Diverse Turtle Fauna from the Late Eocene of Georgia Including the Oldest Records of Aquatic Testudinoids in Southeastern North America

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Abstract.—The Late Eocene (Chadronian NALMA) Hardie Mine local fauna of the Clinchfield Formation in Wilkinson County, Georgia, preserves the most diverse turtle fauna in the Eocene of southeastern North America. This fauna includes at least five taxa including a dermochelyid, a cheloniid, a trionychid, a testudinoid, and an unidentified cryptodire. Chelonioids and trionychids are the most common turtles in this near-shore marine deposit. The aquatic testudinoids from the Hardie Mine site represent the oldest records from southeastern North America, a region that exhibits a high diversity of extant aquatic testudinoids.

Compared with the western interior, turtle faunas from the Paleogene of southeastern North America are rare and taxonomically poorly represented. The best known faunas are from the Paleocene of South Carolina (Hutchison and Weems, 1998), the early Eocene of Virginia (Weems, 1988, 1999), and the Middle Eocene of Texas (Westgate, 2001). Faunas from Alabama (Holman and Case, 1988) and Florida (Holman, 2000) are poorly represented with just two taxa each (both faunas reviewed by Holroyd et al., 2005). Thus, the presence of a small, but relatively diverse (at least five species), turtle fauna from the Late Eocene (Chadronian NALMA [North American Land Mammal Age]) Hardie Mine local fauna of Georgia provides a significant window into the history of North American turtles. The Hardie Mine specimens represent a mixed assemblage of marine and freshwater forms including cheloniid s.l. and dermochelyid marine turtles, a trionychid, an unidentified cryptodire, and the first records of aquatic testudinoids from the Paleogene of southeastern North America.

Hardie Mine Fossil Locality

The Hardie Mine site is an inactive open-pit kaolin mine located about 3.9 km north-north-west of Gordon, Wilkinson County, central Georgia (32°54.335′N, 83°21.543′W). Fossiliferous Clinchfield Formation sediments are exposed in the Hardie Mine in two ways: as an approximately 1 m thick stratum of in situ sediments exposed in the north wall of the mine; and as surface spoil pile sediments that are clearly derived from the in situ sediments (see discussion in Westgate, 2001; Parmley and Cicimurri, 2003, 2005; Parmley and Holman, 2003; Parmley and DeVore, 2005:fig.1). These sediments are rich in vertebrate fossils, especially in marine near-shore taxa of sharks, rays, and bony fishes (Westgate, 2001; Parmley and Cicimurri, 2003). The site also yielded fragmentary teeth of at least five taxa of land mammals (unreported fossils in the Georgia College vertebrate fossil collections), a partial humerus of an alcid bird (Chandler and Parmley, 2003), a colubrid snake vertebra (Parmley and Holman, 2003), palaeopheid snake vertebrae (Parmley and DeVore, 2005), and a tooth plate of a chimaeroid fish (Parmley and Cicimurri, 2005). Screen washing and sorting in situ matrix and surface collecting of spoil pile sediments yielded the turtle fossils discussed here.

