

FOSSIL HISTORY OF BILLFISHES (XIPHIOIDEI)

Harry L. Fierstine

ABSTRACT

This review characterizes each of the five extinct and extant families of billfishes and discusses the relevant literature. Families include: Hemingwayidae (monotypic; late Paleocene, Turkmenistan), Blochiidae (1 genus, 2 species; middle Eocene, Italy), Palaeorhynchidae (4 genera, ca. 22 species; early Eocene-possibly early Miocene, Europe, Iran, Russia, U.S.A.), Xiphiidae that includes the subfamilies Xiphiorhynchinae (1 genus, 9 species; early Eocene-late Oligocene, Egypt, Europe, U.S.A.) and Xiphiinae (monotypic; middle Miocene-present, world-wide temperate-tropical seas), and the Istiophoridae (3 genera, 13 species; middle Miocene-present; world-wide temperate-tropical seas). Billfishes first appeared in the region of the ancient Tethys Sea (or Paratethys), except for the Xiphiinae that first appeared in the western North Atlantic Ocean. Fossil specimens of all five billfish families are usually considered to have had the same environmental preferences as extant billfishes, however, those with upper and lower jaws of equal length were probably less adapted for spearing than those with a disproportionately longer rostrum. Three genera, *Aglyptorhynchus*, *Palaeorhynchus*, and *Xiphiorhynchus* existed for approximately 27 million yrs (Ma) before extinction, whereas the four extant genera *Istiophorus*, *Makaira*, *Tetrapturus*, and *Xiphias* have been in existence ca. 11 Ma, 15 Ma, 5 Ma, and 15 Ma, respectively.

The term billfish refers to those perciform fishes with their premaxillaries elongated into a non-protrusible rostrum or bill that is fused distally and usually bears villiform teeth (Schultz, 1987; Fierstine, 1990; Fierstine and Monsch, 2002). These fishes comprise three extinct (Blochiidae, Hemingwayidae, Palaeorhynchidae) and two extant (Istiophoridae, Xiphiidae) families. They are generally classified in the Suborder Scombroidei of the Order Perciformes along with the mackerels, tunas, and their relatives of the family Scombridae (Monsch, 2000; Fierstine, 2001a, 2005; Monsch, 2005; Monsch et al., 2005), or in the Suborder Xiphioidei (Gosline, 1968; Nakamura, 1985; Schultz, 1996; Collette et al., 2006). The relationship of some of these fossil families within, or to the Scombroidei is poorly understood and some authors, notably Casier (1966), Fierstine (1974), Schultz (1987), and Monsch (2000, 2005), have included one or more other extinct taxa (*Acestrus* Woodward, 1901; *Congorhynchus* Darteville and Casier, 1949; *Cylindracanthus* Leidy, 1856; and *Enniskillenius* Casier, 1966) among the billfishes, in spite of the fact that there is no strong evidence that any of these genera had a non-protrusible rostrum.

Since the last review of fossil billfishes (Fierstine, 1990), there have been numerous interesting and important discoveries. Noteworthy reports include the description of a new species, genus, and family of billfish (Hemingwayidae, *Hemingwaya sarissa* Sytchevskaya and Prokofiev, 2002) from the Paleocene of Turkmenistan (Sytchevskaya and Prokofiev, 2002), the description of a new genus and species of billfish with uncertain affinities (*Rotundorhynchus brittanicus* Monsch, 2005) from the London Clay (early Eocene) (Monsch, 2005), a brief description of the most complete specimen of *Xiphiorhynchus* van Beneden, 1871 (Fierstine and Pfeil, 2002), an analysis of the billfish, *Aglyptorhynchus* Casier, 1966, possibly with a mobile rostrum (Fierstine, 2001a, 2005), and the redescription and phylogenetic relationships of the family

Blochiidae (Fierstine and Monsch, 2002). Other articles include descriptions of fossil istiophorid and xiphiid billfishes that were found identical or very similar to recent species (Schultz, 1996; Fierstine, 1998, 1999a, 2001b; Purdy et al., 2001; Carnevale et al., 2002), descriptions of *Palaeorhynchus* Blainville, 1818 (Pharisat, 1991; Bannikov, 1993), discoveries of *Aglyptorhynchus* in deposits bordering the Pacific Ocean (Fierstine, 2001a, 2005), and evidence that fossil tuna vertebrae were punctured by istiophorid billfishes (Schneider and Fierstine, 2004).

The following review describes some of the above publications in greater detail and summarizes the paleohistory of billfishes. For sake of brevity, I have reduced the diagnosis (characterization) of each taxon, but if the reader desires more information, there are abundant citations throughout the paper.

