

TAXONOMIC REVISION AND STRATIGRAPHIC PROVENANCE OF †*HISTIOPHORUS ROTUNDUS* WOODWARD 1901 (TELEOSTEI, PERCIFORMES)

KENNETH A. MONSCH¹, HARRY L. FIERSTINE² and ROBERT E. WEEMS³

¹Department of Vertebrate Zoology, Institute of Zoology, University of Wrocław, ul. H. Sienkiewicza 21, 50-335 Wrocław, Poland, kmensch@biol.uni.wroc.pl;

²Biological Sciences Department, California Polytechnic State University, San Luis Obispo, CA 93407;

³U.S. Geological Survey, MS 926A National Center, 12201 Sunrise Valley Drive, Reston, Virginia 20192

ABSTRACT—Until recently, †*Histiophorus rotundus* Woodward 1901, was known from a single, poorly preserved rostrum from the Tertiary phosphate beds near Charleston, South Carolina, an area from which many fossils have been described. The specimen is relatively featureless externally; its internal anatomy is unknown and the documentation of its geological provenance was poor. In an earlier revision the species was transferred to the fossil billfish genus †*Xiphiorhynchus* Van Beneden, 1871. Here we confirm this designation, supported by new morphological studies of the holotype, recently found specimens of †*Xiphiorhynchus rotundus* (Woodward, 1901), and the stratigraphic record of †*Xiphiorhynchus*. The systematic paleontology we present is a contribution to the taxonomic revision of billfishes world-wide. Because the holotype is heavily phosphatized and the type locality was vaguely described, we discuss the geology of the phosphate mining districts of the Charleston region. Based on our studies, we can narrow the possible age of the holotype to late Oligocene or early Miocene. We suggest †*X. rotundus* was extinct by the Burdigalian.

INTRODUCTION

Until recently, †*Histiophorus rotundus* Woodward, 1901 was known only from the holotype, a single rostrum from the Tertiary phosphate beds near Charleston, South Carolina. This specimen has proven enigmatic because of its unusual proportions, featureless external morphology, unknown internal canal system, and vague locality and age data. The fossil has been assigned to genus *Histiophorus* Cuvier, 1832 (Woodward, 1901), which is an invalid emendation of *Istiophorus* Lacépède, 1801, as well as to the spearfish *Tetrapturus* Rafinesque, 1810 (Monsch, 2000), and provisionally to the marlin *Makaira* Lacépède, 1802 (Fierstine, 2001). Schultz (1987) included the specimen in †*Xiphiorhynchus* Van Beneden, 1871, because of its dimensions and Eocene (sic) age. Unfortunately Schultz (1987) did not supply data or new figures to support this assertion. We here recognize that three distal rostra of †*Xiphiorhynchus* that are part of a collection in the Charleston Museum are similar to the holotype of †*H. rotundus*. The aim of this paper is twofold: to present a revision of †*H. rotundus* that assigns it to genus †*Xiphiorhynchus*, and a determination of the type locality and age based on a recent stratigraphic study of the Charleston, South Carolina area by Weems and Lewis (2002). The systematic paleontology presented here is a part of the on-going revision of fossil billfishes of the world (e.g., Fierstine 1978, 2001; Schultz, 1987; Monsch 2000). We present extensive information on the geologic setting of the holotype. The information about the origin and age of these so-called Ashley Phosphate deposits is applicable to various other fossil taxa that have been described from that unit (e.g., Sloan, 1908; Malde, 1959; Weems and Edwards, 2001). The systematics presented herein are based on Monsch (2000).

Institutional Abbreviations—AMNH, American Museum of Natural History, New York; BMNH, Natural History Museum, London; ChM, Charleston Museum, Charleston, South Carolina; IRSNB, Institut royal des Sciences naturelles de Belgique, Brussels, Belgium; MNHN, Muséum national d'Histoire naturelle, Paris, France.

Anatomical Abbreviations—cc, central canal; D, depth of rostrum; gD, greatest depth of rostrum; gW, greatest width of rostrum; L, reconstructed length of fused portion of rostrum; lcd, dorsal lateral nutrient canal; lcv, ventral lateral nutrient canal; PMX, premaxilla, S, sagittal suture, W, width of rostrum.

GEOLOGICAL SETTING

The information archived with the type specimen of †*X. rotundus* only states that it came from the Tertiary phosphates of the Cooper River near Charleston, South Carolina (Fig. 1). This phosphate-rich rock is a lag-concentrate derived from geologic formations that long ago lay above the late Oligocene Ashley and Chandler Bridge Formations (Sloan, 1908; Weems and Lemon, 1988).

