). This is based on only a few cervicals, but they do show that these taxa do not have the procoelous condition of cervicals 3–8. We have accepted the Lapparent de Broin and Murelaga (1999) hypothesis and coded *Platychelys*, *Notoemys*, and *Dortoka* as state 2, which then becomes the state primitive for Pleurodira, not the unformed (state 0) as used by Gaffney (1996). When the taxa lacking skull data are excluded, this issue becomes moot, as chelids are the only included taxon with the character.

Homoplasy: None. Note, however, that a complete vertebral series is as yet unknown for any bothremydid. *Cearachelys* has three cervicals of unknown position, all procoelous.

Discussion: The procoelous condition (state 1) is a synapomorphy for Pelomedusoides in the MPC, with or without shell-only taxa. It is also not affected by coding of *Platychelys*, *Notoemys*, and *Dortoka* with state 2 or with "?".

This character is used in Antunes and Broin (1988).

129. Vertebrae, caudal articulation pattern: platycoelous, amphicoelous (*Proganochelys*) = 0; formed centra but articulations vary, opisthocoelous and procoelous (*Notoemys*) = 1; all procoelous (*Pelusios*) = 2.

Morphology: The central articulations of the caudals of pleurodires are figured in Tronc and Vuillemin (1974: pl. 13, figs. 4–6, *Erymnochelys*), Gaffney (1990: fig. 130, *Podocnemis*), Meylan (1996: fig. 2, *Araripemys*), and Lapparent de Broin and Murelaga (1999: fig. 6, *Dortoka*).

Primitive condition: As with cervicals, the presumed primitive condition is unformed: amphicoelous or platycoelous.

Homoplasy: None in the MPC, but the sparse distribution of even partially articulated tails may mask a more complex character distribution. Procoelous caudals, as well as many other patterns, appear with Cryptodira.

Discussion: Character state 2 is a synapomorphy for Chelidae + Pelomedusoides (Eupleurodira) and has been known for some time (it was used by Lapparent de Broin and Murelaga, 1999). Character state 1 is also from Lapparent de Broin and Murelaga (1999) and, although ambiguous, it may reflect a pattern of diverse central articulations that are at least not all procoelous. Nonetheless, this is a weak character state, known only from disarticulated caudals in *Dortoka* (Lapparent de Broin and Murelaga, 1999) and two from *Platychelys* (Bräm, 1965) that show opisthocoely as well as procoely.

130. Shoulder girdle, coracoid foramen: present (*Proganochelys*) = 0; absent (*Podocnemis*) = 1.

See Gaffney (1990) for description; also see Rougier et al. (1995).

131. Shoulder girdle, coracoid shape: coracoid a flat plate (*Proganochelys*) = 0; coracoid columnar (*Podocnemis*) = 1.

See Gaffney (1990) for description; also see Rougier et al. (1995).

132. Pelvic girdle, tenth thoracic centrum: not incorporated into sacrum (*Proganochelys*) = 0; incorporated into sacrum (*Pelusios*) = 1.

Morphology: Broin and Murelaga (1999: pl. 12, fig. 5: *Peltocephalus*) figured the sacrum, showing this character, but this area is not well described in the literature (see also Fraas, 1913: *Proterochersis*; Tronc and Vuillemin, 1974: *Erymnochelys*; and Fernandez and Fuente, 1994: *Notoemys*). The presence of the tenth thoracic rib in the sacrum can be determined by the suturing of the distal end to the ilium. The ilium itself is also sutured to the carapace.

Primitive condition: In *Proganochelys* (Gaffney, 1990) the tenth thoracic rib is fused to the ninth costal, and this is presumably the primitive condition. In cryptodires, the tenth rib is usually free.

Homoplasy: None known, but the character is not known in most bothremydids and in many other extinct pleurodires.

Discussion: This character is a synapomorphy for Pleurodira and is presumably related to the sutured pelvis-carapace.

133. Pelvic girdle, pelvis sutured to shell: pelvis articulates only by ligaments, no sutures (*Proganochelys*) = 0; all three bones of pelvis sutured to shell (*Pelusios*) = 1.

Morphology: This character is figured in Rütimeyer (1873: pl. 8), Bräm (1965: pl. 1), Gaffney (1990: figs. 143, 144 for the pelvis alone of *Podocnemis*), and Lapparent de Broin and Murelaga (1999: pl. 12). Considering how widely used this character is for Pleurodira, it is not well described in the literature.

Primitive condition: The outgroups *Proganochelys* and Cryptodira have a free pelvis, which is the primitive condition (Gaffney, 1990). Rougier et al. (1995) described *Palaeochersis* as having a sutured pelvis. Examination of this material by the senior author shows that the pelvis in *Palaeochersis* is not sutured to the carapace or plastron, but rather it has been crushed dorsoventrally to produce a condition that can be mistaken for suturing. The pelvis and adjacent shell surfaces show no signs of sutures, rather they are very similar to the morphology in *Proganochelys*.

Homoplasy: None known.

Discussion: This is a long-used synapomorphy for Pleurodira.

Lapparent de Broin and Murelaga (1999: 150) added a second state, “ligamentous more firmly linked producing a true articulation scar”, and coded it for *Proterochersis* in their dataset. Extensive study of the known material of *Proterochersis* by two of the authors (E.S.G. and P.A.M.) shows no difference in the type of attachment between pelvis and shell in *Proterochersis* and all other pleurodires, so we reject this second character state.

134. Pelvic girdle, dorsal part of ilium columnar: no, inclined with anterior and posterior processes (*Proganochelys*) = 0; columnar, expanded mediolaterally (*Podocnemis*) = 1.

Morphology: In pleurodires the ilium is a relatively thick columnar element, not flattened with anterior and/or posterior processes as in *Proganochelys* and cryptodires (Gaffney, 1990: figs. 143, 144. It is also oriented more vertically in pleurodires than in other turtles.

Primitive condition: In *Proganochelys* the ilium is expanded anteriorly and posteriorly, forming a horizontally oriented, inclined structure. Cryptodires have a wide diversity of ilium shapes, but primitively they have an inclined, mediolaterally flattened shape, similar to *Proganochelys*.

Homoplasy: None known.

Discussion: This character attempts to reflect further information from the pelvic morphology of pleurodires. Perhaps it is correlated with the suturing of the pelvis to the shell.

135. Pelvic girdle, pelvis narrow: ilia and acetabula relatively far from midline (*Proganochelys*) = 0; ilia and acetabula close to midline (*Podocnemis*) = 1.

Morphology: Although this character is somewhat subjective, all pleurodires do have the ilial column and acetabulum closer to each other and to the midline than in other turtles (i.e., *Proganochelys* and cryptodires), producing a narrower pelvis. Presumably this is related to the sutured pelvis-shell. Gaffney (1990: fig 144) compared *Proganochelys*, a cryptodire, and a pleurodire pelvis, showing this condition.

Primitive condition: The wide pelvis of *Proganochelys* and cryptodires is primitive.

Homoplasy: None known; however, a complete pelvis is not preserved for most bothremydids and many other extinct taxa.

Discussion: This character is used by Lapparent de Broin and Murelaga (1999), it is another pleurodire synapomorphy.

136. Pelvic girdle, thyroid fenestra: separate (*Proganochelys*) = 0; confluent (*Podocnemis*) = 1.

Morphology: The thyroid fenestrae of *Proganochelys*, a pleurodire, and a cryptodire are figured in Gaffney (1990: fig. 144). In the advanced state the fenestra is not subdivided down the center by bone.

Lapparent de Broin and Murelaga (1999) divided this character in a series of states based on the fenestra size. *Proterochersis* has slightly larger fenestrae than does *Proganochelys*, but they are still relatively small and widely separated by bone. Rather than calling this a separate state, we identify both as primitive. *Platychelys* has fenestrae that are not separated by bone but are somewhat smaller than those in Eupleurodira. Rather than making this a separate state, we identify it as the advanced condition because the fenestrae are confluent.

Primitive condition: The small, widely separated fenestrae of *Proganochelys* are primitive.

Homoplasy: It is likely that the confluent thyroid fenestrae arose separately in cryptodires and pleurodires.

Discussion: This character is used in Rougier et al. (1995) and Lapparent de Broin and Murelaga (1999).

137. Humerus, shoulder on lateral side of head: present (*Proganochelys*) = 0; absent (*Podocnemis*) = 1.

Morphology: The humerus of pleurodires has a head that is hemispherical and slightly separated from the lateral and medial processes (Zangerl, 1948: fig. 13, *Chedighaii*; Gaffney, 1975a: fig. 12, *Taphrosphys*; Gaffney, 1990: fig. 149, *Podocnemis*; Fernandez and de la Fuente, 1994: fig. 6, *Notoemys*). The curved shoulder found on the lateral side of the articular head in *Proganochelys* and cryptodires is absent in pleurodires.

Primitive condition: *Proganochelys* has a shoulder and an articular head that is not as spherical as in pleurodires. This is presumed to be primitive.

Homoplasy: None in the MPC; however, this character gets harder to identify when looking within various eucryptodire groups. Also, the humerus is not known for many bothremydids and other extinct pleurodires.

Discussion: This is a pleurodire synapomorphy. *Proterochersis* lacks a humerus, however.

138. Carapace, cervical scale: present (*Emydura*) = 0; absent (*Podocnemis*) = 1.

Morphology: The cervical or nuchal scale is an unpaired scale on the anterior margin of the nuchal bone of most turtles. Except in *Hydromedusa* (see Wood and Moody, 1976), it lies between the first marginal scales. It is absent in Pelomedusoides (fig. 265).

Primitive condition: A cervical scale is present in *Proganochelys* (Gaffney, 1990), in primitive cryptodires (Gaffney, 1979b), in the primitive pleurodires *Proterochersis*, *Platychelys*, and *Notoemys* (Fernandez and de la Fuente, 1994), and in nearly all chelids. Presence of this scale is clearly the primitive condition.

Homoplasy: Loss of the cervical scale occurs independently within the Pleurodira (all members of the Pelomedusoides and one chelid, *Elseya*, fide Pritchard and Trebbau, 1984) and Cryptodira (some testudinids). It is variable within *Dortoka* (Lapparent de Broin and Murelaga, 1999).

Discussion: The absence of a cervical scale is a synapomorphy for the Pelomedusoides.

This character was used by Antunes and Broin (1988), Broin (1988), Gaffney (1988), Gaffney and Meylan (1988), Meylan (1996), Tong et al. (1998), and Lapparent de Broin and Murelaga (1999).

139. Carapace, nuchal bone width: nuchal bone two or more times wider than length (*Platychelys*) = 0; nuchal bone width greater than length but less than two times (*Euraxemys*) = 1; nuchal bone width approximately equals length (*Foxemys*) = 2; nuchal width less than length (*Teneremys*) = 3; nuchal bone greatly emarginated (unique to *Araripemys*) = 4.

Morphology: The width versus length of the nuchal bone in dorsal view (figs. 254–274) is arbitrarily subdivided into four states. This character is used in Lapparent de Broin and Murelaga (1999); we have slightly modified it. *Araripemys* (Meylan, 1996) has a uniquely emarginated nuchal, making it hard to compare with other turtles, so it is given state 4, unique to that taxon.

Primitive condition: Both *Proganochelys* and primitive cryptodires have a very wide (state 0) nuchal, and this occurs in *Platychelys* and *Notoemys*, but the character is indeterminate in *Palaeochersis* and *Proterochersis*.

Homoplasy: Quite a lot, within Selmacryptodira, Chelidae, Pelomedusidae, and Podocnemididae, but for this analysis the CI is 0.66. Nuchal width is often variable within a species. Nonetheless, some patterns are apparent in the MPC.

Discussion: The change from state 0 to state 1 is a synapomorphy for *Dortoka* + Eupleurodira, the parvorder Megapleurodira, and state 1 is primitive for nearly all groups in Eupleurodira. State 3 is unique to *Teneremys* and state 4 is unique to *Ararip-*

emys. *Foxemys* and *Polysternon* are united by state 2.

This character is used in Lapparent de Broin (2000b), who agreed that the wide condition is primitive.

140. Carapace, pygal notch: present, wide and shallow (*Proganochelys*) = 0; present, narrow and spherical (unique to *Proterochersis*) = 1; absent, margin smooth (*Podocnemis*) = 2.

Morphology: The pygal notch in *Proganochelys* is figured in Gaffney (1990: figs. 69–77) and in *Palaeochersis* by Rougier et al. (1995). The pygal notch of *Proterochersis* has not been figured. The absent condition can be seen in nearly all other turtles.

Primitive condition: Presumably, the presence of a pygal notch is primitive for turtles.

Homoplasy: None, although some cryptodires acquire an emarginated posterior carapace margin.

Discussion: The posterior carapace emargination or pygal notch in *Proterochersis* is so different from that in *Proganochelys* that a separate state is identified for it. In this we follow Lapparent de Broin and Murelaga (1999) who also used two states for the pygal notch. Rougier et al. (1995) used "marginals not separated by an anal notch", but we think that this obscures a more complex situation.

141. Carapace, neural series completeness: neurals reach suprapygal (*Euraxemys*) = 0; to eighth costals (*Podocnemis*) = 1; to seventh costals (*Foxemys*) = 2; to sixth costals (*Chedighaii*) = 3; neurals absent or discontinuous (*Araiochelys, Emydura*) = 4.

Morphology: The neural bones of the carapace usually make up the midline of the shell between the nuchal and suprapygal. In most turtles they form a continuous series between the nuchal and suprapygal; in others, some or all costals meet on the midline. In some forms neurals are completely absent. The neurals reaching the suprapygal and forming a complete series is state 0 (fig. 254), reaching to the eighth costals is state 1 (fig. 272), reaching to the seventh costals is state 2 (fig. 259), reaching to the sixth costals is state 3 (fig. 264), and discontinuous or absent neurals is state 4 (fig. 263).

Primitive condition: The neural series of *Proganochelys* is not completely known. However, the neural series in such primitive cryptodires as *Kayentachelys* and *Pleurosternon* is complete (state 0), as are those of *Platychelys* (Bräm, 1965) and *Notoemys* (Fernandez and de la Fuente, 1994). The neural series is complete among Pelomedusoides in *Euraxemys*, *Cearachelys*, and some *Araripemys*.

Homoplasy: Interruption of a complete neural series by costals meeting on the midline occurs within Podocnemididae and Bothremydidae. Among the Cryptodira, trionychids, kinosternids, and dermatemydids all have posterior costals meeting on the midline. *Cearachelys* is apparently a reversal in which the complete neural series is reacquired. The pelomedusids independently lose a full neural series. The CI is 0.42.

Discussion: State 1 is a synapomorphy for the epifamily Podocnemidinura, and state 2 has equivocal support for Bothremydidae, except for *Cearachelys*, which has a complete set of neurals.

A variant of this character is used in Antunes and Broin (1988), Meylan (1996), Tong et al. (1998), Lapparent de Broin and Murelaga (1999), and Lapparent de Broin (2000b).

142. Carapace, iliac scar position: iliac scar absent (*Chelydra*) = 0; iliac scar restricted to costals 7 and 8 (*Pelusios*) = 1; iliac scar on costals 7, 8, and suprapygal (*Taphrosphys*) = 2.

Morphology: The ilium of pleurodires articulates with the bones of the carapace in a sutural contact. The elements with which the ilium articulates vary among species in the suborder (Lapparent de Broin and Murelaga, 1999: pl. 12). In some the articulation is only with costals 7 and 8, and in others the suprapygal and or peripheral elements are also involved. For example, in *Notoemys* the ilium articulates with the eighth costals and suprapygal, while in *Platychelys* it articulates with the eighth costals, suprapygal, and eleventh peripherals (Fernandez and de la Fuente, 1994). State 1 is the scar on costals 7 and 8 (Lapparent de Broin and Murelaga, 1999: pl. 12, fig. 5), and state 2 is the scar on costals 7, 8, and the suprapygal (fig. 265).

Primitive condition: For turtles, the absence of a scar is primitive; the two states are derived. Contact of the ilium in *Platychelys* includes the eighth costals, suprapygal, and eleventh peripherals (Fernandez and Fuente, 1994). In *Araripemys*, the ilium contacts the seventh and eighth costals and the suprapygal. Thus, it appears that contact to the suprapygal may be primitive for pleurodires. Antunes and Broin (1988) argued that the inclusion of the suprapygal in this contact in bothremydids is a reversal to the primitive condition. However, Lapparent de Broin (2000b: 45) considered suprapygal contact primitive for Pelomedusoides. We are uncertain of the evidence that contact to the suprapygal is lost and regained.

Homoplasy: There is individual variation in this contact within the specimens of *Chedighaii barberi* figured by Zangerl (1948, one figure shows suprapygal contact and one does not) and within recent specimens of *Podocnemis expansa* and *P. unifilis* seen by the senior author.

Discussion: Lapparent de Broin and Werner (1998) indicated that broad contact with costal 8 and narrow contact with neural 7 and the suprapygal are the general condition for bothremydids. However, contact in *Kurmademys* is on costals 7 and 8 only (ISIR 278), so the issue is still ambiguous. The area is known in only a few bothremydids.

A related character is used in Lapparent de Broin and Murelaga (1999), which reflects the scar shape. It is also used in Antunes and Broin (1988) and Lapparent de Broin (2000b).

143. Carapace, first costal length: costal 1 shorter or equal to twice the length of costal 2 (*Euraxemys*) = 0; costal 1 more than twice the length of costal 2 (*Foxemys*) = 1.

Morphology: The elements of the anterior portion of the shell of turtles include a first costal bone that is longer anteroposteriorly than the more posterior costals (state 1, fig. 259). In the most primitive turtles, the first costal is not longer than more posterior costals. However, in many forms the first costal is anteroposteriorly long, often two or more times longer than the second costal. This is a gradational character that is arbitrarily defined as the condition where the anteroposterior length of costal 1 is more than twice that of the second costal. This identifies the more extreme end of a gradational character and may be slightly more objective than dividing the character into more states.

Primitive condition: In *Proganochelys* and *Platychelys* the first costal is approximately as long as those of the more posterior costals. This is the best evidence for the primitive condition of this character in pleurodires.

Homplasy: The first costal is anteroposteriorly longer than the more posterior costals in most turtles. However, first costals that are more than twice as long as the second are not common, but they do occur in *Dortoka*, *Kurmademys*, Bothremydini, Taphrosphyini, *Podocnemis*, and some chelids. In the MPC, the CI is 0.33 and the character arises three times.

Discussion: In the MPC, this character is synapomorphic for the infrafamily Bothremydodda (consisting of the tribes Bothremydini and Taphrosphyini), but its rather subjective nature is a problem.

144. Carapace, position of four-sided neural: neural 1 (*Euraxemys*) = 0; neural 2 (*Cearachelys*) = 1; neural 3 (*Araripemys*) = 2; four-sided neural absent (*Platemys*) = 3.

Morphology: Characterizing the neural morphology is a very dubious business. Multiple attempts have been made to characterize neural bone morphology, and none has been satisfactory. One way is to count the sides contacting surrounding elements, considering each contact a side (Auffenberg, 1974). This produces a formula running from anterior to posterior, as in *Euraxemys*: 4-6-6-6-6-6-6-6. In this case the four-sided or quadrangular neural is first (state 0, fig. 265). The four-sided neural may be the second, as in *Cearachelys*: 6-4-6-6-6-6-6-4 (state 1, fig. 258), or it may be the third neural, as in *Araripemys*: 6-6-4-6-6-6-6-4 (state 2; Meylan, 1996: fig. 1). In most Pleurodira, the posterior neurals are all six-sided, but the position of the reversed or four-sided neural varies. In some cases, including some pleurodires, reversal in neural orientation occurs via two consecutive five-sided neurals, as in *Brasilemys* (Lapparent de Broin, 2000b: fig. 4).

Primitive condition: Only neurals 4–7 are known for *Proganochelys*, and these all seem to be six-sided. Meylan and Gaffney (1989) have argued that the primitive condition for *Casichelydia* is 4-6-6-6-6-6-6, and this is what we have chosen for state 0. However, *Kayentachelys* (Gaffney et al., 1987) has the second neural four-sided (although there is individual variation), *Platychelys* and *Notoemys* have the second and fourth neurals four-sided, and *Proterochersis* is unknown, so the primitive neural pattern is still unclear.

Homoplasy: In the MPC, the four-sided first neural is primitive and pervasive throughout the pleurodires, with the other conditions mostly appearing independently, with a CI of 0.75. The neural 2 four-sided condition does unite *Cearachelys* with the two possible *Galianemys* shells, AMNH 30550 and AMNH 30551. In any case, these characters occur widely as individual variation among many species of turtles, and they can be highly variable within species in some families (Auffenberg, 1976; Meylan, 1984, 1987).

Discussion: Lapparent de Broin and Murelaga (1999) used a variation of this character in their dataset. Lapparent de Broin (2000b: 45) implied that state 1 may be primitive for Pelomedusoides. In the MPC analyzed here, state 1 is synapomorphic for Cearachelyini (supporting the AMNH 30550 and AMNH 30551 shells as belonging to *Galianemys*) and, independently, for *Notoemys* + *Platychelys*.

145. Carapace, neural series pattern: irregular, neurals 2 and 4 quadrangular, alternating in width (*Platychelys*) = 0; irregular, width even (*Kayentachelys*) = 1; regular, most hexagonal, coffin-shaped (*Podocnemis*) = 2; neurals absent (*Platemys*) = 3; neurals discontinuous (*Araiochelys*) = 4.

Morphology: This is another feeble attempt to use neural diversity as a character. Lapparent de Broin and Murelaga (1999) and Fuente and Iturralde-Vinent (2001) used "regular" versus "irregular" to distinguish the common casichelydian pattern of one quadrangular neural (in the anterior part of the series) followed by hexagonal, coffin-shaped neurals, from the "irregular" neural pattern of alternating contacts and widths. Lapparent de Broin and Murelaga (1999) used the "irregular" as one state, but this is a diverse group, and we have subdivided it. The taxa placed in this group by Lapparent de Broin and Murelaga (1999) all have more than two quadrangular neurals in common, but the position and width of these neurals vary. They also have a high occurrence of asymmetry, with many five- and seven-sided neurals. *Kayentachelys* has the neural width the same for the series (state 1, Gaffney et al., 1987), while *Notoemys* (Fernandez and Fuente, 1994) and *Platychelys* (Lapparent de Broin, 2001) have an alternating width pattern (state 0). *Dortoka* (Lapparent de Broin and Murelaga, 1999), irregular but somewhat unique, is also coded as state 0. The common pattern, state 2, is seen in the Eupleurodira (fig. 265). *Araiochelys* has the discontinuous condition, state 4 (fig. 263).

Primitive condition: The primitive condition would be "irregular" as one state, but as we have subdivided them, there is no clear primitive pattern. We have arbitrarily chosen the *Platychelys* condition as "0". Note that the neurals known for *Proganochelys* (4–7) do show the "regular", coffin-shaped pattern, so state 2 could be argued as primitive. Because many neurals are missing in *Proganochelys*, it is coded as "?".

Homoplasy: The "regular", state 2 condition has evolved at least once within pleurodires and at least once within cryptodires.

Discussion: This character is from Lapparent de Broin and Murelaga (1999), but they basically recognized only two states outside of chelids. We have recognized more states in the "irregular" condition, because the absence of "regular" includes a series of states that are not the same. It is difficult to specifically define patterns in common because bilateral asymmetry is common among the early pleurodire shells. Nonetheless, the "regular" pattern (state 2) does support a group, the Eupleurodira.

146. Carapace, neural number: more than eight (*Kayentachelys*) = 0; eight (*Cearachelys*) = 1; seven (*Foxemys*) = 2; six or fewer (*Kurmademys*) = 3.

Morphology: The neural bones are easily counted, but some may not be fused to the underlying vertebral spines and might not be considered separate neurals (e.g., the posterior neurals of *Kayentachelys* and *Platychelys*, but this can also occur as an individual variation throughout chelonians).

This is the argument for making this a separate character from character 141 (see below).

Primitive condition: This is difficult to assess because *Proganochelys* and *Palaeochersis* lack complete series. We have chosen the "more than eight" as primitive because of its occurrence in outgroups such as *Kayentachelys* and *Platychelys*.

Homoplasy: Even though the CI is 0.42, homoplasy is extensive for these character states due to variation within chelids, pelomedusids, cryptodires, *Platychelys*, and *Araripemys*. The loss of neurals within Bothremydidae could be more widespread than shown in the MPC, because the generically indeterminate shells from Tunisia (e.g., "*Eusarkia*", "*Gafsachelys*") show neural loss, and some of them seem to be Taphrosphyini.

Discussion: This is very similar to character 141, which might be considered just another way of counting neurals. Deleting either results in the same MPC, but deleting them does affect the placement of the poorly known shell-only taxa.

Although this is a widely variable character, the MPC shows that seven neurals (state 2) is a synapomorphy for podocnemidids + bothremydids + *Teneremys*. Similarly, despite independent acquisition in cryptodires and elsewhere, eight neurals (state 1) is a synapomorphy for pleurodires, with *Proterochersis* unknown.

A version of this character appears in Lapparent de Broin and Murelaga (1999).

147. Carapace, length of contact between peripheral 1 and costal 1 in dorsal view: no contact due to large nuchal (*Dortoka*) = 0; wide contact so that anterior margin of peripheral 1 is less than twice the length of costal 1 contact (*Rosasia*) = 1; narrow contact, so that anterior margin of peripheral 1 is twice or more the length of costal 1 contact (*Foxemys*) = 2; no contact due to small nuchal (unique to *Araripemys*)= 3.

Morphology: This character is a modification of one used by Lapparent de Broin and Murelaga (1999). Their character states are: "wide contact (0), wide contact or no contact (1), wide or narrow contact (2)" (Lapparent de Broin and Murelaga, 1999: 150). Apart from their not inconsiderable entertainment value, the state characterizations are useless. In an effort to squeeze something objective out of this mess, we have arbitrarily divided a fairly continuous character into wide (state 1, fig. 261) and narrow (state 2, fig. 259) by comparing the relative width of the anterior and posterior margins.

Primitive state: The character is not known for *Proganochelys, Australochelys*, *Palaeochersis*, and *Proterochersis*, and there is no obvious distribution pattern in the MPC for a primitive condition for turtles. The state 0 was chosen arbitrarily.

Homoplasy: Lots. The width of the contact between the first peripheral and the first costal is highly variable in turtles. However, the condition in *Dortoka* with anterolateral notches in the nuchal for the first peripherals seems to be autapomorphic. Although the CI is merely 0.33 due to rampant equivocality, state 2 appears six times independently in the MPC, and state 1 appears seven times.

Discussion: The narrow contact could be a synapomorphy for eupleurodires, although it is variable in pelomedusids (and probably in chelids, if enough shells are examined). The first peripheral shape could be characterized in other ways, comparing margin length with costal length, for example, but there does not seem to be any advantage in doing this.

This character is from Lapparent de Broin and Murelaga (1999) and, even as modified, we use it with reservations, but it reflects our effort to include as much of Lapparent de Broin's work on shells as possible.

148. Carapace, axillary process contacts first costal: no contact (*Proganochelys*) = 0; contact present, separated from posterior margin, may be placed in middle of costal (*Chedighaii*) = 1; contact present, placed on posterior border close to second costal (*Dortoka*) = 2.

Morphology: The dorsal process of the hyoplastron may contact the first costal and form a sutural surface. Lapparent de Broin and Murelaga (1999) used this character as two states, and we follow that here. State 1 is a contact area that is often curved and lies in the middle of the costal or at least separated from the posterior edge (Zangerl, 1948: fig. 7, *Chedighaii*). In state 2 (Lapparent de Broin and Murelaga, 1999: pl. 3, fig. 12a), the axillary buttress lies on the posterior edge of costal 1, very close to the contact with costal 2.

Primitive condition: *Proganochelys* and *Kayentachelys* have no axillary buttress contact on the first costal, and this is presumably the primitive state.

Homoplasy: This character has reversals within chelids, pelomedusids, and podocnemidids, as well as within *Taphrosphys sulcatus*. Probably a more extensive study of recent pleurodire shells would show more within-species variation, although the CI is 0.5.

Discussion: Although the character shows a fair amount of homoplasy at the generic and specific levels, state 1 is synapomorphic for the Bothremydidae and state 2 pulls together *Dortoka* and eupleurodires.

Lapparent de Broin and Werner (1998) have an extensive discussion of the axillary buttress meeting the carapace in pleurodires. Unfortunately, most of the literature on pleurodire shells lacks figures and detailed morphology on the internal shell morphology, such as buttress attachments, limiting the value of this and other internal shell characters.

149. Carapace, axillary process extent on ventral surface of peripherals: reaches peripheral 2 (*Platychelys*) = 0; reaches anterior margin of peripheral 3 (*Emydura*) = 1; reaches onto main body or posterior edge of peripheral 3 or is restricted to peripheral 4 (*Chedighaii*) = 2.

Morphology: The axillary process of the hyoplastron can extend anteriorly onto the peripherals, as well as medially, onto the first costal. The character states are continuous but can be divided because it is easy to see the sutural area separated by interperipheral sutures. State 0, the buttress reaching the second peripheral, can be seen in *Proganochelys* (Gaffney, 1990: fig. 102). In state 1 the buttress reaches nearly to the peripheral 2–peripheral 3 contact, which can be seen in some chelids and some podocnemidids (Tronc and Vuillemin, 1974: pl. 13, fig 1). In state 2 the buttress reaches the main body of peripheral 3 (Zangerl, 1948: fig. 4).

Primitive condition: The anterior extension of the axillary buttress to peripheral 2 is found in *Proganochelys*, and it seems to be primitive for turtles.

Homoplasy: Except for homoplasy within chelids and podocnemidids, and a reversal in MNHN GDF 801, this character shows no reversals or homoplasy within pleurodires.

Discussion: The state 2 condition, restriction of the axillary contact to the middle or posterior part of peripheral 3, is a synapomorphy for *Dortoka* + Eupleurodira.

This character is used by Lapparent de Broin and Werner (1998) and Lapparent de Broin and Murelaga (1999).

150. Carapace, inguinal buttress: short or absent, not making extensive contact with costal 5 (*Proganochelys*) = 0; inguinal buttress of hypoplastron contacts costal 5, extending medially onto it (*Chedighaii*) = 1.

Morphology: This character is best seen in a ventral view of the fifth costal, which shows the articulation surface. When the plastron is present, the contact area is usually obscured. *Proganochelys* shows state 0 (Gaffney, 1990: fig. 76) and Lapparent de Broin and Murelaga (1999) show state 1 for *Dortoka* (Lapparent de Broin and Murelaga, 1999: fig. 1) and *Polysternon* (Lapparent de Broin and Murelaga, 1999: pl. 5).

Primitive condition: *Proganochelys* has no inguinal buttress contact (state 0).

Homoplasy: State 1 has evolved at least three times in the MPC and is variable within the Pelomedusidae and the Podocnemididae.

Discussion: This character supports uniting *Teneremys* and the Podocnemidoidea. This character is used by Lapparent de Broin and Murelaga (1999) and Fuente and Iturralde-Vinent (2001).

151. Carapace, supramarginal scales: 12 or more pairs (*Proganochelys*) = 0; 3 pairs (*Proterochersis*) = 1; absent (*Podocnemis*) = 2.

Morphology: Supramarginal scales showing states 0 and 1 are figured in Gaffney (1990: fig. 105). Their absence, state 2, can be seen in figure 264.

Primitive condition: *Proganochelys* and *Palaeochersis* have 12 or more supramarginals.

Homoplasy: The most parsimonious explanation for the distribution of this character in the MPC requires the reappearance of supramarginals in *Platychelys* and *Proterochersis*. The absence of supramarginals in nearly all cryptodires requires that state 1, three pairs of supramarginals in the earliest pleurodires, evolve from state 2, no supramarginals. Although this seems unlikely, it is apparently the case in *Macrochelys* (P.A.M., personal obs.), and the loss of supramarginals in cryptodires and pleurodires independently, the more likely hypothesis as far as supramarginals are concerned, is not supported by the MPC.

Discussion: Total loss of supramarginals, state 2, is a synapomorphy for Casichelydia in the MPC. State 1, three supramarginals, evolves twice (or is lost once) within that group. As discussed above, the reappearance of supramarginals seems unlikely, and it is only one step away from the independent loss of them within pleurodires and in cryptodires.

This character was used for Eupleurodira by Gaffney and Meylan (1988) and in datasets by Lapparent de Broin and Murelga (1999) and Fuente and Iturralde-Vinent (2001).

152. Carapace, vertebral scale width: equal to or wider than pleural scales (*Proterochersis*) = 0; narrower than pleural scales (*Foxemys*) = 1.

Morphology: State 0, wide vertebrals, is figured in Gaffney (1990: fig. 105); narrow vertebrals, state 1, is figured in figure 264. The wide vertebrals of *Proterochersis*, *Platychelys*, and *Notoemys* are distinct from *Dortoka* and Eupleurodira, with their narrow ones.

Primitive condition: *Proganochelys* has wide vertebrals, state 0.

Homoplasy: Narrow vertebrals have evolved twice, once within Selmacryptodira and once within Pleurodira.

Discussion: Some specimens of *Platychelys* seem to have vertebral scales that are about as wide as some of the pleural scales, but others have wider vertebrals.

This character is a synapomorphy for *Dortoka* + Eupleurodira.

153. Carapace, vertebral scale 1 reaches anterior margin of shell: no, first marginal scales meet on midline (*Podocnemis*), or cervical scale is present (chelids) = 0; yes (*Araripemys*) = 1.

Morphology: In most turtles the first marginal scales and the cervical scale or marginal scales alone (Pelomedusoides) intervene between the first vertebral scale and the shell margin. In MNHN GDF 801 ("*Platycheloides* cf. *nyasae*" of Broin, 1980: pl. 1) and *Araripemys*, the first marginal scales do not meet on the midline, and the first vertebral reaches the anterior shell margin (Meylan, 1996: fig. 1).

Primitive condition: First marginal scales meeting medially occurs in all Pelomedusoides outgroups.

Homoplasy: The character occurs twice, independently, in the MPC.

Discussion: This character does not form groups in the MPC, more evidence of staunch objectivity. Or poor judgment.

154. Carapace, nuchal embayment: absent (*Emydura*) = 0; present (*Chedighaii*) = 1.

Morphology: The anterior margin of the nuchal bone is curved, concave anteriorly, and centered on the midline in this character (fig. 264). When the margin is straight or convex anteriorly, the character is absent (fig. 265). A slight groove where the sulcus separates the first two marginals is not an embayed nuchal.

Primitive condition: Although the anterior margin of the nuchal is recessed from the peripherals in *Proganochelys*, and does not look like the condition in bothremydids, we have coded it as embayed. *Kayentachelys* also has a concave edge to the nuchal, but it has a different shape from the incised V-shape of *Chedighaii*.