The Hardie Mine Clinchfield sediments were deposited during the Eocene Jackson Sea transgression, but their age within the Eocene has been unclear (Westgate, 2001). Westgate (2001) suggested the Hardie Mine sediments were deposited either during the late Middle Eocene (Dockery, 1996) or early in the Late Eocene (Huddelstun and Hetrick, 1986). New vertebrate and invertebrate faunal evidence, however, clearly points to a Late Eocene age (Chadronian NALMA, estimated at 34.5–35.5 Ma on the Eocene time scale of Woodburne, 2004) for the fossil-bearing Clinchfield sediments of the mine (see discussions in Parmley and Cicimurri, 2003; Parmley and Holman, 2003).
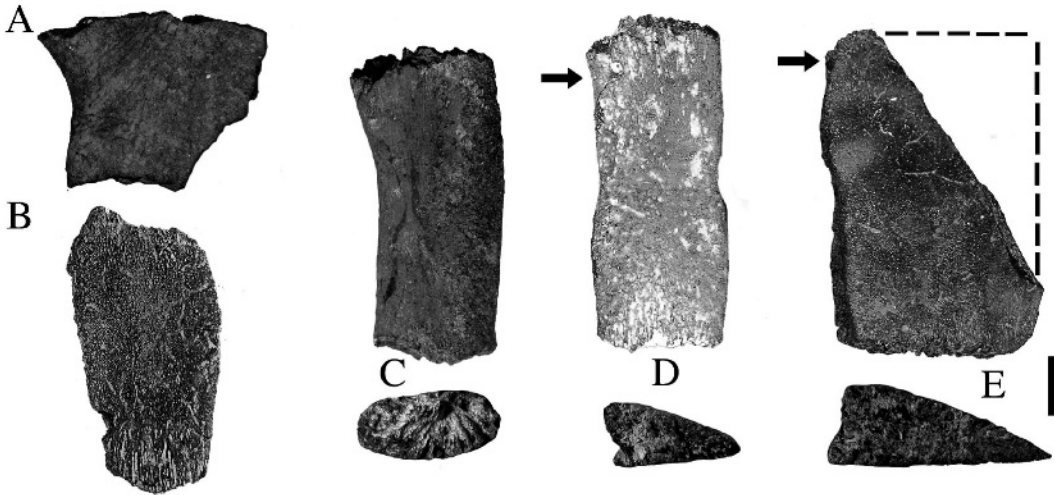
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FIG. 1.   Cheloniids s.l. (A) GCVP 7107, left prefrontal in ventral view, anterior edge is at the top. (B) GCVP 7108, neural, dorsal view. (C) GCVP 7109, right second peripheral, ventral and anterior sutural views. (D) GCVP 7110, narrow peripheral with rib pit (position indicated by arrow), dorsal and suture views. (E) GCVP 7111, wide peripheral with rib pit (position indicated by arrow), dorsal and suture views. Scale bar = 1 cm.

SYSTEMATIC PALEONTOLOGY

Testudines Batsch, 1788
Cryptodira Cope, 1868
Chelonioidea Baur, 1893
Cheloniidae Bonaparte, 1832 s.l.
Figure 1

Material.—GCVP 7107 (GCVP = Georgia College and State University Vertebrate Paleontology Collections), partial left prefrontal; GCVP 7108, neural; GCVP 7109, right second peripheral; GCVP 7110, peripheral with rib pit; GCVP 7111, peripheral with rib pit; GCVP 7112, fragmentary peripheral; GCVP 7113, additional shell fragments.

Description.—The only known skull element is a partial left prefrontal (GCVP 7107; Fig. 1A). Anteroposterior length (3.1 cm) and thickness (1.0 cm) of GCVP 7107 indicates that it belonged to a relatively large turtle (> 70 cm estimated shell length). The lateral side of the element retains the smooth orbital boundary, and its posterior and medial edges preserve the natural suture with the frontal. The prefrontal-frontal suture is not straight, corresponding to two facets of the anterior frontal that diverge from each other at oblique angles. The medial edge of the prefrontal has a partial suture indicating its contact with the right prefrontal. The anterior part of GCVP 7107 shows a fresh break and so the complete length of the prefrontal contact and the suture with the maxillae are lost.

The costal and peripheral fragments are not sculptured as in some Paleogene stem-cheloniids (e.g., *Argillochelys* Lydekker 1889a). A single weathered neural (GCVP 7108; Fig. 1B)

is subhexagonal and shows no indication of a keel. Four peripherals are known. GCVP 7109 (Fig. 1C) is a right second peripheral. It is cylindrical and lacks a rib pit, however, a shallow depression on the ventral side of its posterior end accommodates the first costal rib that inserted into the next peripheral. The other three peripherals (GCVP 7110–7112) are more wedge-shaped in cross-section and wider mediodistally than GCVP 7109. GCVP 7110 and GCVP 7111 (Fig. 1D,E) preserve rib pits and differ from each other in mediodistal width. GCVP 7110 is relatively narrower and more than twice as long anteroposteriorly than mediodistally. GCVP 7111 and the more fragmentary GCVP 7112 (not figured) are relatively wider mediodistally and are not more than twice as long anteroposteriorly.