The type specimen of †*X. rotundus* is dense and heavy. This is because its original pore space largely has been filled with additional phosphatic minerals emplaced during one or more phosphatization episodes. Recent work by Riggs et al. (2000) indicates that in the Carolinas there were three discrete intervals of time during which phosphate-enrichment occurred. These were at 21 to 18 Ma, 10.8 to 11.5 Ma, and 9.0 to 8.6 Ma. Analyses of phosphate clasts from basal lag gravels of units younger than 8.6 Ma show that this material accumulated through reworking of phosphate formed in one of the three episodes of phosphate enrichment. This makes it highly unlikely that the phosphate-impregnated type specimen of †*X. rotundus* originated from any of the units from the Charleston area that are younger than 8.6 Ma (late Miocene), for example the widespread lower Pliocene Goose Creek Limestone.

Conversely, although the mid-Oligocene Ashley Formation directly underlies the phosphate district, it is a dense calcarenite that is nearly impervious to ground water flow. For this reason, fossil vertebrate specimens found within the Ashley are not secondarily phosphate-enriched, because phosphate-rich water could not flow through the Ashley. This groundwater reality makes it virtually certain that the secondarily phosphatized type specimen of †*X. rotundus* originally came from a stratigraphic

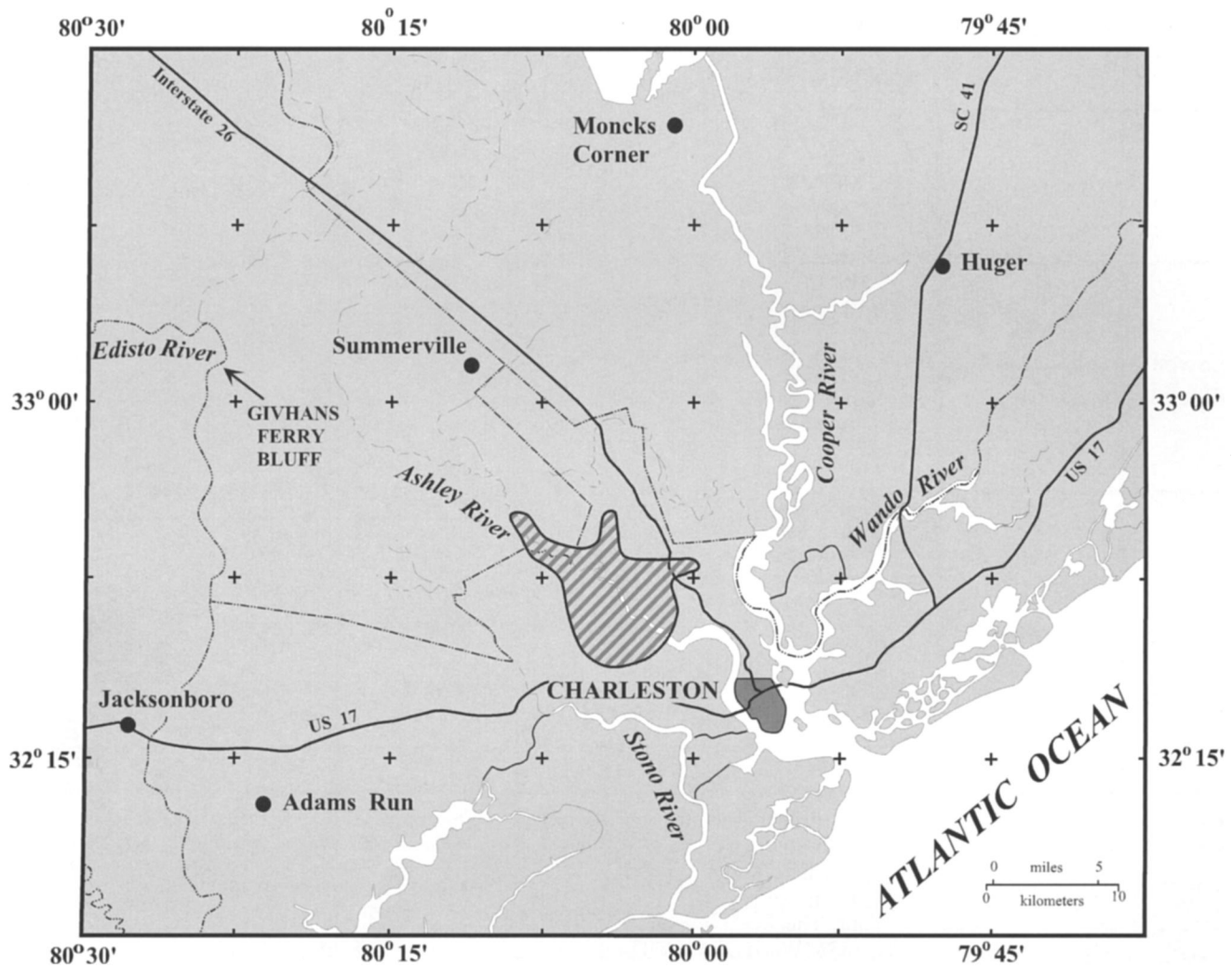


FIGURE 1. Map showing the region around Charleston, SC (which itself is marked by a dark gray area). Diagonally ruled area represents the major region of land phosphate mining in the late nineteenth and early twentieth centuries. In addition, other much smaller areas were mined locally in this region and major dredging operations for river bottom phosphate were undertaken along portions of the Ashley, Cooper, and upper Wando rivers. Fossil bones and teeth were recovered from all of these operations. Crosses mark the corner edges of 7.5-minute USGS quadrangle maps.

horizon higher than the Ashley (i.e., no older than upper Oligocene (Chattian)). The known plausible source beds for this specimen are summarized in Fig. 2 (with locality information in Fig. 1) and described as follows.