FOSSIL RECORD

Hemingwayidae

Sytchevskaya and Prokofiev (2002) described a new family, genus and species of billfish (*Hemingwaya sarissa* Sytchevskaya and Prokofiev, 2002) (Fig. 1) from the Late Paleocene of Turkmenistan based on about 16 partial counterparts. Their interpretation of the material (plus a reinterpretation of the caudal skeleton by Prokofiev, 2004) included: an elongated body with an elongate, high first dorsal fin (D1) and first anal fin (A1), and short, low second dorsal fin (D2) and second anal fin (A2); anus and origin of A1 are located far anteriorly at the level of eighth vertebra; the rostrum is formed mainly by the premaxillae that bear small villiform teeth; lower jaw slightly shorter than the rostrum and with small villiform teeth; pectoral fin short; pelvic fin absent; caudal skeleton consists of two separate hypural plates; caudal fin forked with bases that overlap the hypural plates (hypurostegy); approximately 30–40 vertebrae total (15–20 precaudal and 15–20 caudal vertebrae); the last five or six caudal vertebrae each bear a lateral parapophysis; body and postorbital part of the head bear six longitudinal rows of modified scales or scutes. Maximum body length is 30–40 cm. Based on morphological and not on biostratigraphic evidence, the authors concluded that the *H. sarissa* inhabited the epipelagic zone, did not swim actively or enter great depths, and captured their food in short darts. They also hypothesized that the Hemingwayidae is a sister group to the Istiophoridae.

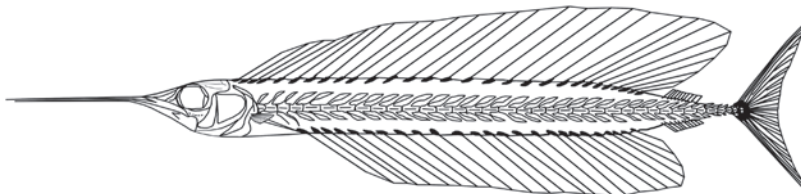


Figure 1. Skeletal reconstruction of *Hemingwaya sarissa* Sytchevskaya and Prokofiev, 2002. Modified from Sytchevskaya and Prokofiev (2002).

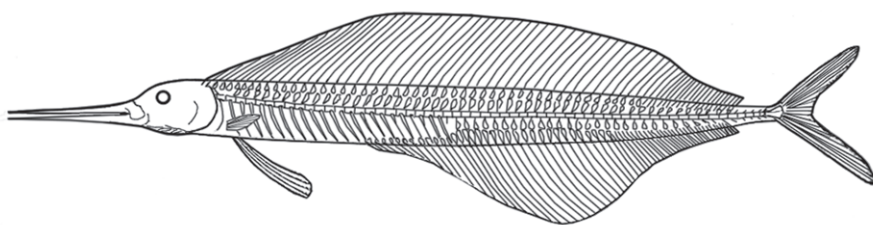


Figure 2. Skeletal reconstruction of a generalized species of *Palaeorhynchus* Blainville, 1818. Modified from Pharissat (1991) and Bannikov (1993).

Palaeorhynchidae

I have not studied in detail any specimens of the three genera that are commonly included in the family Palaeorhynchidae (*Homorhynchus* van Beneden, 1873; *Palaeorhynchus* Blainville, 1818; *Pseudotetrapturus* Danil'chenko, 1960), therefore I have relied mostly on Pharissat (1991), Bannikov (1993), and Monsch (2000) for their identification, morphology, and paleoecology. I have tentatively added a fourth genus (*Aglyptorhynchus* Casier, 1966) to the family, one that I have studied extensively (Fierstine, 2001a, 2005; H. Fierstine and R. Weems, California Polytechnic State University, unpubl. data). Both *Aglyptorhynchus* and *Palaeorhynchus* exhibit a downturned flange on their maxillae.

Homorhynchus, *Palaeorhynchus*, and *Pseudotetrapturus* are only represented by counterparts, some of them as whole skeletons, whereas *Aglyptorhynchus* is known from 3-dimensional bones, none as whole skeletons. Counterparts of palaeorhynchids have provided good information on measurements and meristics, but little on the morphology of individual bones, whereas specimens of *Aglyptorhynchus* have provided detailed knowledge of many individual bones, but no data on total number of vertebrae, morphology of fins, body depth or length, structure of lateral line, and scale pattern.

Homorhynchus is composed of three species, one from the middle Eocene of France, another from the middle Eocene of Belgium, and a third species from the early Oligocene of Switzerland and Russia (Monsch, 2000). Maximum body length is ca. 60 cm (Woodward, 1901). According to Danil'chenko (1960), the body length is about 8–12 times the body height, the rostrum is considerably longer than the lower jaw, there are 50–55 total vertebrae, number of rays in D1 are about twice the number of vertebrae, there is no D2 or A2, the caudal fin is hypurostegic, and pectoral and pelvic fins are present. *Homorhynchus colei* (Agassiz, 1844) has small scales, about 120–160 along the length of the body, and there are small teeth on the lower jaw and the posterior half of the rostrum. Monsch (2000) noted that the centra are slightly constricted and the neural and hemal spines are spine-like, not expanded as reported by Danil'chenko (1960).