Discussion.—The allocation of some of this material to the Cheloniidae s.l. is based on their large size, thickness, and phenetic resemblance to that of extant sea turtles (GCVP 7108 and most of the undescribed costal fragments). The referred specimens and cheloniids share thick and spongy (cancellous) bone. Furthermore, the anterior peripherals can be confidently assigned to Cheloniidae s.l. because they are diagnostically cylindrical (GCVP 7109, GCVP 7110). In contrast, the posterior peripherals are acutely triangular in cross section (GCVP 7111 [Fig. 1E], GCVP 7112). In this respect, the posterior peripherals of cheloniids s.l. are similar to those of ''macrobaenids'' (sensu Parham and Hutchison, 2003), an extinct grade of basal cryptodires. Macrobaenids persisted into the Paleo-
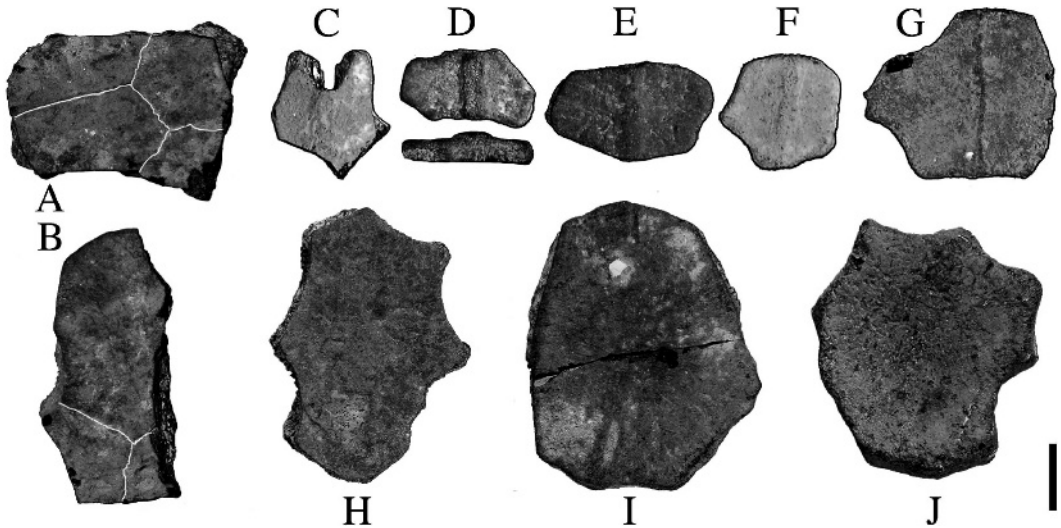
FIG. 2. Dermochelyidae. (A) GCVP 7114, juncture of four ossicles, dorsal view. (B) GCVP 7115, juncture of three ossicles, dorsal view. (C–G) GCVP 7116–7120, respectively, small, ridged ossicles, dorsal view (and suture view of GCVP 7117, [D]) (H–J) GCVP 7121–7123 respectively, large, unridged ossicles, dorsal view. Scale bar = 1 cm.

cene in Asia and North America and are reported from the Paleocene of the southeastern United States (Hutchison and Weems, 1998; Parham and Hutchison, 2003). We think an assignment to Cheloniidae s.l. is more likely than to the macrobaenidae because of the following circumstantial evidence: (1) the preponderance of sea turtle material at the site; (2) the lack of any other definitive macrobaenid material (although see comments in description of GCVP 7137 below); and (3) no Eocene macrobaenids are known (Parham and Hutchison, 2003).

The cheloniid s.l. material cannot be referred to a specific taxon. With the exception of GCVP 7109, it is not possible to tell the specific peripheral these specimens belong to. Given these uncertainties, we cannot determine whether there is more than one taxon represented.