Only one Oligocene stratigraphic unit, the Chandler Bridge Formation (Sanders et al., 1982; Weems and Sanders, 1986), is currently documented above the Ashley Formation in the old phosphate-mining district. However, at least one other upper Oligocene unit must have been present. Samples of rock phosphate from this district, processed for dinoflagellates, have yielded dinocyst assemblages indicative of two slightly different ages: an early Miocene (early Aquitanian) flora and a late Oligocene (late Chattian) flora (Lucy E. Edwards, U.S. Geological Survey, pers. comm.; Miocene data cited previously in Weems and Lemon, 1988). The late Oligocene flora is indistinguishable from the flora found in the Chandler Bridge Formation. These floral assemblages indicate that, in the past, there were at least two phosphatized calcareous units in the Charleston region, now gone, that lay above the noncalcareous quartz-phosphate sands of the Chandler Bridge Formation.

The Aquitanian rock phosphate almost certainly was derived

from the Edisto Formation (Sloan, 1908). The only likely correlative unit for the other (upper Oligocene) phosphatized quartzose calcarenite is an unnamed quartzose calcarenite, here informally designated as the "Givhans Ferry beds," that occurs at the Givhans Ferry bluff beneath the type section of the Edisto Formation. Recent auger drilling, directly across the Edisto River from this bluff, penetrated below river level a phosphate pebble bed at the base of the Givhans Ferry beds. This lag bed, lying on typical Ashley Formation calcarenite, indicates an unconformity between these two units.

A number of widespread and often thick Miocene units occur in eastern Georgia (Weems and Edwards, 2001), but only patches of some of these are known from the Charleston region (Weems and Lewis, 2002). Today, only the basal Aquitanian Edisto Formation occurs specifically in the area of the old phosphate mines (Sloan, 1908; Weems and Lemon, 1988), though some younger Miocene units presently are known to occur in outlying regions (Weems and Lewis, 2000).

We can be fairly certain that the phosphatized type specimen of †*X. rotundus* came from one of these upper Oligocene or Miocene horizons, but it is impossible to be sure which one. It is

