

SYNONYMY OF THE PYCNODONT *PHACODUS PUNCTATUS* DIXON, 1850, AND ITS OCCURRENCE IN THE LATE CRETACEOUS OF THE SOUTHEASTERN UNITED STATES

G. E. HOOKS, III¹, DAVID R. SCHWIMMER², and G. DENT WILLIAMS², ¹Alabama Museum of Natural History, The University of Alabama, Box 870340, Tuscaloosa, Alabama 35487-0340; ²Department of Chemistry and Geology, Columbus State University, Columbus, Georgia 31907-5645

Materials assignable to the pycnodont fish *Phacodus punctatus* Dixon, 1850, have been collected in the Late Cretaceous deposits of the southeastern United States. Previously reported from the Chalk (Cenomanian–Campanian) of England (Woodward, 1902–1912), the Ouled Abdoun (Maastrichtian) of Morocco (Arambourg, 1952), and the Continguiaba Formation (Turonian) of Brazil (Santos and Figueiredo, 1988), this is the first North American record of this taxon. Thus far, specimens have been collected from Mississippi, Alabama, and Georgia, in strata ranging from the Santonian to early Campanian.

Institutional Abbreviations—ALAM, Alabama Museum of Natural History, The University of Alabama; BMNA British Museum (Natural History); CSUK, Columbus State University Cretaceous Collections; LSUMNS, Louisiana State University Museum of Natural Science.

SYSTEMATIC PALEONTOLOGY
Order PYCNODONTIFORMES Berg, 1940
Family *incertae sedis*
PHACODUS Dixon, 1850

Type Species—*Phacodus punctatus* Dixon, 1850.

Revised Diagnosis—Teeth subcircular to oval, covered with numerous, fine pits. Vomer with three or five rows of teeth. Prearticular with

three rows of teeth, teeth in lateral rows nearly as long as wide. In the prearticular and vomer, teeth in rows between the medial and lateral rows smaller than lateral teeth. (Modified from Arambourg, 1952.)

PHACODUS PUNCTATUS Dixon, 1850
(Fig. 1)

Phacodus punctatus var. *africanus* Arambourg, 1952:227–228, pl. XXXVII, figs. 27, 28.

Phacodus sergipensis Santos and Figueiredo, 1988:447–451, fig. 1.

Holotype—BMNH 25829, from the Chalk (Turonian), Lewes, England.

Referred Material—Tombigbee Sand Member of the Eutaw Formation (Santonian): ALAM 988.2.458, fragment of vomer, Dallas Co., Alabama (Fig. 1D); LSUMNS V-6665, three fragmentary prearticulars, Clay Co., Mississippi. Eutaw Formation (Santonian): CSUK-96-2-1, vomer, Chattahoochee Co., Georgia (Fig. 1A). Blufftown Formation (lower Campanian): CSUK-97-2-9, fragment of left prearticular, Barbour Co., Alabama (Fig. 1B); CSUK-97-2-10, right prearticular, Russell Co., Alabama (Fig. 1C).

Distribution—England, Morocco, Brazil, and southeastern United States.

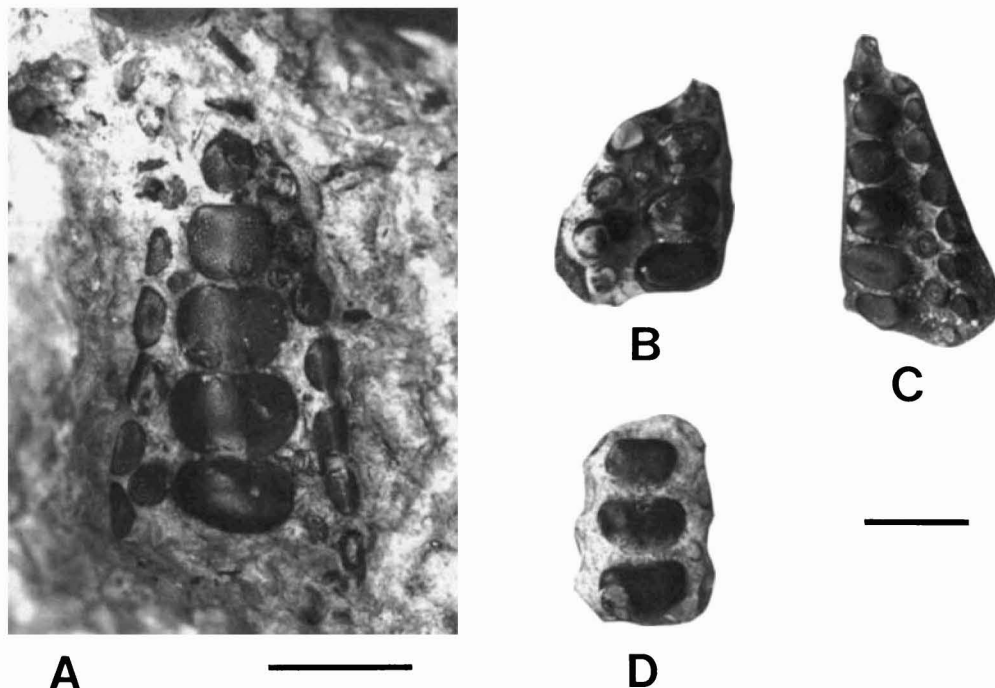


FIGURE 1. *Phacodus punctatus*. A, CSUK-96-2-1, vomer; B, CSUK-97-2-9, fragment of left prearticular; C, CSUK-97-2-10, right prearticular; D, ALAM 988.2.458, fragment of vomer. Scale bars equal 1 cm.