Palaeorhynchus (Fig. 2) is composed of 9–11 species and is by far the most studied genus in the family. Specimens have been identified in the middle Eocene (Italy) (A. Bannikov, et al., Russian Academy of Sciences, unpubl. data), late Eocene (Russia), early Oligocene (Croatia, France, Italy, Iran, Yugoslavia), late Oligocene (Germany, Romania, Russia, Switzerland), and possibly the early Miocene (Germany, Switzer-

land). Monsch (2000) gave the following diagnosis for the genus: upper and lower jaws straight, elongated and of equal length; vertebrae 50–60 in number; dorsal fin elements about equal to the number of vertebrae.

Palaeorhynchus parini Bannikov, 1993 (late Eocene, Caucasus, Russia) is based on six specimens. Unusual morphological features of the species are as follows: 60 total vertebrae (37 are caudal), the posterior part of the maxillary projects ventrally, pectoral fins short and located high on body; pelvic fins long; a single hypural plate bearing a fused parhypural with a hypurapophysis; single epural; lower lobe of caudal fin longer than upper.

Pharisat (1991) studied over 300 specimens of *P. glarisianus* Blainville, 1818, from eastern France (early Oligocene) and his characterization of the species included: maximum size > 1.5 m total length, body length (without caudal fin) is ca. 10–12 times body height; rostra and lower jaws of equal length and both with six to seven rows of conical teeth; rostra ranging in length from one-half to two-thirds the length of the head; dorsal and anal fins high and elongate and each composed of three parts; small cycloid scales cover the entire body from head to hypural plate; lateral line sinuous; caudal fin forked and hypurostegic with the lower lobe slightly more elongate than the upper. Monsch (2000) noted that the dorsal and anal fins of *P. glarisianus* are single fins and do not represent anything other than an elongate D1 and A1, and that the neural and hemal spines are modified with distal plate-like extensions.

Pharisat (1991) discussed the paleoecology of the deposits in eastern France where *P. glarisianus* was collected. He concluded that the ocean was shallow, warm, and well oxygenated in the upper layers, but was poorly oxygenated with a high concentration of hydrogen sulfide at the bottom layer. Arambourg (1967) and Pharisat (1991) suggested that *Palaeorhynchus* inhabited the epipelagic zone and may have used the elongated ventral lobe of its caudal fin to assist feeding at the surface or to swim out of the water like a flying fish (e.g., *Cypselurus*). I disagree with their suggestion because the ventral lobe was not long or stiff enough to produce the thrust to suspend the body out of the water, and the pectoral fins were not long or stiff enough and the body lacked the squarish cross-section to provide the needed lift for gliding.

Pseudotetrapturus Danil'chenko, 1960 (late Eocene, Caucasus, Russia) is monotypic (*P. luteus* Danil'chenko, 1960) and is known by very few specimens. The holotype is a very poorly preserved head, thus its interpretation is equivocal. The species is characterized by a lower jaw that is nearly as long as the upper, jaws that are curved inward at their tip and bear tiny teeth, 45–50 vertebrae, and large cycloid scales. Maximum body size is estimated at 4 m.

Aglyptorhynchus (Fig. 3) is composed of ca. 10 species that are found in various deposits of the early Eocene (Belgium, England), middle Eocene (Belgium), late Oligocene (Belgium, U.S.A.), and middle Miocene (U.S.A.). The genus differs from other scombroid and xiphioid fishes by having a tripartite celous occipital condyle (Fig. 3C), an opisthocelous first vertebra (Fig. 3D), a maxilla with a large expanded ventral flange (Fig. 3B), and a well developed subtemporal fossa (Fierstine, 2005). The premaxillae fuse anteriorly into an elongated rostrum that contains (in cross-section) one to two pairs of large diameter lateral nutrient canals, and usually an unpaired central canal. The lower jaw has a fused symphysis and is deeper than the corresponding section of the rostrum, especially posteriorly. Longitudinal ridges and sulci cover the dorsal and lateral surfaces of the premaxillae and lateral surface of the dentaries (Figs. 3B, F). The ventral surface of each premaxilla and the dorsal surface