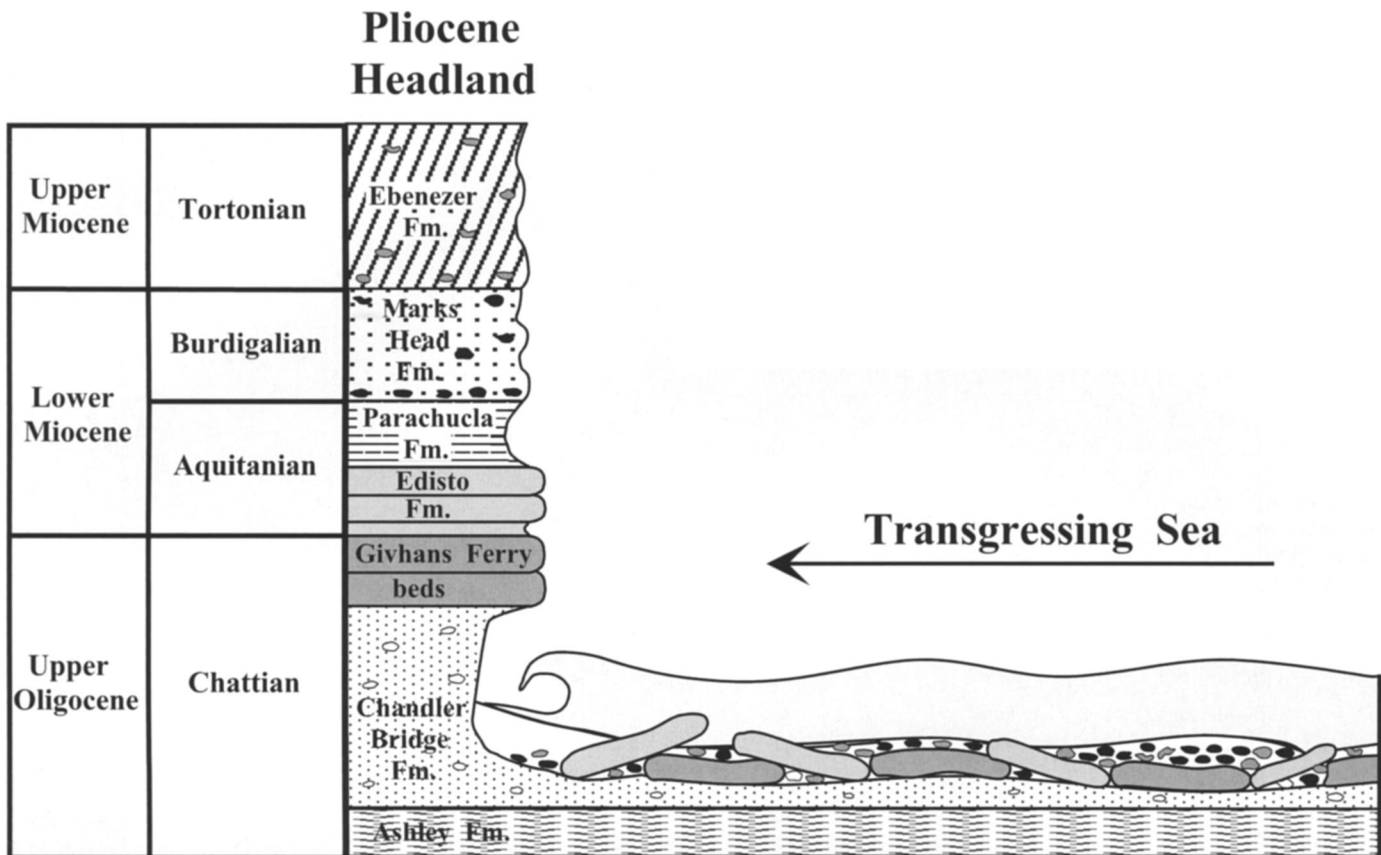


FIGURE 2. Diagram showing the process by which the Charleston area phosphate deposits formed. Wave action along the edge of a transgressing sea, probably at the beginning of Goose Creek deposition during the early Pliocene, undercut older high ground underlain by at least six stratigraphic units, namely the Chandler Bridge Formation, Givhans Ferry beds, Edisto Formation, Parachucla Formation, Marks Head Formation, and Ebenezer Formation. Undercut ledges of phosphatized limestone in the Givhans Ferry beds and the Edisto Formation collapsed into the advancing waters as large blocks, along with phosphate rubble from other units. Finer sands and clays were swept away, leaving phosphatized blocks of Edisto and Givhans Ferry beds, pebble to cobble-size chunks of phosphate, and worn bone fragments of other units to be buried beneath the shallow sea bottom as a jumbled mass of detrital blocks. It is this mass of detrital debris that constituted the phosphate deposits mined in the Charleston region in the late 1800s and early 1900s.

noteworthy, however, that all four specimens of †*X. rotundus* (including ChM GPV4864 from the Chandler Bridge Formation) have been found in the vicinity of Charleston, S.C., and nowhere else. †*X. rotundus* has not been found among the abundant billfish remains recovered over the years from the Miocene (Burdigalian through lower Tortonian) Calvert, Choptank, or St. Marys Formations in the Chesapeake Bay region of Virginia and Maryland. Similarly, †*X. rotundus* has not been found among the abundant vertebrate remains recovered from the Miocene (Burdigalian) Pungo River Formation at the Lee Creek Mine in North Carolina. If this species existed along the Atlantic coast during the Burdigalian to Tortonian portion of the Miocene, it is likely that its remains would have been found outside of the Charleston region. Thus, the absence of any specimens of †*X. rotundus* from elsewhere within the Atlantic Coastal Plain strongly suggests that it was extinct by the Burdigalian, at least along the Atlantic seaboard of the United States. This in turn strongly suggests (along with the occurrence of a supplementary specimen in the Chandler Bridge Formation) that the type specimen of †*X. rotundus* originally came from an upper Oligocene (Chattian) deposit (the Chandler Bridge Formation, or the unnamed beds at Givhans Ferry) or from the lower Miocene (Aquitanian) Edisto Formation or Parachucla Formation.