Homoplasy: The embayed condition seems to have arisen at least six times, as reflected in the low CI of 0.2.

Discussion: The embayed nuchal occurs in three of the five Bothremydini species in which it is known, so it might be interpreted as a tribe Bothremydini synapomorphy. It supports uniting *Teneremys* and MNHN GDF 801.

This character is in Antunes and Broin (1988).

155. Carapace, first thoracic rib: large (close to size of first costal rib) and separated form first costal rib (*Platychelys*) = 0; small (smaller than first costal rib) and closely attached to first costal rib (*Podocnemis*) = 1.

Morphology: State 0 is clear in *Proganochelys* (Gaffney, 1990: figs. 76, 77) in which the first thoracic rib is as large as the first costal (= second thoracic) rib and is widely separated from it. *Proterochersis*, *Notoemys*, and *Platychelys* have smaller first thoracic ribs that are closer to the first costal rib than in *Proganochelys*, but they are not as small or as close as in other pleurodires. Furthermore, the degree of proximity of the two ribs and the relative size of thoracic rib 1 vary among *Proterochersis*, *Platychelys*, and *Notoemys*. Lapparent de Broin and Murelaga (1999) and Fuente and Iturralde-Vinent (2001) used four character states to reflect these differences. However, this only produces unique, autapomorphic character states for *Platychelys* and *Notoemys*, losing some potential information. We take a more inclusive view of first thoracic rib size and only use two states. State 1 is figured in Tronc and Vuillemin (1974: pl. 13, fig 1).

Each rib that is associated with a thoracic vertebra can be identified by the number of that vertebra. After the first thoracic rib, each rib is also fused distally to a costal bone and can be identified as a costal rib of a particular number. Because the first thoracic rib has no associated costal bone, the numbering of the following ribs is offset so that thoracic rib 2 is also costal rib 1, thoracic rib 3 is costal rib 2, and so on. There is no preferred identification of the rib heads as to thoracic or costal.

Primitive condition: *Proganochelys* shows the primitive state.

Homoplasy: None known, but *Notoemys* and *Platychelys* may be considered equivocal because the character is gradational.

Discussion: The eupleurodires + *Dortoka* have state 1; *Notoemys* may also have this state, however.

This character is used in Gaffney et al. (1991), Lapparent de Broin and Murelaga (1999), and Fuente and Iturralde-Vinent (2001).

156. Carapace, costovertebral tunnel: wide anteriorly and posteriorly only (*Proganochelys*) = 0; wide for entire length (*Platychelys*) = 1; narrow for entire length (*Chedighaii*) = 2.

Morphology: The costovertebral tunnel is the space formed between the free part of the thoracic rib and the overlying costal bone; the thoracic centrum defines it medially. State 0 is figured in Gaffney (1990: fig. 78), and state 1 is figured in Bräm (1965: pl. 1, fig. 5).

Primitive condition: The *Proganochelys* condition, state 0, is unique to that taxon at present, so the primitive condition is ambiguous.

Homoplasy: The entire length being wide occurs only in *Platychelys* and *Notoemys*, although *Chelus* and some emydids approach this condition.

Discussion: The conditions of the costovertebral tunnel are not identical in *Proganochelys* and *Proterochersis*. *Proterochersis* has a wide tunnel, not reduced along costals 2–6 as in *Proganochelys*, but not as wide as in *Notoemys* and *Platychelys*.

This character is used in Lapparent de Broin and Murelaga (1999) and Fuente and Iturralde-Vinent (2001).

157. Carapace, articulation facet on thoracic rib 1: absent, anterior edge smooth (*Proganochelys*) = 0; swollen facet or tubercle on anterior margin of first thoracic rib (*Platychelys*) = 1.

Morphology: On the medial end of the first thoracic rib, there is a swollen tubercle that looks like an articulation facet (Bräm, 1965: pl. 1, fig. 5). This occurs only in *Platychelys* and *Notoemys*. Although it is close to the centrum articulation, it does not seem to be for a cervical articulation. It is probably an articulation site for the dorsal process of the scapula.

Primitive condition: The absence of a facet, as in *Proganochelys*, is primitive.

Homoplasy: None.

Discussion: This character is a synapomorphy for *Notoemys* + *Platychelys*.

158. Plastron, mesoplastra: present and meet on midline (*Proganochelys*) = 0; present, wider than long (*Platychelys*) = 1; present, roughly equidimensional (*Chedighaii*) = 2; absent (*Emydura*) = 3.

Morphology: The medially meeting mesoplastra, state 0, are figured in Gaffney (1990: figs. 92, 105). State 1, transversely elongate mesoplastra, are figured in Bräm (1965: pl. 1, fig. 2) and Lapparent de Broin (2001: fig. 1). The equidimensional, that is, rounder, mesoplastra can be seen in figure 264.

Primitive condition: Medially meeting mesoplastra occur in *Proganochelys* and seem to be primitive for turtles. The two pairs of medially meeting mesoplastra seen in *Proter-*

ochersis seem to be an autapomorphy for this taxon.

Homoplasy: Medially meeting mesoplastra have evolved twice, with one being a reversal in *Pelusios*. Among pleurodires, mesoplastra have been lost at least three times: in *Dortoka, Araripemys*, and chelids. In cryptodires, they may have been lost only once.

Discussion: Transverse mesoplastra not meeting on the midline are a synapomorphy for *Platychelys* + *Notoemys*, although there is another occurrence within extinct chelids and a similar condition exists in *Pelusios broadleyi*.

If the equidimensional shape of *Pelomedusa* is primitive for Pelomedusidae, then state 2 is synapomorphic for Pelomedusoides; if not, state 2 is synapomorphic for the magnafamily Podocnemidera.

This character is used in Gaffney et al. (1991), Rougier et al. (1995), Lapparent de Broin and Murelaga (1999), and Fuente and Iturralde-Vinent (2001).

159. Plastron, trapezoidal entoplastron: entoplastron arrow-shaped with posterolateral processes (*Proganochelys*) = 0; entoplastron more trapezoidal (*Podocnemis*) = 1.

Morphology: The entoplastron varies in shape in turtles, and this character is one aspect. The arrow-shaped entoplastron, state 0, is figured in Gaffney (1990: fig. 92), and the more trapezoidal shape is in figure 264.

Primitive condition: *Proganochelys* has state 0.

Homoplasy: *Araripemys* has a reversal to something similar to, but not identical to, the primitive condition.

Discussion: The trapezoidal entoplastron, even though it may be somewhat irregularly shaped (e.g., *Kayentachelys*, *Proterochersis*), is a casichelydian synapomorphy.

This character is used in Lapparent de Broin and Murelaga (1999).

160. Plastron, epiplastra meet on midline: no, at least in ventral view (*Proganochelys*) = 0; yes, meet on midline in ventral view (*Foxemys*) = 1.

Morphology: The separated condition, state 0, is figured in Gaffney (1990: figs. 92, 105) and the midline meeting condition in figure 264. Lapparent de Broin and Murelaga (1999) differentiated meeting in ventral view versus meeting in dorsal view, but the absence of a dorsal contact would only be relevant for *Proganochelys* and *Palaeochersis* and the condition is only known for *Palaeochersis* (which has the epiplastra separated dorsally and ventrally).

Primitive condition: Presumably the complete separation of epiplastra by the entoplastron is primitive for turtles, as it is likely in *Proganochelys* and occurs in *Palaeochersis* and primitive cryptodires (*Kayentachelys*).

Homoplasy: Cryptodires evolve medially meeting epiplastra independently of pleurodires.

Discussion: This character is a synapomorphy for the parvorder Megapleurodira, consisting of all pleurodires minus *Proterochersis*. This character is used in Lapparent de Broin and Murelaga (1999) and Fuente and Iturralde-Vinent (2001).

161. Plastron, dorsal epiplastral process: large, reaching or nearly reaching carapace (*Proganochelys*) = 0; small or absent (*Podocnemis*) = 1.

Morphology: The dorsal process of the epiplastron is figured in Gaffney (1990: figs. 92–97). The absent condition can be seen in all the Pelomedusoides (e.g., Rütimeyer, 1873: pl. 8, fig. 6; Lapparent de Broin and Murelaga, 1999: pl. 2, fig. 5b).

Primitive condition: *Proganochelys*, *Palaeochersis*, and *Proterochersis* have the presumed primitive condition of a large dorsal process of the epiplastron.

Homoplasy: The dorsal process has been lost independently in cryptodires and within pleurodires.

Discussion: This character is a synapomorphy for the parvorder Megapleurodira (all Pleurodira minus *Proterochersis*) and for the Cryptodira.

This character is used in Rougier et al. (1995) and Fuente and Iturralde-Vinent (2001).

162. Plastron, intergular scales: two (one pair) intergular scales (*Proterochersis*) = 0; one intergular scale on midline (*Foxemys*) = 1.

Morphology: A pair of intergulars (state 0) is figured in Gaffney (1990: fig. 105). A single intergular can be seen in figure 264.

Primitive condition: *Proganochelys* has one pair of intergulars.

Homoplasy: None.

Discussion: The single intergular is a synapomorphy for the parvorder Megapleurodira (all pleurodires minus *Proterochersis*). This character is used in Lapparent de Broin and Murelaga (1999) and Fuente and Iturralde-Vinent (2001).

163. Plastron, gular projections: present (*Proganochelys*) = 0; absent (*Podocnemis*) = 1.

Morphology: The conical anterior processes on the epiplastra and entoplastron that are formed where the gular scales are attached can be seen in Gaffney (1990: fig. 105). Figure 264, state 1, shows the smooth margin when the projections are absent.

Primitive condition: *Proganochelys* and *Proterochersis* have gular projections.

Homoplasy: The projections have been lost independently in cryptodires and within pleurodires. Lapparent de Broin (2000b) argued on the basis of morphology that the gular projections of *Proterochersis* and *Proganochelys* are not homologous, but this is ambiguous in the MPC.

Discussion: This character is synapomorphic for the Megapleurodira, which is all Pleurodira minus *Proterochersis*.

164. Plastron, anterior lobe of plastron short, wide at base, and semicircular in outline: width/length of 2.0 or less (*Podocnemis*) = 0; width/length of more than 2.1 (*Chedighaii*) = 1.

Morphology: The plastron in primitive turtles like *Proganochelys*, *Proterochersis*, and *Kayentachelys* includes a long and narrow anterior lobe (Gaffney, 1990: fig. 105). However, the anterior lobe of the plastron in bothremydids and some other pleurodires is much shorter than its width across the base (state 1, fig. 264). Homology of this character is difficult to argue, however, because of the simple nature of the character. This shape has been used as a character for the Bothremydidae (Antunes and Broin, 1988).

Primitive condition: Clearly a plastron in which the anterior lobe is longer than wide is the primitive condition for turtles. Within the Pleurodira, chelids, pelomedusids, *Araripemys*, *Euraxemys*, and most podocnemidids have longer anterior plastral lobes that are longer than half the width at the base.

Homoplasy: *Bairdemys*, a shweboemydine podocnemidid, shows a very similar, short, rounded, anterior plastral lobe that is broad across the base (fig. 275). In addition, a reversal to the longer, primitive condition occurs in the bothremydid *Polysternon*.

Discussion: The addition of *Cearachelys* and the possible *Galianemys*, AMNH 30550 and AMNH 30551, to the shells known for bothremydids indicates that a short anterior plastral lobe is not universal for the family (fig. 314). The anterior lobe of *Kurmademys* is not completely known, but the hyoplastra have parallel lateral sides, which suggests that this form also did not have the very short, rounded anterior lobe seen in other bothremydids. Thus it appears that the short anterior plastral lobe is more likely a synapomorphy for the infrafamily Bothremydodda (Bothremydini and Taphrosphyini).

This character is used in Antunes and Broin (1988) and Lapparent de Broin and Werner (1998).

165. Plastron, pectoral scales on entoplastron: absent (*Euraxemys*) = 0; present (*Foxemys*) = 1.

Morphology: The bony plastron of turtles is primitively covered by a set of seven plastral scales. The fourth set, the pectorals, covers most of the hyoplastron and, in the most primitive of turtles, the mesoplastron (state 0; Gaffney, 1990: fig. 105). In species in which the first three pairs of plastral scales are either reduced in size or absent, the pectorals may reach anteriorly to the entoplastron (state 1, fig. 259).

Primitive condition: In *Proganochelys*, *Proterochersis*, *Platychelys*, *Notoemys* (Fernandez and Fuente, 1994), *Euraxemys*, *Araripemys*, and the Pelomedusidae, the pectoral scales are located posterior to the entoplastron. This seems to be the primitive condition. The primitive condition also appears to be present in the bothremydids, *Cearachelys*, and the probable *Galianemys*, AMNH 30050 and AMNH 30551.

Homoplasy: Overlap of the pectoral scales onto the entoplastron may be a synapomorphy for the superfamily Podocnemidoidea, but if this is the case, then it is reversed at least in *Cearachelys*, *Galianemys*, and *Rosasia*. The pectoral scales also reach the entoplastron in some members of the Cheli-

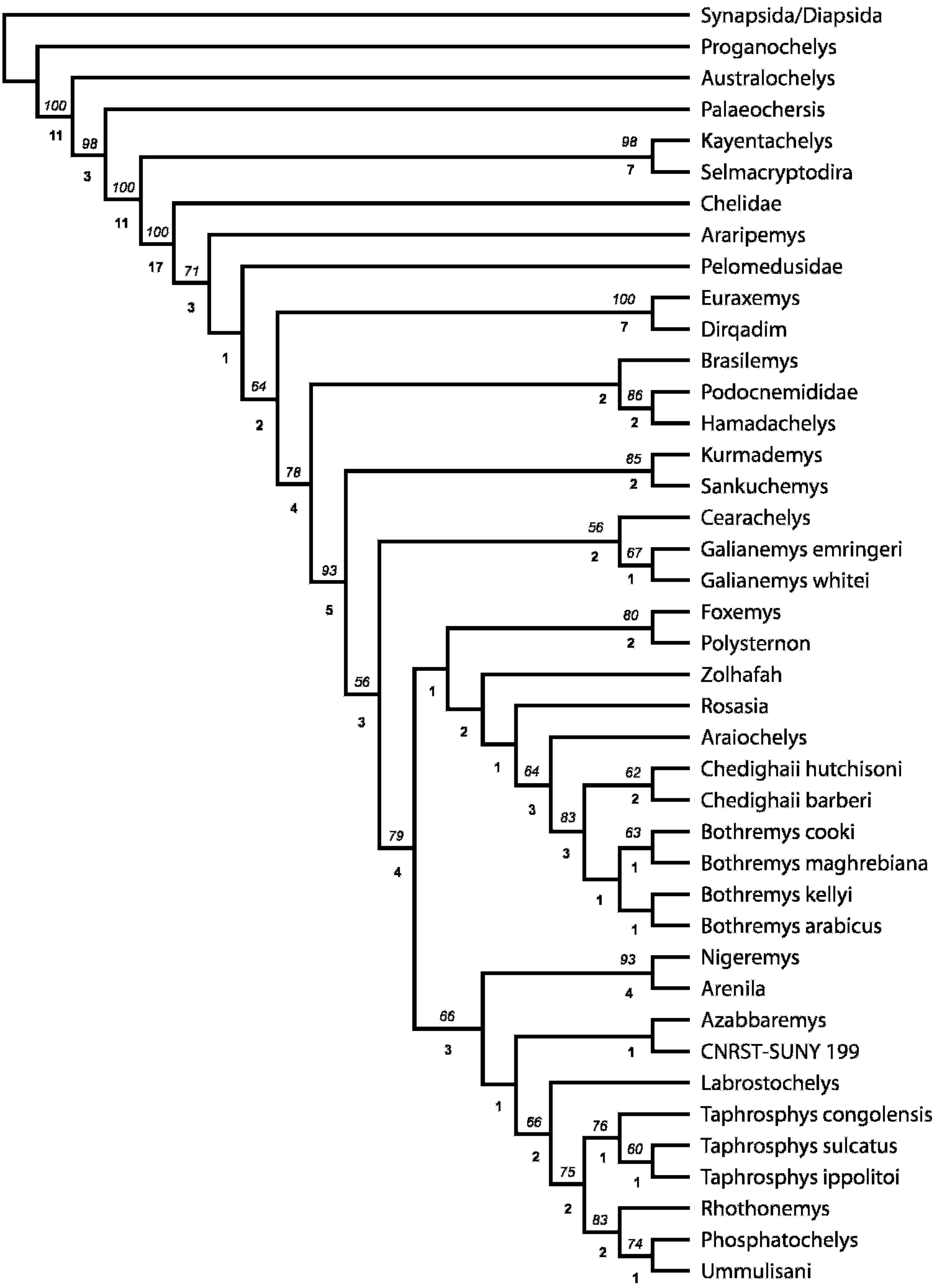


Fig. 288. Cladogram 1, the most parsimonious cladogram (MPC) of the dataset in appendix 3, all shell-only (asterisked) taxa excluded. PAUP* 4.0 analysis of 41 taxa and 175 characters, all characters unweighted and unordered, character list in appendix 2. The result is one cladogram with 382 steps, a consistency index of 0.60, a retention index of 0.81, a rescaled consistency index of 0.49, and a homoplasy index of 0.39. Bootstrapping (upper numbers) was run using 100 replicates. Bremer decay indices (lower numbers) were obtained using TreeRot version 2 (Sorenson, 1999).

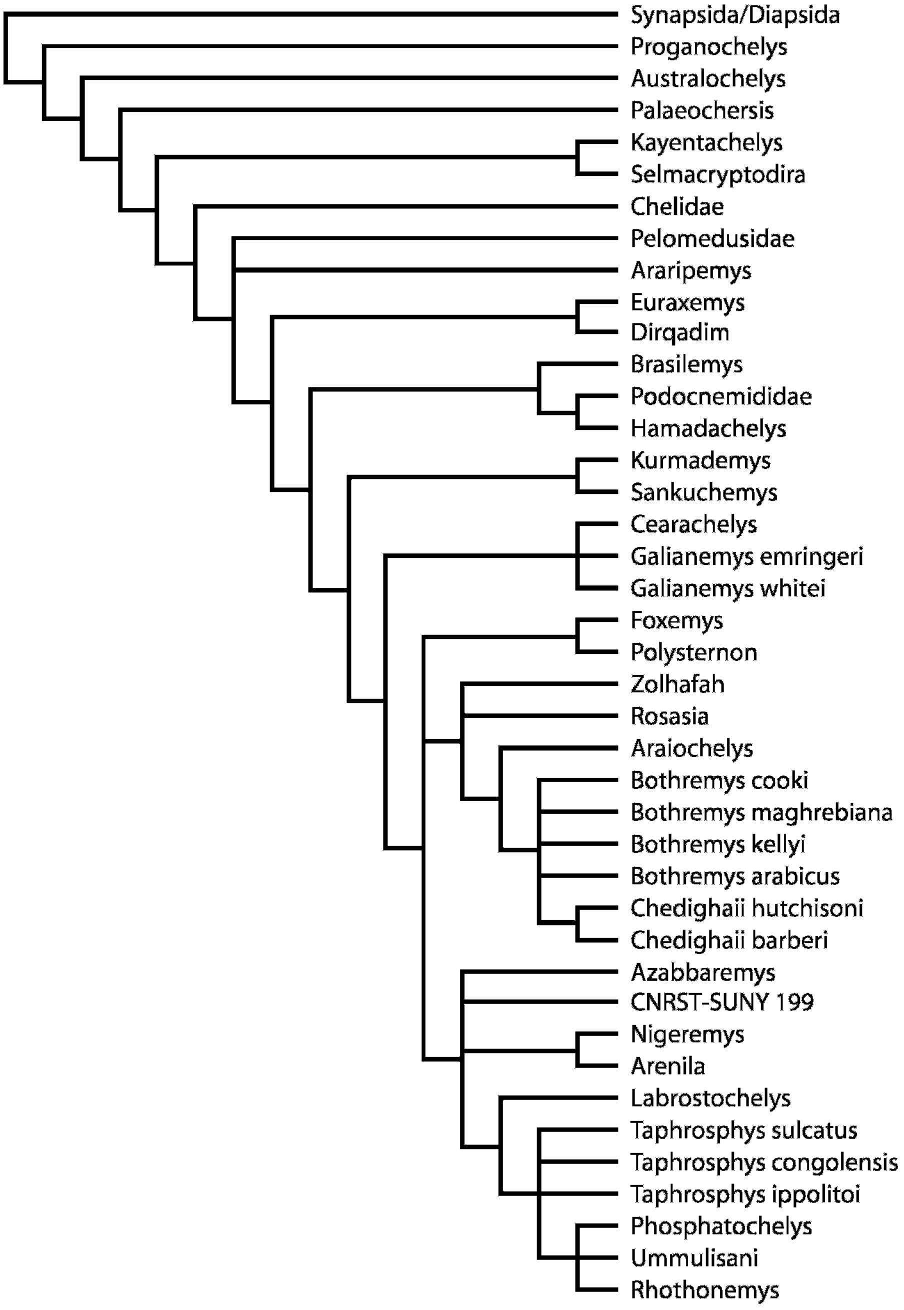


Fig. 289. Consensus cladogram of 38 trees using same matrix as in figure 288, but including all trees one step shorter, 383 steps. Shell-only taxa excluded.

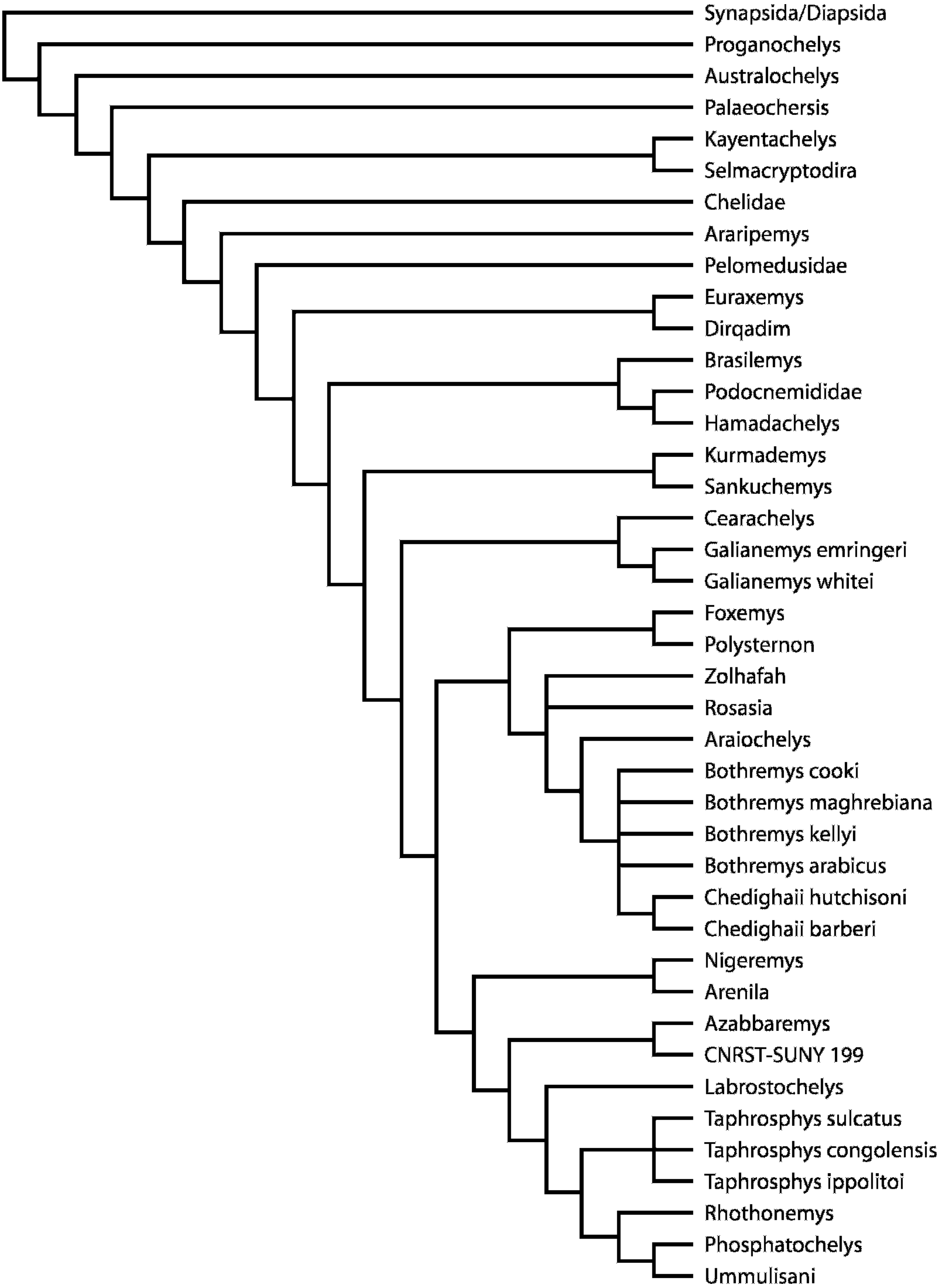


Fig. 290. Consensus cladogram of 63 trees resulting from an analysis of the matrix in appendix 3 with the removal of characters 31 and 110 (see text for discussion).

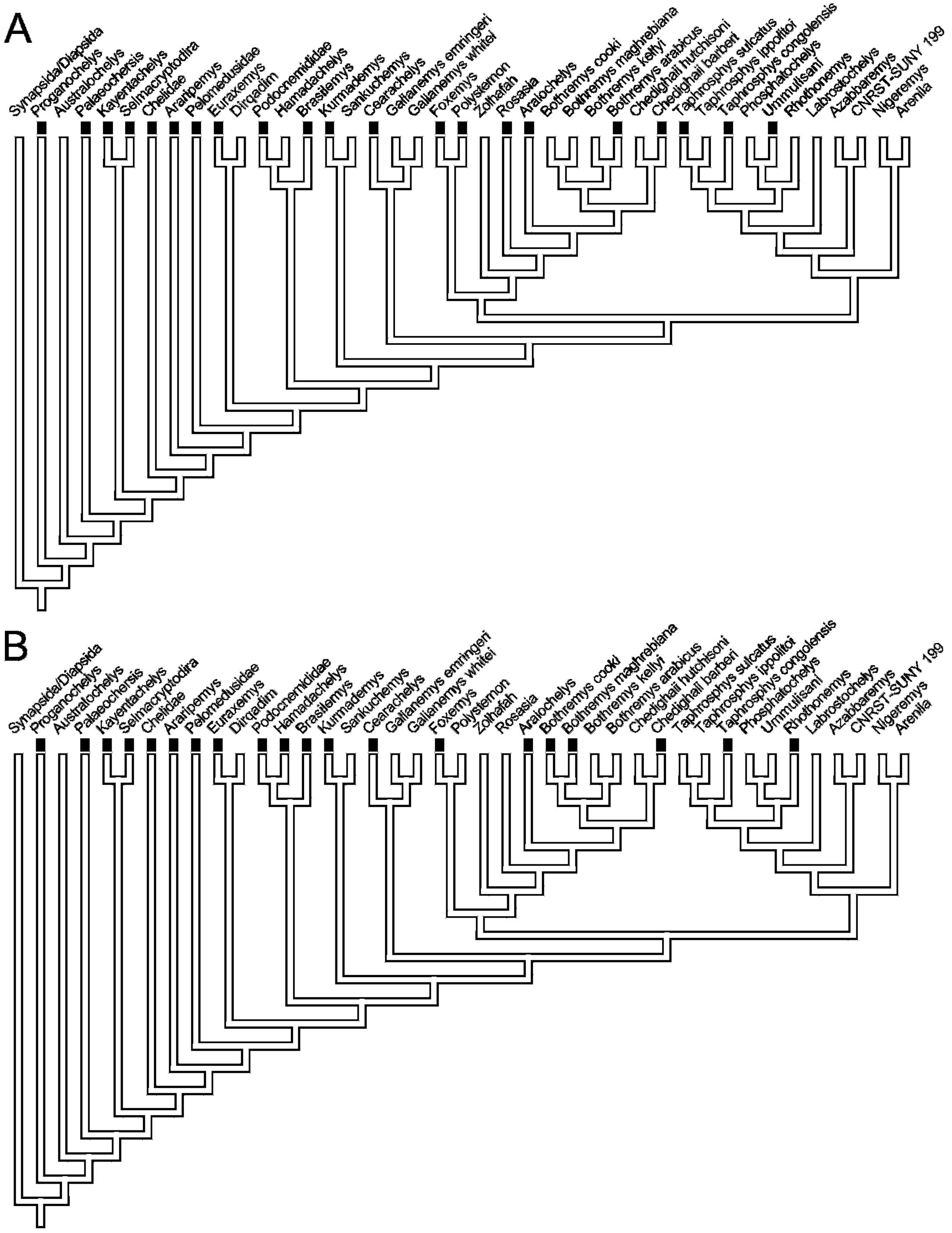


Fig. 291. **A**, cladogram 1 (MPC) from figure 288 showing in solid blocks those taxa represented by shells in addition to skulls. **B**, cladogram 1 (MPC) from figure 288 showing in solid blocks those taxa represented by lower jaws in addition to skulls.

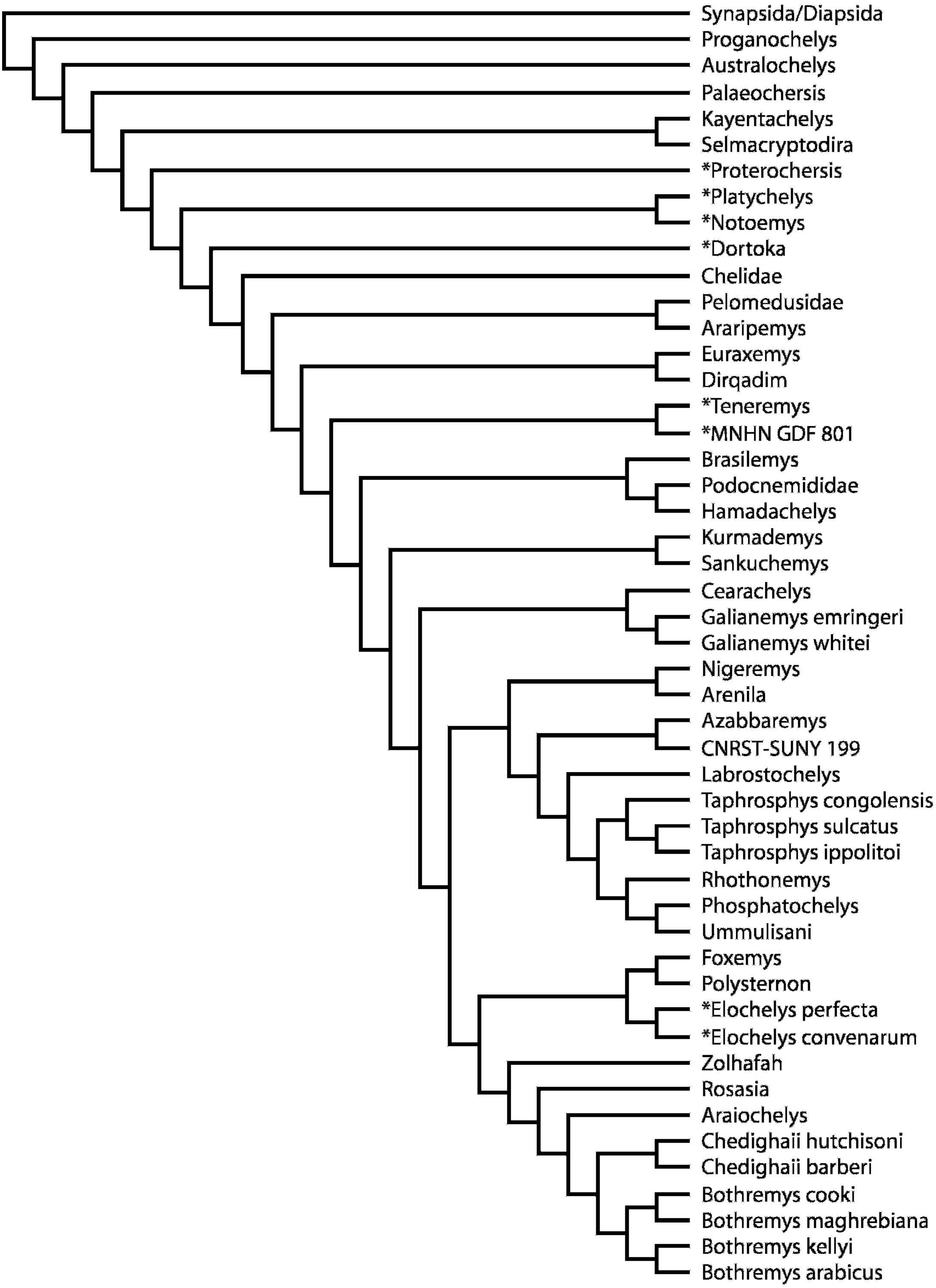


Fig. 292. Cladogram 2, a PAUP* 4.0 analysis of the same dataset (appendix 3) that produced cladogram 1 shown in figure 288, but modified by the addition of a selected group of eight shell-only taxa, indicated by asterisk (*), resulting in a single cladogram of 422 steps.