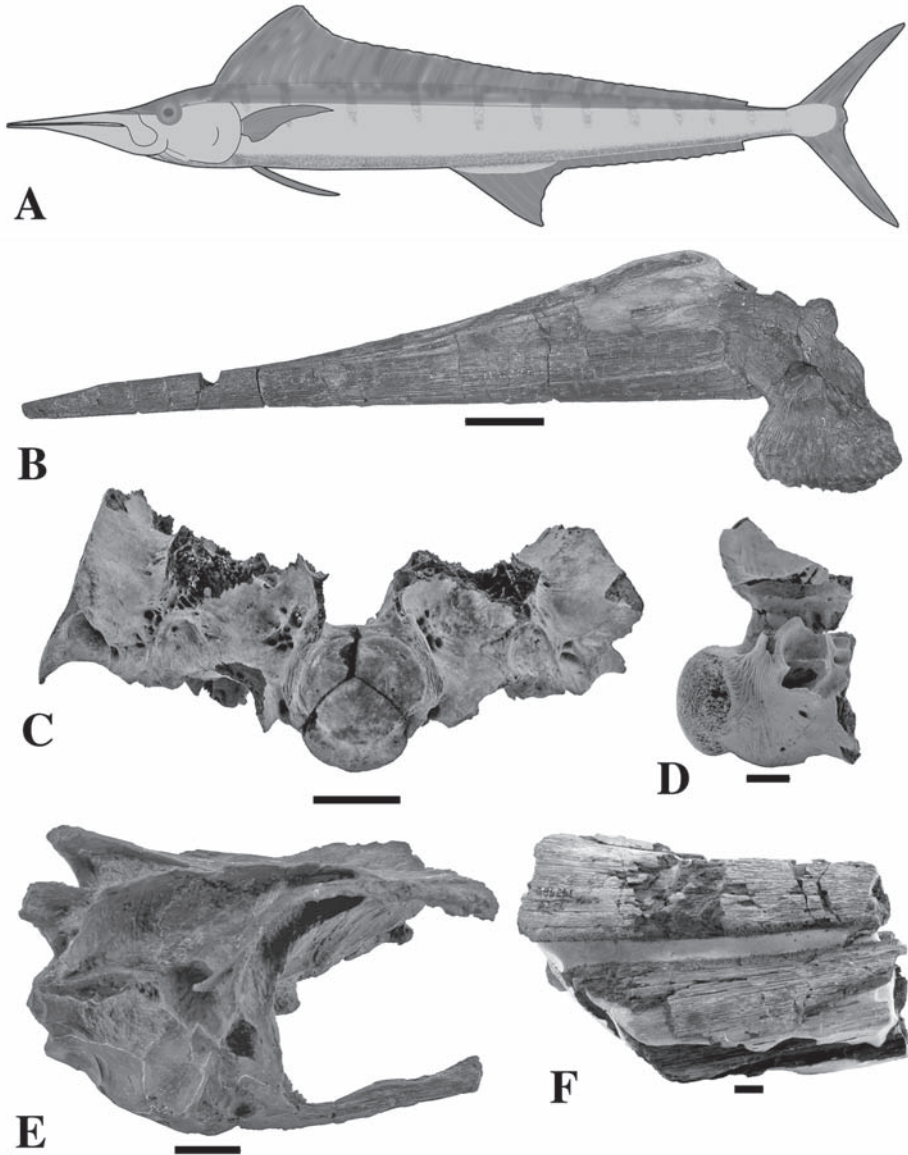


Figure 3. *Aglyptorhynchus* Casier, 1966. (A) Reconstruction of the external morphology of a generalized *Aglyptorhynchus*. (B) Left lateral view of the rostrum of *A. maxillaris* Fierstine, 2001a, (UCMP 123170), holotype, late Oligocene, Yaquina Formation, Oregon, U.S.A. (C) Posterior view of the neurocranium of *A. robustus* (Leidy, 1860), (ChM PV6951) Ashley Formation, late Oligocene, South Carolina, U.S.A. (D) Left lateral view of the first vertebra of *A. robustus*; museum number, formation and age same as C. (E) Right lateral view of the neurocranium of *A. columbianus* Fierstine, 2005, (UMBW 29536), late Oligocene, Lincoln Creek Formation, Washington, U.S.A. (F) Right lateral view of the partial rostrum and lower jaw of *A. columbianus* (LACM 143980), holotype; formation and age same as E. Scale equals 30 mm (B), 20 mm (C, E), and 10 mm (D, F).

of each dentary bear a band of villiform denticles (or their alveoli) approximately 2–20 denticles wide; the two bands on the fused section of the rostrum nearly join together, except for a narrow edentulous area. The maxillae have a large condyle for articulation with the ethmoid and the angular has a large depression on its lateral surface for a ligamentous attachment of the maxillary flange. Scales are large, oval, and cycloid.

Vertebrae of *Aglyptorhynchus* are usually discovered as isolated units, therefore the vertebral count is unknown. Centra are hourglass-shaped and amphicelous, except for the first vertebra. Fierstine and Weems (2004) reported that a specimen of five articulating precaudal vertebrae had elongated and expanded neural spines, and each spine articulated with the dorsal prezygapophysis posterior to it to form an overlapping unit. The expanded spines are thin and fragile, and their overlap probably does little to stiffen the axial skeleton. The caudal skeleton consists of at least four vertebrae, possibly five. The hypural plate is a large, fan-shaped structure with a shallow posterior notch. The parhypural is fused into the plate and bears a well-developed parhypurapophysis.

