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# *XIPHACTINUS VETUS* AND THE DISTRIBUTION OF *XIPHACTINUS* SPECIES IN THE EASTERN UNITED STATES

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The ichthyodectid genus *Xiphactinus* includes the largest teleost fish known in North American Late Cretaceous strata. The single species currently recognized in North America (Bardack, 1965) is *Xiphactinus audax,* which has been reported to range geographically from Saskatchewan to west Texas within the Late Cretaceous interior seaway, and from north-central Texas to New Jersey on the Gulf and Atlantic Coastal Plains. The stratigraphic range of *X. audax,* as the species is presently construed, is Cenomanian to lower Maastrichtian (Russell, 1988, 1993).

Many natural history museums display specimens or casts of complete individuals of *Xiphactinus audax,* including several noteworthy large (over 4.0 m) specimens with a well-preserved *Gillicus arcuatus* or other fish in the gut area (Figure 1). Most museum display specimens of *X. audax* come from the Niobrara Chalk Formation in western Kansas, where this species is common and often well preserved.

Joseph Leidy and Edward D. Cope independently described the taxon as *Xiphactinus audax* Leidy 1870 and *Portheus molossus* Cope, 1871. Although Cope's type specimen was a finely preserved individual, whereas Leidy's type was an isolated pectoral fin spine, the rules of priority (Ride, et al. 1985) require that the widely-known name *Portheus molossus* be suppressed as a junior synonym. In their early descriptions of *Xiphactinus* and *Portheus,* Leidy and Cope followed prevailing practice and recognized numerous species, all of which, at least for North America, were subsequently subsumed into the single species *X. audax* by Bardack (1965), which was the last substantive taxonomic analysis of the genus.

The type description of *Xiphactinus audax* by Leidy (and that of *Portheus molossus* by Cope), and most subsequent studies of *X. audax,* were based on specimens from the upper Coniacian to lower Campanian Smoky Hill Member of the Niobrara Chalk. Well-preserved *Xiphactinus audax* specimens, although incomplete, are also found in the Coniacian Ector Member of the Austin Chalk in north-central Texas. Younger fossils of *Xiphactinus* in Western Interior deposits include common, but usually poorly preserved, incomplete skeletons from the lower Pierre Shale, including the lower Campanian Sharon Springs Member in Kansas, Nebraska, South Dakota and Wyoming (Russell, 1988), and the lower Campanian Pembina Member in Manitoba (Bardack, 1968; Nicholls and Russell, 1990).

*Xiphactinus* is also widely reported from the Gulf and Atlantic Coastal Plains, either as *Xiphactinus* sp. or *X. audax.* Reported occurrences include the upper Campanian Demopolis Formation in northeastern Mississippi (Manning and Dockery, 1992), the middle Campanian Blufftown Formation in western Georgia (Case and Schwimmer, 1988), the upper Campanian Black Creek Formation in North Carolina (Robb, 1989), and the upper Campanian Marshalltown Formation and the lower Maastrictian Mount Laurel and Navesink formations in New Jersey (Gallagher, et al., 1986, Gallagher, 1993) and Delaware (Lauginiger, 1986). Most of these remains are isolated teeth and vertebrae, although rare jaw fragments are known (Fig. 2D, U). Attribution of these eastern Coastal Plain fossils to *Xiphactinus audax* is generally based on the presence of large, relatively slender, hollow-based teeth, with thin, smooth, glossy enamel (see Fig. 2F–Z). Such teeth come presumably from the premaxilla, anterior maxilla or anterior dentary. Also found associated in the same strata are proportionately large, teleostean vertebral centra (Fig. 3G–L). These centra have paired dorsal and (in some) ventral depressions for neural and hemal arches, which are not fused to the centra, and two additional pairs of dorso-lateral and lateral depressions. This morphology, again, is typical of *Xiphactinus audax* and other Ichthyodectidae (Patterson and Rosen, 1977).

## A SECOND NORTH AMERICAN SPECIES OF *XIPHACTINUS*

We have determined that two, clearly differentiable forms of large ichthyodectid teeth and vertebrae are present in the eastern Coastal Plain Upper Cretaceous outcrop. Both tooth types (Fig. 2) include large individuals (crowns measured to 6.5 cm length and extrapolated to 8.0 cm from broken specimens) with glassy, smooth enamel surfaces. One tooth form (Fig 2D, E) is characteristic of *Xiphactinus audax* (Fig. 2A–C) in being nearly straight, with a round to oval cross section and anterior and posterior borders without carinae. Deposits including this tooth form also contain axially round ichthyodectid vertebrae (Fig. 3C–F), which are indistinguishable from typical *X. audax* (Fig. 3A, B). These *X. audax* morphologies have been observed in the lower Mooreville Formation in western Alabama (Applegate, 1970), the Tombigbee Member of the Eutaw Formation in eastern Mississippi and central Alabama (Fig. 3F), and in the lower Blufftown Formation in eastern Alabama (Fig. 3C–E). These stratigraphic occurrences range from the middle Santonian to the lowermost Campanian stage (chronologically up through Nannofossil Zone 19 of Sissingh, 1977).