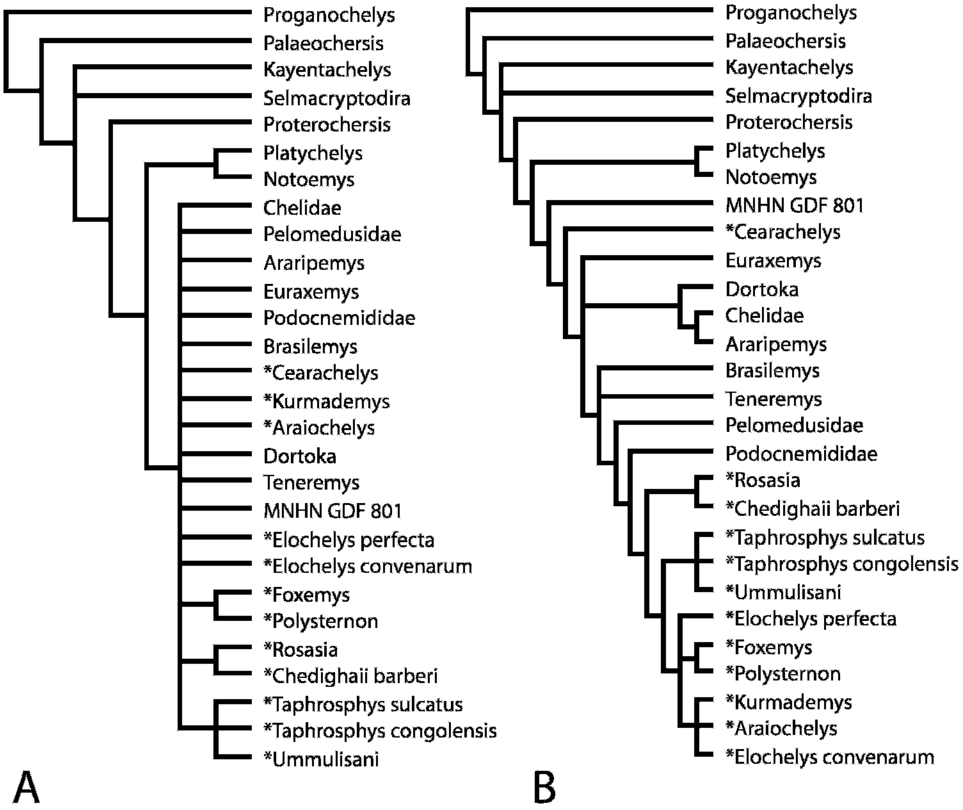


Fig. 293. Cladograms based on a dataset reduced (partitioned) by the removal of all skull-only taxa and all cranial characters resulting in a matrix of 28 taxa and 39 characters. Members of the Bothremydidae indicated by asterisk (*). **A**, consensus cladogram of 2704 trees at 108 steps without weighting; **B**, consensus cladogram of 250 trees produced by character weighting using the rescaled consistency index option in PAUP* 4.0.

dae (*Emydura*), Trionychoidea (some *Adocus*, *Basilemys*, and *Nanhsiungchelys*), and Emydidae (*Clemmys*). The CI is 0.33.

Discussion: Among the bothremydids for which we have data, only *Cearachelys*, *Galianemys*, and *Rosasia* lack this overlap.

A variant of this character is used in Lapparent de Broin and Murelaga (1999).

166. Plastron, pectoral scales on epiplastron: no, far behind epiplastra (*Cearachelys*) = 0; yes, on epiplastra or epiplastron-hyoplastron suture (*Foxemys*) = 1.

Morphology: The bony plastron of turtles is primitively covered by a set of seven plastral scales. The fourth set, the pectorals, covers most of the hyoplastron and, in the most primitive of turtles, the mesoplastron (state 0; Gaffney, 1990: fig. 105). In species in which the first three scale pairs are reduced in size or absent, the pectorals may reach anteriorly to the epiplastron (state 1, fig. 259).

Primitive condition: Absence of pectoral scale-epiplastron contact seems to be the primitive condition. It appears to be absent in basal Pelomedusoides including *Araripemys*, *Euraxemys*, the probable *Galianemys* (AMNH 30050 and AMNH 30551), *Cearachelys*, and *Rosasia*.

Homoplasy: This contact occurs in most podocnemidids (but it is absent in at least some *Podocnemis erythrocephala*, *P. sextuberculata*, *P. unifilis*, and *Peltocephalus*).

Discussion: The derived condition of this character is present in *Kurmademys*, *Polysternon*, *Foxemys*, and *Elochelys* (including *Elochelys convenarum* Laurent et al., 2002). This character supports monophyly of the subtribe Foxemydina (*Polysternon,*

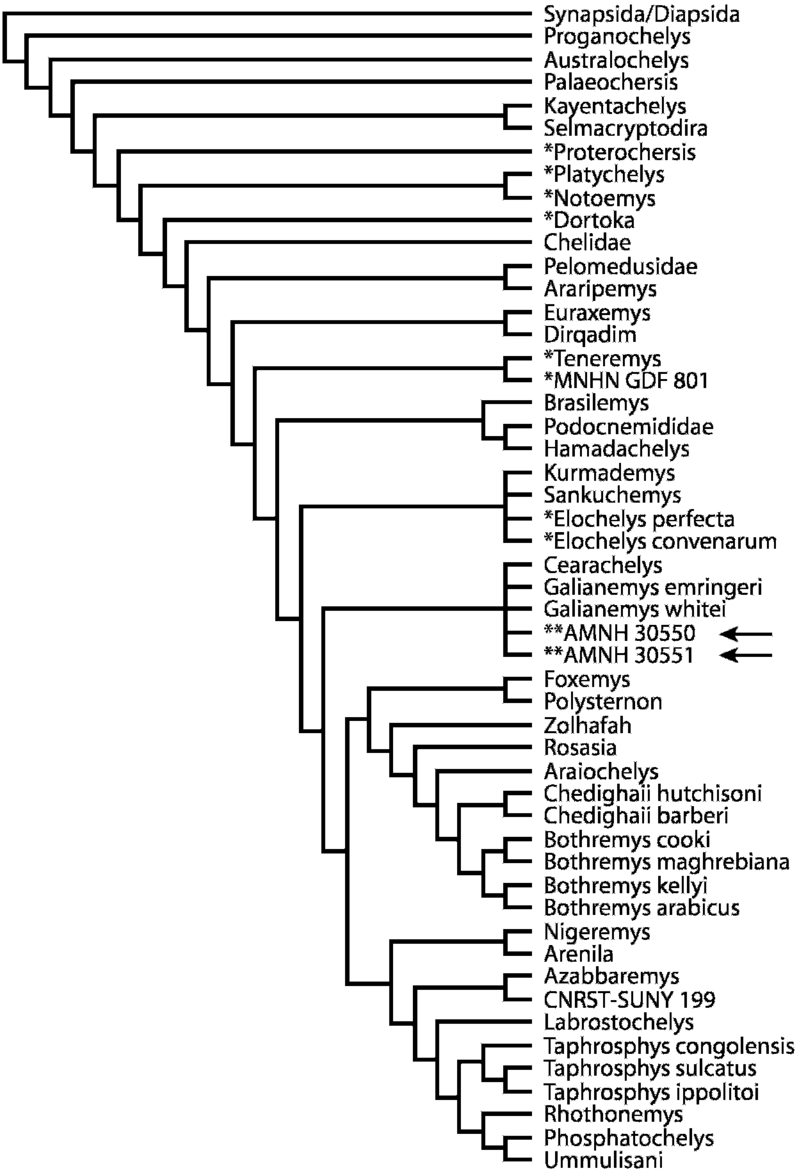


Fig. 294. Consensus cladogram of 186 trees, at 428 steps, produced by the addition of two shells, AMNH 30550 and AMNH 30551 (indicated by arrow), to the data combination used for figure 292, cladogram 2. All shell-only taxa indicated by asterisk (*). The two shells are grouped with the Cearachelyini and are found in the same units as *Galianemys*, the Cenomanian Kem Kem beds of Morocco, and may be the shells of one or both species of this genus. The addition of these shells to the matrix also moves *Elochelys* from the Foxemydina to the Kurmademydini, reflecting the few characters supporting *Elochelys* as a member of the Foxemydina.

Foxemys, Elochelys) within the tribe Bothremydini.

167. Plastron, pectoral-abdominal scale sulcus crosses mesoplastron: yes (*Cearachelys*) = 0; no, anterior to mesoplastron (*Kurmademys*) = 1.

Morphology: The plastron in primitive turtles like *Proganochelys*, *Proterochersis*,

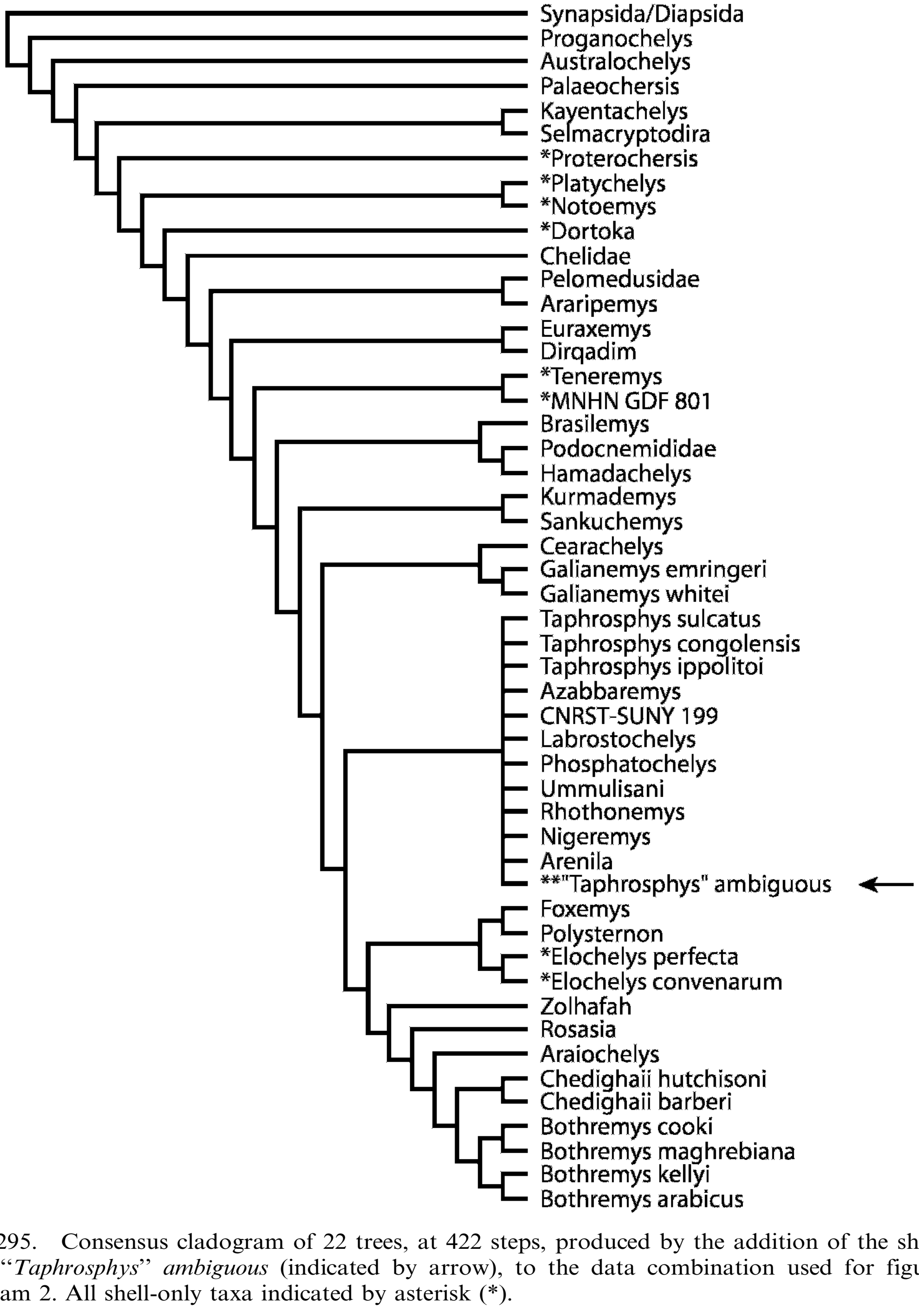


Fig. 295. Consensus cladogram of 22 trees, at 422 steps, produced by the addition of the shell-only taxon, "*Taphrosphys*" *ambiguous* (indicated by arrow), to the data combination used for figure 292, cladogram 2. All shell-only taxa indicated by asterisk (*).

and *Kayentachelys* includes large medially meeting mesoplastra that are covered in part by the pectoral and abdominal scales. Thus, the pectoral-abdominal scale sulcus crosses the mesoplastron primitively (state 0; Gaffney, 1990: fig. 105) as well as in later turtles (state 0, figs. 258, 264). In more derived turtles in which the mesoplastra are present, this sulcus may be anterior to the mesoplastron (state 1, fig. 259).

Primitive condition: Contact of the pectoral-abdominal sulcus on the mesoplastron is

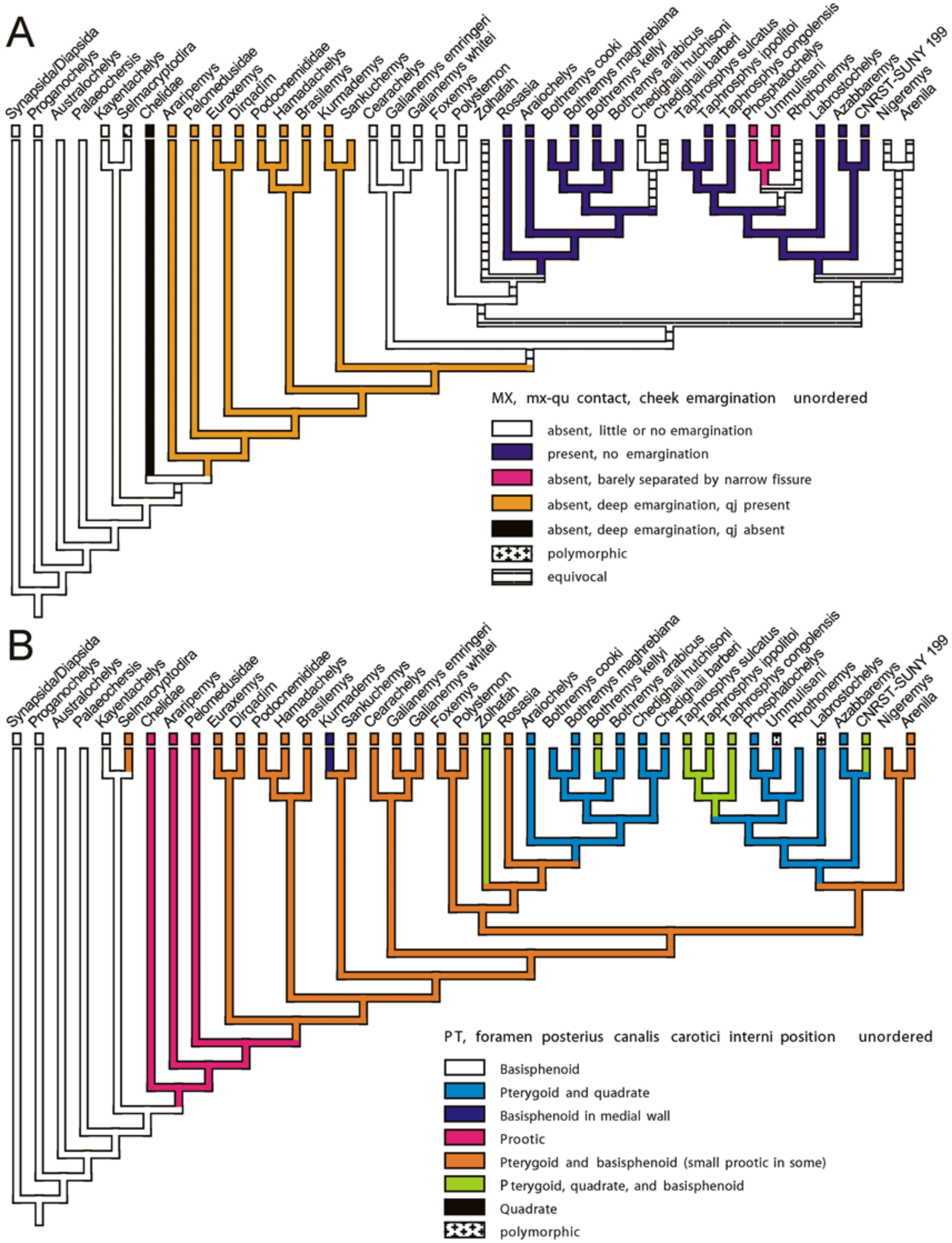


Fig. 296. **A**, cladogram 1, distribution of states for character 39; **B**, cladogram 1, distribution of states for character 74.

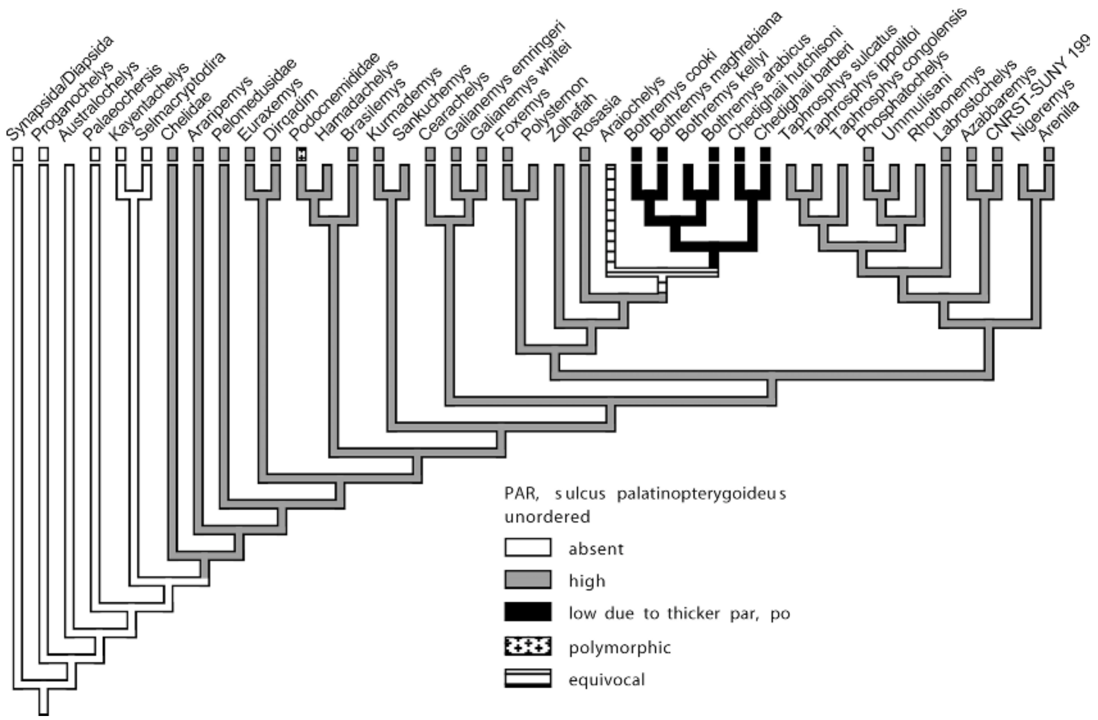


Fig. 297. Cladogram 1, distribution of character states for character 17.

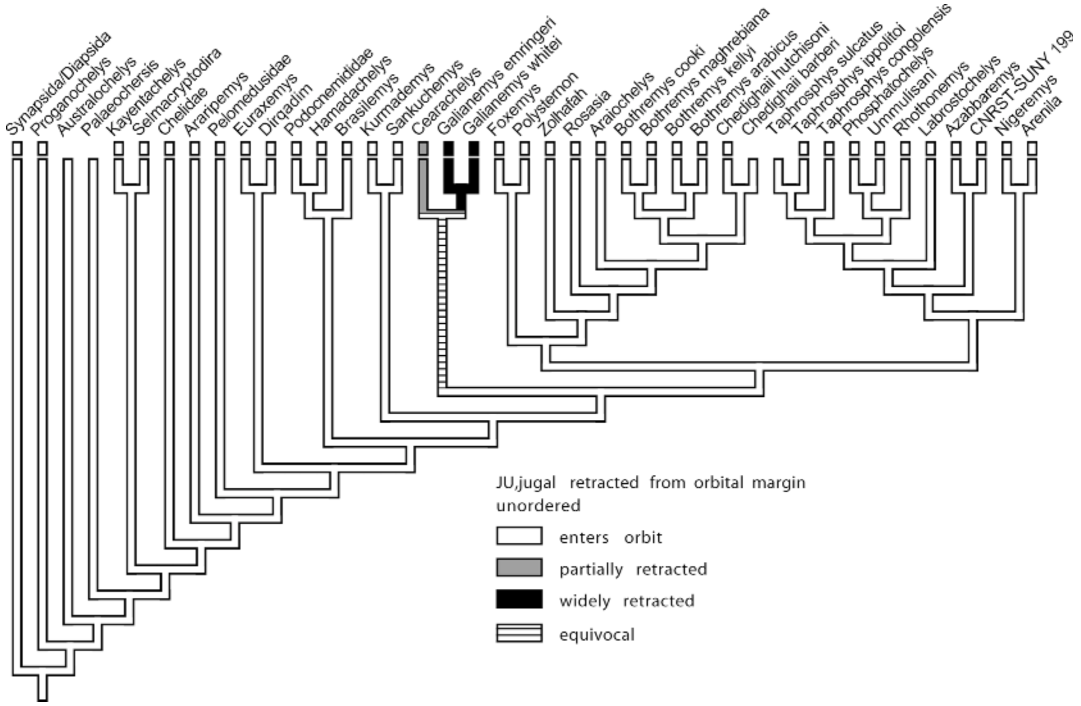


Fig. 298. Cladogram 1, distribution of character states for character 20.

clearly the primitive condition for turtles. The primitive condition is also seen in pleurodires such as *Platychelys*, *Euraxemys*, *Bothremys*, *Rosasia*, *Pelomedusa*, and some *Podocnemis*. This feature appears to show the primitive condition in most of the Bothremydidae.

Homoplasy: The known distribution of this relatively homoplastic character within the Pleurodira suggests that is has appeared at least four times within the Bothremydidae alone. The CI is 0.25.

Discussion: This character supports monophyly of the subtribe Foxemydina within the Bothremydini.

This character is used by Antunes and Broin (1988), and Meylan (1996).

168. Plastron, size and shape of ischial suture: attachment absent (*Proganochelys*) = 0; large and linear or V-shaped (*Podocnemis*) = 1; small and round or triangular (*Taphrosphys*) = 2.

Morphology: In all pleurodires the pelvis sutures to the carapace dorsally and to the xiphiplastron ventrally. The pubic attachment is typically a narrow diagonal suture angled from posterolateral to anteromedial in the middle of the xiphiplastron and does not vary very much. The ischial scar is more variable in shape. In most forms it is a linear or V-shaped contact that is nearly as large as or larger than the pubic suture and is located along the posteromedial portion of the xiphiplastron (state 1, fig. 259, 260; Zangerl, 1948: fig. 11). In a few bothremydid taxa (state 2, fig. 265; Gaffney, 1975a: fig. 11) this suture is reduced to a small circle, much smaller than the pubic scar.

Primitive condition: The absent state is primitive for turtles; state 1 is primitive for pleurodires.

Homoplasy: The ischial suture of *Araripemys* is also quite small, but it is located more posteriorly on the posterior limits of the xiphiplastron.

Discussion: The derived condition of state 2, a relatively small, circular or triangular ischial suture on the xiphiplastron, is known only in *Taphrosphys sulcatus*, *T. congolensis*, and *Ummulisani* and is an equivocal Taphrosphyini synapomorphy. The presence of an ischial attachment scar is a pleurodire synapomorphy.

169. Plastron, posterior lobe wider than pelvis: no, pelvis visible in ventral view (*Proganochelys*) = 0; yes, pelvis hidden by wide posterior lobe (*Podocnemis*) = 1.

Morphology: The posterior lobe of the plastron is relatively narrow and V-shaped in *Proganochelys* and *Palaeochersis*, but wider and U-shaped in most Casichelydia (state 1, fig. 264). Although this character is somewhat subjective, the degree of pelvis exposure in ventral view helps make it more objective (compare Gaffney [1990: fig. 88] and Rougier et al. [1995: fig. 2] with Gaffney and Meylan [1991: 335]).

Primitive condition: Based on *Proganochelys*, the narrow posterior lobe is primitive.

Homoplasy: None in the MPC, but within Eucryptodira a narrow posterior plastron exposing the pelvis has evolved in chelydrids, trionychids, and a number of extinct forms.

Discussion: Although the wide posterior lobe is a synapomorphy for Casichelydia, it is such a simple character, with homoplasy within cryptodires, that its usefulness is limited.

This character is used in Lapparent de Broin and Murelaga (1999) as "pelvis width … pelvis wider than posterior lobe", but it is the plastron that is varying in size, not the pelvis.

170. Plastron, intergular scale: small (*Cearachelys*) = 0; large intergular, separating gulars and humerals (*Taphrosphys*) = 1; large intergular, very small gulars, and partial humeral separation (*Dortoka*) = 2.

Morphology: The intergular scales are the anteriormost scales of the plastron. In *Proganochelys*, *Proterochersis*, and *Kayentachelys* they are relatively short scales that cover the anterior one-third of an anteriorly exposed entoplastron (state 0; Gaffney, 1990: fig. 105). In the genus *Taphrosphys* among the Pelomedusoides and in some chelids, the intergular coverage of the entoplastron is much expanded and it separates both the gular and the humeral scales (state 1, fig. 265). State two occurs only in *Dortoka* in our analysis.

Primitive condition: The small intergular (paired or single) widely occurs in outgroups.

Homoplasy: *Hydromedusa* is close to the *Taphrosphys* condition. Within the Bothre-

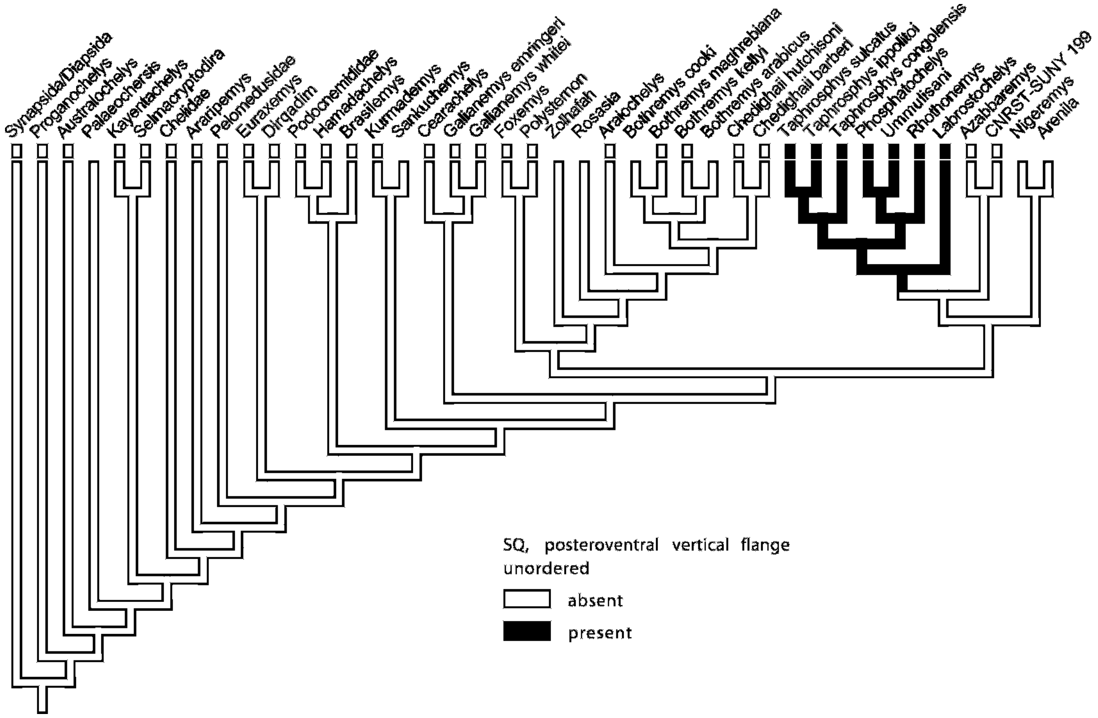


Fig. 299. Cladogram 1, distribution of character states for character 25.

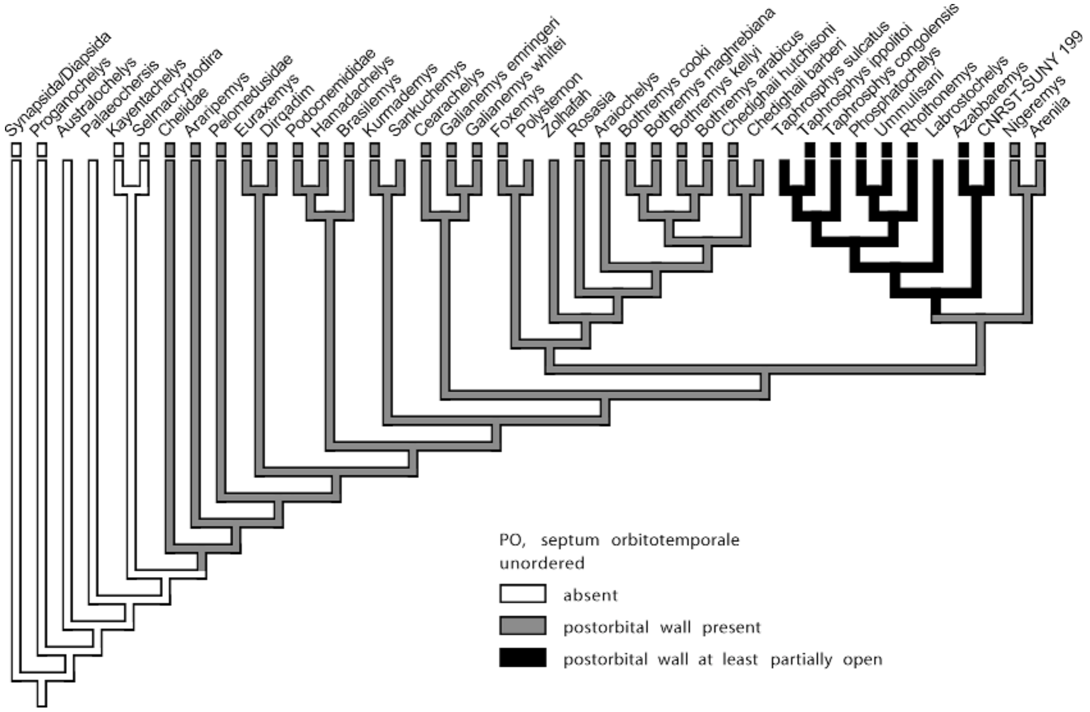


Fig. 300. Cladogram 1, distribution of character states for character 28.

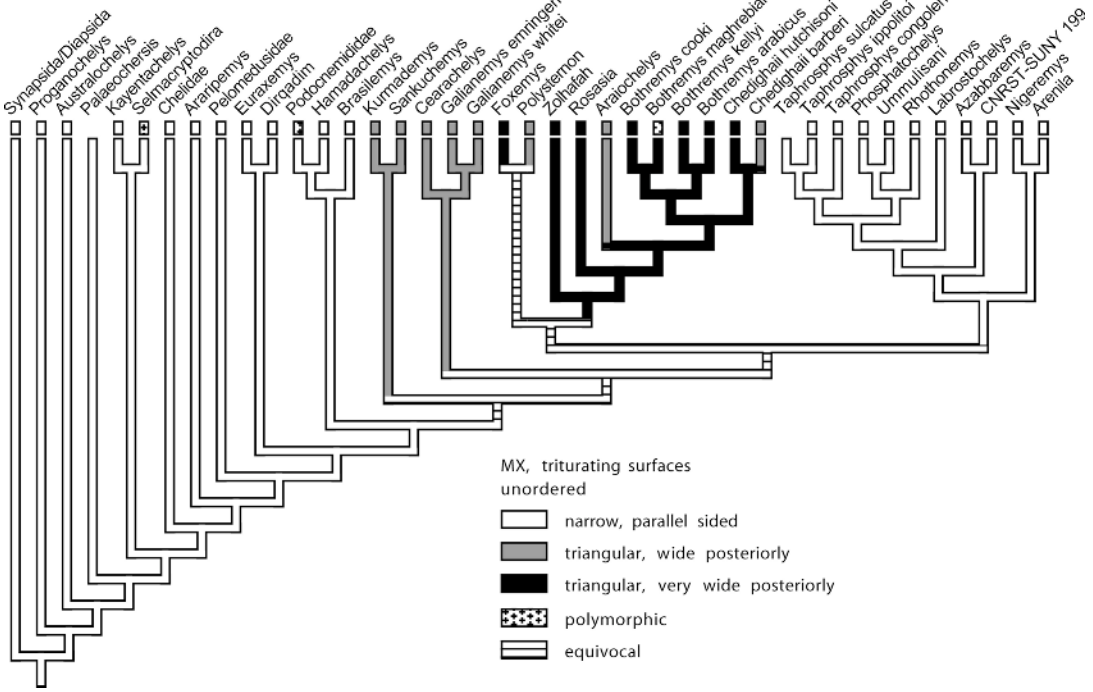


Fig. 301. Cladogram 1, distribution of character states for character 34.

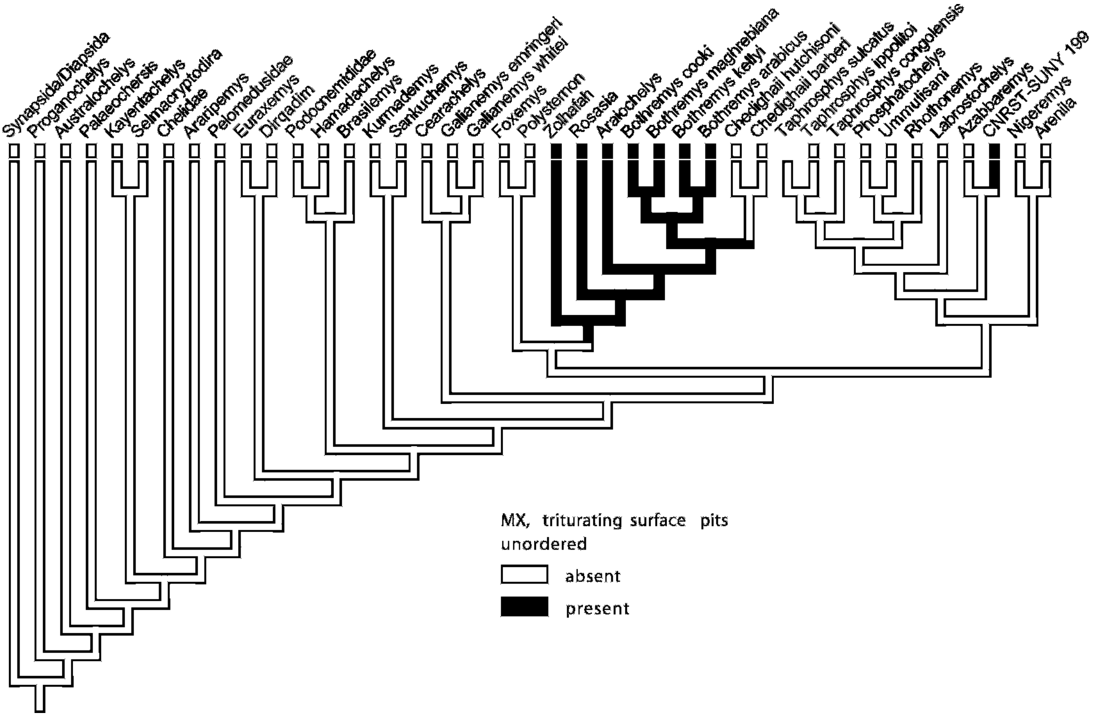


Fig. 302. Cladogram 1, distribution of character states for character 35.