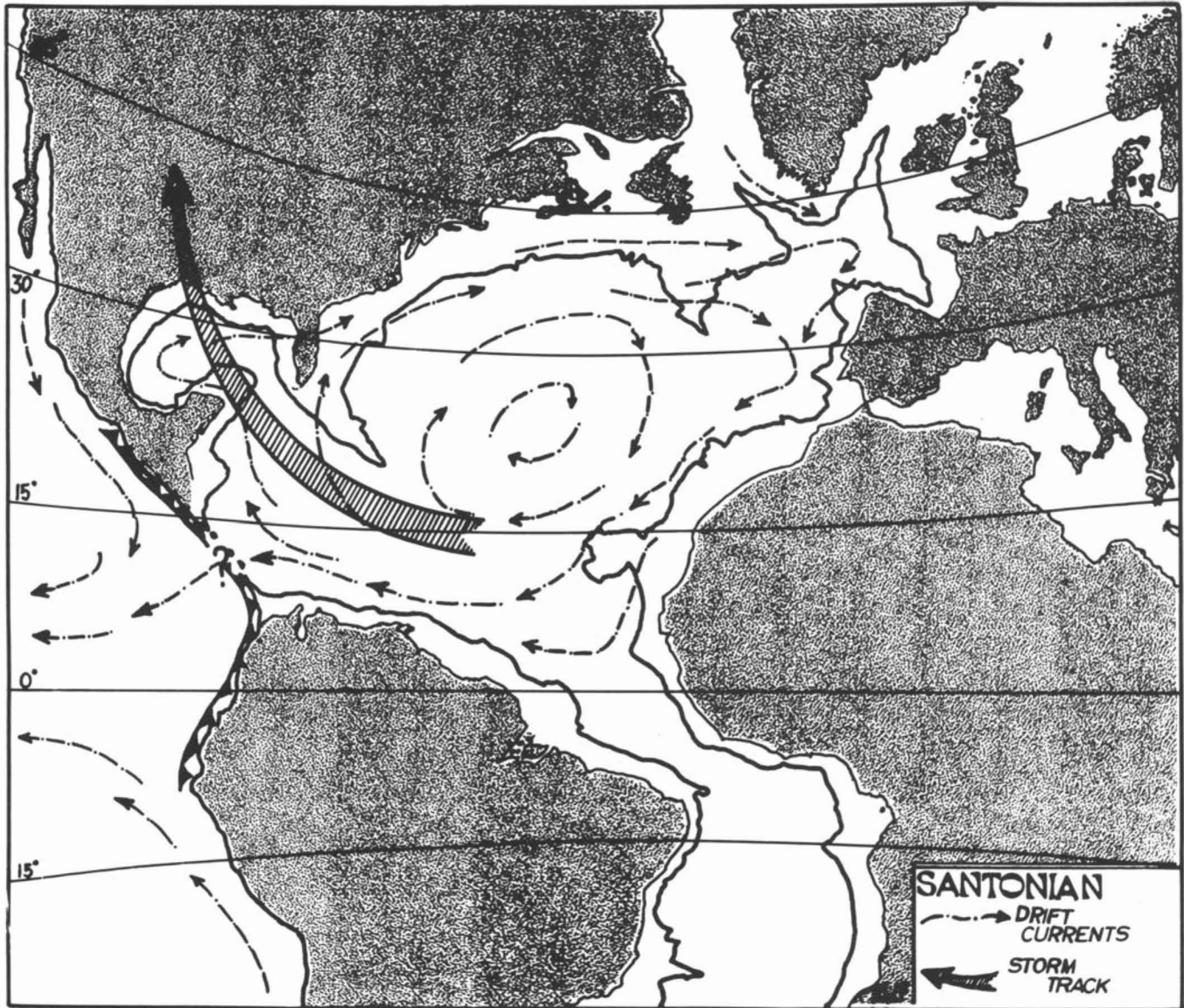


FIGURE 2. Reconstruction of Late Cretaceous (Santonian) circum-Atlantic continental configuration and drift currents. Reconstruction by William J. Frazier, Columbus State University, based largely on Scotese et al., 1988.

Stratigraphic Range—Turonian–Maastrichtian.

Diagnosis—As for genus.