Dermochelyidae Lydekker, 1889b
Figure 2

Material.—GCVP 7114, juncture of four ossicles; GCVP 7115, juncture of three ossicles; GCVP 7116–7123, isolated ossicles; GCVP 7124, additional isolated ossicles.

Description.—One or more species of leatherback sea turtles (Dermochelyidae) is represented by dozens of bony plates. Unlike other turtles, the shells of dermochelyids are comprised of hundreds of ossicles that interlock to form a bony mosaic or corselet. In two specimens, GCVP 7114 and 7115 (Fig. 2A,B), the junction of multiple ossicles is preserved. The rest of the present collection includes isolated ossicles that range in size from 2–6 cm at the widest point. The smaller ossicles are correspondingly thinner and some (Fig. 2C–G) have raised ridges on their dorsal surface but no corresponding ventral groove or angle. Many of the larger ossicles (Fig. 2H–J) have scalloped edges that interlocked with other ossicles.

Discussion.—Dermochelyid ossicles do not resemble shell elements of any other sea turtle. Wood et al. (1996) reviewed the morphological characters for Cenozoic leatherbacks, highlighting important shell characters for the diagnosis of clades. Many of these characters are based on the presence and/or morphology of ossicle ridges. The smaller ridged ossicles in our sample correspond to the morphology of *Egyptemys* Wood, Johnson-Gove, Gaffney, and Maley, 1996 by having a rounded ridge that is represented only on the dorsal surface. None of the larger ossicles have ridges, but we cannot be certain whether these are just interridge ossicles of a large *Egyptemys*-like turtle or from a nonridged species. Ridgeless dermochelyids are known from the Paleocene (*Arabemys* Tong, Buffetaut, Thomas, Roger, Halawani, Memesh, and Lebret, 1999), Eocene (*Natemys* Wood, Johnson-Gove, Gaffney, and Maley, 1996), and Miocene (*Psephophorus* Meyer, 1846). It is possible that the small ridged ossicles and large unridged ossicles are from the same species because carapacial ridges are more developed in juveniles than in adults in many turtle species. We conservatively refer both the smaller ridged and larger unridged ossicles to Dermochelyidae *incerta sedis*.
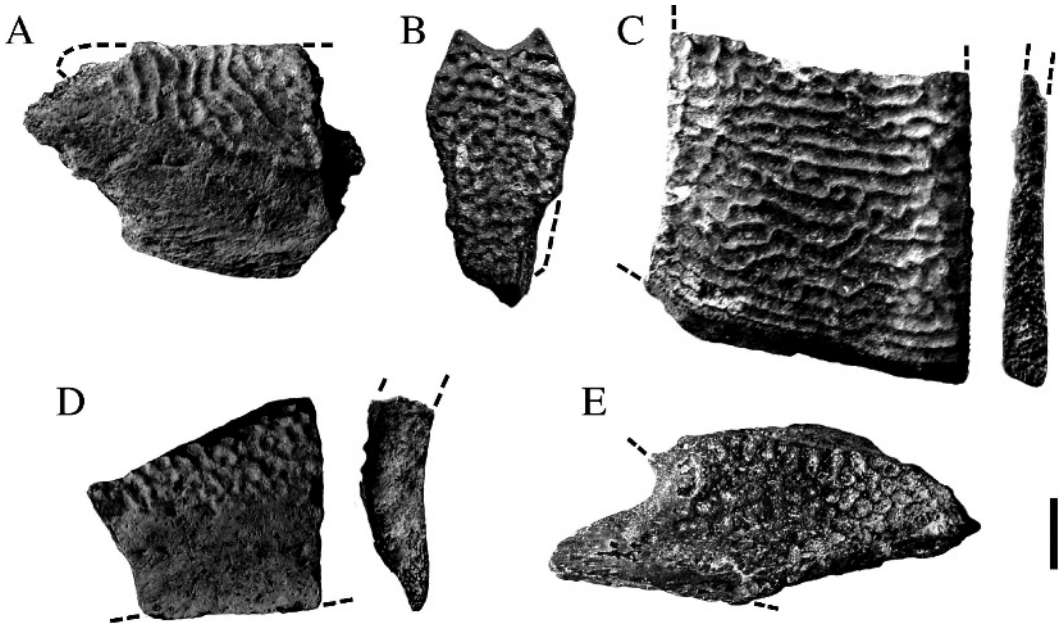
FIG. 3. Trionychinae. (A) GCVP 7125, nuchal, dorsal view. (B) GCVP 7126, neural, dorsal view. (C) GCVP 7127, distal costal fragment, dorsal and suture views. (D) GCVP 7128, xiphiplastron fragment, dorsal view. (E) GCVP 7129, hyo- or hypoplastron lateral fragment, ventral view. Scale bar = 1 cm.