Aglyptorhynchus probably had a mobile rostrum due to the structure of its articulation with the ethmoid, and had a mobile head due to the ball and socket joint with the first vertebra. These are unusual features in a xiphioid fish. Based on figures and descriptions in Bannikov (1993), *P. parini* has a ventral flange on its maxilla and a caudal skeleton similar to *Aglyptorhynchus*. Danil'chenko (1960, plate 23, fig. 1) illustrated a series of vertebrae of *Pseudotetrapturus luteus*, each with a lateral ridge that looks nearly identical to the ridge on the middle precaudal vertebrae of *Aglyptorhynchus*. Possibly, similarities in the maxilla, middle precaudal vertebrae, and caudal skeleton are synapomorphic features of palaeorhynchids.

Remains of *Aglyptorhynchus* are found in strata that were deposited at various depths, types of water, and temperatures. Two strata, the London Clay (early Eocene) and Chandler Bridge Formation (late Oligocene, South Carolina), were probably deposited nearshore in a shallow (10–50 m), low energy, tropical environment (Taylor, 1978; King, 1981; Prothero, 1994; R. E. Weems, United States Geological Survey, pers. comm.). The Chandler Bridge Formation was deposited in an estuary or lagoon (Sanders et al., 1982). Two late Oligocene strata on the west coast of the U. S., the Lincoln Creek and Yaquina Formations, were deposited at depths > 100 m and at sea surface temperatures ranging from 20–24 °C (Fierstine, 2001a, 2005). The Pungo River Formation (middle Miocene, North Carolina) was deposited at a depth greater than 50–60 m in a warm-temperate to subtropical environment that persisted year-round (Purdy et al., 2001).

Blochiidae

The family Blochiidae (Fig. 4) is only known as counterparts from deposits at Monte Bolca (middle Eocene), Italy, with the exception that Schultz (1987) suggested some rostral fragments described by Darteville and Casier (1949) from the Congo (Eocene), might belong to *Blochius*. There is a single genus, *Blochius* Volta 1796, and three nominal species, *B. longirostris* Volta 1796, *B. macropterus* de Zigno 1887, and "*Blochius*" *moorheadi* Eastman 1911. Fierstine and Monsch (2002) redescribed, illustrated, and compared 63 specimens of *B. longirostris*, including the holotype

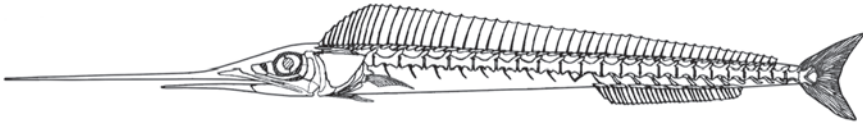


Figure 4. Skeletal reconstruction of *Blochius longirostris* Volta, 1796. From Fierstine and Monsch (2002).

and paratypes, and the only known specimens (holotypes) of *B. macropterus* and “*Blochius*” *moorheadi*, with its putative fossil and extant relatives. They concluded that “*Blochius*” *moorheadi* is a *nomen dubium* because it is too poorly preserved and defies an accurate interpretation. *Blochius macropterus* is a single specimen (right counterpart) that also is poorly preserved and difficult to interpret. Thus, the diagnosis of the Blochiidae is based on the morphology of *B. longirostris*.

Blochius longirostris has a rostrum composed of premaxillae that are usually longer than the lower jaw and that has longitudinal ridges and sulci; lower jaw with a fused symphysis; 24 elongate, hour-glass shaped vertebrae without neural spines (except for last few caudals); caudal complex composed of two vertebrae, one epural, and two hypural plates; two rows of large overlapping scutes running from opercle to caudal peduncle; D1 long and high, and probably depresses into a groove; A1 much shorter than D1; no D2 or A2; pelvic fins small; lunate caudal fin with hypurostegy. Due to the state of preservation of the specimens, Fierstine and Monsch (2002) were unable to obtain information on the morphology of the skull, dentition, and internal structure of the rostrum.

Based on an assessment of the paleoenvironment of Monte Bolca by Landini and Sorbini (1996) and on the morphology of *B. longirostris*, Fierstine and Monsch (2002) suggested that *B. longirostris* had a sinuous swimming pattern and engulfed its prey by swimming over its food, that it was restricted to shallow, tropical water (< 100 m) in the north central Tethys Sea, and inhabited and fed throughout the water column.

Xiphiidae

Fierstine and Monsch (2002) performed a cladistic analysis using morphological data on all well-defined extinct and extant billfishes. The analysis joined *Xiphias* Linnaeus, 1758, and *Xiphiorhynchus* into a sister group, thus they included them as monotypic subfamilies in the Xiphiidae. The discovery of a nearly complete head of a *Xiphiorhynchus*-like fish from the Early Oligocene of Austria (Fierstine and Pfeil, 2002) added new morphological data to support this relationship. The family Xiphiidae is characterized by a rostrum composed of paired premaxillae, an elongate ethmoid, and anterior extensions of the frontals; in cross-section the rostrum usually contains a central canal or series of central chambers; nasal is absent in adult; dentary with a fused symphysis; D1 and A1 are short; no pelvic fins; lack of visible scales in adult; precaudal vertebrae are cube-shaped vertebrae with a smooth surface texture; cleithrum with an elongate dorsal ramus.