SYSTEMATIC PALEONTOLOGY

Order PERCIFORMES Bleeker, 1859
 Suborder SCOMBROIDEI Bleeker, 1859
 Family SCOMBRIDAE Rafinesque, 1815
 Subfamily XIPHIINAE Swainson, 1839
 Tribe †XIPHIORHYNCHINI Regan, 1909
 Genus †XIPHIORHYNCHUS van Beneden, 1871

†XIPHIORHYNCHUS ROTUNDUS (Woodward, 1901)
 (Fig. 3, Table 1)

†*Histiophorus rotundus* Woodward, 1901:495, fig. 18/3.

†*Histiophorus rotundus* Woodward: Leriche, 1942:93.

†*Istiophorus rotundus* (Woodward): Fierstine, 1978:7.

†*Xiphiorhynchus rotundus* (Woodward): Schultz, 1987:146, fig. 5, table 2.

†*Tetrapturus rotundus* (Woodward): Monsch, 2000:150, fig. 7.54.

?†*Makaira rotundus* (Woodward): Fierstine, 2001:36.

Holotype—†*Histiophorus rotundus*, BMNH P8799 (Fig. 3A): distal rostrum, upper Oligocene–early Miocene “Tertiary phosphate beds,” Cooper River, South Carolina, U.S.A.

Referred Specimens—Three distal rostra: ChM GPV2026 (South Carolina, no other data); ChM PV2697 (upper Oli-

gocene–lower Miocene “Tertiary phosphate beds,” Magnolia Phosphate Mine, Charleston County, South Carolina); ChM PV4864 (Chandler Bridge Formation, late Oligocene, South Carolina).

Emended Species Diagnosis—Differs from other xiphiorhynchid billfish (which are characterized by two pairs of lateral nutrient canals and usually a central canal) by having a massive rostrum (distal fused portion) with its greatest depth more than one-fourth of its total length and nearly round in cross-section throughout its length, with a depth/width ratio greater than 0.70.

Description—The holotype (BMNH P8799) is poorly preserved proximally, but otherwise complete to its distal tip. The surface is badly worn, and rather smooth with a slight fibrous texture, except for three shallow grooves near the distal tip. We believe these grooves are on the dorsal surface and represent sutures formed by fusion of the premaxillae and a trace of the sagittal suture (Fig. 3A). From the specimen it is not clear to what degree these premaxillae are fused. Fierstine and Pfeil (2002) confirmed that the dorsal aspect of the †*Xiphiorhynchus* bill is composed of premaxillae. There are no denticles or alveoli to confirm whether we are correct in our recognition of the ventral and dorsal side of the holotype. The specimen has a greatest depth/total length (gD/L) value of 0.34 and a proximal D/W value of 0.84 (Table 1). We lack direct information on its internal morphology because canals are not visible at the broken proximal end and the specimen has never been sectioned or CT-scanned. Nevertheless, we believe the rostrum has two pairs of lateral nutrient canals and probably a central canal, based on the internal anatomy of the referred specimens.

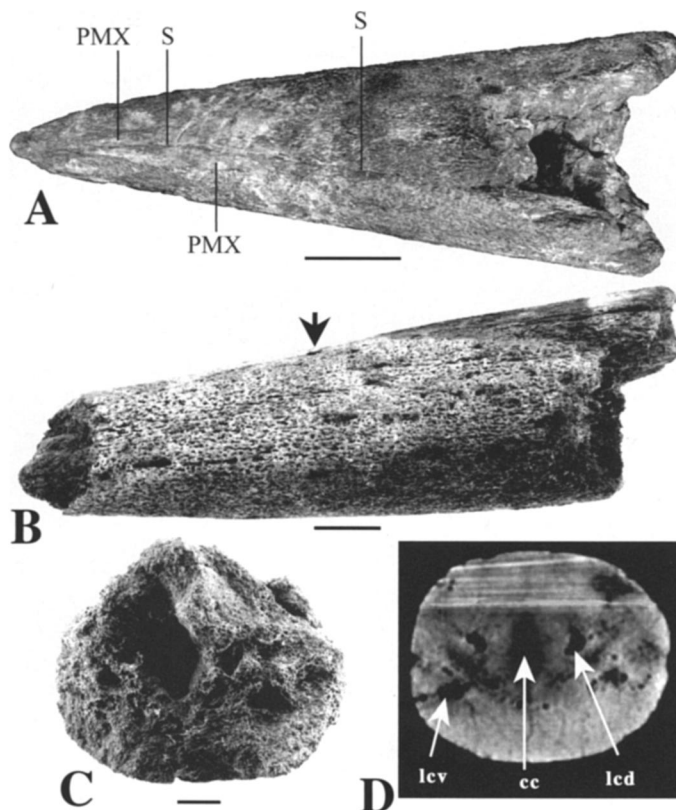


FIGURE 3. Distal rostra of †*Xiphiorhynchus rotundus* (Woodward, 1901). **A**, holotype, BMNH P8799, dorsal view, scale equals 50 mm; **B–D**, distal rostrum of †*Xiphiorhynchus rotundus* (Woodward, 1901) (ChM PV4864, referred specimen, late Oligocene, Chandler Bridge Formation, South Carolina). **B**, lateral view, scale equals 20 mm; **C**, proximal view, scale equals 10 mm; **D**, computer aided tomography image taken 107 mm from proximal end of specimen (indicated by arrow in B). See text for definition of abbreviations.