Trionychidae Gray, 1825
Trionychinae Fitzinger, 1826
Figure 3

Material.—GCVP 7125, partial nuchal; GCVP 7126 neural; GCVP 7127, costal; GCVP 7131, costal; GCVP 7128, partial xiphiplastron; GCVP 7129, hyo- or hypoplastron; GCVP 7130, additional isolated fragments of the carapace and plastron.

Description.—Only one complete element is represented and multiple individuals are likely. A fragment of a nuchal (GCVP 7125; Fig. 3A) exhibits a broad unsculptured free margin. Of the two neurals, one is complete (GCVP 7126; Fig. 3B) and typical of a central neural of trionychines. Also typical of trionychines, the costals (e.g., GCVP 7127; Fig. 3C) and neurals exhibit a well-defined sculpture of pits and ridges that usually become organized into longitudinal ridges near the free margin of the shell. The costals thicken distinctly near the free margins and have unsculptured, steep to gently tapered margins. The first costal fragments exhibit well-defined suprascapular depressions. The plastral fragments (GCVP 7128, 7129; Fig. 3D, E) are robust and well sculptured. The buttress area of a hyo- or hypoplastron (GCVP 7129; Fig. 3E) shows two robust lateral spikes and a well-defined termination of the sculptured area.

Discussion.—Isolated trionychid material is relatively common in the Clinchfield sediments of the Hardie Mine, and it is the only turtle Westgate (2001) reported from the Hardie Mine local fauna. He assigned 17 shell fragments to *Trionyx* sp. indet. Based on Meylan's (1987) revision of the extant Trionychidae, fragmentary fossil trionychid material are better referred only to Trionychidae unless sufficient evidence shows otherwise. The large size of the Hardie Mine costals coupled with their open sculpture, and the unsculptured and tapered free margin of several of the elements exclude the Plastomeninae Hay, 1908 and agree with the Trionychinae. There appears to be no data to support more than one trionychid present in the Hardie Mine sample and all the fragments are referred to Trionychinae. Without a complete nuchal and a complete medial margin of the first costal or first neural, these fossils cannot be differentiated from the two common Eocene trionychines, *Apalone* Rafinesque, 1832 and ''*Aspideretes*'' (Hay, 1904), although no confirmed genera other than *Apalone* are known since the Bridgerian NALMA (Hutchison, 1992).