Xiphiorhynchinae

The monotypic subfamily (and therefore, *Xiphiorhynchus*) (Fig. 5) is characterized by having a rostrum that is round to oval in cross-section and its ventral and ventrolateral surfaces are covered with villiform teeth (or their alveoli); in cross-section, the rostrum contains two pairs of lateral longitudinal canals with the more dorsal pair situated closer to the mid-line than the more ventral pair; lower jaw is robust and equal or subequal in length to the rostrum.

Xiphiorhynchus is composed of approximately nine species, plus the undescribed species mentioned by Fierstine and Pfeil (2002) from the Austrian Oligocene, that have been found in Eocene deposits of Belgium (*X. elegans* van Beneden, 1871), Egypt (*X. aegypticus* Weiler, 1929), England [*X. eocaenicus* (Woodward, 1901); *X. priscus* (Agassiz, 1844)], and U.S.A. [*X. cf. eocaenicus* (Woodward, 1901); *X. homalorhampus* (Cope, 1869); *X. kimblalocki* Fierstine and Applegate, 1974], and in the Oligocene deposits of Belgium [*X. rupeliensis* (Leriche, 1909)], Hungary [*X. hungaricus* Weiler, 1943], and the U.S.A. [*X. rotundus* (Woodward, 1901)]. What little we know about *Xiphiorhynchus* is based on fragmentary and poorly preserved specimens. Of the nine putative species, six are known only by the holotype, five are known only by a single rostral fragment, and one is known only by several isolated vertebrae. Two holotypes have been lost or misplaced (*X. homalorhampus* and *X. hungaricus*). With the exception of the undescribed specimen, *X. priscus* is the only species with a skull and no skull has been found articulated with a rostrum or vertebra.

The discovery of a fairly complete, well-preserved head (including anal, dorsal, and pectoral fins, and eleven articulating precaudal vertebrae) of a *Xiphiorhynchus*-like specimen from the early Oligocene, Austria (Fig. 5B), offers a unique opportunity to learn more about the morphology of the Xiphiorhynchinae (Fierstine and Pfeil, 2002). Because the specimen is so complete and its morphology is somewhat different than the skulls attributed to *X. priscus*, I based my diagnosis of both the Xiphiidae and Xiphiorhynchinae (see above) partly on the anatomy of the Austrian specimen.

Other recent advances in our knowledge of *Xiphiorhynchus* are as follows: The holotype of *X. rotundus* (Woodward, 1901) is a poorly preserved rostrum with the vague provenance of Tertiary phosphate beds near Charleston, South Carolina. Monsch et al. (2005) described additional specimens of *X. rotundus* (Fig. 5C) that were collected in the Charleston region, and were able to narrow the age of the specimen to late Oligocene or early Miocene. The holotype of *X. eocaenicus* (Woodward, 1901), a distal rostrum, probably was collected in the Selsey Formation (early middle Eocene), England. It was the only known specimen until Fierstine and Starnes (2005) identified a distal rostrum from the Moodys Branch Formation, late middle Eocene, Mississippi, as *Xiphiorhynchus cf. X. eocaenicus*. They noted that this discovery represents the first record of a species of *Xiphiorhynchus* in deposits on both sides of the North Atlantic Ocean. Since the original discovery of *X. kimblalocki* Fierstine and Applegate, 1974, in the Yazoo Clay Formation (late Eocene, Mississippi) (Fig. 5D), additional specimens have been recovered from the Yazoo Clay Formation in Louisiana (Fierstine and Stringer, unpubl. data). In their study of the late Cenozoic marine deposits in the Sacaco area of Peru, de Muizon, and DeVries (1985) list *cf. Xiphiorhynchus* in the Pisco Formation (late early Pliocene). There was no description of the specimen(s), and I doubt their identification was correct, particularly since this record would extend the last appearance of the genus approximately 20 million yrs.