The second large ichthyodectid attributed here to *Xiphactinus* has enlarged teeth that are moderately compressed laterally, slightly recurved (presumably posteriorly and medially), with an anterior or antero-lingual carina. Many teeth also have a second, posterior, carina. Some specimens have their external surfaces configured into full-length facetts (e.g., Fig. 2F–I, Q, R), whereas others are smooth on lingual and labial surfaces (e.g. Fig. 2M–P, S, T). Six large ichthyodectiform vertebrae have been found at one locality in western Georgia, in association with more than twenty-five teeth of this second *Xiphactinus* morphology (Fig. 3G–L). These vertebrae are oval, rather than round, in axial profile, and two (presumably posterior) vertebrae have a flat or slightly concave ventral surface (e.g. Fig. 3G–J). All vertebrae in this assemblage are markedly lower dorso-ventrally than are vertebrae of *Xiphactinus audax* (compare Fig. 3K with Fig. 3B). This second ichthyodectid tooth and vertebral morphology appears in middle Campanian to lower Maastrichtian deposits in the eastern Gulf of Mexico and Atlantic Coastal Plains (as listed below under Systematics). Most significantly, all occurrences of the faceted, carinate large teeth and the single known site with flattened and oval ichthyodectid vertebrae are in strata younger than all occurrences of typical *Xiphactinus audax.* This is true for both the Western Interior and the eastern Coastal Plains: *X. audax* in its entire geographic range occurs in the Turonian through lower Campanian, whereas the ichthyodectid with carinate tooth morphology first occurs in the middle Campanian.

We believe the younger taxon, thus far known only in the eastern United States and only from isolated teeth, vertebrae, and a single jaw fragment, is a separate species properly named *Xiphactinus* (*Polygonodon*) *vetus* (Leidy, 1856). Leidy's generic name *Polygonodon* preceded *Xiphactinus* and, therefore, by general taxonomic protocol all *Xiphactinus* species should be replaced into *Polygonodon.* However, since *Xiphactinus* is in very common use and since Leidy considered *Polygonodon* to be a reptile genus, we believe that Articles 23(b) and 79 (the "fifty-year rule") of the International Code of Zoological Nomenclature (Ride, et al., 1985) justify retention of *Xiphactinus* and suppression of the generic name *Polygonodon.* A ruling on this matter will be requested from the I.C.Z.N., and the systematics below assume that permission is granted to suppress *Polygonodon* in favor of *Xiphactinus.*

**Institutional abbreviations: AMNH**, American Museum of Natural History, New York City, New York; **ANSP**, Academy of Natural Sci-