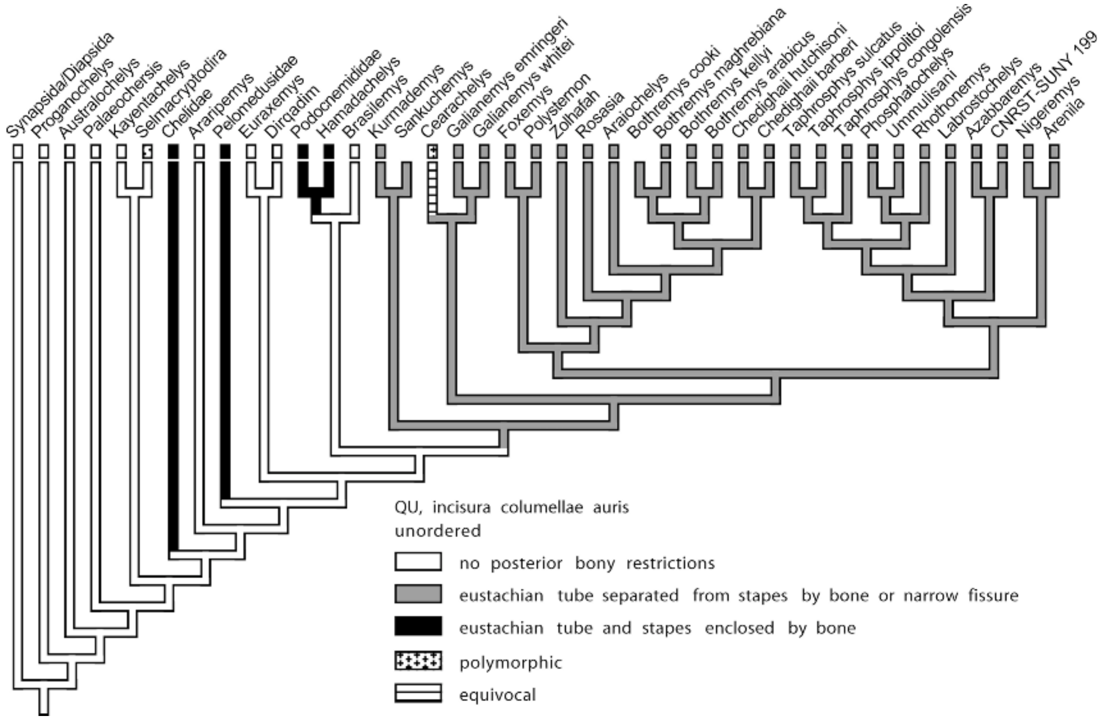


Fig. 303. Cladogram 1, distribution of character states for character 52.

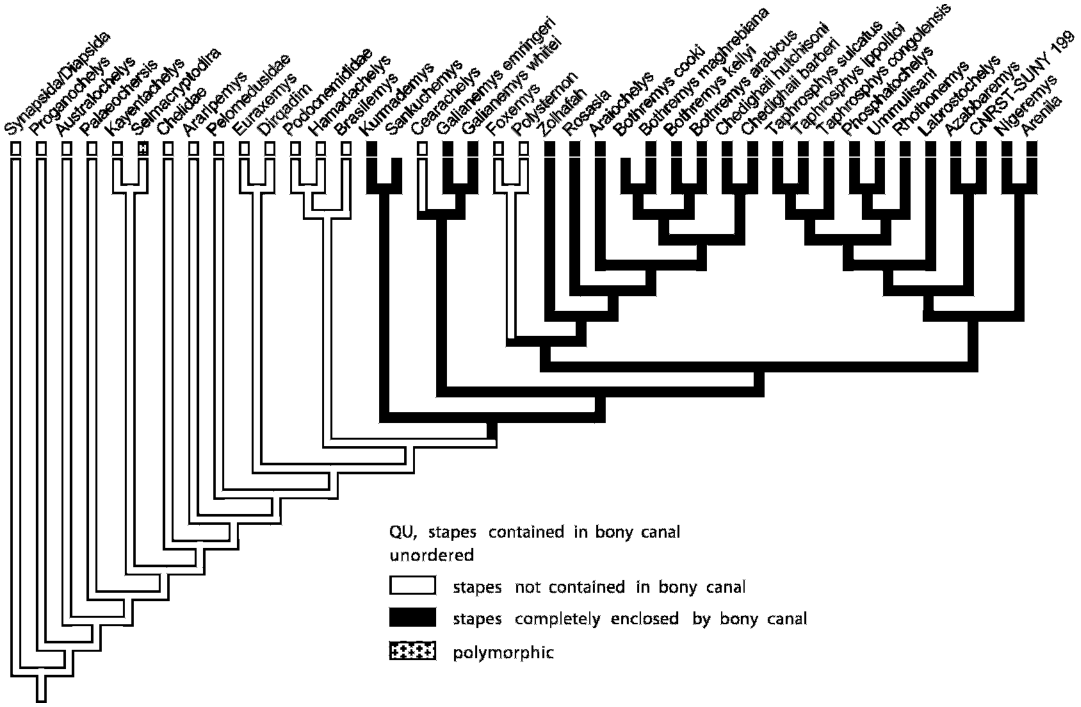


Fig. 304. Cladogram 1, distribution of character states for character 53.

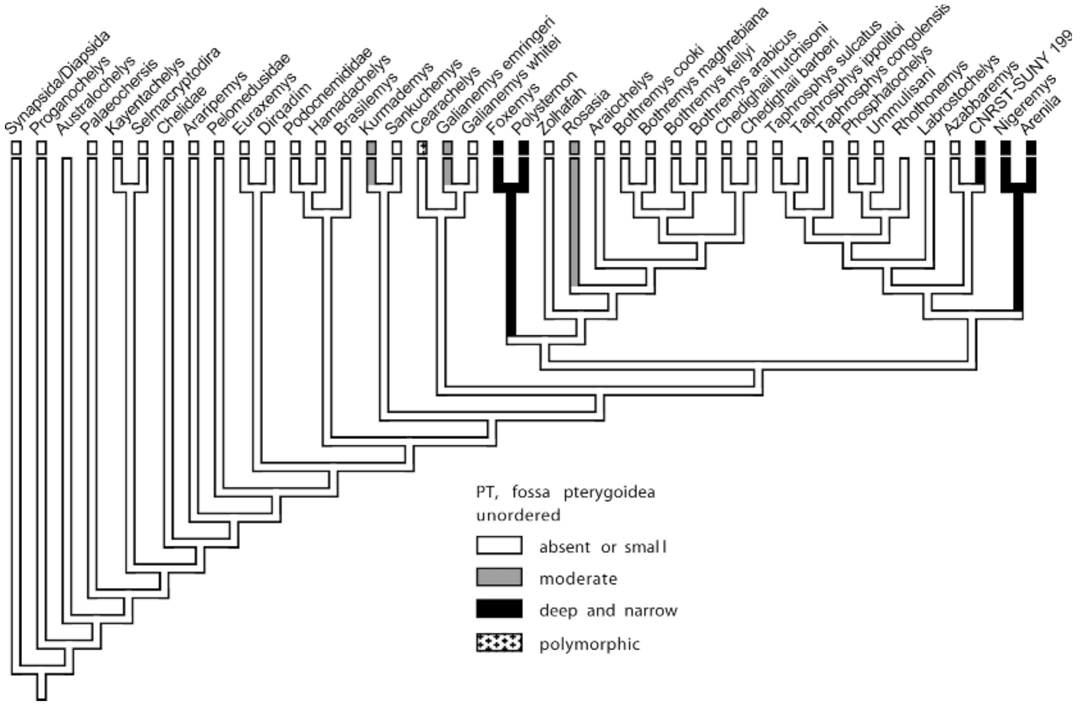


Fig. 305. Cladogram 1, distribution of character states for character 68.

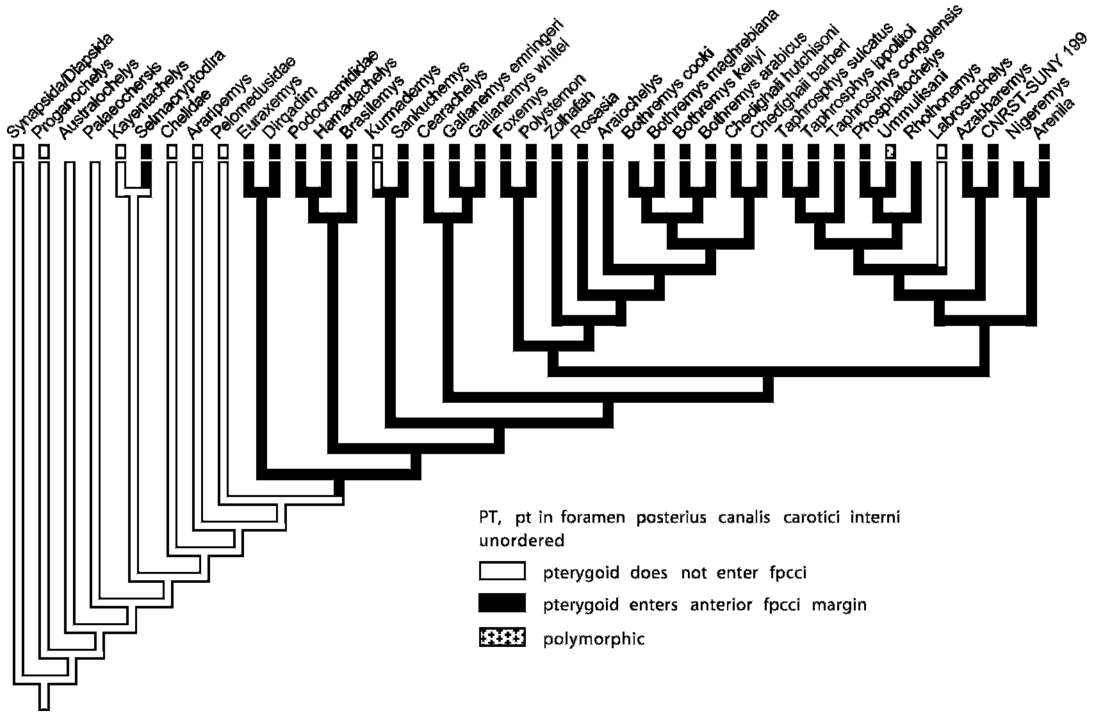


Fig. 306. Cladogram 1, distribution of character states for character 75.

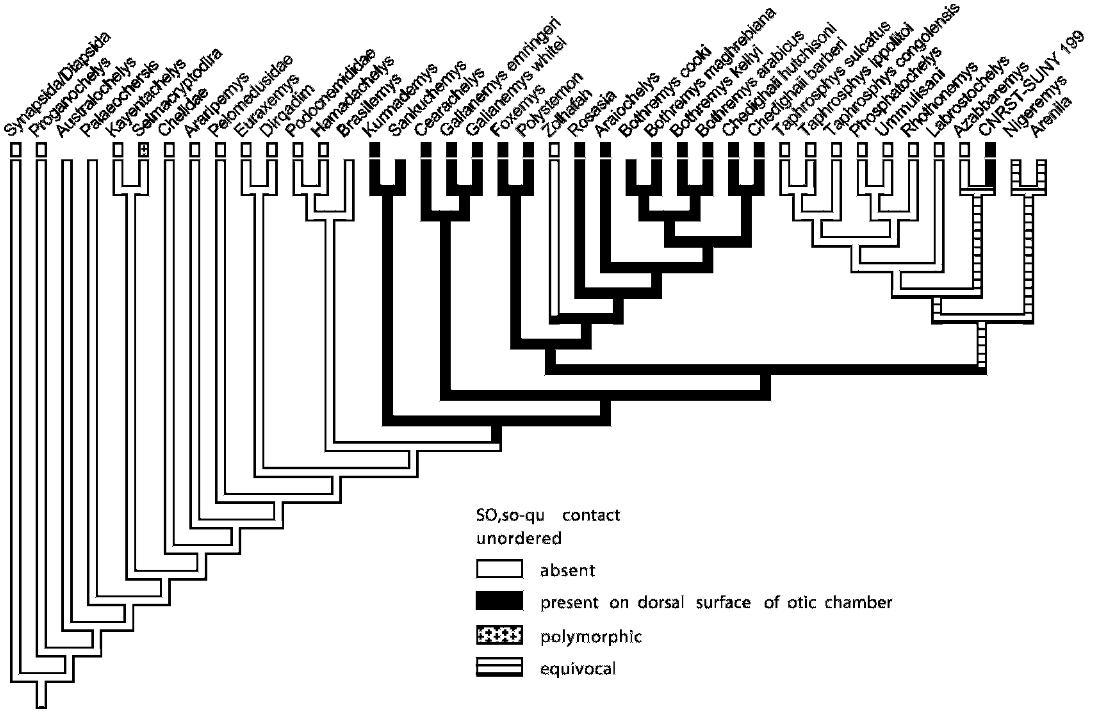


Fig. 307. Cladogram 1, distribution of character states for character 79.

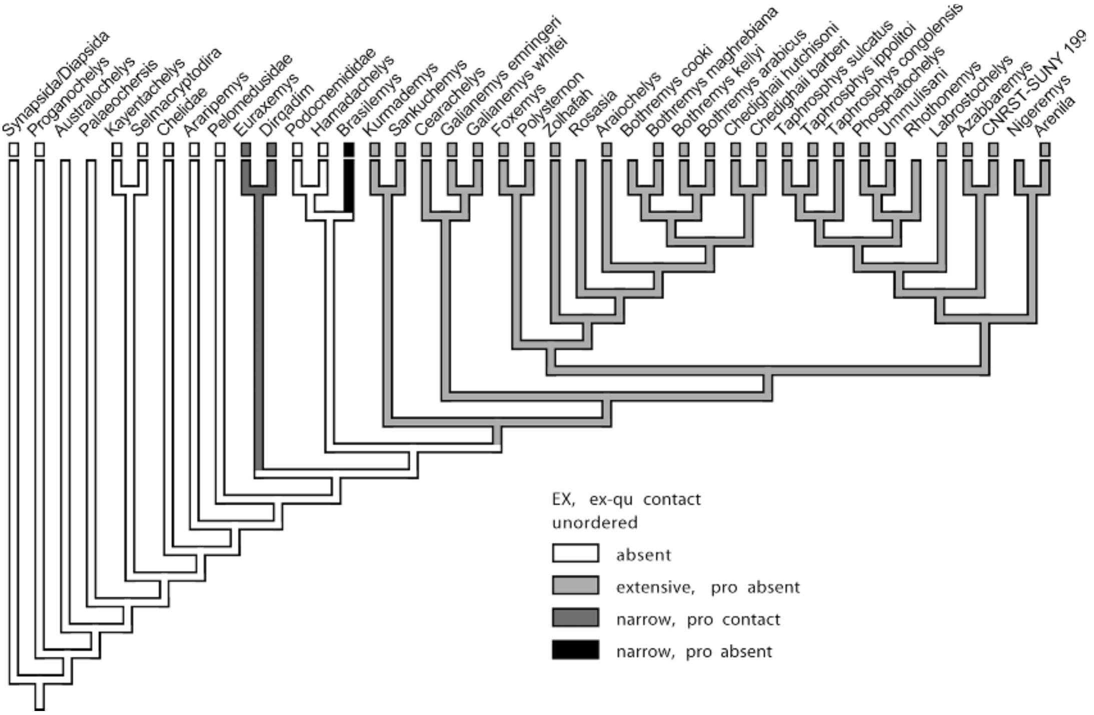


Fig. 308. Cladogram 1, distribution of character states for character 85.

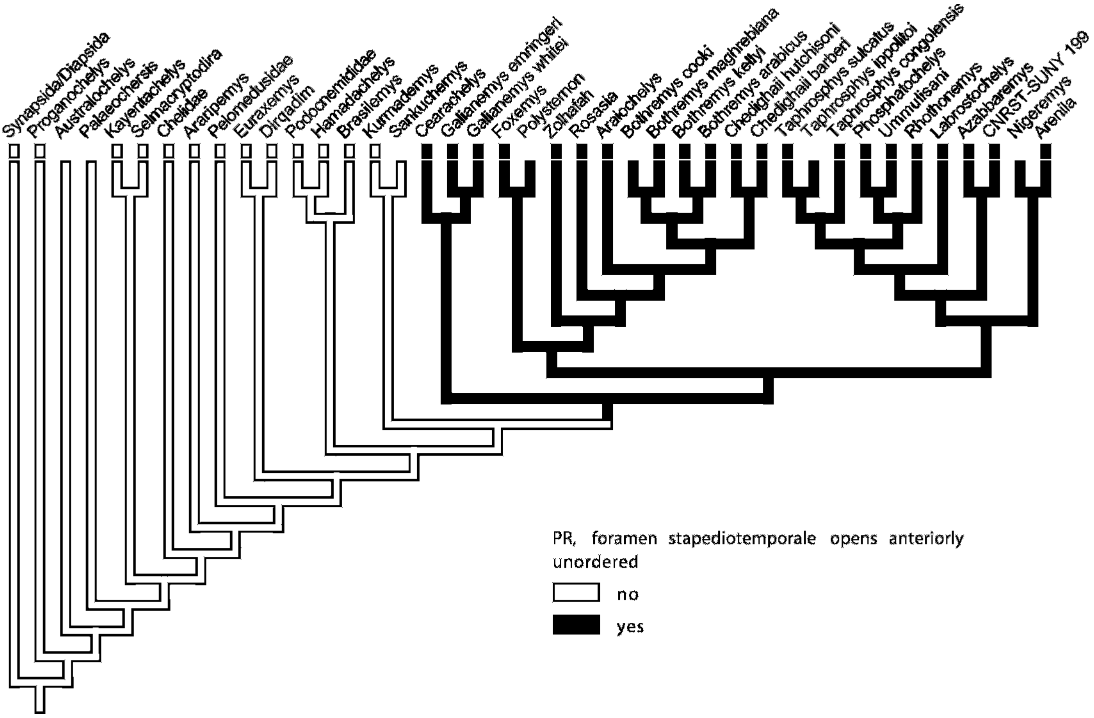


Fig. 309. Cladogram 1, distribution of character states for character 92.

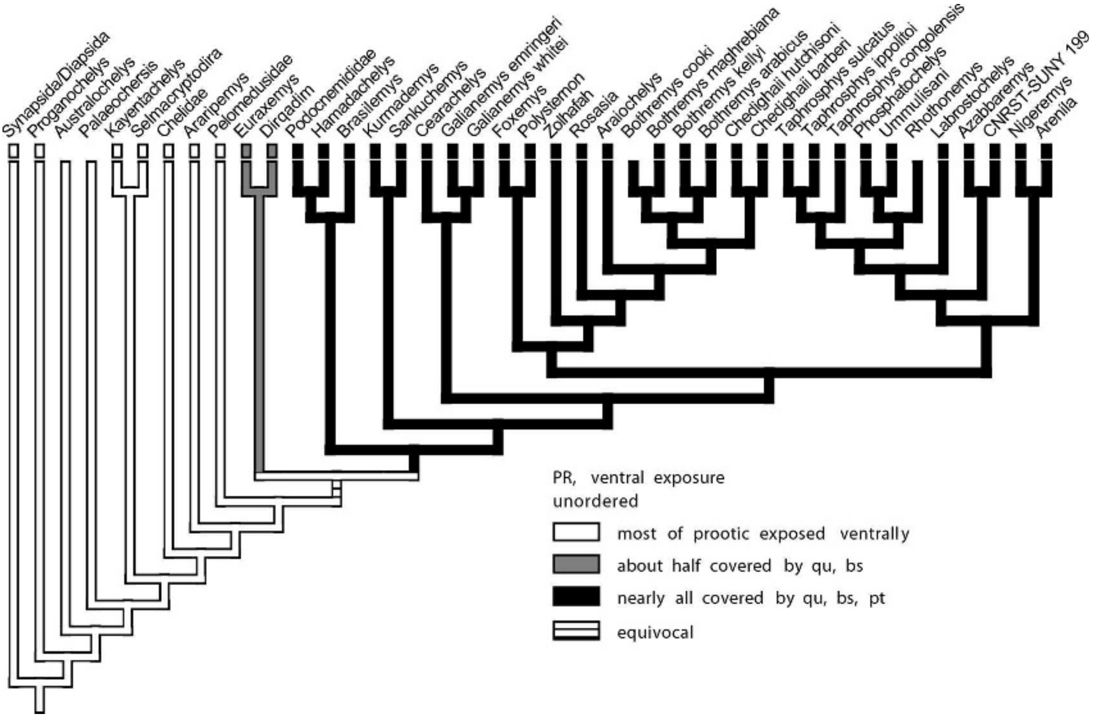


Fig. 310. Cladogram 1, distribution of character states for character 94.

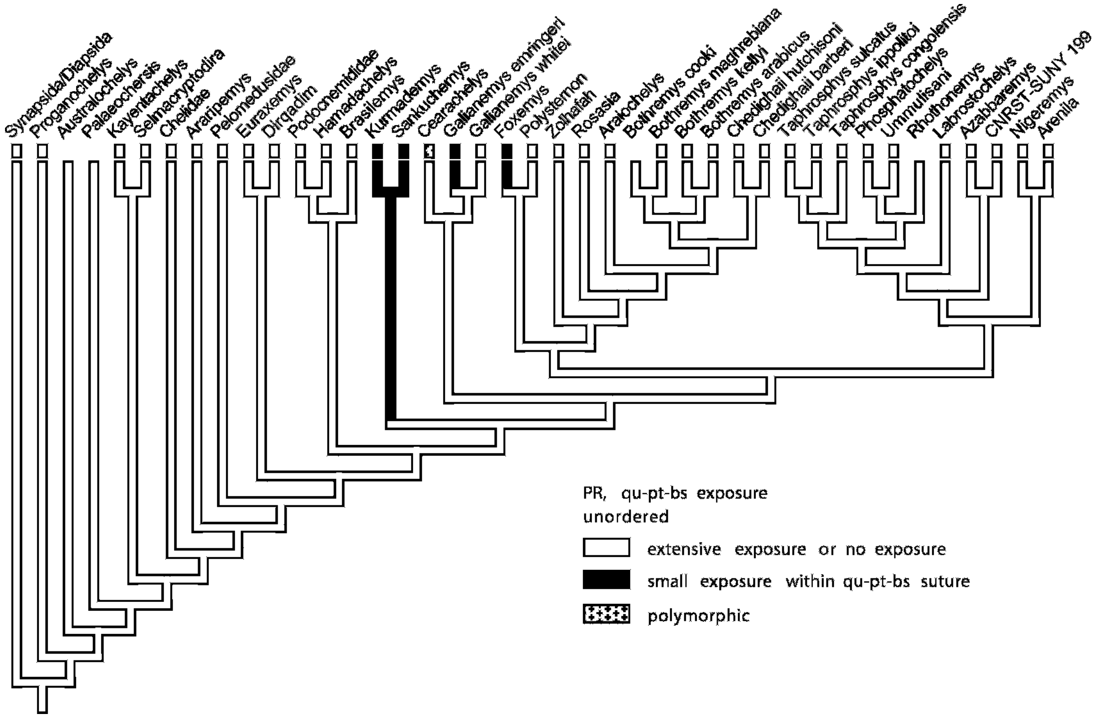


Fig. 311. Cladogram 1, distribution of character states for character 95.

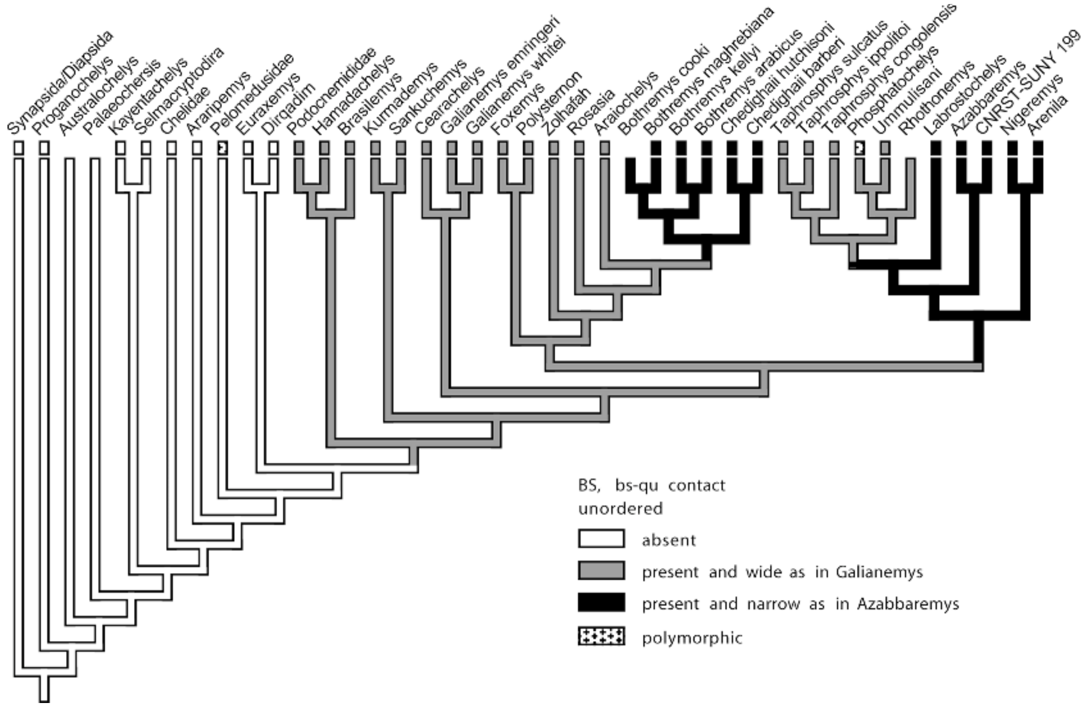


Fig. 312. Cladogram 1, distribution of character states for character 104.

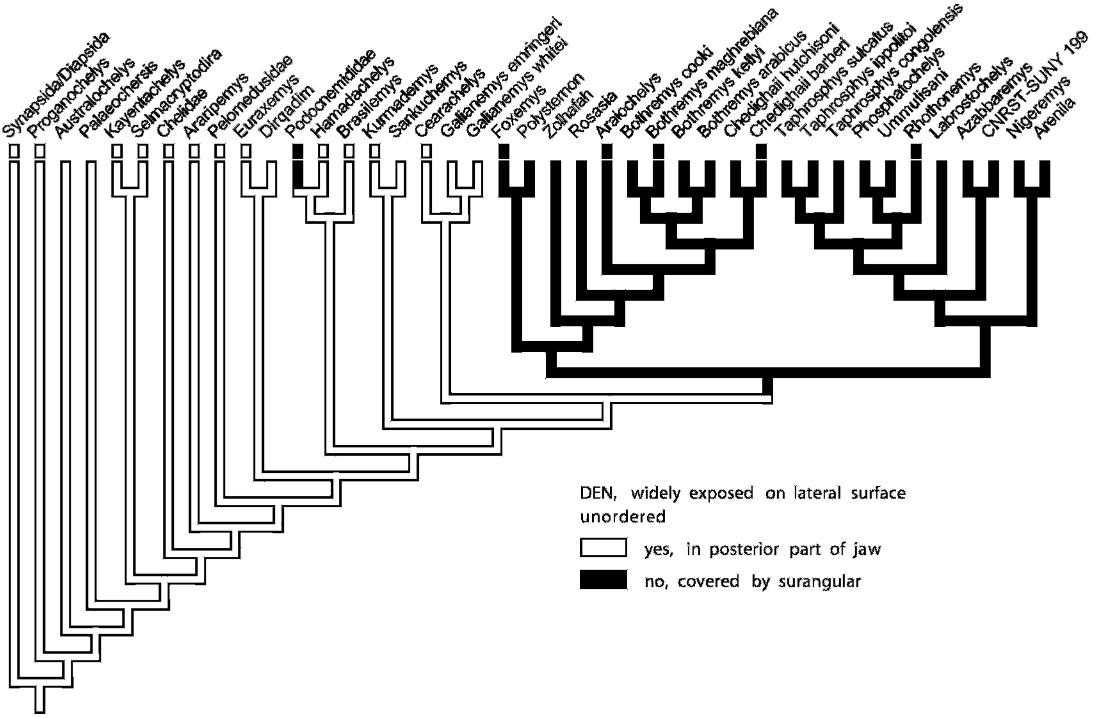


Fig. 313. Cladogram 1, distribution of character states for character 119.

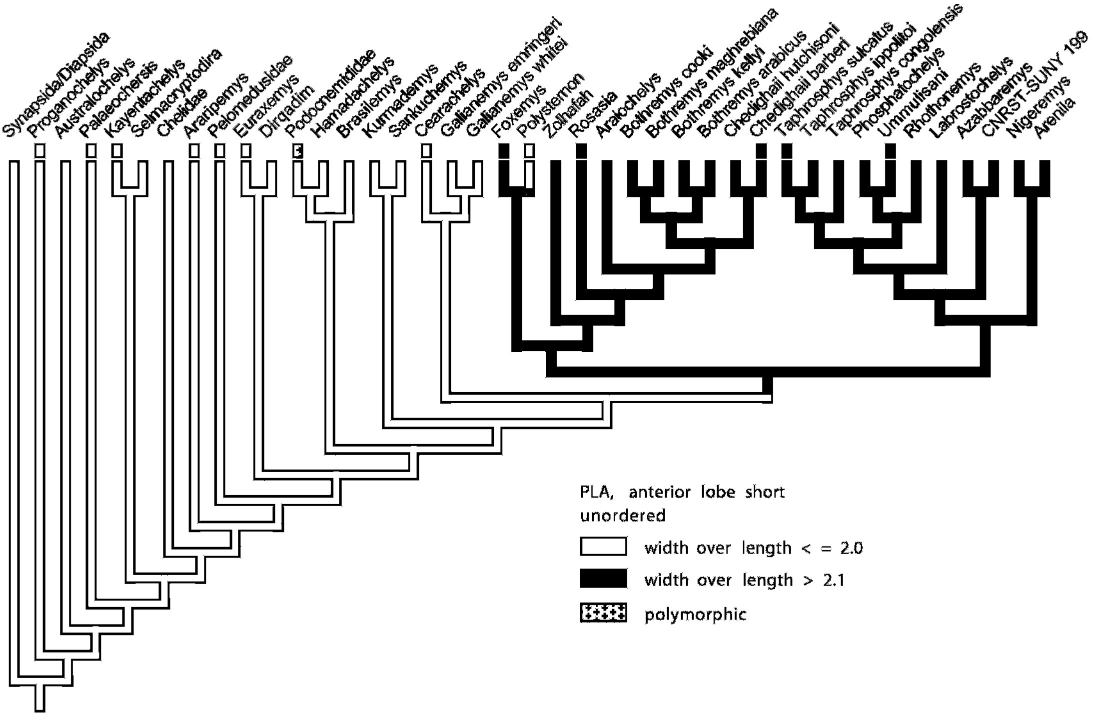


Fig. 314. Cladogram 1, distribution of character states for character 164.

mydidae, a large intergular occurs twice: in the Taphrosphyini and in *Elochelys*.

Discussion: Within the Bothremydidae, the derived condition is a synapomorphy for *Ummulisani* + *Taphrosphys*. This character has been used to argue for the close relation of *Elochelys* and *Taphrosphys* (Lapparent de Broin and Werner, 1998: 163); however, our analysis suggests a close relationship among *Elochelys, Foxemys*, and *Polysternon*, requiring the large intergular to be acquired twice within the Bothremydidae.

The relative sizes of the anterior plastral scales vary considerably in turtles. However, most of this variation is relatively continuous and does not form readily recognizable groupings. This character is one attempt to use this variation but does not attempt to use all of it.

171. Plastron, axillary/inguinal scales: present (*Kayentachelys*) = 0; absent (*Emydura*) = 1.

Morphology: The small bridge scales can be seen in cryptodire shells (state 0, Zangerl, 1969: fig. 1). State 1 is their absence (fig. 258).

Primitive condition: The absence of information about these scales in the outgroups (*Proganochelys, Australochelys, Palaeochersis*) makes it difficult to determine the primitive chelonian condition; presumably the presence of the scales is primitive.

Homoplasy: None known in pleurodires, although there may be multiple losses within Cryptodira.

Discussion: A problem with this character is the frequent damage to the bridge area of shells, making it difficult to determine the presence or absence of axillary or inguinal scales. In the MPC, *Proterochersis* is the only pleurodire definitely known to have these scales (Gaffney, 1990: fig. 105), so their absence is a Megapleurodira synapomorphy.

172. Plastron, abdominal scale narrow: abdominal midline sulcus length equals or exceeds that of anal scale (*Podocnemis*) = 0; abdominal midline length less than anal scales (*Taphrosphys*) = 1; abdominal scales do not meet on the midline (*Araripemys*) = 2.

Morphology: Most of the paired scales of the turtle plastron meet and share a common sulcus on the midline. The length of that midline sulcus for the abdominal scute is primitively one of the longest such midline sulci and is equal to or longer than the length of the anal scales at the midline (state 0, figs. 257–264). In some bothremydids, the abdominal scale is significantly narrowed on the midline (state 1, figs. 265, 267). In *Araripemys* the abdominal scales do not meet on the midline (state 2; Meylan, 1996: fig. 2).

Primitive condition: Abdominal scales in *Proganochelys, Kayentachelys*, and most Selmacryptodira are broad at the midline, suggesting that this is the primitive condition.

Homoplasy: The narrowed condition appears to occur several times within the Pleurodira. Among the Cryptodira, lateral displacement of the abdominals and loss occur in the Chelydridae and Kinosternidae (Hutchison and Bramble, 1981).

Discussion: Although this character shows homoplasy, it occurs only once within the Podocnemidoidea and, in the MPC, is a synapomorphy of a subset of the Taphrosphyini: *Taphrosphys* + *Ummulisani.*

173. Plastron, anterior lobe reaches carapace edge: anterior margin of plastron reaches same level or beyond anterior margin of carapace (*Cearachelys*) = 0; anterior margin of plastron well posterior to the anterior margin of the carapace (*Foxemys*) = 1.

Morphology: In most turtles the anterior lobe of the plastron is nearly as long as or longer than the anterior margin of the carapace. This can be seen in the primitive turtles *Proganochelys*, *Proterochersis*, and *Kayentachelys* (state 0; Gaffney, 1990: fig. 105). This is also the case in chelids, podocnemidids, pelomedusids, *Euraxemys*, *Araripemys*, and some bothremydids such as the probable *Galianemys* (AMNH 30550 and AMNH 30551) and *Cearachelys*. In the known Bothremydini the anterior limit of the plastron is well posterior to the anterior limit of the carapace (state 1, fig. 264).

Primitive condition: Approximate alignment of the anterior ends of the plastron and carapace is considered to be the primitive condition for turtles.