TABLE 1. Selected morphometric measurements (mm) and ratios of the holotype (BMNH P8799) and three referred specimens (ChM GPV2026, PV2697, PV4864) of †*Xiphiorhynchus rotundus* (Woodward, 1901). See text for definition of abbreviations.

Measurements or ratios	Specimens			
	BMNH P8799	ChM GVP2026	ChM PV2697	ChM PV4864
Actual Length	313	225	190	210
Estimated Length with Reconstructed tip (L)	313	335	235	295
Greatest width proximally (gW)	111.8	78.5	~53.7	78.0
Estimated gW/L	0.36	0.23	0.23	0.26
Greatest depth proximally (gD)	~106	~66.0	51.2	62.5
Estimated gD/L	0.34	0.29	0.27	0.31
D/W proximally	0.84 ¹	0.73 ²	0.89 ³	0.87 ⁴
D/W distally	—	0.73 ⁵	0.97 ⁶	0.73 ⁷

¹Measured 97 mm from broken proximal end.

²Measured 65 mm from broken proximal end.

³Measured 78 mm from broken proximal end.

⁴Measured 50 mm from broken proximal end.

⁵Measured 30 mm from broken distal end.

⁶Measured 50 mm from broken distal end.

⁷Measured 28 mm from broken distal end.

These new specimens are distal rostra as well, with their anterior tips missing. The actual length of the specimens varies between 190 and 225 mm, and we estimate their actual lengths to have been between 235 and 335 mm (Table 1). Where not eroded, the surface of these specimens is fibrous (“woody”). Specimens ChM PV4864 (Fig. 3B–D) and ChM GPV2026 have a very shallow, ventral, mid-line groove. None of the referred specimens possesses denticles or alveoli. In every specimen, the maximum depth is about 30% of the estimated total length (Table 1). All of the rostra in question are nearly round throughout: proximally and distally they are almost as deep as they are wide (Table 1). CT scans have been taken of ChM PV4864 and ChM GPV2026. The scan image of the first of these two (Fig. 3D) shows a central canal and two pairs of nutrient canals. A CT scan taken at 140 mm from the proximal broken end of ChM PV2026 shows both a dorsal and a ventral left lateral nutrient canal.

Discussion—Species identification of billfish based solely on the morphology of a partial, isolated rostrum is a risky activity. Fierstine and Voigt (1996) showed that there is considerable intraspecific and interspecific variability in the states of taxonomic characters of xiphiid bills. Since we lack information on intraspecific variability of the rostrum of the nine recognized species of †*Xiphiorhynchus*, it is possible that these are variants of one, two, or three species. On what basis, then, do we recognize †*X. rotundus* as a distinct species?

First, there is a difference in morphology. Only four species, †*Xyphiorhynchus elegans* van Beneden, 1871 (upper Eocene, Gent, Belgium), †*Xyphiorhynchus eocaenicus* (Woodward, 1901) (middle Eocene, England), †*Xyphiorhynchus homalorhamphus* (Cope, 1869) (?Eocene, New Jersey, U.S.A.), and †*Xyphiorhynchus priscus* (Agassiz, 1844) (lower Eocene, London Clay, England) need to be considered on the basis of taxonomic priority, because *X. rotundus* would become a junior synonym if it was found to be similar morphologically to any one of them. Of these four, the holotype of †*X. homalorhamphus* has been lost and we may never know its true morphology. Five specimens identified as †*X. homalorhamphus* (in two lots: AMNH 8430, 8431) are relatively slender with a gW less than 40 mm. The holotype of †*X. elegans* (IRSNB P642) is also very slender with a gW less than 25 mm. The holotype of †*X. priscus* (MNHN PTE474) is a skull without a rostrum. Fierstine and Pfeil