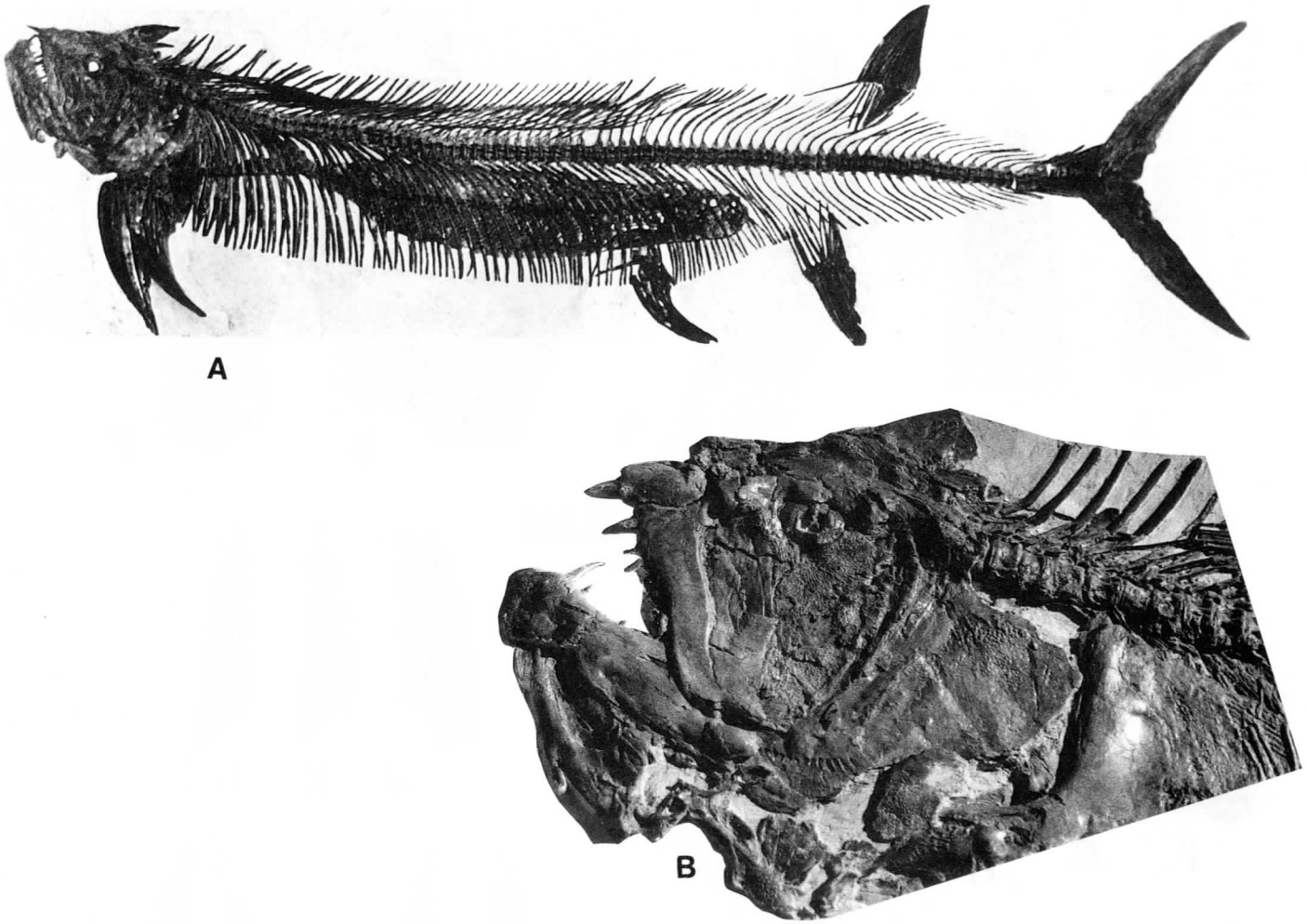



FIGURE 1. (**A**, **B**) *Xiphactinus audax,* representative specimens from the Smoky Hill Chalk, Niobrara Fm., Kansas; **A**, large (4.0 m) complete individual with a *Gillicus arcuatus* inside gut area, photograph courtesy of Sternberg Museum of Natural History. **B**, head of large individual, showing the positions of hypertrophied dentary and maxillary/premaxillary teeth, photograph courtesy of Elizabeth L. Nicholls.

ences, Philadelphia, Pennsylvania; **CSUK**, Columbus State University, Cretaceous Research Collections, Columbus, Georgia; **CVNHM**, Chattahoochee Valley Natural History Museum, Seale, Alabama; **LACM,** Los Angeles County Museum of Natural History, Los Angeles, California; **NJSM**, New Jersey State Museum, Trenton, New Jersey; **USNM**, United States National Museum of Natural History, Washington, D.C.