Discussion—The original description of *Phacodus punctatus* (Dixon, 1850) was based on a fragment of the lower jaw containing six worn teeth. This specimen was later figured by Woodward (1902–1912) with another specimen, a vomer. Woodward's figures provided the comparative information used by Arambourg (1952) in describing *Phacodus punctatus* var. *africanus*, from the Maastrichtian of Morocco. Arambourg's description was based on a well preserved vomer and two lower jaw fragments which, he noted, differed slightly from the English specimens in size and shape of the teeth. Differences in tooth shape were also used by Santos and Figueiredo (1988) to characterize a new species, *Phacodus sergipensis*. This taxon was based on a single vomer from the Turonian of Brazil. Comparison of described materials of *Phacodus* indicates variation in tooth shape among specimens and among teeth in the same specimen (Fig. 1; Woodward, 1902–1912: pl. XXXIV, figs. 7,8; Arambourg, 1952:pl. XXXVII, figs. 27,28; Santos and Figueiredo, 1988:fig. 1). Such variation has been observed in the pycnodont genus *Anomoedus* by one of the present authors (GEH) and in pycnodonts in general by Nursal (1996). Unfortunately, the small number of known specimens of *Phacodus* prohibits reliable statistical anal-

ysis to determine the significance of these variations, therefore, the taxonomic validity of these characters is questionable. Santos and Figueiredo also noted the presence of five rows of teeth in the vomer of *Phacodus sergipensis*, compared to three rows in *Phacodus punctatus*. The two extra rows of teeth were between the medial and lateral rows, and extended only along the posterior half of the vomer. These two extra rows of teeth are present in a North American specimen of *Phacodus*, CSUK-96-2-1 (Fig. 1A), and extend along the entire length of the vomer. The extreme variation in these extra rows of teeth, from complete absence to presence along the entire vomer, among the small number (four) of specimens of *Phacodus*, makes this character suspect. Taking into account the questionable nature of the aforementioned characters used to distinguish between the various *Phacodus* materials from England, Morocco, and Brazil, we consider *Phacodus punctatus* var. *africanus*, and *Phacodus sergipensis* to be junior synonyms of *Phacodus punctatus* to which we have assigned the North American materials.

For most of the past two centuries pycnodont systematics has, at best, been problematic. This is largely due to the fact that most pycnodont taxonomy is based entirely on tooth characteristics of the prearticular and vomer, the most robust pycnodont bones and the most likely to be preserved. The difficult task of finding taxonomically useful characters

on only two bones is further complicated by the large amount of variation that these bones exhibit, as mentioned above. Nursal (1996) published a badly-needed revision of pycnodonts which was not limited to jaw characteristics. Unfortunately, the only materials thus far recovered for *Phacodus* are portions of the prearticular and vomer. This makes it impossible to assign *Phacodus* to any category below the level of order. It seems unlikely that any further systematic resolution of *Phacodus* will be forthcoming until more complete materials of this genus are found.

DISCUSSION

The newly-described and referred specimens extend the geographic range of *Phacodus punctatus* to include southeastern North America, along with North Africa, Brazil, and England. Given that pycnodonts were slow-moving, non-pelagic creatures, this distribution implies dispersal along contiguous continental shelves with limited open-sea crossings. A similar geographic distribution may be observed among the Late Cretaceous coelacanth fishes of the *Macropoma-Macropomoides-Megalocoelacanthus* clade (Schwimmer, et al., 1994), which are also principally distributed in North Africa, western Europe, and many sites in southeastern North America. These fishes too appear to be shelf-based species.

Wide Atlantic oceanic distribution of non-pelagic fishes may reflect the relatively short distances then prevailing between the landmasses, compared with the modern world after nearly 100 million years of additional seafloor spreading. Typical Late Cretaceous paleogeographic reconstructions (e.g. Scotese, et al, 1988) show nearly continuous continental shelves between northeastern North America, western Europe, North Africa, and eastern South America. Ocean drift currents affected by Coriolis force would have clockwise gyres (Fig. 2) in the Atlantic Ocean of the Late Cretaceous, enhancing the spread of taxa from the European, western African or eastern South American shelves to the Gulf of Mexico, in this configuration. The only open-ocean crossings that were necessary to distribute *Phacodus punctatus* as delineated here are the hops from Africa to Brazil and from Brazil to the Southeastern USA Coastal Plain. These would have involved deep-water traverses of less than 1,000 km, precisely in the direction of prevailing surface currents.

Striking comparison in geographic distribution may be made between these fishes and the common, endemic North American species *Xiph-*

hactinus audax. This large, streamlined, presumably fast-swimming, Late Cretaceous teleost apparently crossed the Interior and Gulf seas during much of the mid-Late Cretaceous. *Xiphactinus audax* was built along the lines of many larger modern pelagic fishes such as the Scombridae (tuna and mackerel), yet it was apparently restricted to the one continent. Its geographic range overlapped with *Phacodus punctatus* in the Gulf Coastal Plain (Schwimmer et al., 1997), yet did not achieve trans-Atlantic distribution. Reasons for the selectivity of paleogeographic distribution among Late Cretaceous marine fish guilds remains an important avenue of future research.

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