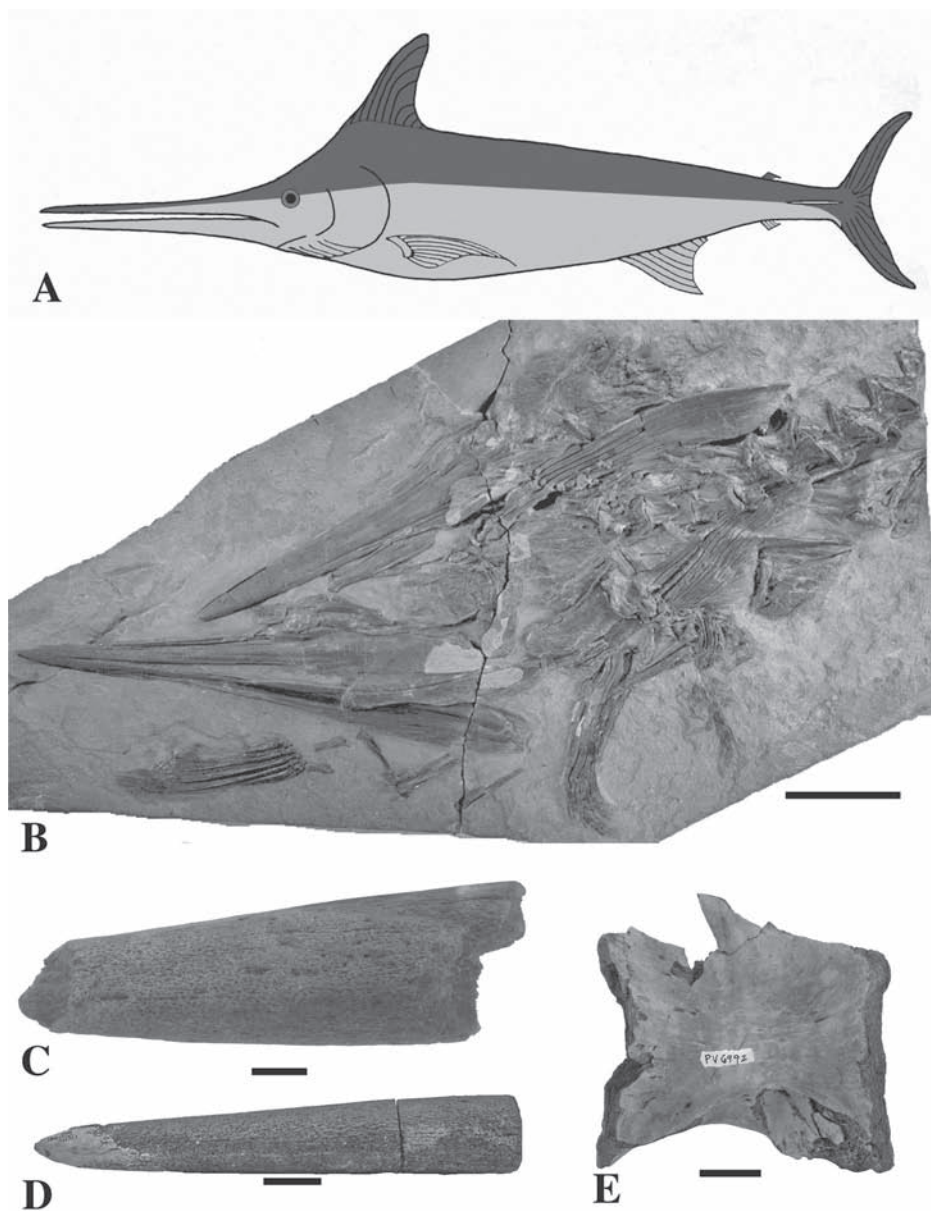


Figure 5. *Xiphiorhynchus* van Beneden, 1871. (A) Reconstruction of the external morphology of a generalized *Xiphiorhynchus*. (B) Head and anterior vertebrae of an undescribed *Xiphiorhynchus*-like billfish (BSM 1984 I 60), Paisslberg Formation, early Oligocene, Austria. (C) Left lateral view of a partial distal rostrum of *X. rotundus* Woodward, 1901, (ChM PV4864), Chandler Bridge Formation, late Oligocene, South Carolina, U.S.A. (D) Left lateral view of the distal rostrum of *X. kimblalocki* Fierstine and Applegate, 1974, holotype, (LACM 25575.1), Yazoo Clay Formation, late Eocene, Mississippi, U.S.A. (E) Right lateral view of an abdominal vertebra of *Xiphiorhynchus* sp. (ChM PV6992), Ashley Formation, late Oligocene, South Carolina, U.S.A. Scale equals 20 cm (B), 20 mm (C–E).

Monsch (2005) reexamined and refigured the holotype of *X. parvus* Casier, 1966 (BMNH P.21306), a small distal rostrum from the London Clay (early Eocene), and concluded that it lacked an important diagnostic feature of *Xiphiorhynchus* by having only two (one pair) nutrient canals rather than four (two pair). Monsch did not align the specimen with any billfish family or genus.

If determined by consensus, *Xiphiorhynchus* normally inhabited shallow, near-shore, marine water in a tropical setting (Casier, 1966; Taylor, 1978; Sanders, 1980; Breard, 1991). Exceptions include some specimens of *X. priscus* that were associated with a deepwater ichthyofauna based on otoliths (Stinton, 1966), and the holotype of *X. kimblalocki* that was collected in a deposit that accumulated in a deep, marine environment (Manning, 2003).

Xiphiinae

This monotypic subfamily (Fig. 6) is characterized by having a rostrum that is flat in cross-section and lacks dentition in the adult; in cross-section, the rostrum contains only one pair of lateral longitudinal canals and usually a series of central chambers; lower jaw is weak and much shorter than the rostrum.