## SYSTEMATIC PALEONTOLOGY

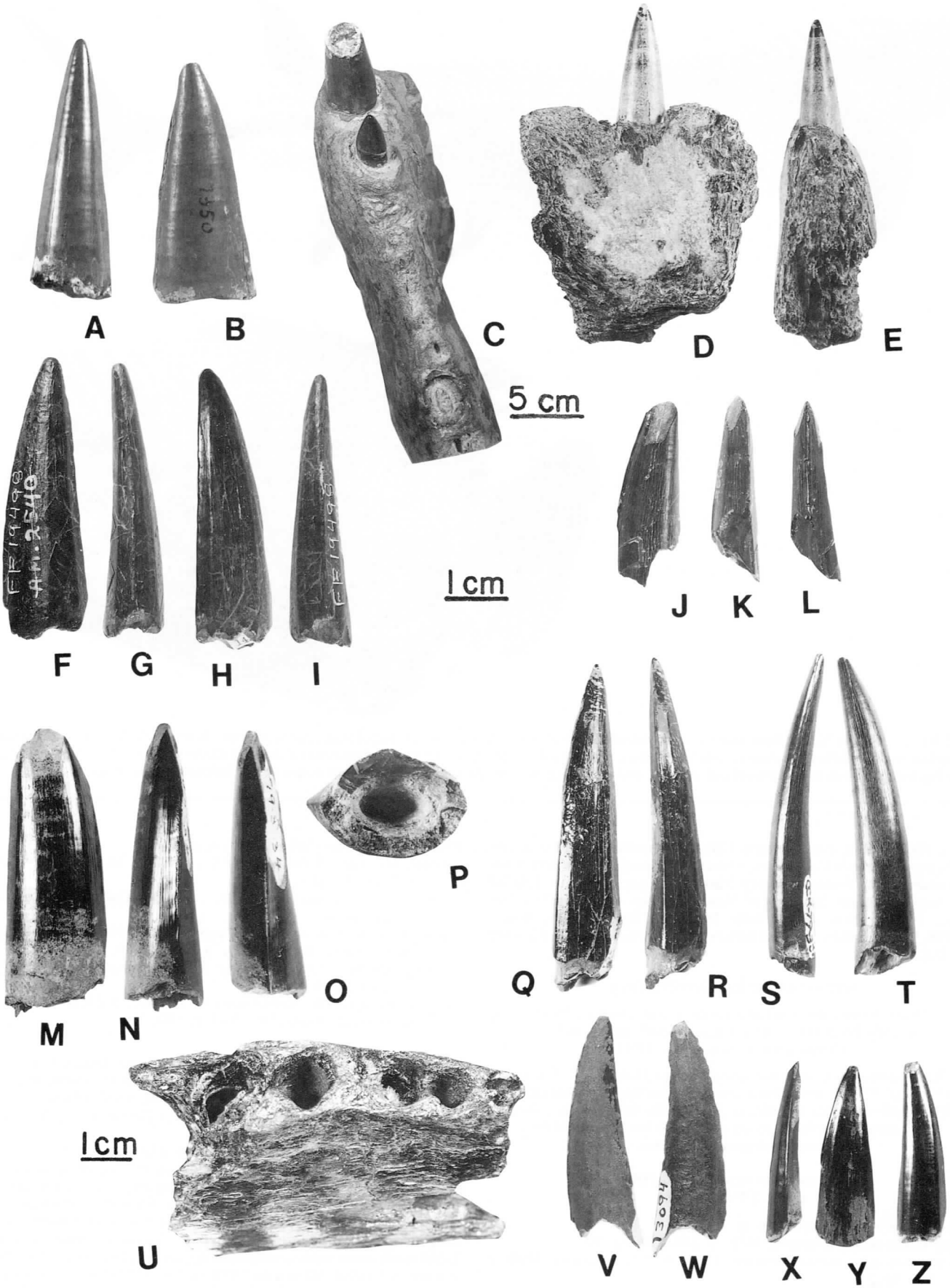
Order ICHTHYODECTIFORMES Bardack and Sprinkle, 1969
Family ICHTHYODECTIDAE Patterson and Rosen, 1977
Genus XIPHACTINUS Leidy, 1870

**Type species**—*Xiphactinus audax* Leidy, 1870, p. 12. Bardack (1965, p. 37–38) presented a complete synonymy to that date.
**Diagnosis**—Bardack's (1965, p. 37) generic diagnosis is followed here except as modified to accommodate tooth and vertebral morpohologies of *X. vetus.*

*XIPHACTINUS VETUS* Leidy, 1856
(Figs. 2 F–Y, 3 G–L)

*Polygonodon vetus* Leidy, 1856, p. 221.
*Polygonodon rectus* Emmons, 1858, p. 218–219, fig. 37.
*Mossasaurus* (sic) *rectus* Emmons, 1858, p. 218; Emmons, 1860, p. 208, fig. 3.
*Polygonodon vetus*: Leidy, 1864, p. 76, fig. 34, pl. 9, figs. 12, 13.
*Portheus angulatus* Cope, 1872, p. 337–338; Kerr, 1875, p. 32.
*Polygonodon rectus*: Miller, 1967, p. 229.
*Xiphactinus audax*: Schwimmer, 1981, p. 84, pl. 10, fig. 7; Schwimmer, 1986, p. 115, pl.1, figs. H, I.
*Xiphactinus* sp.: Lauginiger, 1986, p. 55–56; Gallagher, et al., 1986 (partim), p. 31.
*Xiphactinus* sp. cf. *X. audax*: Gallagher, et al., 1986 (partim), p. 25.
*Xiphactinus audax*: Robb, 1989, p. 77, 82–83, fig. 20; Case and Schwimmer, 1988, p. 300, fig. 6.29; Manning and Dockery, 1992, p. 12–13, fig. 5.
*Xiphactinus angulatus*: Schwimmer et. al, 1992, p. 51A.
*Xiphactinus audax*: Gallagher, 1993, p. 100, 111.

**Material**—Thirty-five teeth, six vertebrae, one dentary fragment.
**Hypodigm**—Holotype: a single tooth, AMNH FF 19498. Paratypes: *Polygonodon rectus* Emmons, 1858, two teeth, ANSP 15330 and 15324, and USNM 7447 (cast of ANSP 15330); *Portheus angulatus* Cope, 1872, a single tooth, AMNH 2863.
**Diagnosis**—A species of *Xiphactinus* which differs from the only other known species by the following characters: hypertrophied anterior teeth elongate, slender, slightly curved lingually and posteriorly, with faint to strongly developed carina present along the full length of the anterior border. A second carina is often present on the posterior border. External enamel may form full-length vertical facets around perimeter. Basal tooth cross section elliptical, appearing polygonal when enamel surface is faceted. Maximum tooth crown length known (incomplete) 6.5 cm, estimated to reach 8.0 cm; maximum cross-sectional basal dimension 1.6 cm. Smaller, presumably posterior dentary and maxillary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teeth generally like anterior teeth, usually bicarinate, strongly compressed, slightly curved, lengths typically ranging from 1.5 to 3.0 cm.