Homoplasy: In addition to those bothremydids with the derived condition described above, this condition occurs in some cryptodires with reduced plastra including *Chelydra*, *Macrochelys*, *Staurotypus*, *Claudius*, and *Sternotherus*.

Discussion: This character is a synapomorphy for the tribe Bothremydini. The character is gradational at best, and it can be ambiguous if the articulated carapace and plastron are held at varying angles of view.

174. Plastron, anal notch: absent (*Kayentachelys*) = 0; present (*Taphrosphys*) = 1.

Morphology: The posterior lobe of the plastron has a recessed or embayed posterior margin on the midline (state 1, fig. 264).

Primitive condition: The straight or posteriorly convex margin is primitive, as this occurs in *Proganochelys* (Gaffney, 1990) and *Palaeochersis* (Rougier et al., 1995).

Homoplasy: None known in the MPC, but within Selmacryptodira many taxa may acquire at least a shallow anal notch, and within Chelidae some (e.g., some *Chelodina*) may also have a nearly absent anal notch.

Discussion: The anal or xiphiplastral notch is a pleurodire synapomorphy, possibly related to the sutured pelvis.

The character is used in Antunes and Broin (1988), Lapparent de Broin and Murelaga (1999), Lapparent de Broin (2000b), and Fuente and Iturralde-Vinent (2001).

175. Shell, surface texture: surface rough with radiating ridges diverging from the posteromedial part (growth center) of the vertebral and pleural scale areas, as in *Proganochelys* = 0; weakly granulated polygons, "pelomedusoid" pattern, also as in chelids = 1; strongly granulated polygons, as in *Taphrosphys* = 2; fine, striated ridges as in *Polysternon* = 3; smooth, as in *Cearachelys* = 4; numerous small pits, as in *Araripemys* = 5; texture as in *Dortoka* = 6.

Morphology: The surface of the shell of many turtles is textured or sculptured; in others the shell is quite smooth. Within the Pleurodira a few species have radiating patterns of raised ridges, including *Platychelys* and *Notoemys* (state 0). Others, such as *Araripemys*, have patterns of numerous small pits (state 5). In certain members of the Bothremydidae, Chelidae, and Podocnemididae, there is a pattern of reticulate and anastomosing furrows and/or long striations that do not radiate from growth centers (state 1). At least in the Podocnemididae, these may be limited to the bridge. Broin (1977) called this texture "décoration pélomédusidienne". She described it as fine vascular grooves more or less dichotomous and discontinuous.

Primitive condition: The shell surface of *Proganochelys* has a pattern of radiating raised ridges (state 0; Gaffney, 1990: figs. 73, 74). The same pattern appears to have been present in *Proterochersis*, *Platychelys*, and *Notoemys*. This may be the primitive condition for pleurodires. However, within the Pelomedusoides, neither the pelomedusids nor most podocnemidids have well-developed shell surface texture.

Homoplasy: Shell surface sculpturing similar to that observed within some bothremydines occurs also in some chelids (AMNH 103702) and some *Podocnemis*.

Discussion: The pattern of reticulate furrows and/or long striations has been used to recognize shell material of the Bothremydidae (Antunes and Broin, 1988: character C-8; Lapparent de Broin 2000b: 67) or *Taphrosphys* (Antunes and Broin, 1988; character H-1; Broin, 1977; Lapparent de Broin and Werner, 1998: 41). Lapparent de Broin (2000b) argued that the carapace in bothremydids is more strongly decorated than in the other Pelomedusoides; that there are deeper short dichotomous sulci similar to marine cryptodires in *Bothremys* and sulci often united into salient polygons in *Taphrosphys*.

In our survey of bothremydid shells, we have found some inconsistencies in the distribution of these characters. In the primitive bothremydids, *Kurmademys* and *Cearachelys*, there is an extremely fine surface texture of very small raised areas that are only visible under magnification. Also, there are *Taphrosphys*-like polygons in *Araiochelys*, a bothremydine on the basis of skull morphology. *Polysternon* and *Foxemys*, also bothremydines, have surface texture, but these do not resemble those of other bothremydids. *Polysternon* is described (Broin, 1977) as having grooves that are deeper and larger than those generally seen in "décoration pélomédusidienne". They are described as sinuous, longitudinal and continuous, and disposed in scale areas of the carapace anterior-posteriorly (Broin, 1977).

The senior author thinks that this character should be dropped because the various states are difficult to identify objectively and consistently over a wide range of taxa. Making limited comparisons at the specific level for alpha taxonomic decisions should be done, but wide comparisons of all pleurodires becomes very subjective. Attempts to use surface texture in the highly ornamented Trionychidae have led to similar frustration. However, removing the character produces the same MPC. Nonetheless, state 1, if it can be recognized consistently, is a synapomorphy for Eupleurodira.

Innumerable authors have used surface texture as a character in studies of pleurodires, with some of the more explicit being Antunes and Broin (1988), Lapparent de Broin and Werner (1998), Lapparent de Broin and Murelaga (1999), and Lapparent de Broin (2000b). Lapparent de Broin and Murelaga (1999) use "decoration" states, similar to the ones used here.

SUMMARY

This study shows that pleurodires had a more extensive and more complex evolutionary history than has been realized. The discovery of new taxa of extinct groups has revealed a diversity of morphologies indicating a remarkable diversity of feeding and sensory strategies. The recognition of this new diversity is based on the discovery and description of many new skulls of pleurodires in this and other recent papers. Most previous work has been based on the shell, which in pleurodires in general, and in the Pelomedusoides in particular, is relatively conservative morphologically, masking the magnitude of pleurodire diversity.

The known history of the Pleurodira begins in the Late Triassic of Germany with the very high-domed, tortoiselike shells of *Proterochersis*. More than two dozen *Proterochersis* shells have been found in freshwater, stream-deposited sediments. Although they may have been aquatic, the high-domed shell is commonly assumed to indicate purely terrestrial turtles, however, it is also consistent with an adaptive response to large predators, like phytosaurs and metoposaurs. Although known only from the shell, *Proterochersis* is hypothesized as the sister taxon to all other pleurodires because it lacks the reduced scale arrangement of other pleurodires. Between the Late Triassic and Late Jurassic there is a long hiatus in the pleurodire record. The Late Jurassic yields a sparse pleurodire fauna of near-shore marine taxa of the family Platychelyidae, which is known from central Europe and the Caribbean. This family survives into the Early Cretaceous of South America. The Platychelyidae is the sister group to all remaining pleurodires, that is, the nanorder Eupleurodira consisting of the hyperfamilies Cheloides and Pelomedusoides.

It is in the latter part of the Early Cretaceous that pleurodire diversity sharply increases, supporting the idea that a significant amount of the earlier record is missing. The Cheloides, consisting of the family Chelidae, is the sister group to the Pelomedusoides. Chelids appear in the fossil record in the Albian at about the same time as the Pelomedusoides, but it is likely that this basal divergence took place earlier because of the high diversity of Pelomedusoides in the Early Cretaceous that we have been able to document with this study. Evidence for monophyly of the Chelidae is supported by the presence in all chelids of biconvex fifth and biconcave seventh cervical vertebrae (character 128) and the extreme cheek emargination extending into the temporal region (character 39).

At least four major clades of Pelomedusoides are known by the Albian. These are based on the genera *Araripemys* (Araripemydidae), *Euraxemys* (Euraxemydidae), *Brasilemys* (Podocnemidinura), and *Cearachelys* (Bothremydidae) from the Albian Santana Formation of Brazil, which shows that the major groups of Pelomedusoides were already established. A possible fifth lineage is *Teneremys*, from the Early Cretaceous of northern Africa. Based primarily on shell characters, *Teneremys* is resolved in this study as the sister taxon to the superfamily Podocnemidoidea, but it is as yet too poorly known for a well-tested relationship hypothesis.

The family Araripemydidae consists of one taxon, *Araripemys barretoi* from the Aptian–Albian of Brazil. Description of new cranial material suggests a possible sister-group relationship to the extant family Pelomedusidae based on extensive temporal and cheek emargination (character 14), but this relationship is only weakly supported. *Araripemys*, although highly autapomorphic in many features, may represent the first record of the Pelomedusidae, a lineage still important in the recent African fauna. Regardless of whether they are sister taxa, they are outgroups to all the remaining Pelomedusoides because they lack the advanced feature of a partial or full covering of the prootic (character 94). *Araripemys* is characterized by very thin, narrow triturating surfaces and a shell that lacks mesoplastra and has the first costals reaching the shell margin. *Araripemys* was a near-shore, probably marine, possibly freshwater predator, very similar in habitus to recent turtles that prey on fish (trionychids, long-necked chelids).

The new family Euraxemydidae consists of two new genera: *Euraxemys essweini*, n. gen. et sp., from the Albian Santana Formation of Brazil, and *Dirqadim schaefferi*, n. gen. et sp., from the Cenomanian Kem Kem beds of Morocco. Members of the Euraxemydidae share the unique possession of a medial process of the quadrate partially covering the prootic (character 94) and narrowly contacting a ventral process of the exoccipital, in contrast to all other pleurodires, which have either complete exposure or complete covering of the prootic ventrally. Furthermore, they possess a ventral process of the exoccipital that is exposed at the lateral margin of the basioccipital in an elongate foot (character 86). The Euraxemydidae is hypothesized as the sister group to the families Podocnemididae and Bothremydidae, which together form the superfamily Podocnemidoidea. Members of the superfamily Podocnemidoidea have the processus interfenestralis of the opisthotic and most of the prootic covered ventrally by the quadrate and basisphenoid (characters 94 and 99). The Euraxemydidae provides a model for the primitive condition for many other characters in the superfamily Podocnemidoidea.

Brasilemys is the oldest member of the diverse group represented by the family Podocnemididae, which in the Recent fauna contains eight species divided into three genera currently living in South America and Madagascar. *Brasilemys*, from the Albian Santana Formation, the Cenomanian *Hamadachelys* from Morocco, and the Podocnemididae make up the epifamily Podocnemidinura. This clade is united by the possession of a cavum pterygoidei formed by the basisphenoid and pterygoid (character 69). The family Podocnemididae is known from the Cretaceous to the Recent and is known from all continents except Australia and Antarctica.

Cearachelys is the oldest known of the Bothremydidae, a now extinct family that appears to be the most diverse family among the Pleurodira, reaching its greatest diversity later in the Late Cretaceous and Paleogene. All pleurodires known from the Early Cretaceous Santana Formation, including *Cearachelys*, were probably near-shore marine species, although some may have been fresh-water. In the Santana fauna, *Euraxemys* and *Brasilemys* may have been more generalized predators, with *Araripemys* more specialized for fish-eating. However, it is *Cearachelys* that may have begun the bothremydid trend toward a crushing feeding apparatus with a habitus similar to that of the Recent emydid *Malaclemys*.

The Late Cretaceous reveals the persistence of euraxemydids in North Africa and a slight increase in diversity of podocnemidids in South America. The big event in pleurodire evolution at this time, however, is the explosive radiation of the Bothremydidae. This rapid expansion in morphological diversity can be observed in four clades, recognized as tribes, namely the Kurmademydini, Cearachelyini, Bothremydini, and Taphrosphyini. Although the oldest bothremydid is the Albian *Cearachelys* from Brazil, the most basal clade, and sister group to all other bothremydids, is the Maastrichtian tribe Kurmademydini from India. The two genera in the Kurmademydini have extensive temporal and cheek emargination. *Kurmademys* has a broad, triangular triturating surface, while that of *Sankuchemys* is narrower, with an accessory triturating ridge. The phylogenetic position of the Kurmademydini is based, among other characters, on the persistence of the fossa precolumellaris (character 56), which is absent in all other bothremydids. The Kurmademydini were most likely freshwater forms with lifestyles resembling those of the Recent pelomedusids *Pelomedusa* and *Pelusios*.

The tribe Cearachelyini consists of two genera, *Cearachelys* from the Albian of Brazil and *Galianemys* from the Cenomanian of Morocco. They have the triangular, posteriorly expanded triturating surfaces typical of bothremydids (character 34). Their monophyly is supported by the presence of a jugal that is retracted from the orbital margin (character 20). While the Kurmademydini are found in freshwater sediments, as is *Galianemys*, *Cearachelys* is in the presumably near-shore marine Santana Formation. The broad jaws of the Cearachelyini genera suggest that their lifestyles may have been comparable to broad-jawed emydids like *Graptemys* and *Malaclemys*.

The tribe Bothremydini is characterized by the very broad preorbital part of the skull with very wide triturating surfaces, often with conical pits on the skull and jaws (characters 34, 35). The function of the pits is unknown, but they may have allowed the animal to hold and crush slippery, ovoid prey, like gastropods. The Bothremydini are the most long-ranging bothremydids, extending from the Late Cretaceous Santonian to the Eocene Ypresian. Geographically, this clade is widespread, extending from its peak diversity area of North Africa to North America, Europe, and the Middle East. Although most are near-shore marine, the European subtribe Foxemydina and the North American species *Chedghaii hutchisoni* are known from freshwater sediments. This radiation of broad-jawed, probable molluscivores is unique among turtles. In the genus *Graptemys*, the females of four species approach the morphology seen in the Bothremydini, but they are much smaller, nonmarine turtles with a very restricted distribution. Among marine cryptodires many species have enlarged triturating surfaces, but none has produced the inflated face seen in members of this tribe.

The tribe Bothremydini consists of *Foxemys mechinorum* from the Campanian–Maastrichtian of France; *Polysternon provinciale* from the Campanian of Europe; *Zolhafah bella* from the Maastrichtian Dakla Formation of Egypt; *Rosasia soutoi* from the Campanian–Maastrichtian of Portugal; *Araiochelys hirayamai*, n. gen. et sp. and *Bothremys maghrebiana*, n. sp. from the Danian phosphates of the Ouled Abdoun Basin, Morocco; *Bothremys cooki* from the Maastrichtian Navesink Formation of New Jersey; *Bothremys kellyi*, n. sp. from the Ypresian phosphates of the Ouled Abdoun Basin, Morocco; *Bothremys arabicus* from the Santonian of Jordan; *Chedighaii hutchisoni*, n. gen. et sp. from the Campanian Kirtland Formation of New Mexico; and *Chedighaii barberi*, n. gen. from the Campanian of Arkansas, Alabama, Kansas, and New Jersey.

The tribe Taphrosphyini has a variety of triturating surfaces but lacks the wide, triangular surfaces typical of the other bothremydids. Members of the Taphrosphyini are characterized by the presence of a jugal-quadrate contact (character 22), the absence of a maxilla-quadratojugal contact (character 38), and the absence of a supraoccipital-quadrate contact (character 79). Among the Bothremydidae, the Taphrosphyini is the most diverse morphologically. The feeding surfaces show surprising variation. The long, narrow skull of *Labrostochelys* is similar to the skull of some fish-eating trionychids, while the very short skull of *Phosphatochelys* is similar to some cheloniids. Other skulls, such as those of *Azabbaremys* and *Arenila*, are large and massive, but without broadly expanded triturating surfaces, while *Ummulisani* has very narrow and deep labial ridges. The nasal regions of Taphrosphyini also show wide diversity. *Rhothonemys* has nasal openings and cavities that are more than twice the size of the orbits, in contrast to the nasal openings in *Labrostochelys*, which are smaller than the relatively small orbits. This diversity in the skull morphology of the Taphrosphyini is mostly evident in the Paleogene of North Africa, but the group is also known from the East Coast of North America, central Africa, and (based on shells) Europe and South America. All the Taphrosphyini are near-shore marine.

The tribe Taphrosphyini consists of *Taphrosphys sulcatus* from the Danian Hornerstown Formation of New Jersey; *Taphrosphys congolensis* from the Paleocene of Cabinda, west Africa; *Taphrosphys ippolitoi*, n. sp. and

Labrostochelys galkini, n. gen. et sp. from the Danian phosphates of the Ouled Abdoun Basin, Morocco; *Phosphatochelys tedfordi* and *Ummulisani rutgersensis*, n. gen. et sp. from the Ypresian phosphates of the Ouled Abdoun Basin of Morocco; *Rhothonemys brinkmani*, n. gen. et sp. from the Paleogene phosphates of the Ouled Abdoun Basin of Morocco; *Azabbaremys moragjonesi* from the Paleocene Teberemt Formation of Mali; *Nigeremys gigantea* from the Maastrichtian of Niger; and *Arenila krebsi* from the Maastrichtian Dakla Formation of Egypt.

When the skull morphology of the members of the Taphrosphyini is considered alongside that of the other three tribes, it becomes apparent that the family Bothremydidae has the greatest range of skull forms of any turtle family yet known. In fact, the skull morphologies of many turtle families seem remarkably uniform in comparison (e.g., Testudinidae, Kinosternidae, Pelomedusidae, Trionychidae, Carettochelyidae). Even in families with relatively diverse skull morphologies (e.g., Geoemydidae, Chelidae), variation generally occurs in one or two major aspects of their structure (triturating surface and cheek completeness in geoemydids; cheek emargination in chelids). There are also families with bizarre skull morphologies (e.g. Nanhsiungchelyidae, Protostegidae), but these are not diverse, at least as they are now known. In no other family do we see the extremes exemplified by the skulls of *Cearachelys*, *Bothremys*, *Labrostochelys*, *Azzabaremys*, *Rhothonemys*, and *Phosphatochleys*. It is this remarkable variation in skull morphology that has allowed us to formulate a strong hypothesis of bothremydid relationships in spite of the presence in Pelomedusoides of remarkably uniform shells.

A phylogenetic analysis of the core dataset of 41 taxa, 122 cranial characters, and 52 postcranial characters relies on comparative descriptions of these taxa. The analysis using PAUP results in one most parsimonious cladogram of 382 steps and a consistency index of 0.6. A Bremer decay analysis shows that the family Bothremydidae is strongly supported at five steps, the tribes Cearachelyini and Kurmademydini have an index of 2, and the tribe Taphrosphyini has an index of 3. The tribe Bothremydini becomes unresolved at one step and is the most weakly supported of these groups. The addition of selected, shell-only taxa with low missing data to the core dataset results in one equally parsimonious cladogram, which is resolved as (*Proterochersis* (Platychelyidae (*Dortoka* (Chelidae (Pelomedusidae + *Araripemys*) (Euraxemydidae (*Teneremys* (Podocnemididae + *Hamadachelys* + *Brasilemys* (Bothremydidae)))))))). A partitioned dataset consisting only of cranial characters (excluding all shell-only taxa) results in one equally parsimonious cladogram identical to the most parsimonious cladogram resulting from the whole dataset; however, a partitioned dataset consisting only of postcranial characters (excluding all skull-only taxa) resulted in 2704 trees, the consensus of which lacks resolution for nearly all of the Pelomedusoides, but which does resolve more basal pleurodires.

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APPENDIX 1
Morphology Description Outline

PREFRONTAL

- I. Preservation
- II. Contacts
  - A. Prefrontal on midline
  - B. Maxilla anteroventrolaterally
  - C. Frontal posteriorly
  - D. Palatine ventrally
  - E. Parietal posterolaterally (in *Phosphatochelys* and *Ummulisani*)
- III. Structures
  - A. Dorsal plate
    - 1. Dorsal margin of apertura narium externa, protruding, or flat
    - 2. Dorsal margin of orbit, very wide, narrow
    - 3. Ventral surface: sulcus olfactorius
  - B. Ventral process, forms edge of foramen orbitonasale

FRONTAL

- I. Preservation
- II. Contacts
  - A. Frontal on midline
  - B. Prefrontal anteriorly
  - C. Postorbital posterolaterally
  - D. Parietal posteriorly
- III. Structures
  - A. Orbital margin posteromedially
  - B. Ventral surface: sulcus olfactorius

PARIETAL

- I. Preservation
- II. Contacts of dorsal plate
  - A. Parietal on midline
  - B. Frontal anteriorly
  - C. Postorbital laterally
  - D. Quadratojugal posterolaterally
- III. Structures of dorsal plate
  - A. Emargination
  - B. Ventral process lateral to sulcus palatinopterygoideus
- IV. Contacts of processus inferior parietalis
  - A. Palatine anteroventrally
  - B. Pterygoid ventrally
  - C. Prootic posteroventrally
  - D. Supraoccipital posteriorly
- V. Structures of processus inferior parietalis
  - A. Foramen interorbitale
  - B. Width
  - C. Foramen nervi trigemini: parietal anterodorsally, prootic dorsolaterally, pterygoid ventrally

JUGAL

- I. Preservation
- II. Contacts of lateral plate
  - A. Maxilla anteroventrally
  - B. Postorbital dorsally
  - C. Quadratojugal posterodorsally
  - D. Quadrate posteroventrally
- III. Structures of lateral plate
  - A. Orbital margin, present or absent (PO-MX contact)
  - B. Cheek emargination
- IV. Contacts of medial process
  - A. In floor of orbit (dorsal view)
    - 1. Maxilla anteriorly and laterally
    - 2. Palatine medially
  - B. In septum orbitotemporale, i.e. postorbital wall (posterior view and anterior view)
    - 1. Postorbital dorsomedially
    - 2. Palatine ventromedially
    - 3. Pterygoid posteriorly (lateral and/or posterior views)
    - 4. Maxilla ventrally
- V. Structures of medial process
  - A. Fossa orbitalis floor
  - B. Septum orbitotemporale
  - C. Triturating surface

QUADRATOJUGAL

- I. Preservation
- II. Contacts
  - A. Parietal medially
  - B. Quadrate posteroventrally
  - C. Squamosal posterodorsally
  - D. Postorbital anterodorsally
  - E. Jugal anteroventrally/anteriorly
  - F. Maxilla anteroventrally
- III. Structures
  - A. Flat plate in temporal roof, usually C shaped
  - B. Cheek emargination margin
  - C. Temporal emargination margin

SQUAMOSAL

- I. Preservation
- II. Contacts
  - A. Quadrate anteriorly, and anteromedially
  - B. Opisthotic medially: on dorsal, posterior, and ventral surfaces
  - C. Quadratojugal anterodorsolaterally
- III. Structures
  - A. Cone-shaped bone fitting around antrum postoticum of quadrate
  - B. Flatter vs. rounder
  - C. Vertical flange on ventral surface

POSTORBITAL

- I. Preservation
- II. Contacts of lateral plate
  - A. Frontal anteromedially
  - B. Jugal ventrally
  - C. Quadratojugal posteriorly
  - D. Parietal posteromedially
  - E. Maxilla anteroventrally
  - F. Quadrate ventrolaterally
- III. Structures of lateral plate
  - A. Orbital margin
  - B. Temporal emargination
- IV. Contacts of medial process
  - A. In septum orbitotemporale, facing fossa orbitalis
    - 1. Frontal dorsomedially
    - 2. Palatine ventrally

- 3. Jugal ventrolaterally
- 4. Parietal medially
- B. In septum orbitotemporale, facing fossa temporalis
  - 1. Parietal dorsomedially
  - 2. Pterygoid ventromedially
  - 3. Jugal ventrolaterally
  - 4. Palatine ventrally
- V. Structures of medial process
  - A. Part of roof and lateral wall of sulcus palatinopterygoideus
  - B. Septum orbitotemporale, facing fossa orbitalis
  - C. Septum orbitotemporale, facing fossa temporalis

PREMAXILLA

- I. Preservation
- II. Contacts
  - A. Maxilla posterolaterally
  - B. Premaxilla medially on midline
  - C. Vomer posteriorly
- III. Structures on dorsal surface
  - A. Floor of fossa nasalis, beginning choanal division
  - B. Margin of apertura narium externa
  - C. Foramen praepalatinum and associated grooves
- IV. Structures on ventral surface
  - A. Vertical labial ridge with horizontal medial plate
  - B. Labial ridge of triturating surface: notched, curved, sharp, blunt
  - C. Midline concavity, often defined by ridge that is continuous with lingual ridge/medial margin of triturating surface
  - D. Accessory ridges or troughs
  - E. Width, length of premaxilla

MAXILLA

- I. Preservation
- II. Contacts of vertical plate
  - A. Premaxilla anteromedially
  - B. Jugal posterodorsally
  - C. Quadratojugal posteriorly
  - D. Quadrate posteriorly
  - E. Prefrontal anterodorsally
- III. Structures of vertical plate
  - A. Orbital margin
  - B. Foramen orbito-nasale
  - C. Fossa nasalis: choanal passages (anterior part, otherwise see horizontal plate)
  - D. Apertura narium externa
  - E. Cheek emargination
- IV. Contacts of horizontal plate
  - A. Premaxilla anteromedially
  - B. Vomer medially
  - C. Other maxilla medially on midline
  - D. Palatine posteromedially
  - E. Jugal posterolaterally
- V. Structures of horizontal plate
  - A. Width
  - B. Shape: triangular vs. parallel
  - C. Medial process
  - D. Apertura narium interna
  - E. Triturating surface
    - 1. Labial ridge: (a) deep vs. shallow, (b) thick vs. thin, (c) curved vs. straight
    - 2. Pits, accessory ridges, etc.
    - 3. Width to lingual margin
    - 4. Palatine/jugal contribution
  - F. Dorsal surface: floor of fossa orbitalis
    - 1. Foramen orbito nasale
    - 2. Foramen alveolare superius
    - 3. Margin of fossa orbitalis
  - G. Anterior wall of fossa temporalis

VOMER

- I. Preservation
- II. Contacts
  - A. Premaxillae anteriorly
  - B. Maxillae anterolaterally
  - C. Palatines posteriorly
- III. Structures
  - A. Apertura narium interna, straight vs. dumb-bell shaped, choanal passages
  - B. Size, thick central bar
  - C. Trough on dorsal surface
  - D. Foramen praepalatinum

PALATINE

- I. Preservation
- II. Contacts
  - A. Maxilla anterolaterally
  - B. Vomer anteromedially
  - C. Other palatine medially on midline
  - D. Pterygoid posteriorly
  - E. Only on dorsal surface: parietal (processus inferior parietalis)
    - 1. Parietal
    - 2. Floor of fossa orbitalis: (a) maxilla anterolaterally, (b) jugal laterally, (c) postorbital posterolaterally
- III. Structures on dorsal surface
  - A. Fossa orbitalis floor
  - B. Foramen orbito-nasale
  - C. Apertura narium interna
  - D. Dorsal process to parietal
  - E. Dorsal process to postorbital and jugal forming anterior floor of sulcus palatinopterygoideus
  - F. Foramen palatinum posterius (penetrates to ventral surface)
- IV. Structures on ventral surface
  - A. Triturating surface contribution
  - B. Apertura narium interna
  - C. Foramen palatinum posterius
  - D. Choanal passages, dorsal arching of palate

QUADRATE

- I. Preservation
- II. Contacts on lateral surface
  - A. Quadratojugal anterodorsally
  - B. Maxilla anteriorly
  - C. Jugal anterodorsally
  - D. Postorbital anterodorsally
  - E. Squamosal posterodorsally
- III. Structures on lateral surface
  - A. Skull roof temporal/cheek emargination
  - B. Cavum tympani
    - 1. Incisura columellae auris: (a) open vs. closed, (b) eustachian tube separated from stapes, by bone or narrow fissure
    - 2. Antrum postoticum
    - 3. Fossa precolumellaris
    - 4. Sulcus eustachii
    - 5. Ventrolateral shelf below cavum tympani
- IV. Contacts on dorsal and anterior surface

A. Prootic anteromedially
B. Opisthotic posteromedially
C. Supraoccipital medially
D. Squamosal posteriorly and posterolaterally
V. Structures on dorsal and anterior surface
A. Foramen stapedio-temporale (see Prootic)
VI. Contacts on ventral surface
A. Pterygoid anteromedially
B. Basisphenoid medially
C. Basioccipital posteromedially
D. Prootic medially
VII. Structures on ventral surface
A. Fossa pterygoidea (see Pterygoid)
B. Foramen posterius canalis carotici interni
C. Condylus mandibularis
1. Position relative to condylus occipitalis
VIII. Contacts on posterior surface
A. Squamosal dorsolaterally
B. Opisthotic dorsomedially
C. Exoccipital medially
D. Basioccipital ventromedially
E. Prootic ventromedially
IX. Structures on posterior surface
A. Fenestra postotica: (a) subdivisions for lateral head vein and stapedial artery
B. Aditus canalis stapedio-temporalis
C. Cavum acustico-jugulare
D. Incisura columellae auris
E. Foramen chorda tympani superius/inferius

PTERYGOID

I. Preservation
II. Contacts on ventral surface
A. Palatine anteriorly
B. Other pterygoid anteromedially
C. Basisphenoid posteromedially
D. Prootic posteriorly
E. Quadrate posterolaterally
III. Structures on ventral surface
A. Processus trochlearis pterygoidei, size, angle to midline
B. Quadrate ramus
C. Fossa pterygoidea (depression for M. pterygoideus)
D. Cavum pterygoidei (includes carotid, overhung by pterygoid)
E. Foramen posterius canalis carotici interni
1. May also have quadrate, basisphenoid, or prootic inmargin
F. Foramen palatinum posterius
G. Pterygoid flange
IV. Contacts on dorsal surface
A. Contacts of processus trochlearis pterygoidei
1. Postorbital dorsolaterally
2. Jugal anterolaterally
3. Palatine anteroventrally
4. Parietal anterolaterally
B. Contacts of crista pterygoidea
1. Parietal anterodorsally
2. Prootic posterodorsally
3. Quadrate posterolaterally
4. Palatine anteriorly
5. Basisphenoid medially
V. Structures on dorsal surface
A. Processus trochlearis pterygoidei
B. Sulcus palatinopterygoideus
1. Formed by PO, PA, PT, PAL
C. Foramen palatinum posterius
1. Canalis nervi vidiani, foramen nervi vidiani
D. Crista pterygoidea
1. Foramen nervi trigemini
E. Sulcus/canalis cavernosus
F. Foramen caroticum laterale

SUPRAOCCIPITAL

I. Preservation
II. Contacts
A. Parietals dorsally and anteriorly
B. Prootic anterolaterally
C. Quadrate laterally
D. Opisthotic posterolaterally
E. Exoccipitals posteroventrally
III. Structures
A. Crista supraoccipitalis
B. Cavum labyrinthicum
1. Canalis semicircularis posterior
2. Canalis semicircularis anterior
3. Recessus labyrinthicus supraoccipitalis
4. Foramen aquaducti vestibuli
C. Foramen magnum

EXOCCIPITAL

I. Preservation
II. Contacts
A. Supraoccipital dorsally
B. Opisthotic laterally
C. Quadrate ventrolaterally
D. Basioccipital ventrally
E. Prootic anteriorly
F. Basisphenoid anteriorly in ventral view
III. Structures
A. Foramen magnum
B. Condylus occipitalis (BO present or absent)
C. Foramen nervi hypoglossi
D. Foramen jugulare posterius (open or closed)
E. Foramen jugulare anterius
F. Fenestra postotica
G. Ventral process

BASIOCCIPITAL

I. Preservation
II. Contacts
A. Basisphenoid anteriorly
B. Quadrate laterally
C. Exoccipitals posterodorsally
D. Opisthotic laterally
III. Structures
A. Condylus occipitalis
B. Tuberculum basioccipitale
C. Median concavity on ventral surface
D. Relative size, short vs. long

PROOTIC

I. Preservation
II. Contacts
A. Parietal dorsomedially
B. Quadrate laterally
C. Supraoccipital posterodorsally
D. Pterygoid ventrally
E. Opisthotic posteriorly
III. Structures
A. Fossa temporalis exposure
1. Foramen nervi trigemini (in suture with pterygoid, parietal), close to foramen stapedio-temporale

        - 2. Foramen stapedio-temporale (in suture with quadrate), visible in dorsal view or not
    - B. Cavum acustico-jugulare exposure
        - 1. Fenestra ovalis (with opisthotic)
        - 2. Foramen cavernosum (with quadrate)
        - 3. Foramen nervi facialis (VII)
        - 4. Aditus canalis stapedio-temporalis
    - C. Cavum labyrinthicum exposure
        - 1. Canalis semicircularis anterior
        - 2. Recessus labyrinthicus prooticus
        - 3. Canalis semicircularis horizontalis
        - 4. Hiatus acusticus
        - 5. Fossa acustico-facialis: (a) foramen nervi facialis, (b) foramen nervi acustici
    - D. Ventral surface exposure
        - 1. Foramen nervi facialis
        - 2. Foramen posterius canalis carotici interni

OPISTHOTIC

- I. Preservation
- II. Contacts
    - A. Supraoccipital anteromedially
    - B. Prootic anteriorly
    - C. Quadrate anterolaterally
    - D. Squamosal posterolaterally
    - E. Exoccipital posteromedially
- III. Structures
    - A. Foramen jugulare posterius
    - B. Fenestra postotica
        - 1. Lateral head vein (more medial)
        - 2. Stapedial artery (more lateral, mostly quadrate)
    - C. Processus interfenestralis
        - 1. Covered ventrally or exposed
        - 2. Fenestra ovalis (with prootic)
        - 3. Fenestra perilymphatica
    - D. Cavum labyrinthicum
        - 1. Canalis semicircularis horizontalis
        - 2. Canalis semicircularis posterior
        - 3. Recessus labyrinthicus opisthoticus
        - 4. Foramen medialis, externum, internum nervi glosspharyngii (IX)
        - 5. Hiatus acusticus
    - E. Cavum acustico-jugulare
        - 1. Foramen jugulare anterius
        - 2. Recessus scalae tympani

BASISPHENOID

- I. Preservation
- II. Contacts on ventral surface
    - A. Pterygoids anterolaterally
    - B. Basioccipital posteriorly
    - C. Prootic laterally
    - D. Quadrate laterally (Podocnemididae and Bothremydidae)
- III. Structures on ventral surface
    - A. Foramen posterius canalis carotici interni
    - B. Ventral midline concavity
    - C. Cavum pterygoidei
- IV. Contacts on dorsal surface
    - A. Pterygoid anterolaterally
    - B. Prootic laterally
    - C. Palatines anteriorly
    - D. Basioccipital posteriorly
- V. Structures on dorsal surface
    - A. Rostrum basisphenoidale
    - B. Sulcus cavernosus
    - C. Sella turcica
    - D. Dorsum sellae
    - E. Foramen anterius canalis carotici interni
    - F. Processus clinoideus
    - G. Foramen nervi abducentis (VI)
    - H. Foramen caroticum laterale
    - I. Hiatus acusticus

DENTARY

- I. Preservation
- II. Contacts
    - A. Coronoid posterodorsally
    - B. Surangular posterolaterally
    - C. Angular posteroventrally
- III. Structures
    - A. Fusion of rami at symphysis
    - B. Posterior extent on lateral surface
    - C. Posterior extent on medial surface
    - D. Labial ridge
    - E. Lingual ridge, and symphyseal wedge
    - F. Shape of triturating surface
    - G. Pit
        - 1. Size
        - 2. Contacts
    - H. Symphyseal hook
    - I. Sulcus cartilaginis meckelii
    - J. Foramen intermandibularis medius
    - K. Foramen alveolare inferius
    - L. Foramen dentofaciale majus
    - M. Limits of rhamphotheca
    - N. Extent of jaw adductor musculature on dentary

ANGULAR

- I. Preservation
- II. Contacts
    - A. Dentary anteriorly
    - B. Prearticular dorsally
    - C. Articular posteriorly
    - D. Surangular posteroventrally
- III. Structures
    - A. Contribution to margin of sulcus cartilaginis meckelii
    - B. Foramen intermandibularis caudalis
    - C. Foramen intermandibularis oralis

SURANGULAR

- I. Preservation
- II. Contacts
    - A. Dentary anteriorly
    - B. Coronoid anterodorsally
    - C. Angular posteroventrally
    - D. Articular posteromedially
- III. Structures
    - A. Fossa meckelii
    - B. Foramen nervi auriculotemporalis
    - C. Contribution to area articularis
    - D. Retroarticular process

CORONOID

- I. Preservation
- II. Contacts
    - A. Dentary anteriorly and laterally
    - B. Surangular posterolaterally
    - C. Prearticular posteromedially
- III. Structures
    - A. Processus coronoideus
    - B. Fossa meckelii
    - C. Triturating surface

ARTICULAR
 I. Preservation
 II. Contacts
  A. Surangular laterally
  B. Angular ventrally
  C. Prearticular medially
 III. Structures
  A. Area articular
  B. Fossa meckelii
  C. Retroarticular process
  D. Foramen posterius chorda tympani
PREARTICULAR
 I. Preservation
 II. Contacts
  A. Coronoid anterodorsally
  B. Articular posteromedially
  C. Angular ventrally
 III. Structures
  A. Fossa meckelii
  B. Foramen intermandibularis medius
  C. Foramen intermandibularis oralis
  D. Foramen intermandibularis caudalis
SPLENIAL
 I. Preservation
 II. Contacts
 III. Structures

APPENDIX 2

CHARACTER LIST

Taxonomic examples of character states are indicated in parentheses.