Testudinoidea Fitzinger, 1826
Figure 4

Material.—GCVP 7132, posterior part of left hyoplastron; GCVP 7133, posterior part of right hyoplastron; GCVP 7134, distal part of left xiphiplastron; GCVP 7135, distal part of right xiphiplastron; GCVP 7136, proximal part of a right costal.
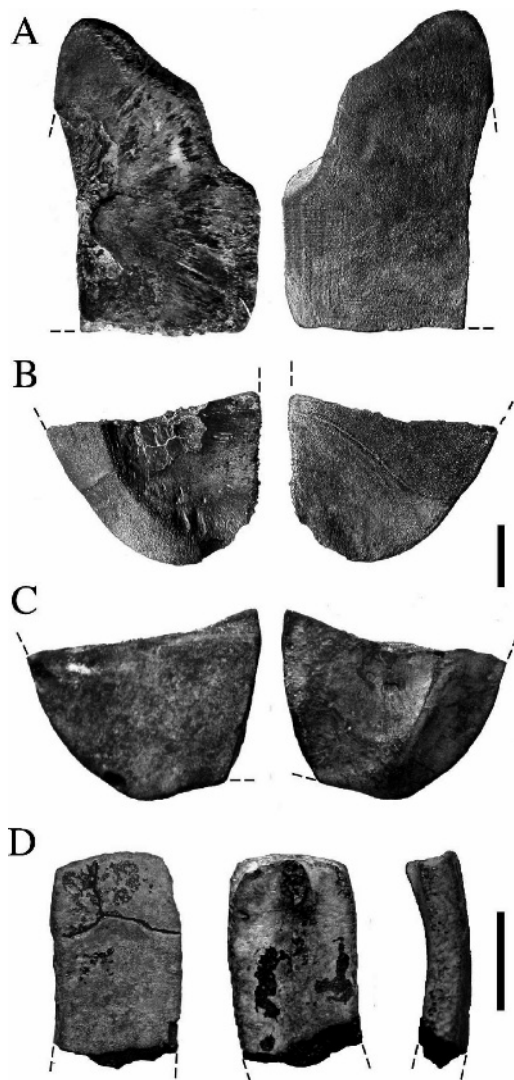
FIG. 4. Testudinoidea. (A) GCVP 7132, partial left hyoplastron, dorsal and ventral views. (B) GCVP 7134, left xiphiplastron fragment, dorsal and ventral views. (C) GCVP 7135, right xiphiplastron fragment, dorsal and ventral views. (D) GCVP 7136, proximal part of right costal 3 or 5, dorsal, visceral, and posterior sutural views. Scale bar = 1 cm.

Description.—The hyoplastron (GCVP 7132; Fig. 4A) lacks the bridge area, is water worn, and no sulci are evident. There may be an extremely faint indication of the humeral-pectoral sulcus crossing the anterior part of the element just posterior to the gular suture. Up to three faint growth lines are visible parallel to the medial and posterior sutures. These show no interruption for a humeral-pectoral sulcus further suggesting an anterior placement. The sutures are all dentate, but the dentations

exhibit a vertical orientation. There is no indication of a humeral-pectoral sulcus although the ventral edge of the lateral part of the preserved posterior suture is slightly rounded. If the sulcus has not been obliterated by abrasion, its apparent absence coupled with the sutural orientation may indicate a kinetic joint along the hyo-hypoplastron with a coincident pectoral abdominal sulcus. The embayment for the entoplastron indicates that the entoplastron was longer than broad. The humeral strongly overlaps the dorsal surface. Seven growth lines can be discerned. The maximum anteroposterior length is 51 mm.

The xiphiplastra (GCVP 7134, 7135; Figs. 4B–C) are well preserved but lack the anterior margins caused by breakage. The free margins are rounded and not notched at the anal-femoral sulcus. The medial margin is dentate and swollen dorsally in the anal scale region. The anal-femoral sulcus is finely incised, sinuous, and not reaching the hypoplastral suture. Faint growth lines on GCVP 7134 parallel the anal-femoral sulcus and dorsal margins of the scales. The ventral surface is flat except for the area bordering the anal notch where it is slightly down-turned. The anal and femoral scales overlap strongly onto the thickened dorsal surface but taper posteriorly and the anal terminates before reaching the midline. The size of the fragments is roughly comparable to that represented by the hyoplastron. The elements exhibit a fine silky texture with fine growth lines and probably indicate a single taxon.

The proximal part of a right costal (GCVP 7136; Fig. 4D) is small and stout. An intervertebral sulcus extends dorsally indicating a costal 3 or 5. There is no indication of a costal carina, surface sculpture, or distinct dorsal thickening. The broken base of the rib head is ovoid and anteriorly-posteriorly compressed. The body of the costal thickens slightly distally suggesting that it may be a costal 5. Although there is no direct indication of a buttress scar, the distal thickening is centrally located suggesting that a buttress may have articulated centrally as in emydids. If so, there is no comparable costal lengthening toward the distal end.