Vertebral centra oval to D-shaped in axial profile, hemal and neural processes unknown. Ventral surface of centrum convex in anterior vertebrae, grading to flat, ventral surfaces in posterior abdominals, and further grading to a narrow concave central area between deep ventral pits in caudal vertebrae.

**Occurrence and age**—Mississippi: Demopolis Formation (upper Campanian), Frankstown, Prentiss County (Manning and Dockery, 1992); Alabama: Blufftown Formation (middle Campanian), South Fork Cowikee Creek, Barbour County; Georgia: Blufftown Formation (middle Campanian), Hannahatchee Creek, Stewart County (Case and Schwimmer, 1988); North Carolina: Black River Formation (Upper Campanian), Cape Fear River, Duplin County [type locality of *Portheus angulatus,* Cope, 1872 and *Polygonodon rectus* Leidy] (Emmons, 1858; Leidy, 1856; Cope, 1872; Miller, 1967); and Phoebus Landing, Bladen County (Robb, 1989); Delaware: Marshalltown? Formation (upper Campanian), Chesapeake & Delaware Canal, (Lauginiger, 1984); New Jersey: "Green-sand" (Navesink or Hornerstown formations, upper Campanian and lower Maastrichtian), Bladen, Monmouth County [type locality of *Polygonodon vetus*] (Leidy, 1856); Marshalltown Formation (upper Campanian), Ellisdale, Monmouth County; Marshalltown or Navesink formations (upper Campanian to lower Maastrichtian), Big Brook, Freehold, Monmouth County; (Gallagher et al., 1986; Lauginiger, 1986; Gallagher, 1993).

**Discussion**—*Xiphactinus vetus* is known to date from teeth, vertebrae, and a jaw fragment. The peripheral faceting present to various degrees on many teeth of this species (e.g. Fig. 2F–I, Q, R) presents a nearly polygonal cross-section, which led to both Joseph Leidy's generic name "*Polygonodon,*" and E. D. Cope's specific in "*Portheus angulatus.*" The relationship between the faceted tooth morphology and the smooth carinate tooth morphology is unclear, but they do co-occur. It is plausible that one morphology represents the characteristically enlarged premaxillary fangs of *Xiphactinus* (see Fig. 1) and the other morphology represents large dentary teeth. The contention that these *X. vetus* teeth, the putative *X. vetus* centra, and the dentary fragment, all come from a species of *Xiphactinus* is strongly supported by the large size and characteristically glassy-smooth enamel surfaces of teeth, the thecodont origin of the teeth in the jaw fragment, and by the vertebral morphology, notably the pattern of peripheral pits, unfused arches and large size.

The only North American Cretaceous fish with similar teeth is *Protosphyraena,* which has a single pair each of very large, straight, rostral and anterior dentary teeth, and rows of many modest-size posterior teeth, all of which are very compressed, sharply carinate, and have smooth enamel. However, we reject the idea that the teeth in consideration can represent a form of *Protosphyraena* because the large teeth here are curved, and because few posterior teeth attributable to *Protosphyraena* are found in the same strata. Logically, if a *Protosphyraena* were the source of so many large teeth, one should find equal or greater numbers of posterior *Protosphyraena* teeth in these same deposits.

A large, oval-shaped basioccipital from an ichthyodectiform was found in the upper Campanian Demopolis Chalk in eastern Mississippi. The original specimen is part of the Memphis Pink Palace Museum collection, and a cast of the specimen is deposited in the Los Angeles County Museum of Natural History (LACM 134395). It is demonstrably ichthyodectiform, based on the shape of the occipital face (which is not a smooth inverted cone, contra Bardack, 1965, fig. 7). This specimen co-occurs with carinate, faceted *Xiphactinus* teeth (Manning and Dockery, 1992), and its oval ventral outline is consistent with the oval shape of presumably anterior *Xiphactinus vetus* centra (e.g., Fig. 3K, L). By contrast, *Xiphactinus audax* has a circular occipital condyle, congruent with its circular anterior vertebrae.

In northeastern Mississippi and eastern Alabama, both species of *Xiphactinus* are known from superjacent strata. The eastern Alabama relationship of species is evident within a single unit, the Blufftown Formation, which contains only typical *X. audax* in the basal portion of early Campanian age (e.g., Figs. 2D, E, 3C–E), and only *X. vetus* in the uppermost few meters which are of middle Campanian age (e.g., Fig. 2Q, R). Based on this stratigraphic unit, one may delimit the cutoff between species near the top of Nannofossil Zone 19, within the uppermost lower Campanian.