1. NA, nasals: (0) present (*Emydura*) or (1) absent (*Pelusios*).
2. LA, lacrimal: (0) present (*Proganochelys*) or (1) absent (*Emydura*).
3. LA, lacrimal foramen: (0) present (*Proganochelys*) or (1) absent (*Emydura*).
4. PF, meet on midline in dorsal view: (0) no (*Proganochelys*) or (1) yes (*Pelusios*).
5. PF, preorbital skull broad: (0) narrow (*Galianemys*) or (1) very broad (*Bothremys*).
6. PF, anterior margin: (0) straight, broadly convex margin (*Pelomedusa*) or (1) narrow midline process, at least partially dividing nares (*Bothremys*).
7. PF, pf-pal contact: (0) absent (*Galianemys*) or (1) present in anterior wall of fossa orbitalis (*Bothremys*).
8. PF, pf-vo contact: (0) absent (*Proganochelys*) or (1) present (*Chelydra*).
9. PF, fissura ethmoidalis: (0) very wide (*Proganochelys*) or (1) narrow (*Pelusios*).
10. PF, pf-pa contact: (0) absent (*Galianemys*) or (1) present (*Phosphatochelys*).
11. FR, orbits facing upwards: (0) facing more laterally (*Galianemys*) or (1) facing more dorsally (*Bothremys*).
12. FR, foramen interorbitale: (0) high (*Galianemys*) or (1) low (*Bothremys*).
13. PA, qj-pa contact: (0) absent (*Proganochelys*) or (1) present, with qj large (*Euraxemys*) or (2) present, with qj small (*Phosphatochelys*).
14. PA, temporal emargination: (0) absent, slight, moderate (*Proganochelys*) or (1) extreme (*Kurmademys*) or (2) intermediate (*Galianemys*).
15. PA, pa-sq contact: (0) present (*Proganochelys*) or (1) absent (*Pelusios*).
16. PA, contacts pt at base of processus trochlearis pterygoidei: (0) absent (*Pelusios*) or (1) present, ventral parietal process on lateral side of sulcus palatinopterygoideus (*Bothremys*).
17. PA, sulcus palatinopterygoideus: (0) absent (*Proganochelys*) or (1) high (*Galianemys*) or (2) low due to thicker pa, po (*Bothremys*).
18. PA, enters orbital margin: (0) no (*Galianemys*) or (1) yes (*Phosphatochelys*).
19. ST, supratemporal: (0) present (*Proganochelys*) or (1) absent (*Pelusios*).
20. JU, jugal retracted from orbital margin: (0) enters orbit (*Pelusios*) or (1) partially retracted (*Cearachelys*) or (2) widely retracted (*Galianemys*).
21. JU, narrow dorsoventrally: (0) broader (*Bothremys*) or (1) narrower (*Taphrosphys, Labrostochelys*).
22. JU, ju-qu contact: (0) no (*Bothremys*) or (1) yes (*Azabbaremys*).
23. JU, exposure in triturating surface: (0) no exposure (*Pelusios*) or (1) small exposure (*Galianemys*) or (2) greater exposure (*Bothremys*).
24. SQ, posterior projection: (0) lacks projection (*Galianemys*) or (1) projects posteriorly, forming distinct process (*Bothremys*).
25. SQ, posteroventral vertical flange: (0) absent (*Galianemys*) or (1) present (*Labrostochelys*).
26. SQ, lateral tubercle: (0) absent (*Galianemys*) or (1) present (*Labrostochelys*).
27. PO, fossa orbitalis posterior enlargement: (0) absent (*Galianemys*) or (1) present (*Bothremys*).
28. PO, septum orbitotemporale: (0) absent (*Proganochelys*) or (1) postorbital wall closed (*Galianemys*) or (2) postorbital wall at least partially open (*Phosphatochelys*).
29. PO, size: (0) short (*Euraxemys*) or (1) long (*Galianemys*).
30. PM, protrudes anteriorly beyond labial ridge: (0) no, slightly (*Galianemys*) or (1) yes, in ventral view projects moderately at least (*Bothremys*).
31. PM, midline depression: (0) absent, shallow, indistinct (*Euraxemys*) or (1) present and distinct (*Bothremys*).
32. PM, midline dorsal process: (0) present, meeting nasals (*Proganochelys*) or (1) absent, low (*Galianemys*) or (2) present, partially, completely separates apertura narium externa (*Araiochelys*).
33. PM, dorsal sulcus: (0) smooth surface (*Bothremys*) or (1) sulcus on dorsal surface, parallel to anterior margin (*Phosphatochelys*).
34. MX, triturating surfaces: (0) narrow (*Taphrosphys*) or (1) wider (*Galianemys*) or (2) widest (*Bothremys*).

35. MX, pits: (0) absent (*Kurmademys*) or (1) present (*Bothremys*).
36. MX, accessory ridge: (0) absent (*Galianemys*) or (1) present (*Euraxemys*).
37. MX, labial ridge below orbit: (0) shallower (*Galianemys*) or (1) very deep ventrolateral to orbit (*Bothremys*).
38. MX, mx-qj contact: (0) absent (*Euraxemys*) or (1) present (*Galianemys*) or (2) absent due to qj absence (*Emydura*).
39. MX, mx-qu contact, cheek emargination: (0) absent, little or no emargination (*Galianemys*) or (1) present, no emargination (*Azabbaremys*) or (2) absent, barely separated by narrow fissure (*Phosphatochelys*) or (3) absent, deep emargination, qj present (*Euraxemys*) or (4) absent, deep emargination, qj absent (*Emydura*).
40. MX, orbital-narial bar width: (0) width intermediate (*Galianemys*) or (1) broad (*Bothremys*) or (2) extremely broad (*Labrostochelys*) or (3) extremely narrow (*Phosphatochelys*).
41. MX, dorsal process onto skull roof: (0) mx not constricting pf (*Galianemys*) or (1) extends dorsomedially constricting pf (*Bothremys cooki*).
42. MX, ventral rim of orbit: (0) rim with distinct margin (*Galianemys*) or (1) rim absent, continuous slope (*Bothremys*).
43. MX, exposure in orbital floor: (0) mx broadly exposed in floor of orbit (*Galianemys*) or (1) narrowly or not exposed (*Azabbaremys*).
44. VO, mx-vo contact: (0) present (*Proganochelys*) or (1) absent (*Azabbaremys*).
45. VO, absent: (0) present, paired (*Proganochelys*) or (1) present, single (*Galianemys*) or (2) absent (*Pelusios*).
46. VO, vomerine teeth: (0) present (*Proganochelys*) or (1) absent (*Pelusios*).
47. VO, central bar: (0) sutured at both ends (*Galianemys*) or (1) sutured only anteriorly (*Azabbaremys*) or (2) absent.
48. PAL, foramen palatinum posterius: (0) in floor of orbit (*Chelydra*) or (1) behind orbit, in floor of sulcus palatinopterygoideus (*Pelusios*).
49. PAL, dorsally arched palate: (0) absent (*Galianemys*) or (1) present (*Azabbaremys*).
50. PAL, contribution to triturating surface: (0) little or none (*Euraxemys*) or (1) moderate to extensive (*Bothremys*).
51. QU, antrum postoticum: (0) absent, open incisura columellae auris (*Proganochelys*) or (1) small (*Bothremys*) or (2) absent, closed incisura (*Azabbaremys*) or (3) moderate-large (*Galianemys*).
52. QU, incisura columellae auris: (0) no posterior bony restrictions (*Euraxemys*) or (1) eustachian tube separated from stapes by bone or narrow fissure (*Foxemys*) or (2) eustachian tube and stapes enclosed by bone (*Podocnemis*).
53. QU, stapes contained in bony canal: (0) no (*Euraxemys*) or (1) yes (*Bothremys*).
54. QU, sulcus eustachii: (0) without ventral process (*Bothremys*) or (1) with ventral process (*Labrostochelys*).
55. QU, trough on closed incisura columellae auris ridge: (0) absent (*Bothremys*) or (1) present (*Galianemys*).
56. QU, fossa precolumellaris: (0) very small to absent (*Galianemys*) or (1) present but shallow (*Euraxemys*) or (2) deep and well defined (*Pelusios*).
57. QU, shelf below cavum tympani: (0) absent (*Galianemys*) or (1) lower portion of cavum tympani unusually deep (*Bothremys*).
58. QU, medial process reaches braincase: (0) absent (*Chelydra*) or (1) present (*Pelusios*).
59. QU,qu-bo contact: (0) absent (*Euraxemys*) or (1) present (*Galianemys*).
60. QU, condylus mandibularis position: (0) posterior to or on bo-bs suture (*Galianemys*) or (1) anterior to bo-bs suture (*Pelusios*) or (2) posterior to condylus occipitalis (*Nigeremys*).
61. QU, fully formed cavum tympani: (0) absent (*Proganochelys*) or (1) present (*Pelusios*).
62. QU, cavum tympani with acute posterior edge: (0) no (*Proganochelys*) or (1) acute edge, also enclosed stapes (*Pelusios*).
63. QU, middle ear with complete lateral wall: (0) not complete (*Proganochelys*) or (1) complete (*Pelusios*).
64. QU, cavum tympani curved dorsally: (0) no (*Proganochelys*) or (1) yes (*Palaeochersis*).
65. QU, covers op laterally: (0) no (*Proganochelys*) or (1) yes (*Australochelys*).
66. QU, pocket for stapes articulation: (0) present (*Proganochelys*) or (1) absent (*Australochelys*).
67. QU, cranioquadrate space: (0) relatively open (*Proganochelys*) or (1) a well defined canal (*Australochelys*).
68. PT, fossa pterygoidea: (0) absent or small (*Pelusios*) or (1) moderate (*Galianemys whitei*) or (2) deep and narrow (*Foxemys*).
69. PT, cavum pterygoidei: (0) absent (*Pelusios*) or (1) present (*Podocnemis*).
70. PT, processus trochlearis pterygoidei: (0) absent (*Proganochelys*) or (1) present (*Pelusios*).
71. PT, posteroventral flange: (0) absent (*Chelydra*) or (1) present, medial and ventral to processus trochlearis pterygoidei (*Pelusios*).
72. PT, processus pterygoideus externus: (0) without vertical plate (*Pelusios*) or (1) with vertical plate (*Chelydra*).
73. PT, trigeminal ridge (pt + qu): (0) absent (*Galianemys*) or (1) ridge extending posteroventrally from foramen nervi trigemini to condylus mandibularis (*Phosphatochelys*).
74. PT, foramen posterius canalis carotici interni position: (0) bs (*Proganochelys*) or (1) pt + qu (*Araiochelys*) or (2) bs in medial wall (*Kurmademys*) or (3) pr (Pelomedusidae) or (4) pt + bs (also + pr) (*Euraxemys*) or (5) pt + qu + bs (*Taphrosphys*) or (6) qu (*Labrostochelys*).
75. PT, pt in foramen posterius canalis carotici interni: (0) pterygoid does not enter foramen posterius canalis carotici interni position (*Pelusios*) or (1) pterygoid enters anterior foramen posterius canalis carotici interni position margin (*Galianemys*).

76. PT, foramen caroticum laterale: (0) present (*Emydura*) or (1) absent (*Pelusios*).
77. PT, midline contact: (0) longer (*Galianemys*) or (1) very short (*Dirqadim*).
78. EPT, absent: (0) epipterygoid present (*Chelydra*) or (1) epipterygoid absent (*Pelusios*).
79. SO, so-qu contact: (0) absent (*Pelusios*) or (1) present on dorsal surface of otic chamber (*Bothremys*).
80. SO, crista supraoccipitalis: (0) low to absent (*Proganochelys*) or (1) distinct sagittal plate (*Pelusios*).
81. SO, wide occipital plate: (0) wide occipital plate with depressions (*Proganochelys*) or (1) absent (*Pelusios*).
82. EX, foramen jugulare posterius: (0) not formed in bone (*Proganochelys*) or (1) closed partially (*Galianemys*) or (2) closed completely (*Azabbaremys*).
83. EX, recessus scalae tympani: (0) not formed in bone (*Proganochelys*) or (1) formed in bone, also fenestra perilymphatica (*Pelusios*).
84. EX, condylus occipitalis: (0) basioccipital plus both exoccipitals (*Euraxemys*) or (1) exoccipitals only (*Pelusios*).
85. EX, ex-qu contact: (0) absent (*Pelusios*) or (1) extensive, pr absent (*Galianemys*) or (2) narrow, pr contact (*Euraxemys*) or (3) narrow, pr absent (*Brasilemys*).
86. EX, ventral process: (0) absent (*Pelusios*) or (1) present (*Euraxemys*).
87. BO, short: (0) long, length divided by width = > 0.60 (*Pelusios*) or (1) short, length divided by width = < 0.59 (*Bothremys*).
88. BO, thick: (0) bo + bs thick (*Proganochelys*) or (1) thinner (*Pelusios*).
89. BO, bo-op contact: (0) absent (*Galianemys*) or (1) present (*Pelomedusa*).
90. PR, hyomandibular nerve: (0) in canalis cavernosus (*Chelydra*) or (1) in its own canal (*Podocnemis*).
91. PR, foramen stapediotemporale: (0) not a canal (*Proganochelys*) or (1) formed in bone as a canal (*Pelusios*).
92. PR, foramen stapediotemporale opens anteriorly: (0) no (*Pelusios*) or (1) yes (*Galianemys*).
93. PR, foramen stapediotemporale/foramen nervi trigemini: (0) separated by most of prootic (*Pelusios*) or (1) separated by narrow bar of prootic (*Bothremys*).
94. PR, ventral exposure: (0) most of prootic exposed ventrally (*Emydura*) or (1) about half covered by qu + bs (*Euraxemys*) or (2) nearly all covered by qu, bs, pt (*Taphrosphys*).
95. PR, qu-pt-bs exposure: (0) extensive exposure or no exposure (*Pelusios*) or (1) small exposure within qu-pt-bs suture (*Kurmademys*).
96. PR, processus trochlearis oticum: (0) absent (*Proganochelys*) or (1) present (*Chelydra*).
97. PR, plane of fenestra ovalis: (0) inclined (*Proganochelys*) or (1) vertical (*Chelydra*).
98. OP, processus interfenestralis expanded ventrally: (0) narrow ventrally (*Proganochelys*) or (1) expanded ventrally (*Pelusios*).
99. OP, processus interfenestralis covered ventrally: (0) visible ventrally (*Emydura*) or (1) covered ventrally (*Bothremys*).
100. OP, fenestra postotica closed medially: (0) open (*Euraxemys*) or (1) closed by op, qu contact (*Taphrosphys*).
101. OP, fenestra postotica a short slit: (0) more open (*Euraxemys*) or (1) small, horizontal slit (*Galianemys*).
102. OP, processus paroccipitalis: (0) projects posteriorly beyond sq (*Euraxemys*) or (1) smaller, anterior to sq (*Galianemys*).
103. OP, thin horizontal flange: (0) absent (*Galianemys*) or (1) present on posterior edge (*Chedighaii hutchisoni*).
104. BS, bs-qu contact: (0) absent (*Euraxemys*) or (1) present, wider (*Galianemys*) or (2) present, very narrow (*Azabbaremys*).
105. BS, interpterygoid vacuity: (0) large and open (*Proganochelys*) or (1) small, absent (*Pelusios*).
106. BS, ventral outline: (0) elongate, lacking sutured pterygoids (*Proganochelys*) or (1) triangular (baenids) or (2) pentagonal (*Taphrosphys*) or (3) very elongate (*Araripemys*) or (4) V-shaped (*Arenila*).
107. BS, processus clinoideus: (0) present, with canal (*Pelusios*) or (1) absent, foramen nervi abducentis is a groove (*Bothremys*).
108. BS, skull akinetic: (0) no, open basipterygoid articulation (*Proganochelys*) or (1) yes, basipterygoid articulation fused (*Australochelys*).
109. BS, cultriform process: (0) rodlike, thin (*Proganochelys*) or (1) broad, flat, absent (*Australochelys*).
110. BS, sella turcica/dorsum sellae: (0) deep, well-defined (*Bothremys*) or (1) shallow, low margins (*Taphrosphys sulcatus*).
111. BS, ventral bs/bo tubercle: (0) single (*Proganochelys*) or (1) paired (*Australochelys*) or (2) absent (*Pelusios*).
112. CA, columella auris: (0) without footplate (*Proganochelys*) or (1) with wide footplate (*Pelusios*).
113. SP, splenial: (0) present (*Proganochelys*) or (1) absent (*Pelusios*).
114. DEN, high lingual ridge: (0) no (*Pelusios*) or (1) yes (*Bothremys*).
115. DEN, pits: (0) no (*Euraxemys*) or (1) yes (*Bothremys*).
116. DEN, U-shaped lingual ridges: (0) absent (*Euraxemys*) or (1) form U-shape, also wedge (*Bothremys*).
117. DEN, sutured symphysis: (0) symphysis fused (*Bothremys*) or (1) symphysis sutured (*Euraxemys*).
118. DEN, triturating surfaces: (0) narrow (*Euraxemys*) or (1) wide posteriorly (*Cearachelys*).
119. DEN, widely exposed on lateral surface: (0) yes, in posterior part of jaw (*Euraxemys*) or (1) no, covered by surangular (*Bothremys*).
120. SUR, foramen nervi auriculotemporalis: (0) absent (*Proganochelys*) or (1) present (*Podocnemis*).
121. COR, wide lateral exposure: (0) no (*Euraxemys*) or (1) yes (*Bothremys*).

122. PRA, fossa meckelii open anteriorly: (0) closed by long ang-pra contact (*Euraxemys*) or (1) more open, short pra-ang contact (*Bothremys*).
123. ART, processus retroarticularis: (0) long, posterior (*Bothremys*) or (1) short, absent (*Pelusios*) or (2) long, posteroventral (*Podocnemis*).
124. VT, cervical ribs: (0) present (*Proganochelys*) or (1) absent (*Pelusios*).
125. VT, cervical zygapophyses: (0) separate (*Proganochelys*) or (1) some fused (*Podocnemis*).
126. VT, cervical postzygapophyses: (0) separated from each other (*Proganochelys*) or (1) postzygapophyses elevated on neural spine (*Podocnemis*).
127. VT, cervical centrum: (0) not formed (*Proganochelys*) or (1) formed, wider than high (*Platychelys*) or (2) formed, usually higher than wide (*Podocnemis*).
128. VT, cervical articulations: (0) amphicoelous, platycoelous (*Proganochelys*) or (1) (2))3))4))5))6))7))8) (*Pelusios*) or (2) (2((3((4((5))6))7((8) (*Emydura*).
129. VT, caudals: (0) platycoelous (*Proganochelys*) or (1) formed centra but variable (*Notoemys*) or (2) only procoelous (*Pelusios*).
130. SH, coracoid foramen: (0) present (*Proganochelys*) or (1) absent (*Podocnemis*).
131. SH, coracoid shape: (0) flat plate (*Proganochelys*) or (1) columnar (*Podocnemis*).
132. PEL, tenth thoracic centrum: (0) not incorporated into sacrum (*Proganochelys*) or (1) incorporated into sacrum (*Pelusios*).
133. PEL, pelvis sutured to shell: (0) no (*Proganochelys*) or (1) yes (*Pelusios*).
134. PEL, ilium columnar: (0) no, inclined, with anterior, posterior processes (*Proganochelys*) or (1) columnar, expanded mediolaterally (*Podocnemis*).
135. PEL, narrow: (0) pelvis widely placed (*Proganochelys*) or (1) ilia close to midline (*Podocnemis*).
136. PEL, thyroid fenestra: (0) small (*Proganochelys*) or (1) large, broadly confluent (*Podocnemis*).
137. HUM, shoulder on lateral side of head: (0) present (*Proganochelys*) or (1) absent (*Podocnemis*).
138. CAR, cervical scale: (0) present (*Emydura*) or (1) absent (*Podocnemis*).
139. CAR, nuchal width: (0) width 2 times wider than length, or more (*Platychelys*) or (1) width greater than length, but less than 2 times (*Euraxemys*) or (2) width equals length (*Foxemys*) or (3) width less than length (*Teneremys*) or (4) *Araripemys* condition.
140. CAR, pygal notch: (0) present, wide (*Proganochelys*) or (1) present, narrow, spherical (*Proterochersis*) or (2) absent, margin smooth (*Podocnemis*).
141. CAR, neural series completeness: (0) to suprapygal (*Euraxemys*) or (1) to costals 8 (*Podocnemis*) or (2) to costals 7 (*Foxemys*) or (3) to costals 6 (*Chedighaii*) or (4) neurals discontinuous or absent (*Emydura*).
142. CAR, iliac scar: (0) absent (*Chelydra*) or (1) costals 7 and 8 (*Pelusios*) or (2) costals 7 and 8 and suprapygal (*Taphrosphys*).
143. CAR, costal one length: (0) costal 1 shorter or equal to 2 times length of costal 2 (*Euraxemys*) or (1) costal 1 two times longer than 2nd costal (*Foxemys*).
144. CAR, position of four sided neural: (0) neural one (*Euraxemys*) or (1) neural two (*Cearachelys*) or (2) neural three (*Araripemys*) or (3) four-sided neural absent (*Platemys*).
145. CAR, neural series pattern: (0) irregular, 2 and 4 quadrangular, alternating in width (*Platychelys*) or (1) irregular, width even (*Kayentachelys*) or (2) regular, most hexagonal, coffin-shaped (*Podocnemis*) or (3) neurals absent (*Platemys*) or (4) discontinuous (*Araiochelys*).
146. CAR, neural number: (0) more than 8 (*Kayentachelys*) or (1) 8 neurals (*Cearachelys*) or (2) 7 neurals (*Foxemys*) or (3) 6 or less (*Kurmademys*).
147. CAR, peripheral 1/ costal 1 contact length: (0) no contact (*Dortoka*) or (1) wide contact, anterior margin less than 2× contact (*Rosasia*) or (2) narrow contact, anterior margin 2× contact (*Foxemys*) or (3) *Araripemys.*
148. CAR, axillary process contacts costal 1: (0) no contact (*Proganochelys*) or (1) contact present but separated from costal 2 suture (*Chedighaii*) or (2) contact present and close to costal 2 (*Dortoka*).
149. CAR, axillary process extent: (0) reaches peripheral 2 (*Platychelys*) or (1) reaches anterior edge of peripheral 3 (*Emydura*) or (2) main body of peripheral 3 (*Chedighaii*).
150. CAR, inguinal buttress: (0) short or absent (*Proganochelys*) or (1) extends medially to center of costal 5 (*Chedighaii*).
151. CAR, supramarginal scales: (0) 12 (*Proganochelys*) or (1) 3 (*Proterochersis*) or (2) none (*Podocnemis*).
152. CAR, vertebral scale width: (0) equal to or wider than pleural scales (*Proterochersis*) or (1) narrower than pleural scales (*Foxemys*).
153. CAR, vertebral scale 1 reaches anterior margin of shell: (0) no, first marginal scales meet on midline (*Podocnemis*) or (1) yes (*Araripemys*).
154. CAR, nuchal embayment: (0) no (*Emydura*) or (1) yes (*Chedighaii*).
155. CAR, first thoracic rib: (0) larger and separate (*Platychelys*) or (1) smaller and closer to 2nd rib (*Podocnemis*).
156. CAR, costovertebral tunnel: (0) large anteriorly and posteriorly only (*Proganochelys*) or (1) large entire length (*Platychelys*) or (2) small (*Chedighaii*).
157. CAR, thoracic rib one facet: (0) anterior edge smooth (*Proganochelys*) or (1) swollen articulation facet, tubercle (*Platychelys*).
158. PLA, mesoplastra: (0) present, meet on midline (*Proganochelys*) or (1) present, wider than long (*Platychelys*) or (2) present, rounder (*Chedighaii*) or (3) absent (*Emydura*).
159. PLA, entoplastron trapezoidal: (0) arrow-shaped with posterolateral processes (*Proganochelys*) or (1) more trapezoidal (*Podocnemis*).

160. PLA, epiplastra meet in midline: (0) separated by entoplastron (*Proganochelys*) or (1) meet in midline (*Foxemys*).
161. PLA, dorsal epiplastral process: (0) very large (*Proganochelys*) or (1) small or absent (*Podocnemis*).
162. PLA, intergular scales: (0) one pair (*Proterochersis*) or (1) one intergular scale (*Foxemys*).
163. PLA, gular projections: (0) present (*Proganochelys*) or (1) absent (*Podocnemis*).
164. PLA, anterior lobe short: (0) width over length < = 2.0 (*Podocnemis*) or (1) width over length > 2.1 (*Chedighaii*).
165. PLA, pectorals on entoplastron: (0) no (*Euraxemys*) or (1) yes (*Foxemys*).
166. PLA, pectorals on epiplastron: (0) no, far behind epiplastron (*Cearachelys*) or (1) on epiplastron, on epi-hyoplastron suture (*Foxemys*).
167. PLA, pectoral on mesoplastron: (0) yes (*Cearachelys*) or (1) anterior to mesoplastron (*Kurmademys*).
168. PLA, ischial attachment shape: (0) absent (*Proganochelys*) or (1) large and linear (*Podocnemis*) or (2) small and equidimensional (*Taphrosphys*).
169. PLA, posterior lobe wider than pelvis: (0) no (*Proganochelys*) or (1) yes (*Podocnemis*).
170. PLA, large intergular scale: (0) small (*Cearachelys*) or (1) large, separating gulars and humerals (*Taphrosphys*) or (2) large, very small gulars, humeral and partial pectoral separation (*Dortoka*).
171. PLA, axillary/inguinal scales: (0) present (*Kayentachelys*) or (1) absent (*Emydura*).
172. PLA, abdominal scale narrow: (0) midline length abdominal = > midline length anal (*Podocnemis*) or (1) midline length abdominal < midline length anal (*Taphrosphys*) or (2) abdominals do not meet (*Araripemys*).
173. PLA, anterior lobe reaches carapace edge: (0) yes (*Cearachelys*) or (1) no (*Foxemys*).
174. PLA, anal notch: (0) absent (*Kayentachelys*) or (1) present (*Taphrosphys*).
175. Shell texture: (0) rough surface without clear pattern (*Proganochelys*) or (1) weak granulated polygons (chelids) or (2) strong granulated polygons (*Taphrosphys*) or (3) fine, striated ridges (*Polysternon*) or (4) smooth (*Cearachelys*) or (5) pits (*Araripemys*)(6) or "microreticulation" (*Dortoka* fide deBroin).

APPENDIX 3
DATA MATRIX

Single asterisk indicates shell-only taxa added in analysis shown in figure 292. Double asterisk indicates taxa with large amounts of high missing data, added individually, as seen in figures 294 and 295.

Synapsida/Diapsida
000000(01)0000000000(01)0000000000000000000000-
000000000000000000000000000000000000000(01)
0000000000000000000000000000000000000000000-
0000000000000?????????????????????????????????

Proganochelys
00000010000000000000000000000000000000000000-
0000000000000000000000000000000000000000000-
?000000000000000000000000000000000000000000-
000000000000????0000001000000000000000000?0000

Australochelys
??0?00???00??0?????????000???0?0?0000??0?1???1???00-
00?000?01010111???00???????1000????0???????010???-
???00?11?1???????????????????????????????????????-
??????????????????

Palaeochersis
??0?00?0??00?0??0???0??????????0??0??????????1????0000-
0??0?0111111100000???????1000????0???????010?0??-
??1??11?10?????0?????0??00000?00000??0??????????0?-
?????000?00???00???000

Kayentachelys
011000011000000000010000000000100100000000000011-
10000300000000001111111000010000000111100001-
?010000111000100110110210000000010?100000011-
0000?0002000110100020010200101010000?000004

Selmacryptodira
(01)110(01)(01)01(01)0(01)00(01)(01)00(01)10000000-
001(01)(01)10(012)0(01)(01)0(03)000011100(01)0(2-
3)(01)(01)0000000111111100001041 0(01)0(01)11(1-
2)1000(01)10010000111(01)001001101102100000(0-
1)0100(01)000000110000100(012)2(0123)00(01)(12)
(01)(12)(01)0(01)2(01)0(01)02001(01)101?0000(01)-
00(01)0(01)(014)

Chelidae
0110000010(01)00000101000000000010001000(01)0240-
00001101003200020101111111100110030(01)0101-
12100001(01)1100000110001001201102100000(01)0-
010011(01)1222111111110(123)2(01234)(12)(01)(0-
13)(234)(123)2(12)(12)0210(01)120(13)11111?(01)
(01)01101(01)111

Pelomedusidae
111100(01)01000011010100000000010001000(01)0030-
0(01)01212100320002010111111110011003010101-
12110001111000001100000(01)12011021100(01)(0-
1)0010011012121111111111(12)2(123)1002(12)(12)
(01)2(01)2100120(12)11111000011010(01)11

Araripemys
11110?0010100110101000000000100010000000300000??1-
?10130000201011111111001100300110 11(12)1000-
0101100000011000000013?11021100010011011 11210-
11111111114202022(01)3020211112030111 1000?21?-
12015

Euraxemys
11110000100010101010000000001000100010030000 01-
10100300001010111111110011004 1?010111102101-
01100100111000001 1?11?21100010010011112 1211-
1111111120?00212?2?21001202111 1100?011011011

Dirqadim
111100001000100010100000000101010001003000 0??-
1?100300001010111111111001100 41?110111102101-
0110010011100000 11?11?2??????????????????????????-
?????????????????????????????????????

Podocnemididae
1111000010001010(12)0100(01)00000100(01)10(012)0-
(01)00300001(12)1(02)10032000(012)0111111111 1-

0111004100101121000111110020011100001120110211(01)000(01)11012111212111111111(12)2(123)1002(23)1(12)(012)(01)2100120211111(01)11(01)11010011

Hamadachelys

1111000010001010?01000000000010001?0000030000111010032000201111111111011100041?0101121000111?1002001110000112?11?2?1000000100 2??

Brasilemys

??1?????0000???1010000000010????000003??00??1??00300001011111111111011?0041?01?111103011??100200??10000112?11?2?1000?0010?2???1?????1?1??12?11002222?121001???????????????????

Cearachelys

1111000010000210101100000000110?101000100000?1101013(02)000001101111111(01)01100411011111111011 0?1102(01)0111011011101102?110101010001?12?2???111111(13)20?0121(12)?2?21001202111110 00011010014

Galianemys emringeri

1111(01)00010000210101200000011101101000100000??1?1013110100110111111110110041101111101011011102101110110111011 02???

Galianemys whitei

1111000010000210101200000011101 1?1000100000011010131101001101111111001100 41?011111101011011102001110110111011 02??

Kurmademys

1111000010000111101000000001100110100013000 01?1?1013110120111111111110110020101111210101 10?1002101111010112011?2??10101010001??2??11?111?111231102311212100 12?2?????011111??0?11

Sankuchemys

11110???10??011??010??0?????001??1010??00?011101???????111111111001?0?41?0??11?1?10110?1??210??1????112?11?2???

Foxemys

1111100010010010101000010011101102000100010011010131000011101111111120110041?0111111110110?111210??11010112?11?2?110101101101112??11?111111222(12)102221212100 12?211111111(01)11010111

Polysternon

111110?0100?001??010000?00??1011?100010000???1??01310000111111111111201?0041?0?1111111011 0?1??200??1101?112?11?2?????0???????????????1?1??1222(12)10222121210112?2111110111 11010113

Araiochelys

11110110100100 1??0100011001111220110 0?100000110?0111100011101111111001100 11?1?111211101 10?1112001111010111?11?2?11110010110?????????1???????????043212121???2?2?1????10111??0?11

Zolhafah

11111?00100??????10??1???1??01102100??0000011010131100?111011111111100??0051?0101121?1?110?11?200??1101?11101102???

Rosasia

11111000100100?01010001???11?02102100110000011 0101?11?00111011111111110???041?01111?1??0?1??111200??110??11101102???????????????????????1????1122?10221?2?2101???2?11111000?10?0111

Bothremys cooki

1111111010 11???120100?1???11?12202101??11100110101????????????????1001?0???101?????????1????????????????1?11102??11101???1???

Bothremys maghrebiana

111111101011001120100011 0(01)1111220(12)10(01)1111(01)0011010111100011101111111100110011111 11121110110111120011110 1(01)21111102?11110(01)10110??

Bothremys kellyi

11111110101?001??0100?1100111112 02101?1100???1??0111100011101111111100??0?51?0?111211011??11?2001?11011211?11?2???

Bothremys arabicus

??1?1??0?01????12??0??1????1??1??210?????0?0110?01?11?00?1101111111001??011???1?12?110110?11?20???110??211?11?2???

Chedighaii hutchisoni

1111111010110011201000010011 1?1??2001100000111 0101?1100011101111111001100 11?01111211101 10?1112001111011211?11?2???