Discussion.—The shape of the elements and fine texture are consistent with testudinoid turtles (Testudinidae Gray, 1825; Bataguridae Gray, 1870; Emydidae Bell, 1825). The weak anal notch, dorsal narrowing of the anal scale posteriorly, and fine texture differs from testudinids. The batagurids (especially *Echmatemys* Hay, 1906) are the most common turtles in the Eocene of North America. The Georgia specimen differs from *Echmatemys* in the weaker expression of the anal-femoral and caudal notches, rounded rather than pointed xiphiplas-
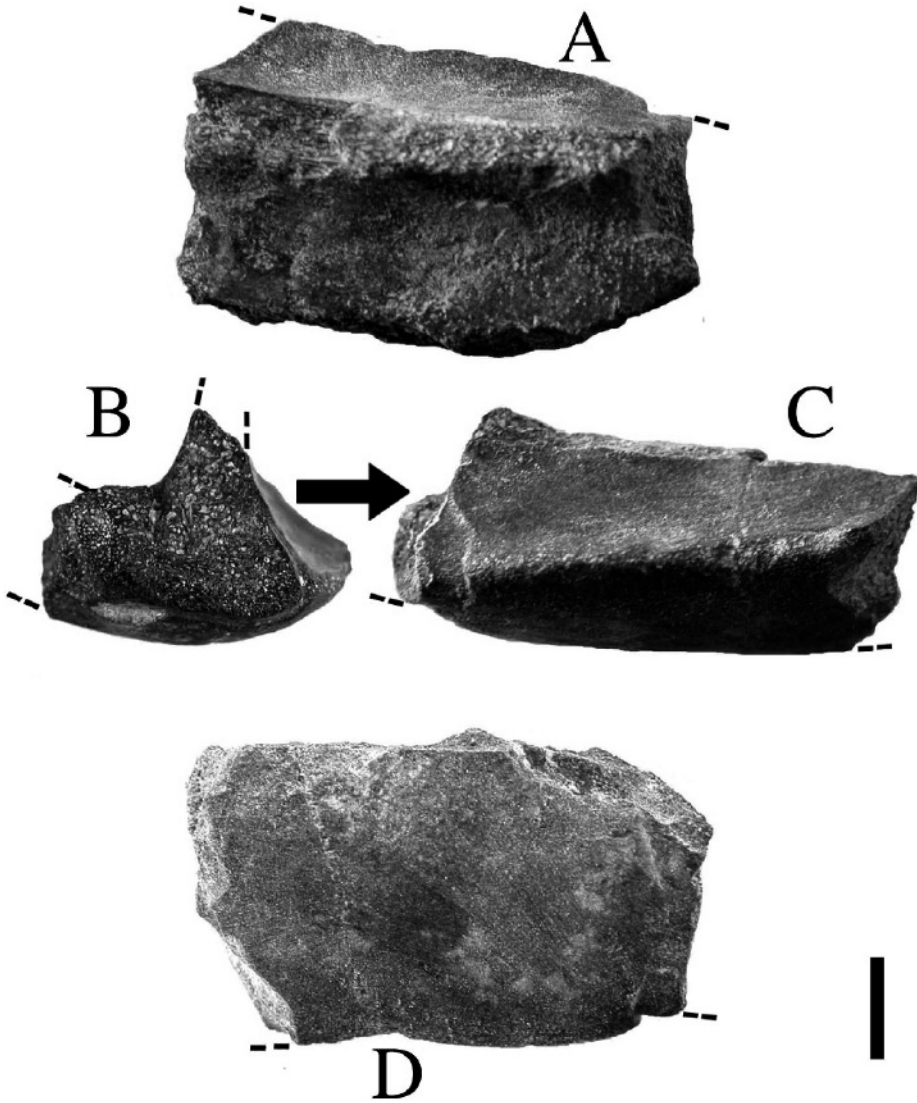
FIG. 5. Cryptodira indet. GCVP 7137, partial peripherals. (A) Dorsal view. (B) Cross-section view of posterior end. (C) Lateral (reversed) view. (D) Ventral view. Scale bar = 1 cm.