(2002) are studying the only known complete head (skull and rostrum) of a †*Xiphiorhynchus* (lower Oligocene, Austrian Alps). According to this study, the holotype of †*X. priscus*, as well as similar skulls identified by Woodward (1901) and Casier (1966), are morphologically different from the Austrian specimen and may not belong to †*Xiphiorhynchus* at all, but to a new xiphiorhynchin genus. Thus, †*X. eocaenicus* is the only remaining species with which †*X. rotundus* could be synonymized. †*Xiphiorhynchus eocaenicus* is known from two distal rostra (holotype BMNH 25744 and BMNH P12204, both from the middle Eocene of England). Similar to †*X. rotundus*, the holotype is long (351 mm) and wide (101 mm) at its proximal end, and its dorsal, ventral, and lateral surfaces are smooth, without alveoli or denticles. Unlike †*X. rotundus*, the holotype (at 150 mm from the distal end) is more depressed in cross-section ($D/W = 0.62$) and there are numerous small foramina, representing two pairs of lateral nutrient canals, a central canal, and possibly other canals as well.

Second, there is an argument based on the chronostratigraphic age of the specimens. All four of the comparative species were found in lower or middle Eocene deposits (Schultz, 1987), whereas we now believe that the holotype of †*X. rotundus* was found in strata no older than late Oligocene, a difference in age possibly as large as 28, but certainly no less than 11 my. It is not unreasonable to hypothesize that an Eocene species of †*Xiphiorhynchus* could have evolved into one or more sister species over this length of time.

CONCLUSIONS

Morphological comparisons of the holotype of “†*Histiophorus rotundus*” with new specimens of this species and with specimens of other †*Xiphiorhynchus* species support the recognition of a separate species †*Xiphiorhynchus rotundus*. Earlier, Schultz (1987) transferred the species to †*Xiphiorhynchus*, but his assignment was poorly considered, without new data to support it. The stratigraphic provenance of the holotype has been narrowed down to the upper Oligocene or lower Miocene horizons of the “Tertiary phosphate beds” in the Charleston, South Carolina region. A provenance from the upper Oligocene beds is more likely, based on the discovery of referred specimen ChM PV4864 in the Chandler Bridge Formation. We suggest that †*X. rotundus* was extinct by the Burdigalian.

ACKNOWLEDGMENTS

We thank P. Forey (BMNH), D. Goujet (MNHN), J. Maisey (AMNH), D. Nolf (IRSNB), and A. Sanders (ChM) for access to specimens in their custody. The Photography Department (BMNH) provided the photo of the holotype. F. Vernaccia (San Luis Diagnostic Center) generously provided CT images at minimal cost. A. Elżanowski (Wrocław) and J. Maisey reviewed different versions of the manuscript. KAM acknowledges M. J. Benton (University of Bristol) and P. Forey for co-supervising the PhD project (University of Bristol) that included work presented here, a LSF grant of the European Union and a ‘Badania Własne’ grant (2020/W/IZ/2001) of the University of Wrocław for financial assistance. REW acknowledges L. Edwards (USGS) and J. Self-Trail (USGS) for their helpful reviews of the geologic portion of the manuscript. We acknowledge two anonymous reviewers whose comments and criticisms helped us to improve this paper.