What remains undetermined are the evolutionary relationships between these two species of *Xiphactinus,* and the presence (or absence) of *X. vetus* in the Western Interior and *X. audax* in the Atlantic Coastal Plain. There are no published reports of *Xiphactinus* species from upper Campanian or overlying strata in the Western Interior, suggesting that *X. audax* disappeared there by middle Campanian time (Russell, 1988, 1993), and was not replaced by *X. vetus.* However, this may be a biased impression created by the absence of good upper Campanian or Maastrichtian marine sections with reported vertebrate collections in the western U.S.A.

There are likewise no confirmable occurrences of *X. audax* in Atlantic Coastal Plain strata and, concomitantly, there are very few reported occurrences of marine vertebrate faunas older than late Campanian in the region (Schwimmer, 1995). Once again, one would not expect a species, in this case *X. audax,* to be found where fossiliferous marine strata of the required age are rare or unstudied.

In summary, the paleogeographic distribution of *Xiphactinus* species across North America is presently poorly constrained because of the disjunct ages of the well-studied marine strata in the east and west. At the present state of knowledge, it appears that *Xiphactinus vetus* ranged from the eastern Gulf of Mexico to the middle Atlantic Coastal Plain, whereas *Xiphactinus audax* ranged across the western continental seas, reaching eastward as far as the eastern Gulf Coastal Plain in Alabama.

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## LITERATURE CITED

Applegate, S. P. 1970. The vertebrate fauna of the Selma Formation in western Alabama: Pt. VIII: the fishes. Fieldiana, Geology Memoirs 3:383–433.

Bardack, D. 1965. Anatomy and evolution of Chirocentrid fishes. The University of Kansas Paleontological Contributions 10:1–88.

———. 1968. Fossil vertebrates from the marine Cretaceous of Manitoba. Canadian Journal of Earth Sciences 5:145–153.

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FIGURE 2. Comparison of teeth of *Xiphactinus* species. Scale bar in center of figure for all illustrations except C and U. (**A–C**) *Xiphactinus audax,* AMNH 7350, Smoky Hill Chalk (Upper Coniacian), Gove County, Kansas; **A**, **B**, large (4th) maxillary tooth, anterior and labial views, showing rounded borders; **C**, occlusal view maxilla/premaxilla, showing large premaxillary tooth with rounded cross-section, and base of maxillary tooth figured in A, B. (**D**, **E**) *Xiphactinus audax,* CVNHM 113, lower Blufftown Formation (lower Campanian), Russell Co., Alabama, dentary fragment with single preserved tooth, medial and posterior views, showing rounded tooth borders. (**F–Z**) *Xiphactinus vetus*: **F–I**, AMNH FF 19498, holotype of *Polygonodon vetus,* Navesink Formation (lower Maastrichtian), Burlington County, New Jersey, labial, posterior, lingual and anterior views; **V–W**, NJSM 13094, Navesink Formation (lower Maastrichtian), Burlington County, New Jersey, showing morphology comparable to F–I; **U**, NJSM 11370, Navesink Formation (lower Maastrichtian), Burlington County, New Jersey, dentary fragment with five alveoli; **J–L**, holotype of "*Portheus angulatus,*" AMNH 2863, Black Creek Formation (upper Campanian), Duplin County, North Carolina, labial, anterior and posterior views; **M–T**, **X–Z**, *Xiphactinus vetus,* upper Blufftown Formation (middle Campanian), Barbour County Alabama and Stewart County, Georgia; M-P, CSUK 79-3-34, labial, posterior, anterior, and basal views, showing sharp anterior and posterior carinae; **Q**, **R**, CVNMH 111, labial and posterior views showing facetted enamel surfaces; **S**, **T**, CSUK 79-3-31, anterior and labial views showing anterior carina and smooth enamel surfaces; **X–Z**, CSUK 79-3-32, posterior tooth, anterior, labial, and posterior views, showing slightly facetted enamel and anterior carina.