Chedighaii barberi

11111??0101?????201?0?010?1???2??100???0000??1???1111?0011?0111?11100???011?0?1?121?10110?111200??1101121111102??11101101?01112???111111112321022112121011202111111100110?0111

Taphrosphys sulcatus

1?1100???00?20???01????0111?00?11???????0????1????311100?1111111111100???15110?011211100101111200111101011 2?1112?????????????1112??111111111112221 0222(12)2121001202111111 10?211?1012

Taphrosphys congolensis

111100?0100?201??0101?00111200?11000001000???1?1?0?11?0011111111111001?0?51?0?0112111011 0?111200?111010112011 02??000?0?????????????????????222??22???1?10????2??1?1?1012?1???12

Taphrosphys ippolitoi

111100?0100??01??0101100111 2?0111000001 0001??1?1?03111001111111111?0110151?0101121110110?1??2001111010112?1112??

Azabbaremys

11110000100000101010010000121101000000010001111111021100011101111111100??0011?0101121110110?1112001111010211011 02??

CNRST-SUNY 199

11110?001000???010100111 0012?01200110?100011111110311000111011111111201?0051?111?121110110?111200111101021 1?11?2??

Labrostochelys

11110110100?201?10101?0111??012200000012001011010011110011101111111001100(16)0?1101121110110?111200?11101021 1?11?2??

Phosphatochelys

1111000011002011111001001112001210001023000??1?1103111001110111111100110111?0101121110110?1112001111010(12)12?11?2???

Ummulisani

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Rhothonemys

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Nigeremys

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Arenila

??110????00?????10100?0???11?0???0000??000001101?0211?0??1121111111201???41?11??12111?110?111200??1?010214?11??

*_Proterochersis_

???11110?0?1??0????00?10000?0010000000011001010

*_Platychelys_

??????????????????1??1001211?11111?00202010(01)(02)1011000011111111000011011010

*_Notoemys_

??1??1?11111????????????11?1????1?11????01??????????1??2?????????????1?012???1111?10020?010111?02000011111???00011??001?

*_Dortoka_

???1?1221???1111?(01)12(01)1100(13)0221210012?311111000?112?0016

*_Teneremys_

????0????00??1?????????0????0????00??????0??11??0??00????1011?11111001?0?41?0??11??????1??1????0????????13?11?2??????10???????1212???1111?132(12)?0?22122?21011??211111?000?1?????1

*MNHN GDF 801

???11111?102(03)10323120121111202111110000110??010

*_Elochelys perfecta_ ??1?1??1122?10222???210????211?111111?11?0111

*_Elochelys convenarum_

???1111?11?3210232121210 0?20211111111111110111

**_“Podocnemis” parva_

???1????1(23)23?10222?2?21?1???2111111100??0??111

**_“Podocnemis” somaliensis_

???1?????123?00231?2?2??0???2111?11????1??11?

**AMNH 30550

???1111?112220123112121001202111111000110??011

**AMNH 30551

???111??1121?0121112121001202111111000?101?011

**_“Taphrosphys” olssoni_

???1?1???12?11????121???01202111111100211??01?

**_“Taphrosphys” ambiguous_

???1?1????????????????????????211111110021 1??12

**_“Platycheloides” nyasae_

??21?????000???????

**_“Eusarkia” rotundiformis_

???1?????224?13331??????012?211?11110??11??11(24)

**_Bairdemys venezuelensis_

????????????????????????????????????0??1?????2241133321?1???0???2111111111110??011

APPENDIX 4

SKULLS MEASURED IN APPENDIX 5

1 *Araripemys barretoi* AMNH 24454
2 *Araripemys barretoi* AMNH 24453
3 *Araripemys barretoi* THUg 1357
4 *Araripemys barretoi* THUg 1907
5 *Euraxemys essweini* FR 4922 (type)
6 *Dirqadim schaefferi* MDEt 41 (type)
7 *Dirqadim schaefferi* AMNH 30038
8 *Sankuchemys sethnai* SDS/VPL 1125 (type)
9 *Kurmademys kallamedensis* ISI R152 (type)
10 *Kurmademys kallamedensis* ISI R158
11 *Kurmademys kallamedensis* ISI R159
12 *Kurmademys kallamedensis* ISI R155A
13 *Kurmademys kallamedensis* ISI R155B
14 *Cearachelys placidoi* BSP 1976 I 160
15 *Cearachelys placidoi* MPSC (type)
16 *Cearachelys placidoi* THUg 1798
17 *Galianemys whitei* AMNH 29987 (type)
18 *Galianemys whitei* AMNH 30027
19 *Galianemys whitei* AMNH 30028
20 *Galianemys whitei* AMNH 30036
21 *Galianemys whitei* AMNH 30555
22 *Galianemys whitei* MDEt 45
23 *Galianemys whitei* AMNH 29986
24 *Galianemys emringeri* AMNH 29985 (type)
25 *Galianemys emringeri* AMNH 30026
26 *Galianemys emringeri* AMNH 30035
27 *Galianemys emringeri* AMNH 30037
28 *Galianemys emringeri* AMNH 30040
29 *Foxemys mechinorum* PAM 511A
30 *Foxemys mechinorum* MDEt 10 (type)
31 *Polysternon provinciale* Costa AE 28
32 *Zolhafah bella* TUB Vb 173 (type)
33 *Araiochelys hirayamensis* THUg 3338 (type)
34 *Bothremys cooki* AMNH 2521 (type)
35 *Bothremys maghrebiana* AMNH 30234
36 *Bothremys maghrebiana* AMNH 30561 (type)
37 *Bothremys maghrebiana* AMNH 30041
38 *Bothremys maghrebiana* AMNH 30522
39 *Bothremys maghrebiana* MHNL 20-268370
40 *Bothremys kellyi* AMNH 50553
41 *Chedighai hutchisoni* KUVP 14765 (type)
42 *Chedighai barberi* ALAB PV 2001.2
43 *Taphrosphys sulcatus* NJSM 11362
44 *Taphrosphys sulcatus* ANSP 15544
45 *Taphrosphys congolensis* MRAC uncataloged
46 *Taphrosphys ippolitoi* AMNH 30042 (type)
47 *Taphrosphys ippolitoi* AMNH 30500
48 *Labrostochelys galkini* AMNH 30043 (type)
49 *Labrostochelys galkini* AMNH 29984
50 *Phosphatochelys tedfordi* AMNH 30008 (type)
51 *Phosphatochelys tedfordi* MDEt 26
52 *Rhothonemys brinkmani* AMNH 30521 (type)
53 *Ummulisani rutgersensis* AMNH 30563 (type)
54 *Ummulisani rutgersensis* AMNH 30569
55 *Azabbaremys moragjonesi* BMNH 16370 (type)
56 *Nigeremys gigantea* MNHN (P) NIR 1 (type)
57 *Arenila krebsi* TUB Vb 641 (type)

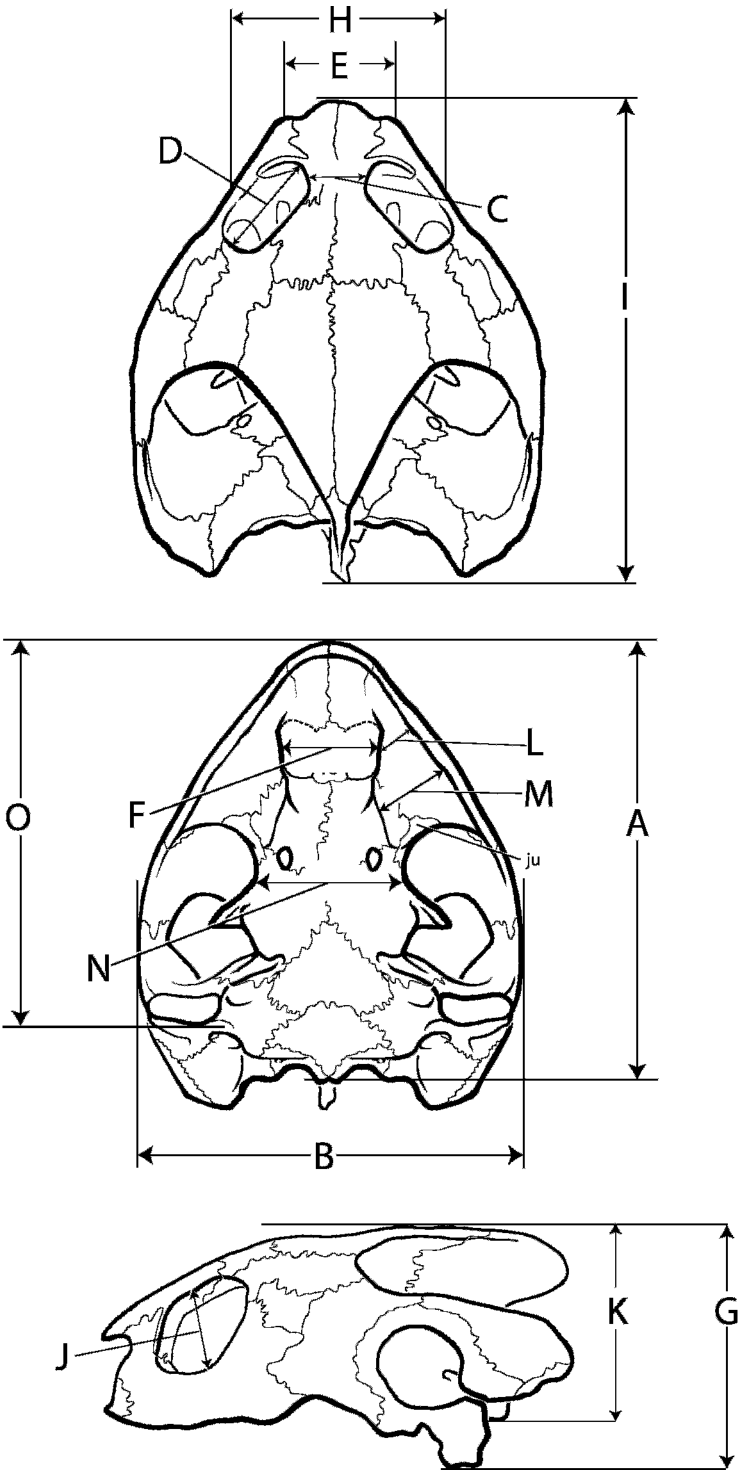

Fig. 315. Positions of skull measurements for appendix 5 on an outline of *Cearachelys*.

APPENDIX 5

SKULL MEASUREMENTS OF TAXA IN APPENDIX 4

See figure 315 for positions of measurements.

	A	B	C	D1	D2	E	F	G	H	I	J1	J2	K	L	M	N	O
1	42.4[a]	35.7	4.6[a]	10.6[a]	8.8	11.8[a]	—	9.4[a]	24.7	38.4[a]	7.9[a]	7.6	12.0[b]	—	—	22.0[b]	34.0
2	—	34.2[b]	—	—	—	—	—	8.7[a]	25.0[b]	—	—	—	—	—	—	—	—
3	35.4	24.4[b]	2.8	—	7.3	7.8[a]	7.9	8.3	15.7	30.3[a]	6.7[a]	6.4	9.5[b]	4.5	3.4	18.8[b]	27.2
4	42.7[a]	29.6	4.2[a]	—	—	8.8[a]	—	9.3	19.9	40.2[a]	8.2[a]	7.0	11.8	—	—	21.6	32.6
5	41.5	30.8	3.1[a]	9.6	10.2[a]	6.7	10.0	17.9	18.7	37.5	9.2	9.6	13.9	5.5	4.6	16.0	31.7
6	38.8	33.5	4.8	10.1	9.2	9.8	10.4[a]	15.9	20.7	34.3[a]	9.5	10.2	13.8	4.6	6.0	19.3	28.0
7	18.3[a]	30.4	5.0[b]	—	—	—	—	14.6[a]	—	—	—	—	11.8	—	—	—	—
8	48.8	49.3	9.0	13.1	11.5	11.2	11.9[a]	9.7[a]	30.3[a]	44.5[a]	5.5[a]	6.7[a]	9.4[a]	5.5	7.0	14.1[a]	33.2[a]
9	47.2	49.4	—	12.8[b]	12.6	9.3	11.6	28.2	25.7	47.2[b]	12.4	12.4	19.4	4.5	8.8	22.2	38.2
10	50.1[a]	48.0[b]	6.8	12.0[a]	13.0[a]	12.8	—	19.5[a]	27.9	—	12.6	14.5[a]	—	—	—	24.9	43.6
11	—	37.2[b]	5.5	—	10.7	—	—	14.5	—	—	—	10.3	—	4.7	8.1	—	—
12	37.2[a]	23.0[b]	—	—	—	—	—	—	—	—	—	—	13.4[a]	—	—	13.5	—
13	35.3	28.6[b]	—	—	8.4	—	—	—	—	—	—	6.7[a]	12.4[b]	—	—	—	—
14	42.3	42.5	8.5[a]	8.3[a]	9.6	8.7[a]	9.1	25.8	26.6	47.5[a]	12.4[a]	9.9	19.1	4.6	11.4	19.9	38.9
15	27.1[a]	37.0	—	—	—	—	—	19.7	—	—	—	—	14.7	—	—	14.8	—
16	31.4	28.7	4.8	7.7	8.0	7.4	6.1[a]	16.0	15.6	34.2	7.6	7.9	12.0	—	6.8	12.0[b]	27.1
17	48.9[a]	46.9	9.8	10.9	11.1	8.9	9.6	25.6	19.3	47.5[a]	9.9	11.1	18.4	6.5	10.2	16.5	45.7
18	45.3[a]	44.0[b]	10.2[b]	—	11.1	—	—	23.9	—	45.2[a]	—	12.0[a]	16.0[b]	—	9.1	17.6	—
19	43.2[a]	41.4	9.5	11.0	10.8	10.7[a]	9.5	21.3	23.5	44.2[a]	10.7	10.7	14.1	6.4[a]	8.5	16.3	37.4[b]
20	47.0[a]	49.2	8.1	11.2	11.2	10.4	10.6	26.9	22.7	44.4[a]	11.1	11.7	18.5	6.4	9.7	18.4	42.9[a]
21	41.7	39.2	7.3	10.5	10.8	9.0[b]	9.9	20.1	23.1	44.6	11.1	10.6	14.2	6.0	7.8	15.4	36.6
22	23.0[b]	22.0[b]	6.0	7.4	6.6	6.8[a]	6.2	12.3[b]	14.4	24.6[b]	6.8	6.9	9.1[b]	4.2	4.9	10.5[a]	—
23	37.7[a]	38.4	7.4[b]	—	10.3	6.8[b]	7.8[b]	21.3[a]	—	39.0[a]	—	10.1	14.2[a]	—	8.7	15.4[b]	34.0[a]
24	46.5[a]	46.0[b]	9.6	10.4	10.4[a]	9.0[b]	10.0[b]	21.0[a]	22.0[b]	46.8[a]	10.1	9.0[a]	20.1[b]	—	8.5	18.4	40.8[a]
25	—	44.0[b]	—	—	—	—	—	—	—	—	—	—	17.3[b]	—	—	—	—
26	54.0	59.7	11.1	11.6	11.5	13.1	14.6	30.7	26.8	54.8[a]	12.2	11.5	21.5[b]	7.6	12.4	24.9	49.6
27	44.7	44.0[b]	9.3	10.2[a]	9.9[a]	11.2[a]	10.8	24.3	22.3	46.6[a]	8.9[a]	8.0[a]	17.5[b]	5.8	8.1	19.5	39.8
28	18.7	18.6	3.8	5.8	6.5[a]	—	3.6	8.6[a]	10.9[a]	21.8[b]	5.4	5.4[b]	6.3[a]	—	3.9	7.6	17.0[b]
29	77.0	91.1	20.3	20.2	—	15.9	12.0	45.8	61.0	85.4	17.3	18.1	34.4	6.3	21.8	34.9	71.3
30	53.5	59.6	14.3	—	14.2	—	—	16.0	—	52.5	—	9.1	14.8	—	15.0	23.9	51.0
31	72.9	85.9	21.0	19.7	18.4	14.5	19.0	39.8	59.8	60.8	14.7	13.2	27.8	6.1	17.0	40.4	53.6
32	68.0	73.0	13.5	16.0	—	23.0	19.0	35.0	51.5	—	17.5	—	31.0	20.0	24.5	32.0	67.0
33	62.8	60.6	15.2	14.4[a]	14.0[a]	16.1	14.2	30.9	38.9	62.8	9.5[a]	9.5[a]	20.0	8.9	12.4	27.4	54.8
34	59.8[a]	72.2[a]	17.3	12.8	12.7	18.7	13.8	—	66.3	62.2[a]	12.7	13.8	32.1[b]	11.7	27.2	34.6[b]	—
35	78.9	91.5	18.0[a]	16.2[a]	13.6	23.8	19.4	45.2	72.6	83.2	14.3	13.0[a]	28.4	21.4[a]	24.4[a]	41.4	71.9

	A	B	C	D1	D2	E	F	G	H	I	J1	J2	K	L	M	N	O
36	74.6	78.9	18.6	14.2	14.2	21.5	15.5	39.6	60.5	70.0[a]	10.9	10.0	28.9	14.1	24.4	37.3	68.2
37	57.4	68.2[b]	14.7	14.5[a]	13.1	17.3	15.5[a]	27.3[a]	46.8	61.0	9.3	—	17.4	7.4	14.7	32.0	50.4
38	67.2[b]	70.2	18.4	—	13.0[a]	—	11.8	37.0	62.0[b]	66.7[a]	—	11.5	24.5	10.1	23.2	32.8	63.0
39	74.0	86.0	17.0	14.7	15.4	24.4	—	35.2	54.6	88.5	11.7	11.4	25.0	10.3	19.7	36.9	71.0
40	111.3	141.9	37.8	25.2	24.0	41.4	32.1	49.9	72[b]	107.6	20.2	20.6	33.4	22.9	38.1	48[a]	120.5
41	119.0[a]	182.0[a]	25.4	25.9	24.8	34.8[b]	—	70.0[b]	—	159.0	25.9	23.9	55.1	—	53.1	56.5	—
42	120.0[a]	131.0[a]	—	—	—	34.0[b]	—	72.0[b]	—	84.0[b]	—	—	45.5[b]	—	30.1	—	120.0[b]
43	44.4[a]	62.0[b]	—	—	—	—	—	44.0	—	—	—	—	30.4	—	—	—	—
44	76.4[a]	42.0	20.3	—	—	—	—	—	—	76.4	—	—	—	—	—	—	—
45	30.6[a]	84.3	—	—	—	—	—	25.5[a]	—	83.4[a]	—	—	23.2[a]	13.0	11.6	48.0[b]	60.0[a]
46	133.7[a]	116.6[a]	28.4	28.3[a]	—	47.3[a]	54.5[a]	61.3	81.0[a]	113.8[a]	12.2[a]	11.5[a]	41.6[a]	23.2	16.2	58.8[a]	105.4
47	101.2[a]	93.4	26.7	—	—	—	—	53.6	—	96.6[a]	—	—	35.5	—	—	—	84.6[a]
48	127.6	91.6	16.7	24.9[a]	24.4[a]	21.7	28.0	36.4[a]	74.0[a]	113.1[a]	16.2[a]	14.9[a]	27.7[a]	13.7	14.9	46.4	104.0
49	101.2[a]	79.4	15.0	17.6	17.9[b]	17.9[b]	22.5[b]	31.8[a]	57.3[a]	96.3[a]	11.1[a]	13.2[a]	22.0[a]	11.9	10.5	38.5[b]	87.6[a]
50	67.2	68.5	26.7	19.0[a]	17.0	23.6	20.2	50.0	51.1	61.7	17.9[a]	18.4[a]	30.3	9.6	14.2	26.1	61.6
51	102.9	102.2	38.0[b]	21.8[a]	—	33.3	29.3	64.0	83.6	74.0[a]	18.4	—	41.3	20.3	28.8	34.3	94.1
52	151.0[a]	121.6	30.3	25.9[a]	24.4[a]	50.0	—	—	94.5	132.0[a]	20.4	23.3[a]	—	—	—	—	—
53	124.0	114.0[a]	37.0	—	25.2	39.5	—	58.0	66.5	97.0	24.0	—	44.0	19.0	—	—	87.0
54	197.0	186.0	75.0	46.0	36.0	71.0	63.5	102.0	123.0	151.0	48.0	50.0	51.0	37.0	32.0	103.0	143.0
55	149.0	169.0	65.7	43.6	42.4	39.3	53.9	110.2	98.0	175.0	38.0	36.2	71.7	31.7	33.8	67.8	126.0
56	182.0	226.0	71.0	34.0	—	68.0	67.0	116.0	133.0	—	37.0	—	83.0	47.0	46.0	115.0	187.0
57	150.0[b]	158.0[b]	68.0[b]	48.0[b]	—	62.0[b]	58.0[b]	108.0[a]	92.0[b]	160.0	30.0[a]	—	68.0	37.0	35.0	124.0[b]	172.0[b]

[a] damaged.

[b] estimated.

APPENDIX 6
ADDITIONAL MEASUREMENTS OF *BOTHREMYS* AND *CHEDIGHAII* SKULLS

	Bothremys maghrebiana	*?Bothremyscooki*	*Chedighaii barberi*								
	AMNH 30031	AMNH 29444	CSU-K 85-7-4	NCSM 14103	NCSM 14227	NCSM 14226	NCSM 18650	NCSM 12766	NCSM 14102	ALAB 2001.2	FMNH PR 247
Distance from lateral edge of basisphenoid to lateral edge of quadrate	28.7	31.6	—	—	75.2	—	56.4	67.3	60.8	49.5	
(Maximum) height of quadrate	21.0	29.2	—	—	70.6	—	50.7	67.6	53.8	50.6	
Anteroposterior width of otic chamber at quadrate suture	15.4	18.6	30.1	30.3	40.6	29.6	25.6	26.8	30.6	25.5	
Skull width at quadrate	79.3	88.0[a]	128.0[a]	—	220[a]	—	152	100[a]	—	126	141[a]
Basioccipital length in ventral view	13.8	6.8[b]	13.0[b]	—	13.9[b]	—	14.7 [b]	12.2[b]	13.6[b]	17.0	17.7
Parietal-frontal suture length measured on ventral surface	—	—	—	—	—	—	—	—	—	58.9	58.0

[a] estimated.

[b] damaged.

APPENDIX 7

ADDITIONAL MEASUREMENTS OF *TAPHROSPHYS* AND *LABROSTOCHELYS* SKULLS

			T. sulcatus	*T. sulcatus*	*T. sulcatus*	*Labrostochelys*	*Labrostochelys*
	T. ippolitoensis	*T. congolensis*	YPM-PU 18707	NJSM 11362	ANSP 15544	AMNH 30043	AMNH 29984
Width of basioccipital	40.2	25.4	32.0	20.3	—	31.4	26.2
Length of basioccipital	24.1	12.5	12.8	12.5	—	16.8	12.8
Length of basisphenoid	21.8	21.9	—	13.0	—	27.9	25.6
Width of basisphenoid	41.5	29.3	—	22.6	—	26.7	19.9
Length from occipital condyle to anterior edge of pterygoids	67.8	30.6	—	40.8	—	57.5	45.9a
Maximum internal width of foramen magnum	15.0	13.2[a]	—	10.5	—	11.1	9.7
Maximum length of parietal	63.6[a]	46.0	—	32.9	34.9	—	—
Maximum width of parietal	45.0[a]	30.2	—	21.4	42.3	26.3a	20.8a
Length from anterior edge of parietal to posterior edge of crista supraoccipitalis	63.8[a]	56.5	—	43.4	46.6	—	—
Length from anterior edge of prefrontal to posterior edge of parietal	114.0[a]	—	—	—	49.8	—	—

[a] damaged.

APPENDIX 8
LOWER JAW MEASUREMENTS

See figure 316 for positions of measurements.

	A	B	C
Araripemys THUg 1907	22.2	26.8	2.6
Araripemys AMNH 24454	23.3	31.3	3.4
Euraxemys FR 4922	32.5	61.0	3.0
Kurmademys ISI R155E	25.3	41.3[a]	8.9
Kurmademys ISI R155D	25.1	39.1	7.1
Kurmademys ISI R155F	24.7	—	6.9
Cearachelys BSP 1976 I 160	26.0	34.0	7.5
Cearachelys THUg 1798	15.3	23.7	3.6
Pelomedusoides incertae sedis AMNH 30029	27.0[a]	—	5.4
Foxemys PAM 511B	39.0	—	16.8
Foxemys MC M2114	20.8	—	4.3
Foxemys MC M2115	19.1	—	4.6
Foxemys MC M2116	24.2	—	8.3
Foxemys MC M2117	22.3	—	5.2
Foxemys MC M2118	36.3	53.9[a]	11.8
Araiochelys THUg	34.2	55.7[a]	6.8
Bothremys cooki AMNH 2521	41.2	—	19.0
Bothremys maghrebiana AMNH 30522	34.2	67.7[a]	14.5
Chedighaii barberi FMNH PR247	58.8	104.0	27.3
Chedighaii barberi ALAB PV 2001.2	68.1	—	22.8
Chedighaii barberi NJSM 12704	52.0	—	24.0
Rhothonemys AMNH 30521	79.0	115.7	17.8
Bothremydini indet AMNH 29989	50.8	—	26.2

[a] reconstructed.

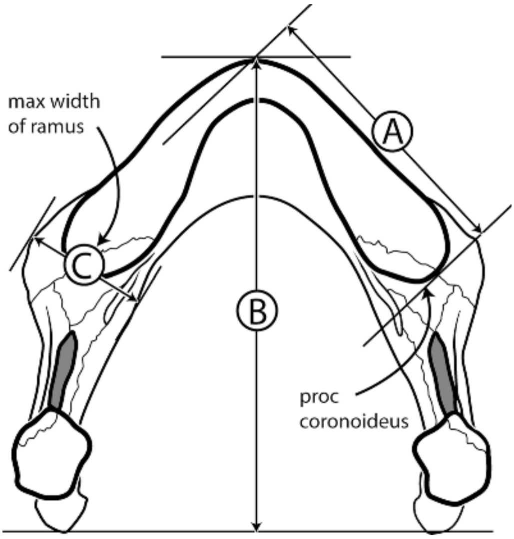

Fig. 316. Positions of lower jaw measurements for appendix 8 on an outline of *Kurmademys*.

APPENDIX 9

APOMORPHY LIST (SEE FIG. 317 FOR NODE NUMBERS)

This list is the PAUP* 4.0 parsimony analysis resulting in Cladogram 1, shown in figures 288 and 317, of the dataset in appendix 3, with all shell-only (asterisked) taxa excluded. All characters are unweighted and unordered. The full character names are listed in appendix 2. Double arrows represent unequivocal transformations in both ACCTRAN and DELTRAN character optimizations. Single arrows represent ACCTRAN optimization only. The first number is the character number, followed by the name in parentheses, the number of steps, the consistency index, and the character state change.

Node 97 → *Proganochelys*
7 (PF, PF-PAL contact), 1, 0.333, 0 → 1
Node 97 → node 96
2 (LA, lacrimal), 1, 1.000, 0 → 1
9 (PF, fissura ethmoidalis), 1, 1.000, 0 → 1
19 (ST, supratemporal), 1, 1.000, 0 → 1
44 (VO, MX-VO contact), 1, 0.167, 0 → 1
45 (VO, absent), 1, 1.000, 0 → 1
46 (VO, vomerine teeth), 1, 1.000, 0 ⇒ 1
61 (QU, fully formed cavum tympani), 1, 1.000, 0 ⇒ 1
63 (QU, middle ear with wall), 1, 1.000, 0 ⇒ 1
65 (QU, covers OP laterally), 1, 1.000, 0 ⇒ 1
66 (QU, pocket for stapes), 1, 1.000, 0 ⇒ 1
67 (QU, cranioquadrate space), 1, 1.000, 0 ⇒ 1
80 (SO, crista supraoccipitalis), 1, 0.500, 0 ⇒ 1
91 (PR, foramen stapediotemporalis), 1, 1.000, 0 → 1
97 (PR, plane of fenestra ovale), 1, 1.000, 0 ⇒ 1
102 (OP, processus paroccipitalis), 1, 0.333, 0 → 1
108 (BS, skull akinetic), 1, 1.000, 0 ⇒ 1
109 (BS, cultriform process), 1, 1.000, 0 ⇒ 1
111 (BS, ventral BS/BO tubercle), 1, 1.000, 0 ⇒ 1
120 (SUR, foramen nervi auriculotemporalis), 1, 0.500, 0 → 1
123 (ART, processus retroarticularis), 1, 0.667, 0 → 1
156 (CAR, costovertebral tunnel), 1, 1.000, 0 → 2
Node 96 → *Australochelys*
42 (MX, ventral rim of orbit), 1, 0.333, 0 ⇒ 1
Node 96 → node 95
62 (QU, cavum tympani with acute edge), 1, 1.000, 0 ⇒ 1
64 (QU, cavum tympani curved dorsally), 1, 1.000, 0 ⇒ 1
105 (BS, interpterygoid vacuity), 1, 1.000, 0 ⇒ 1
106 (BS, ventral outline), 1, 0.500, 0 → 1
Node 95 → node 94
3 (LA, lacrimal foramen), 1, 1.000, 0 ⇒ 1
32 (PM, midline dorsal process), 1, 0.400, 0 ⇒ 1
51 (QU,antrum postoticum), 1, 0.500, 0 ⇒ 3
81 (SO, wide occipital plate), 1, 1.000, 0 ⇒ 1
82 (EX, foramen jugulare posterior), 1, 0.333, 0 → 1
83 (EX, recessus scalae tympani), 1, 1.000, 0 ⇒ 1
88 (BO, thick), 1, 1.000, 0 ⇒ 1
98 (OP, processus interfenestralis), 1, 1.000, 0 ⇒ 1
111 (BS, ventral BS/BO tubercle), 1, 1.000, 1 ⇒ 2
112 (CA, columella auris), 1, 1.000, 0 ⇒ 1
130 (SH, coracoid foramen), 1, 1.000, 0 ⇒ 1
131 (SH, coracoid shape), 1, 1.000, 0 ⇒ 1
136 (PEL, thyroid fenestra), 1, 1.000, 0 ⇒ 1
140 (CAR, pygal notch), 1, 1.000, 0 ⇒ 2
151 (CAR, supramarginal scale), 1, 1.000, 0 ⇒ 2
159 (PLA, entoplastron trapezoidal), 1, 0.500, 0 ⇒ 1
161 (PLA, dorsal epiplastral process), 1, 1.000, 0 ⇒ 1
163 (PLA, gular projections), 1, 1.000, 0 ⇒ 1
169 (PLA, posterior lobe wide), 1, 1.000, 0 → 1
175 (shell texture), 1, 0.833, 0 → 1
Node 94 → node 59
8 (PF, PF-VO contact), 1, 1.000, 0 ⇒ 1
29 (PO, size), 1, 0.333, 0 ⇒ 1
72 (PT, processus pterygoideus externus), 1, 1.000, 0 ⇒ 1
96 (PR, processus trochlearis pterygoidei), 1, 1.000, 0 ⇒ 1
144 (CAR, position of four sided neural), 1, 0.667, 0 → 1
175 (shell texture), 1, 0.833, 1 → 4
Node 59 → Selmacryptodira
74 (PT, foramen posterius canalis carotici interni position), 1, 0.500, 0 ⇒ 4
75 (PT, pt in foramen posterius canalis carotici interni), 1, 0.250, 0 ⇒ 1
Node 94 → node 93
17 (PA, sulcus palatinopterygoideus), 1, 1.000, 0 ⇒ 1
28 (PO, septum orbitotemporale), 1, 1.000, 0 ⇒ 1
39 (MX, MX-QU contact, cheek emargination), 1, 0.571, 0 → 3
48 (PAL, foramen palatinum posterius), 1, 1.000, 0 ⇒ 1
56 (QU, fossa precolumellaris), 1, 0.500, 0 ⇒ 2
58 (QU, medial process), 1, 1.000, 0 ⇒ 1
60 (QU, condylus mandibularis), 1, 0.333, 0 ⇒ 1
70 (PT, processus trochlearis pterygoidei), 1, 1.000, 0 ⇒ 1
71 (PT, posteroventral flange), 1, 1.000, 0 ⇒ 1
74 (PT, foramen posterius canalis carotici interni position), 1, 0.500, 0 ⇒ 3
78 (EPT, absent), 1, 1.000, 0 ⇒ 1
82 (EX, foramen jugulare posterior), 1, 0.333, 1 → 2
90 (PR, hyomandibular nerve), 1, 1.000, 0 ⇒ 1
106 (BS, ventral outline), 1, 0.500, 1 → 2
117 (DEN, sutured symphysis), 1, 0.500, 0 → 1
124 (VT, cervical ribs), 1, 1.000, 0 ⇒ 1
125 (VT, cervical postzygapophyses), 1, 0.500, 0 → 1
126 (VT, cervical postzygapophyses), 1, 1.000, 0 ⇒ 1
127 (VT, cervical centra), 1, 1.000, 0 ⇒ 2
128 (VT, cervical articulation), 1, 1.000, 0 → 1
129 (VT, caudal articulation), 1, 0.500, 0 → 2
132 (PEL, tenth thoracic centrum), 1, 1.000, 0 ⇒ 1
133 (PEL, pelvis sutured), 1, 1.000, 0 ⇒ 1
134 (PEL, dorsal part of ilium), 1, 1.000, 0 ⇒ 1
135 (PEL, narrow), 1, 1.000, 0 ⇒ 1
137 (HUM, shoulder), 1, 1.000, 0 ⇒ 1
139 (CAR, nuchal bone width), 1, 0.750, 0 ⇒ 1
142 (CAR, iliac scar position), 1, 0.667, 0 ⇒ 1
145 (CAR, neural series pattern), 1, 1.000, 1 → 2
146 (CAR, neural number), 1, 0.600, 0 → 1
147 (CAR, peripheral 1/ costal), 1, 0.333, 1 → 2
148 (CAR, axillary process), 1, 0.667, 0 → 1
149 (CAR, axillary process), 1, 1.000, 0 ⇒ 2
152 (CAR, vertebral scale width), 1, 1.000, 0 ⇒ 1

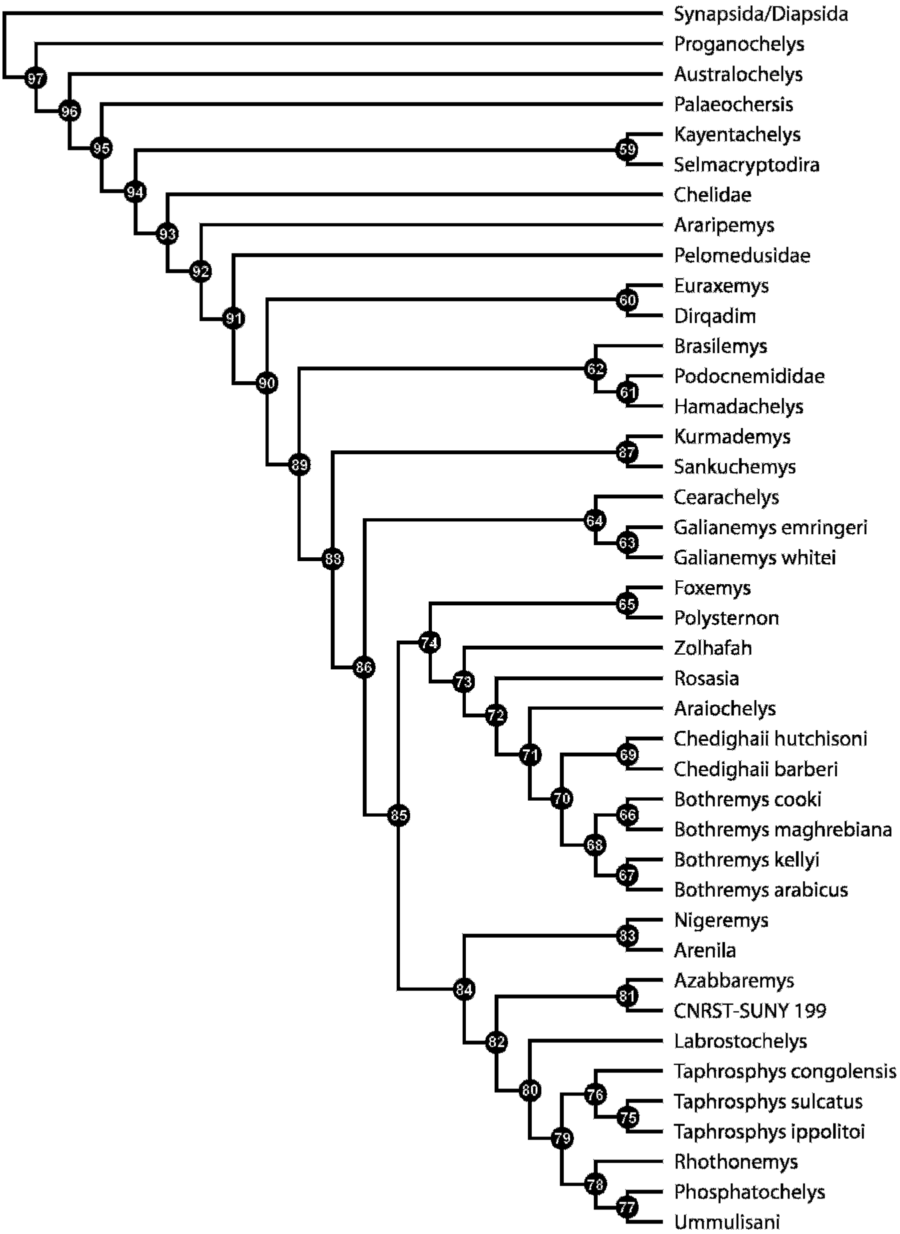

Fig. 317. Cladogram 1 showing numbered nodes for apomorphy list in appendix 9.