LITERATURE CITED

- Agassiz, L. 1833–44. *Recherches sur les Poissons Fossiles* 5. Imprimerie de Petitpierre, Neuchâtel, 160 pp.
- Bleeker, P. E. 1859. *Enumeratio Specierum Piscium hucusque in Archipelago Indico observatarum*. Verhandelingen der Natuurkundige Vereeniging in Nederlandsch Indië 6:1–276.
- Casier, E. 1966. *Faune ichthyologique du London Clay*. British Museum (Natural History), London, 496 pp.
- Cope, E. D. 1869. Descriptions of some extinct fishes previously unknown. *Proceedings of the Boston Society of Natural History* 12: 310–317.
- Cuvier, G., and A. Valenciennes. 1832. *Histoire naturelle des poissons*. Vol. 8 (9, Des Scombéroïdes). F. G. Levrault, Paris, 509 pp.
- Fierstine, H. L. 1978. A new marlin, *Makaira panamensis*, from the Late Miocene of Panama. *Copeia* 1978:1–11.
- Fierstine, H. L. 2001. Analysis and new records of billfish (Teleostei: Perciformes: Istiophoridae) from the Yorktown Formation, early Pliocene of Eastern North Carolina at Lee Creek Mine; pp. 21–69 in C. E. Ray and D. J. Bohaska (eds.), *Geology and Paleontology of the Lee Creek Mine, North Carolina III*. Smithsonian Contributions to Paleobiology 90.
- Fierstine, H. L., and F. Pfeil. 2002. A new species of xiphiorhynchid billfish (Perciformes, Scombroidei) from the Austrian Alps (early Oligocene). *Journal of Vertebrate Paleontology* 22(3, supplement): 53A.
- Fierstine, H. L., and N. Voigt. 1996. Use of rostral characters for identifying adult billfishes (Teleostei: Perciformes: Istiophoridae and Xiphiidae). *Copeia* 1996:148–161.
- Lacépède, B. G. E. 1801. *Histoire naturelle des poissons* 3. Plassan, Imprimeur-Librairie, Paris, 558 pp.
- Lacépède, B. G. E. 1802. *Histoire naturelle des poissons* 4. Plassan, Imprimeur-Librairie, Paris, 728 pp.
- Lerliche, M. 1942. Contribution à l'étude des faunes ichthyologiques marines des terrains tertiaires de la plaine côtière atlantique et du Centre des États-Unis. *Mémoires de la Société Géologique de France* 45:1–111.
- Malde, H. E. 1959. *Geology of the Charleston phosphate area, South Carolina*: U. S. Geological Survey Bulletin, Report B 1079:1–105.
- Monsch, K. A. 2000. *The phylogeny of the scombroid fishes*. Unpublished Ph.D. dissertation, University of Bristol, 272 pp.
- Rafinesque, C. S. 1810. *Caratteri di alcuni nuovi generi e nuove specie di animali e piante della Sicilia, con varie osservazioni sopra i medesimi*. Palermo, 105 pp.
- Rafinesque, C. S. 1815. *Analyse de la Nature, ou Tableau de l'Univers et de Corps Organisés*. Palermo, 224 pp.
- Regan, C. T. 1909. On the anatomy and classification of the scombroid fishes. *Annals and Magazine of the Natural History Museum*, ser. 8 no. 3:66–75.
- Riggs, S., S. Snyder, and D. Ames. 2000. Chronostratigraphy of upper Cenozoic phosphorites on the North Carolina continental margin and the oceanographic implications for phosphogenesis; pp. 369–385 in C. R. Glenn, L. Prevot-Lucas, and J. Lucas (eds.), *Marine Authigenesis: from Global to Microbial*. Society for Sedimentary Geology Special Publication, vol. 66, Tulsa, Oklahoma.
- Sanders, A. E., R. E. Weems, and E. M. Lemon, Jr. 1982. Chandler Bridge Formation, a new Oligocene stratigraphic unit in the lower Coastal Plain of South Carolina; in *Stratigraphic Notes, 1980–1982*. U.S. Geological Survey Bulletin 1529-H:H105–H124.
- Schultz, O. 1987. *Taxonomische Neugruppierung der Überfamilie Xiphioida (Pisces, Osteichthyes)*. *Annalen des Naturhistorischen Museums, Wien, Serie A: für Mineralogie und Petrographie, Anthropologie und Prähistorie* 89:95–202.
- Sloan, E. 1908. *Catalogue of the mineral localities of South Carolina*. *South Carolina Geological Survey Bulletin* 2 (series 4):1–505.
- Swainson, W. 1839. *The Natural History and Classification of Fishes, Amphibians, & Reptiles, or Monocardian Animals* 2. Longman, Orme, Green and Longmans & John Taylor, London, 448 pp.
- Van Beneden, P.-J. 1871. *Recherches sur quelques poissons fossiles de Belgique*. *Bulletin de l'Académie Royale de Belgique* 104:493–517.
- Weems, R. E., and L. E. Edwards. 2001. *Geology of Oligocene, Miocene, and younger deposits in the coastal area of Georgia*. *Georgia Geological Survey Bulletin* 131:1–124.
- Weems, R. E., and E. M. Lemon, Jr. 1988. *Geologic map of the Ladson Quadrangle, Berkeley, Charleston, and Dorchester counties, South*

- Carolina. U. S. Geological Survey Geologic Quadrangle Map GQ-1630 (with text), 1 map sheet.
- Weems, R. E., and E. M. Lemon, Jr. 1989. Geology of the Bethera, Cordesville, Huger, and Kittredge quadrangles, Berkeley County, South Carolina. U. S. Geological Survey Miscellaneous Investigations Series Report I-1854: 2 map sheets.
- Weems, R. E., and W. C. Lewis. 2002. Structural and tectonic setting of the Charleston, South Carolina, region: evidence from the Tertiary stratigraphic record. *Geological Society of America Bulletin* 114: 24–42.
- Weems, R. E., and A. E. Sanders. 1986. The Chandler Bridge Formation (upper Oligocene) of the Charleston, South Carolina region; pp. 323–326 in T. L. Neathery (ed.), *Geological Society of America Centennial Field Guide, Southeastern Section, Geological Society of America*, vol. 6. Boulder, CO.
- Woodward, A. S. 1901. *Catalogue of the Fossil Fishes in the British Museum (Natural History)* 4. British Museum (Natural History), London, 636 pp.

Submitted 2 April 2004; accepted 1 September 2004.