tral ends, the anal scale narrowing posteriorly on the dorsal surface rather than expanding, and a narrow rather than broad notch for the entoplastron. The only two emydids presently described from the latest Eocene are *Pseudographtemys inornata* (Loomis, 1904) and *Chrysemys antiqua* (Clark, 1937) from the Chadronian NALMA of South Dakota (Hutchison, 1996). The Hardie Mine xiphiplastra differ from *P. inornata* and resemble *Chrysemys* in having rounded posterior ends, shallower xiphiplastral notches, weaker anal-femoral notches, and sinusoidal anal femoral sulci. The hyoplastron, however, differs from both in the longer and narrower entoplastral embayment and steep

slope of the epi-hyoplastral suture. If the faint suggestion of a sulcus that crosses the entoplastron is real, the relationships may lie near the *Emys* Duméril, 1806 group or batagurids of the *Rhinoclemmys* Fitzinger, 1835 group. The Hardie Mine turtles cannot be assigned confidently to the emydid or batagurid lineages.

Testudines Bastch, 1788
Cryptodira indet.
Figure 5

Material.—GCVP 7137, articulated portions of two left peripherals.

Description.—The specimen (Fig. 5) consists of about one-third of one and one-half of another

bridge peripheral, both of which lack the plastral and costal sutures. The remaining parts are stoutly constructed and finely cancellous. The bases of the costal and plastral arms form a slightly greater than normal angle suggesting a low domed shell. The body of the peripheral tapers laterally into a strong, progressively upturned, and moderately acute lateral carina that forms a dorsal gutter. The posterior peripheral preserves part of a well-defined intermarginal sulcus that steps-down posteriorly at the sulcus. The ventral surface is broadly convex. The unabraded outer surface is dense and not porous without any distinctive sculpture.

Discussion.—The dense surface bone, finely cancellous construction, distinct scale margins, and overall shape of the fossil does not resemble cheloniids s.l. (see above) and probably represents a brackish or freshwater turtle. We found no close match with any of the turtles with which we are familiar, but the Chelydridae Swainson, 1839 came closest. The specimen resembles primitive chelydrids in the step between the marginals at the sulcus, and thickened and upturned lateral carina. Chelydrids have a wide distribution in the Paleogene (Erickson, 1973; Hutchison, 1982; Hutchison and Pasch, 2004) but have not been reported from the Paleogene of the southeast.

DISCUSSION

Latest Eocene turtle faunas in North America are rare and were best known only from the west. The Hardie Mine local fauna is the most diverse Late Eocene turtle fauna yet discovered in southeastern North America. The fauna includes at least five taxa that are about equally divided between marine and primarily freshwater turtles. Of the marine turtles, both extant families Dermochelyidae and Cheloniidae are represented and common. The Trionychidae are one of the most common nonmarine turtles but they also venture into near-shore brackish and marine environments and generally are the most common ''freshwater'' turtles found in near-shore marine environments in the Paleogene. The testudinoids are poorly represented but compare well with the Emydidae. The presence of another unidentified but probably nonmarine turtle is represented by a single specimen. The extant turtle fauna of the southeast is the most diverse in North America (Kiester, 1971; Hutchison and Archibald, 1986), but in the Eocene the most diverse faunas are found west of the Mississippi (Hay, 1908; Hutchison, 1982). Freshwater turtle faunas from the southeast are rare because of the extensive marine transgressions during the Eocene, extensive extant vegetation covering sediments,

thinness of the geological units, and probably unfavorable diagenetic and taphonomic environments. Despite these obstacles, the Hardie fauna is the most diverse turtle fauna yet known from this region and hints at a greater diversity of latest Eocene turtles than previously known from the southeastern North America region.

The most significant specimens from the Hardie Mine site are the aquatic testudinoids. Holman and Case (1988) and Holman (2000) have identified other specimens from the Eocene of Alabama and Florida as aquatic testudinoids, but reexamination of these specimens found these identifications to be in error (Holroyd et al., 2005). Therefore, the Hardie Mine specimens represent the earliest aquatic testudinoids in southeastern North America, an area that boasts a highly diverse assemblage of extant forms.

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