155 (CAR, first thoracic rib), 1, 1.000, 0 ⇒ 1
158 (PLA, mesoplastra), 1, 1.000, 0 ⇒ 3
160 (PLA, epiplastra meet in midline), 1, 1.000, 0 ⇒ 1
162 (PLA, intergular scales), 1, 1.000, 0 ⇒ 1
168 (PLA, ischial attachment), 1, 0.667, 0 ⇒ 1
171 (PLA, axillary/inguinal), 1, 1.000, 0 → 1
174 (PLA, anal notch), 1, 1.000, 0 ⇒ 1
Node 93 → Chelidae
38 (MX, MX-QJ contact), 1, 0.667, 0 ⇒ 2
39 (MX, MX-QU contact, cheek emargination), 1, 0.571, 3 → 4
44 (VO, MX-VO contact), 1, 0.167, 1 → 0
52 (QU, incisura columellae), 1, 0.400, 0 ⇒ 2
128 (VT, cervical articulation), 1, 1.000, 1 → 2
173 (PLA, anterior lobe reaches carapace edge), 1, 0.500, 0 ⇒ 1
Node 93 → node 92
1 (NA, nasals), 1, 1.000, 0 ⇒ 1
4 (PF, meet on midline in dorsal view), 1, 1.000, 0 ⇒ 1
14 (PA, temporal emargination), 1, 0.500, 0 → 1
15 (PA, PA-SQ contact), 1, 0.500, 0 ⇒ 1
102 (OP, processus paroccipitalis), 1, 0.333, 1 → 0
113 (SP, splenial), 1, 1.000, 0 ⇒ 1
138 (CAR, cervical scale), 1, 1.000, 0 ⇒ 1
Node 92 → node 91
76 (PT, foramen caroticum laterale), 1, 0.500, 0 → 1
150 (CAR, inguinal buttress), 1, 1.000, 0 → 1
154 (CAR, nuchal embayment), 1, 0.333, 1 ⇒ 0
158 (PLA, mesoplastra), 1, 1.000, 3 ⇒ 2
Node 91 → Pelomedusidae
45 (VO, absent), 1, 1.000, 1 ⇒ 2
47 (VO, central bar), 1, 1.000, 0 ⇒ 2
52 (QU, incisura columellae), 1, 0.400, 0 ⇒ 2
84 (EX, condylus occipitalis), 1, 0.333, 0 ⇒ 1
89 (BO, BO-OP contact), 1, 0.500, 0 ⇒ 1
125 (VT, cervical postzygapophyses), 1, 0.500, 1 → 0
141 (CAR, neural series complete), 1, 0.600, 0 ⇒{123}
Node 91 → node 90
14 (PA, temporal emargination), 1, 0.500, 1 → 0
74 (PT, foramen posterius canalis carotici interni position), 1, 0.500, 3 ⇒ 4
75 (PT, PT in foramen posterius canalis carotici interni position), 1, 0.250, 0 ⇒ 1
94 (PR, ventral exposure), 1, 1.000, 0 → 1
99 (OP, processus interfenestralis), 1, 1.000, 0 ⇒ 1
166 (PLA, pectorals on epiplastron), 1, 0.333, 0 → 1
Node 90 → node 60
13 (PA,QJ-PA contact), 1, 0.667, 0 ⇒ 1
36 (MX, accessory ridge), 1, 0.333, 0 ⇒ 1
44 (VO, MX-VO contact), 1, 0.167, 1 → 0
56 (QU, fossa precolumellaris), 1, 0.500, 2 ⇒ 1
82 (EX, foramen jugulare posterior), 1, 0.333, 2 ⇒ 1
85 (EX, EX-QU contact), 1, 1.000, 0 ⇒ 2
86 (EX, ventral process), 1, 1.000, 0 ⇒ 1
106 (BS, ventral outline), 1, 0.500, 2 ⇒ 1
172 (PLA, abdominal scale), 1, 0.667, 0 → 1
Node 60 → *Dirqadim*
15 (PA, PA-SQ contact), 1, 0.500, 1 ⇒ 0
30 (PM, protrudes anteriorly), 1, 0.200, 0 ⇒ 1
77 (PT, midline contact), 1, 0.143, 0 ⇒ 1
Node 90 → node 89
59 (QU,QU-BO contact), 1, 1.000, 0 ⇒ 1
87 (BO, short), 1, 0.500, 0 ⇒ 1
94 (PR, ventral exposure), 1, 1.000, 1 → 2
104 (BS, BS-QU contact), 1, 0.500, 0 ⇒ 1
117 (DEN, sutured symphysis), 1, 0.500, 1 → 0
123 (ART, processus retroarticularis), 1, 0.667, 1 → 0
146 (CAR, neural number), 1, 0.600, 1 → 2
165 (PLA, pectorals on entoplastron), 1, 0.333, 0 ⇒ 1
Node 89 → node 62
69 (PT, cavum pterygoidei), 1, 1.000, 0 ⇒ 1
76 (PT, foramen caroticum laterale), 1, 0.500, 1 → 0
89 (BO, BO-OP contact), 1, 0.500, 0 → 1
123 (ART, processus retroarticularis), 1, 0.667, 0 → 2
139 (CAR, nuchal bone width), 1, 0.750, 1 → 2
141 (CAR, neural series complete), 1, 0.600, 0 ⇒ 1
148 (CAR, axillary process), 1, 0.667, 1 → 2
Node 62 → node 61
13 (PA, QJ-PA contact), 1, 0.667, 0 ⇒ 1
52 (QU, incisura columellae), 1, 0.400, 0 ⇒ 2
147 (CAR, peripheral 1/ costal), 1, 0.333, 2 → 1
Node 61 → Podocnemididae
119 (DEN, widely exposed), 1, 0.500, 0 ⇒ 1
122 (PRA, fossa meckelii), 1, 0.500, 0 ⇒ 1
Node 62 → *Brasilemys*
56 (QU, fossa precolumellaris), 1, 0.500, 2 ⇒ 1
82 (EX, foramen jugulare posterior), 1, 0.333, 2 ⇒ 1
85 (EX, EX-QU contact), 1, 1.000, 0 ⇒ 3
127 (VT, cervical centra), 1, 1.000, 2 ⇒ 1
Node 89 → node 88
27 (PO, fossa orbitalis), 1, 0.500, 0 ⇒ 1
31 (PM, midline depression), 1, 0.333, 0 ⇒ 1
34 (MX, triturating surfaces), 1, 0.333, 0 → 1
38 (MX, MX-QJ contact), 1, 0.667, 0 ⇒ 1
50 (PAL, contribution to triturating surfaces), 1, 0.333, 0 ⇒ 1
52 (QU, incisura columellae), 1, 0.400, 0 ⇒ 1
53 (QU, stapes), 1, 0.333, 0 ⇒ 1
79 (SO, SO-QU contact), 1, 0.250, 0 ⇒ 1
85 (EX, EX-QU contact), 1, 1.000, 0 ⇒ 1
100 (OP, fenestra postotica), 1, 0.500, 0 → 1
102 (OP, processus paroccipitalis), 1, 0.333, 0 ⇒ 1
114 (DEN, high lingual ridge), 1, 0.500, 0 ⇒ 1
116 (DEN, U-shaped lingual ridge), 1, 0.500, 0 ⇒ 1
118 (DEN, triturating surface), 1, 0.333, 0 ⇒ 1
143 (CAR, costal one width), 1, 0.500, 0 → 1
Node 88 → node 86
29 (PO, size), 1, 0.333, 0 ⇒ 1
39 (MX, MX-QU contact, cheek), 1, 0.571, 3 → 0
44 (VO, MX-VO contact), 1, 0.167, 1 → 0
56 (QU, fossa precolumellaris), 1, 0.500, 2 ⇒ 0
60 (QU, condylus mandibularis), 1, 0.333, 1 ⇒ 0
84 (EX, condylus occipitalis), 1, 0.333, 0 → 1
92 (PR, foramen stapediotemporale), 1, 1.000, 0 ⇒ 1
106 (BS, ventral outline), 1, 0.500, 2 ⇒ 1
142 (CAR, iliac scar position), 1, 0.667, 1 → 2
166 (PLA, pectorals on epiplastron), 1, 0.333, 1 → 0
Node 86 → node 64
14 (PA, temporal emargination), 1, 0.500, 0 ⇒ 2
20 (JU, jugal retracted), 1, 1.000, 0 → 1
82 (EX, foramen jugulare posterior), 1, 0.333, 2 ⇒ 1
100 (OP, fenestra postotica), 1, 0.500, 1 → 0
101 (OP, fenestra postotica), 1, 1.000, 0 ⇒ 1
143 (CAR, costal one width), 1, 0.500, 1 → 0
144 (CAR, position of four sided neural), 1, 0.667, 0 → 1
146 (CAR, neural number), 1, 0.600, 2 → 1
165 (PLA, pectorals on entoplastron), 1, 0.333, 1 → 0
175 (Shell texture), 1, 0.833, 1 → 4
Node 64 → *Cearachelys*

27 (PO, fossa orbitalis), 1, 0.500, 1 ⇒ 0
52 (QU, incisura columellae), 1, 0.400, 1 ⇒{02}
53 (QU, stapes), 1, 0.333, 1 ⇒ 0
Node 64 → node 63
20 (JU, jugal retracted), 1, 1.000, 1 → 2
55 (QU, trough on closed ICA), 1, 0.500, 0 ⇒ 1
84 (EX, condylus occipitalis), 1, 0.333, 1 → 0
Node 63 → *Galianemys emringeri*
68 (PT, fossa pterygoidea), 1, 0.333, 0 ⇒ 1
95 (PR, QU-PT-BS exposure), 1, 0.333, 0 ⇒ 1
Node 86 → node 85
24 (SQ, posterior projection), 1, 0.333, 0 → 1
34 (MX, triturating surfaces), 1, 0.333, 1 → 0
39 (MX, MX-QU contact, cheek emargination), 1, 0.571, 0 → 1
57 (QU, shelf below cavum tympani), 1, 1.000, 0 ⇒ 1
93 (PR, foramen stapediotemporalis), 1, 1.000, 0 ⇒ 1
119 (DEN, widely exposed), 1, 0.500, 0 ⇒ 1
120 (SUR, foramen nervi auriculotemporalis), 1, 0.500, 1 ⇒ 0
121 (COR, wide lateral exposure), 1, 0.500, 0 → 1
122 (PRA, fossa meckelii), 1, 0.500, 0 ⇒ 1
141 (CAR, neural series complete), 1, 0.600, 0 ⇒ 2
164 (PLA, anterior lobe short), 1, 0.500, 0 ⇒ 1
Node 85 → node 74
5 (PF, preorbital skull broad), 1, 0.500, 0 ⇒ 1
12 (FR, foramen interorbitalis), 1, 1.000, 0 ⇒ 1
34 (MX, triturating surfaces), 1, 0.333, 0 → 2
154 (CAR, nuchal embayment), 1, 0.333, 0 → 1
173 (PLA, anterior lobe), 1, 0.500, 0 ⇒ 1
Node 74 → node 65
39 (MX, MX-QU contact, cheek emargination), 1, 0.571, 1 → 0
53 (QU, stapes), 1, 0.333, 1 ⇒ 0
68 (PT, fossa pterygoidea), 1, 0.333, 0 ⇒ 2
82 (EX, foramen jugulare posterior), 1, 0.333, 2 ⇒ 1
106 (BS, ventral outline), 1, 0.500, 1 ⇒ 2
139 (CAR, nuchal bone width), 1, 0.750, 1 ⇒ 2
166 (PLA, pectorals on epiplastron), 1, 0.333, 0 ⇒ 1
167 (PLA, pectoral on mesoplastron), 1, 0.250, 0 → 1
Node 65 → *Foxemys*
42 (MX, ventral rim of orbit), 1, 0.333, 0 ⇒ 1
95 (PR, QU-PT-BS exposure), 1, 0.333, 0 ⇒ 1
154 (CAR, nuchal embayment), 1, 0.333, 1 → 0
Node 65 → *Polysternon*
34 (MX, triturating surfaces), 1, 0.333, 2 → 1
60 (QU, condylus mandibularis), 1, 0.333, 0 ⇒ 1
164 (PLA, anterior lobe short), 1, 0.500, 1 ⇒ 0
175 (shell texture), 1, 0.833, 1 ⇒ 3
Node 74 → node 73
23 (JU, exposure in triturating surface), 1, 0.333, 0 ⇒ 1
35 (MX, triturating surface), 1, 0.333, 0 ⇒ 1
115 (DEN, pits), 1, 1.000, 0 → 1
147 (CAR, peripheral 1/ costal), 1, 0.333, 2 → 1
Node 73 → node 72
31 (PM, midline depression), 1, 0.333, 1 ⇒ 2
51 (QU, antrum postoticum), 1, 0.500, 3 → 1
Node 72 → node 71
6 (PF, anterior margin), 1, 0.333, 0 ⇒ 1
7 (PF, PF-PAL contact), 1, 0.333, 0 ⇒ 1
16 (PA, contacts pterygoid), 1, 0.333, 0 → 1
17 (PA, sulcus palatinopterygoideus), 1, 1.000, 1 → 2
30 (PM, protrudes anteriorly), 1, 0.200, 0 ⇒ 1
32 (PM, midline dorsal process), 1, 0.400, 1 ⇒ 2
74 (PT, foramen posterius canalis carotici interni), 1, 0.500, 4 ⇒ 1
107 (BS, processus clinoideus), 1, 1.000, 0 → 1
141 (CAR, neural series compete), 1, 0.600, 2 → 3
Node 71 → *Araiochelys*
5 (PF, preorbital skull broad), 1, 0.500, 1 ⇒ 0
34 (MX, triturating surfaces), 1, 0.333, 2 ⇒ 1
77 (PT, midline contact), 1, 0.143, 0 ⇒ 1
118 (DEN, triturating surface), 1, 0.333, 1 ⇒ 0
145 (CAR, neural series pattern), 1, 1.000, 2 ⇒ 4
146 (CAR, neural number), 1, 0.600, 2 ⇒ 3
147 (CAR, peripheral 1/ costal), 1, 0.333, 1 → 2
167 (PLA, pectoral on mesoplastron), 1, 0.250, 0 ⇒ 1
Node 71 → node 70
11 (FR, orbits facing upward), 1, 0.500, 0 ⇒ 1
37 (MX, labial ridge), 1, 0.500, 0 ⇒ 1
103 (OP, thin horizontal flange), 1, 1.000, 0 ⇒ 1
104 (BS, BS-QU contact), 1, 0.500, 1 ⇒ 2
Node 70 → node 68
40 (MX, orbital-narial bar width), 1, 1.000, 0 ⇒ 1
Node 68 → node 66
41 (MX, dorsal process), 1, 1.000, 0 ⇒ 1
42 (MX, ventral rim of orbit), 1, 0.333, 0 → 1
Node 66 → *Bothremys maghrebiana*
77 (PT, midline contact), 1, 0.143, 0 ⇒ 1
Node 68 → node 67
31 (PM, midline depression), 1, 0.333, 2 ⇒ 1
Node 67 → *Bothremys kellyi*
74 (PT, foramen posterius canalis carotici interni), 1, 0.500, 1 ⇒ 5
Node 70 → node 69
23 (JU, exposure in triturating surfaces), 1, 0.333, 1 ⇒ 0
35 (MX, triturating surface), 1, 0.333, 1 ⇒ 0
39 (MX, MX-QU contact, cheek), 1, 0.571, 1 → 0
44 (VO, MX-VO contact), 1, 0.167, 0 → 1
Node 69 → *Chedighaii hutchisoni*
31 (PM, midline depression), 1, 0.333, 2 ⇒ 1
Node 69 → *Chedighaii barberi*
34 (MX, triturating surfaces), 1, 0.333, 2 ⇒ 1
Node 72 → *Rosasia*
68 (PT, fossa pterygoidea), 1, 0.333, 0 ⇒ 1
165 (PLA, pectorals on entoplastron), 1, 0.333, 1 ⇒ 0
Node 73 → *Zolhafah*
74 (PT, foramen posterius canalis carotici interni), 1, 0.500, 4 ⇒ 5
79 (SO, SO-QU contact), 1, 0.250, 1 ⇒ 0
Node 85 → node 84
22 (JU, JU-QU contact), 1, 1.000, 0 → 1
38 (MX, MX-QJ contact), 1, 0.667, 1 → 0
49 (PAL, dorsally arched palate), 1, 0.500, 0 ⇒ 1
50 (PAL, contribution to triturating surfaces), 1, 0.333, 1 ⇒ 0
77 (PT, midline contact), 1, 0.143, 0 → 1
79 (SO, SO-QU contact), 1, 0.250, 1 → 0
104 (BS, BS-QU contact), 1, 0.500, 1 ⇒ 2
114 (DEN, high lingual ridge), 1, 0.500, 1 → 0
116 (DEN, U-shaped lingual ridge), 1, 0.500, 1 → 0
118 (DEN, triturating surface), 1, 0.333, 1 → 0
168 (PLA, ischial attachment), 1, 0.667, 1 → 2
170 (PLA, intergular scale), 1, 1.000, 0 → 1
172 (PLA, abdominal scale), 1, 0.667, 0 → 1
175 (shell texture), 1, 0.833, 1 → 2
Node 84 → node 82
28 (PO, septum orbitotemporale), 1, 1.000, 1 ⇒ 2

32 (PM, midline dorsal process), 1, 0.400, 1 → 2
43 (MX, exposure), 1, 0.500, 0 ⇒ 1
74 (PT, foramen posterius canalis carotici interni), 1, 0.500, 4 ⇒ 1
Node 82 → node 80
13 (PA,QJ-PA contact), 1, 0.667, 0 ⇒ 2
21 (JU, narrow dorsoventrally), 1, 0.500, 0 → 1
25 (SQ, posteroventral vertical flange), 1, 1.000, 0 ⇒ 1
26 (SQ, lateral tubercle), 1, 1.000, 0 ⇒ 1
29 (PO, size), 1, 0.333, 1 ⇒ 0
54 (QU, sulcus eustachii), 1, 1.000, 0 ⇒ 1
Node 80 → node 79
24 (SQ, posterior projection), 1, 0.333, 1 → 0
33 (PM, dorsal sulcus), 1, 1.000, 0 ⇒ 1
60 (QU, condylus mandibularis), 1, 0.333, 0 → 1
73 (PT, trigeminal ridge (PT), 1, 1.000, 0 ⇒ 1
77 (PT, midline contact), 1, 0.143, 1 → 0
104 (BS, BS-QU contact), 1, 0.500, 2 ⇒ 1
106 (BS, ventral outline), 1, 0.500, 1 ⇒ 2
Node 79 → node 76
32 (PM, midline dorsal process), 1, 0.400, 2 → 1
74 (PT, foramen posterius canalis carotici interni), 1, 0.500, 1 ⇒ 5
167 (PLA, pectoral on mesoplastron), 1, 0.250, 0 → 1
Node 76 → node 75
110 (BS, sella turcica/ dorsum sellae), 1, 1.000, 0 ⇒ 1
Node 75 → *Taphrosphys sulcatus*
87 (BO, short), 1, 0.500, 1 ⇒ 0
Node 79 → node 78
18 (PA, enters orbital margin), 1, 1.000, 0 ⇒ 1
21 (JU, narrow dorsoventrally), 1, 0.500, 1 → 0
37 (MX, labial ridge), 1, 0.500, 0 ⇒ 1
39 (MX, MX-QU contact, cheek emargination), 1, 0.571, 1 → 2
40 (MX, orbital-narial bar width), 1, 1.000, 0 ⇒ 3
43 (MX, exposure), 1, 0.500, 1 → 0
Node 78 → node 77
10 (PF, PF-PA contact), 1, 1.000, 0 ⇒ 1
Node 77 → *Phosphatochelys*
16 (PA, contacts pterygoid), 1, 0.333, 0 ⇒ 1
60 (QU, condylus mandibularis), 1, 0.333, 1 → 0
Node 77 → *Ummulisani*
6 (PF, anterior margin), 1, 0.333, 0 ⇒ 1
51 (QU, antrum postoticum), 1, 0.500, 3 ⇒ 2
80 (SO, crista supraoccipitale), 1, 0.500, 1 ⇒ 0
Node 78 → *Rhothonemys*
30 (PM, protrudes anteriorly), 1, 0.200, 0 ⇒ 1
Node 80 → *Labrostochelys*
6 (PF, anterior margin), 1, 0.333, 0 ⇒ 1
7 (PF, PF-PAL contact), 1, 0.333, 0 ⇒ 1
30 (PM, protrudes anteriorly), 1, 0.200, 0 ⇒ 1
31 (PM, midline depression), 1, 0.333, 1 ⇒ 2
40 (MX, orbital-narial bar width), 1, 1.000, 0 ⇒ 2
49 (PAL, dorsally arched palate), 1, 0.500, 1 ⇒ 0
51 (QU, antrum postoticum), 1, 0.500, 3 ⇒ 1
75 (PT, PT in foramen posterius canalis carotici interni), 1, 0.250, 1 ⇒ 0
Node 82 → node 81
44 (VO, MX-VO contact), 1, 0.167, 0 ⇒ 1
47 (VO, central bar), 1, 1.000, 0 ⇒ 1
Node 81 → *Azabbaremys*
24 (SQ, posterior projection), 1, 0.333, 1 → 0
30 (PM, protrudes anteriorly), 1, 0.200, 0 ⇒ 1
31 (PM, midline depression), 1, 0.333, 1 ⇒ 0
32 (PM, midline dorsal process), 1, 0.400, 2 → 1
51 (QU, antrum postoticum), 1, 0.500, 3 ⇒ 2
77 (PT, midline contact), 1, 0.143, 1 → 0
Node 81 → CNRST-SUNY 199
23 (JU, exposure in triturating surface), 1, 0.333, 0 ⇒ 1
35 (MX, triturating surface), 1, 0.333, 0 ⇒ 1
36 (MX, accessory ridge), 1, 0.333, 0 ⇒ 1
68 (PT, fossa pterygoidea), 1, 0.333, 0 ⇒ 2
74 (PT, foramen posterius canalis carotici interni position), 1, 0.500, 1 ⇒ 5
79 (SO, SO-QU contact), 1, 0.250, 0 → 1
Node 84 → node 83
51 (QU, antrum postoticum), 1, 0.500, 3 ⇒ 2
60 (QU, condylus mandibularis), 1, 0.333, 0 ⇒ 2
68 (PT, fossa pterygoidea), 1, 0.333, 0 ⇒ 2
106 (BS, ventral outline), 1, 0.500, 1 ⇒ 4
Node 88 → node 87
14 (PA, temporal emargination), 1, 0.500, 0 ⇒ 1
16 (PA, contacts pterygoid), 1, 0.333, 0 → 1
55 (QU, trough on closed ICA), 1, 0.500, 0 → 1
95 (PR, QU-PT-BS exposure), 1, 0.333, 0 ⇒ 1
141 (CAR, neural series complete), 1, 0.600, 0 → 3
146 (CAR, neural number), 1, 0.600, 2 → 3
147 (CAR, peripheral 1/ costal), 1, 0.333, 2 → 1
167 (PLA, pectoral on mesoplastron), 1, 0.250, 0 → 1
Node 87 → *Kurmademys*
68 (PT, fossa pterygoidea), 1, 0.333, 0 ⇒ 1
74 (PT, foramen posterius canalis carotici interni position), 1, 0.500, 4 ⇒ 2
75 (PT, PT in foramen posterius canalis carotici interni), 1, 0.250, 1 ⇒ 0
Node 87 → *Sankuchemys*
36 (MX, accessory ridge), 1, 0.333, 0 ⇒ 1
Node 92 → *Araripemys*
11 (FR, orbits facing upward), 1, 0.500, 0 ⇒ 1
50 (PAL, contribution to triturating surface), 1, 0.333, 0 ⇒ 1
77 (PT, midline contact), 1, 0.143, 0 ⇒ 1
106 (BS, ventral outline), 1, 0.500, 2 ⇒ 3
121 (COR, wide lateral exposure), 1, 0.500, 0 ⇒ 1
129 (VT, caudal articulation), 1, 0.500, 2 → 0
139 (CAR, nuchal bone width), 1, 0.750, 1 ⇒ 4
142 (CAR, iliac scar position), 1, 0.667, 1 → 2
144 (CAR, position of four sided neural), 1, 0.667, 0 → 2
147 (CAR, peripheral 1/ costal), 1, 0.333, 2 ⇒ 3
148 (CAR, axillary process), 1, 0.667, 1 → 0
153 (CAR, vertebral scale 1), 1, 1.000, 0 ⇒ 1
159 (PLA, entoplastron trapezoidal), 1, 0.500, 1 ⇒ 0
168 (PLA, ischial attachment), 1, 0.667, 1 ⇒ 2
172 (PLA, abdominal scale), 1, 0.667, 0 ⇒ 2
175 (shell texture), 1, 0.833, 1 ⇒ 5

APPENDIX 10
SHELL MEASUREMENTS (IN MILLIMETERS)

		Carapace		Plastron	
Taxon	Specimen	length	width	length	References
Euraxemys essweini	FR 4922	312	255	248	
Kurmademys kallamedensis	ISI R278	285[a]	254	240[a]	
Cearachelys placidoi	BSP 1976I 160	161	210	178	
	THUg 1798	139	109	116	
Foxemys mechinorum	MDE t 10	470	320[a]	345	Tong et al., 1998
	MDE t 09	—	—	260	
	PAM 548	400[a]	340	340	
	MHNM uncataloged	410	340	330	
Polysternon provinciale	MHNM 1982-857	480[a]	420[a]	410	
	AE uncataloged	510	440	415	
Elochelys perfecta	Specimen no. 1	225[a]	192[a]	—	Nopcsa, 1931
Elochelys convenarum	MDE-Cas2-259	350[a]	275	285	Laurent et al., 2002
Rosasia soutoi	MTA 1	241[a]	220	197[a]	Antunes and Broin, 1988
	MTA 2	440[a]	377[a]	333	
	SGP,[b] uncataloged	375	354	—	
Chedighaii barberi	FMNH P26055	630	604	539	Schmidt, 1940
	ALAB 2001.2	—	—	590	
Taphrosphys sulcatus	YPM(PU) 18706	530[a]	390[a]	370	
Ummulisani	AMNH 30562	—	—	780	
Pelomedusoides indeterminate	AMNH 30551	550	405	433	
(?*Galianemys*)	AMNH 30550	555	398	460	

[a] estimated.

[b] Serviços Geológicos de Portugal.

→

Fig. 318. Skulls used as the basis of the reconstructions seen in the frontispiece. Upper, *Phosphatochelys tedfordi* (AMNH 30008, tribe Taphrosphyini), Eocene; middle, *Bothremys maghrebiana* (skull AMNH 30561, jaws AMNH 30522, tribe Bothremydini), Paleocene; lower, *Labrostochelys galkini* (AMNH 30043, tribe Taphrosphyini), Paleocene, image from CT scan furnished by Tim Rowe, University of Texas at Austin. All are from the Phosphates of Morocco. The orientations shown are the same as in the reconstructions. [F. Ippolito, del.]

Phosphatochelys

Bothremys

Labrostochelys

NOTE ADDED IN PROOF

After conducting additional acid preparation, the senior author has recently reinterpreted a skull fragment among the material belonging to FMNH PR 247, an associated partial skull and shell from the late Cretaceous of Alabama. This specimen was described and figured in Gaffney and Zangerl (1968) as *Bothremys barberi*, and identified here as *Chedighaii barberi* (figs. 162, 163). Because this specimen has an associated partial skull and shell, it was the basis for placing the species "*Podocnemis*" *barberi* Schmidt 1940, the type of which is a shell only (fig. 264), in *Chedighaii*. The newly reinterpreted skull fragment shows that this identification was in error. FMNH PR 247 belongs to *Bothremys* and not to *Chedighaii*. The principal result of this reinterpretation is the questionable generic assignment of the species *barberi*; it could belong to either *Bothremys* or *Chedighaii.* The species *barberi* is not the type species of any genus so its assignment does not affect the taxonomic basis of these genera.

The newly identified skull fragment from FMNH PR 247 consists of a part of the left jugal and maxilla that forms the lateral wall of the triturating surface and cheek. This fragment, although small and not well preserved, shows the lateral part of the pit structure on the triturating surface as seen in *Bothremys* (figs. 128, 133). It should be kept in mind that three of the type specimens assigned to the four known species of *Bothremys* consist of skulls without associated shells and that the type specimen of the type species of *Chedighaii, Chedighaii hutchisoni*, is also a skull. Therefore, the only distinguishing features of these genera are within the skull. All the species of *Bothremys* have well-developed triturating pits, which are absent in *Chedighaii*. The skulls are also different in shape as well as in the presence/absence of triturating pits (figs. 156, 161).

However, in the present paper the senior author has placed the species *barberi* in *Chedighaii* on the basis of the close similarity of the shell of FMNH PR 247 with the type shell of "*Podocnemis*" *barberi*, FMNH P26055. This identification was done with some qualification (see Discussion under *Chedighaii barberi*) due to the apparent absence of confirming skull material. The recognition of triturating pits in the jugal + maxilla skull fragment in FMNH PR 247 makes this identification incorrect: although FMNH PR 247 has triturating pits and is correctly assigned to *Bothremys*, the species assignment of FMNH PR 247 is now unclear.

Whether FMNH PR 247 should be identified as *Bothremys barberi*, *Bothremys cooki*, or one of the other *Bothremys* species is a difficult question because the the skull in FMNH PR 247 is incomplete. When originally described by Gaffney and Zangerl (1968), FMNH PR 247 was readily assigned to the genus *Bothremys* because of the pits in the lower jaws, and the species identification was based on the shell morphology. At the present time, however, shells very similar to the type shell of *barberi* apparently occur in at least two genera associated with both pitted (FMNH PR 247) and nonpitted (ALAB PV 2001.2) skull types. Therefore, at present, we identify FMNH PR 247 as *Bothremys* sp. Another skull/shell association identified as *Chedighaii barberi*, ALAB PV 2001.2, can still be identified as *Chedighaii* on the basis of its skull (figs. 160, 161, 164, 165), which clearly lacks pits and is similar to *Chedighaii hutchisoni*. Its shell is also very similar to the type shell of *"Podocnemis" barberi*, showing that the shell seems to be inadequate for a specific assignment.

The other specimens listed under *Chedighaii barberi* that consist of shells, or parts of shells, are now best identified as: *Chedighaii* or *Bothremys*. The distribution map in figure 18 has been corrected to show this new interpretation. The captions of the figures of ALAB PV 2001.2 and FMNH PR 247 have also been corrected but the text has not. The natural endocast identified as *Chedighaii barberi*, YPM PU 12951 (figs. 166, 167), can still be identified as *Chedighaii* sp. It clearly lacks triturating pits and is similar to *Chedighaii hutchisoni*.

As far as we can determine, none of these changes alter the MPC (Most Parsimonious Cladogram) and cause only minor alterations in the cranial descriptions, which will be corrected in a future paper. The dataset entry for *Chedighaii barberi* (now better identified as *Chedighaii* sp.) is based almost entirely on ALAB PV 2001.2 (an associated skull and shell identifiable as *Chedighaii*), with some carapace entries from FMNH PR 247 and specimens earlier identified by Gaffney and Zangerl (1968) as *Bothremys barberi.* ALAB PV 2001.2 can still be identified as *Chedighaii* because it has a skull with a pitless triturating surface, but the species assignment is questionable as it is distinct from *Chedighaii hutchisoni*.

Further discussion of these questions and the description of the FMNH PR 247 skull fragment will be dealt with in work in progress by the senior author, V. Schneider, and E. Hooks.