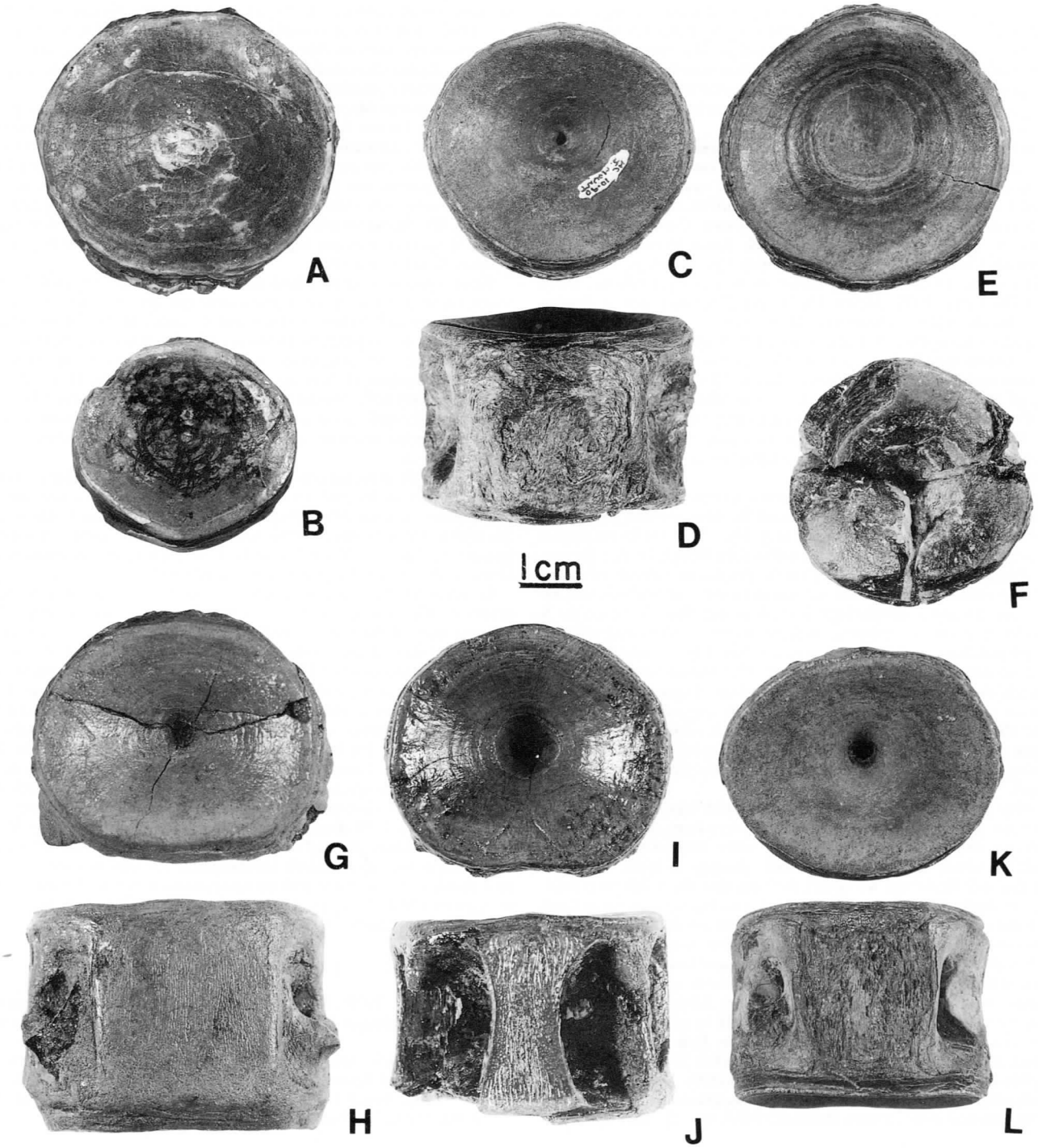


FIGURE 3. Comparison of vertebral centra of *Xiphactinus* species. Scale bar in center of figure for all illustrations. (**A–F**) *Xiphactinus audax*: **A**, **B**, representative specimens from the Niobrara Formation in Kansas, axial views showing round profiles; **A**, AMNH 2372, Smoky Hill Chalk (upper Coniacian), Gove County, Kansas, abdominal; **B**, AMNH 1706, locality unknown, abdominal; **C–F**, *X. audax* vertebrae from the eastern Gulf Coastal Plain; **C–E**, lower Blufftown Formation (lower Campanian), Russell County, Alabama; **C**, **D**, CVNHM 112, abdominal, axial and ventral views; **E**, CVNHM 114, abdominal, axial view; **F**, CSUK 93-17-17, Tombigbee Sandstone Member, Eutaw Formation (upper Santonian), Montgomery County, Alabama, ablated caudal, axial view. (**G–L**) *Xiphactinus vetus,* all from the upper Blufftown Formation (middle Campanian), Stewart County, Georgia, anterior and ventral views showing oval to ventrally flattened morphologies: **G**, **H**, CSUK 89-4-2, posterior abdominal, with flat ventral surface; **I**, **J**, CSUK 94-7-1, caudal, with slightly concave ventral surface; **K**, **L**, CSUK 83-81-3, anterior abdominal, showing oval outline and convex ventral margin.

——— and G. Sprinkle. 1969. Morphology and relationships of saurocephalid fishes. Fieldiana, Geology Memoirs 16:297–340.

Case, G. R. and D. R. Schwimmer. 1988. Late Cretaceous fish from the Blufftown Formation (Campanian) in western Georgia. Journal of Paleontology 62:290–301.

Cope, E. D. 1871. Account of a journey in the valley of the Smoky Hill River in Kansas. Proceedings of the American Philosophical Society 12:174–176.

———. 1872. On the families of fishes of the Cretaceous formation of Kansas. Proceedings of the American Philosophical Society 12: 327–357.

Emmons, E. 1858. Report of the North Carolina Geological Survey: Agriculture of the eastern counties, together with description of the fossils of the marl beds. Raleigh, North Carolina, 315 pp.

Emmons, E. 1860. Manual of Geology. Sower, Barnes & Co., Philadelphia, 290 pp.

Gallagher, W. B. 1993. The Cretaceous/Tertiary mass extinction event in the northern Atlantic Coastal Plain. The Mosasaur 5:75–154.

Gallagher, W. B., D. C. Parris and E. E. Spamer. 1986. Paleontology, biostratigraphy, and depositional environments of the Cretaceous-Tertiary transition in the New Jersey Coastal Plain. The Mosasaur 3:1–35.

Kerr, W. C. 1875. Synopsis of the Vertebrata whose remains have been preserved in the Formations of North Carolina: Report of the Geological Survey of North Carolina, Vol. I. Raleigh, North Carolina, Appendix B, p. 32.

Lauginiger, E. M. 1984. An Upper Campanian vertebrate fauna from the Chesapeake and Delaware Canal. The Mosasaur 2:141–149.

———. 1986. An Upper Cretaceous vertebrate assemblage from Big Brook, New Jersey. The Mosasaur 3:53–61.

Leidy, J. 1856. Notes on the fishes in the collection of the Academy of Natural Sciences of Philadelphia. Proceedings of the Academy of Natural Sciences of Philadelphia VIII (printed 1857), p. 221.

———. 1864. Cretaceous reptiles of the United States. Smithsonian Contributions to Knowledge 192, 135pp, 20 pl.

———. 1870. Remarks on ichthyorudiolites and on certain fossil Mammalia. Proceedings of the Academy of Natural Sciences of Philadelphia 21:12–13.

Manning, E. M. and Dockery, D. T. III. 1992. A guide to the Frankstown vertebrate fossil locality (Upper Cretaceous), Prentiss County, Mississippi. Mississippi Department of Environmental Quality, Office of Geology Circular 4, 43pp.

Miller, H. 1967. Cretaceous vertebrates from Phoebus Landing, North Carolina. Proceedings of the Philadelphia Academy of Natural Sciences 119: 219–235.

Nicholls, E. L. and A. P. Russell. 1990. Paleobiogeography of the Cretaceous Western Interior Seaway of North America: the vertebrate evidence. Palaeogeography, Palaeoclimatology, Palaeoecology 79: 149–169.

Patterson, C. and D. E. Rosen. 1977. Review of Ichthyodectiform and other Mesozoic teleost fishes and the theory and practice of classifying fossils. Bulletin of the American Museum of Natural History 158: 81–172.

Ride, W. D. L., et al. (eds.). 1985. International Code of Zoological Nomenclature, Third Edition. University of California Press, Berkeley and Los Angeles, 338 pp.

Robb, A. J. III. 1989. The Upper Cretaceous (Campanian, Black Creek Formation) fossil fish fauna of Phoebus Landing, Bladen County, North Carolina. The Mosasaur 4:75–92.

Russell, D. A. 1988. A check list of North American marine Cretaceous vertebrates including fresh water fishes. Occasional papers of the Tyrrell Museum of Palaeontology 4, 57pp.

———. 1993. Vertebrates in the Cretaceous Western Interior; pp. 665–680 *in* W. G. E. Caldwell, and E. G. Kauffman (eds.), Evolution of the Western Interior Basin. Geological Association of Canada Special Paper 39, 680p.

Schwimmer, D. R. 1981. A distinctive Upper Cretaceous fauna 3–4 meters below the Blufftown-Cusseta contact in the Chattahoochee Valley; pp. 79–85 *in* J. Reinhardt and T. G. Gibson, (eds.), Georgia Geological Society Guidebook, 16th Annual Field Trip.

———. 1986. Late Cretaceous fossils from the Blufftown Formation (Campanian) in Georgia. The Mosasaur 3:109–123.

———. 1995. East-west provincialism: real or an artifact of parasynchrony? Abstracts with Programs, Geological Society of America Annual Meeting, 27: A–387.

———, J. D. Stewart, and G. D. Williams. 1992. Late Cretaceous *Xiphactinus* fossils in eastern United States are not necessarily *X. audax*. Journal of Vertebrate Paleontology 12 (suppl. to 3): 51A.

Sissingh, W. 1977. Biostratigraphy of Cretaceous calcareous nannoplankton. Geologie en Mijnbouw 56:37–65.

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