The fossil record of *X. gladius* is sparse. Most specimens were collected in the Italian Pliocene. In the only exception to the Pliocene age, Jermanska (1962) identified a segment of an articulated vertebral column with partial dorsal and anal fins, from the middle Miocene of Poland, as a juvenile specimen of *Xiphias* sp. Lawley (1876) identified several rostral fragments from the Italian Pliocene as *X. delfortrieri*, but they were reidentified by Santucci (1923) as *X. gladius*. Sorbini (1988) illustrated, but did not describe, a fairly complete specimen (Fig. 6B) from the Marecchia River deposit (early to middle Pliocene) of eastern central Italy, and Purdy et al. (2001) described a rostral fragment from the Yorktown Formation (early Pliocene), Lee Creek

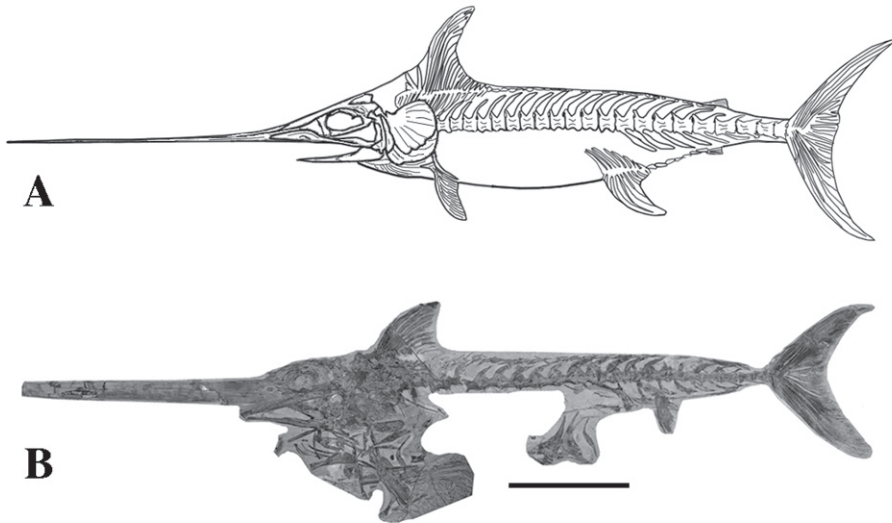


Figure 6. *Xiphias gladius* Linnaeus, 1758. (A) Skeletal reconstruction (modified from Gregory and Conrad, 1937). (B) Lateral view of a nearly complete specimen (MCSNV 106), Marecchia River (early to middle Pliocene), Italy. Scale equals 20 cm (B).

Mine, North Carolina. The only other specimens known are from Holocene (Recent) deposits associated with human activity (Poplin, 1975; Davenport et al., 1993; Johnson, 1993).

Based on an analysis of the fish fauna collected at the Marecchia River locality, Sorbini (1988) considered the environment similar to the modern Atlantic-Mediterranean biogeographic region. He believed that the water depth was often over 100 m, but not far from shore, and the climate was subtropical. Purdy et al. (2001) discussed the paleoecology of the Yorktown Formation and concluded that it represented a mixture of tropical, warm-temperate, and cool-temperate fish that preferred temperature ranges observed off Cape Hatteras, NC today. They also suggested that the water depth was > 50 m and that deposition occurred in the deeper part of the inner shelf.

Monsch (2005) described two distal rostra from the London Clay (early Eocene) as having a near circular cross-section with a large central canal and two (one pair) lateral nutrient canals, and their ventral and lateral surfaces covered with villiform teeth. On the basis of this mix of characters, he established a new genus and species, *Rotundorhynchus brittanicus* Monsch, 2005, but was unable to ally the new genus with any particular billfish clade. The specimens are small (ca. 80 mm long and 20 mm in diameter) and poorly preserved. Until better material is available, the status of *Rotundorhynchus* will remain an enigma.

Istiophoridae

This extant family (Fig. 7) is composed of three genera (Nelson et al., 2004), *Istiophorus* Lacépède, 1801 (one species), *Makaira* Lacépède, 1802 (seven species), and *Tetrapturus* Rafinesque, 1810 (five species). They differ from other xiphioids by the following autapomorphies: prenasals are included in the posterior half of the rostrum; rostrum is round to oval in cross-section with one pair of lateral longitudinal nutrient canals; lower jaw with a toothed prementary at the distal tip; and 24 vertebrae mostly with interlocking neural and hemal spines and zygapophyses to form a stiff unit. Istiophorids are found worldwide in temperate to tropical seas and most species inhabit the oceanic realm.

Istiophorus solidus (van Beneden, 1871), late Eocene, Belgium, is a poorly preserved rostral fragment with one pair of round nutrient canals that are placed more toward the periphery than in other istiophorids. Paired grooves run the length of the dorsal surface and indicate the presence of prenasal bones. The specimen is probably an istiophorid, but its morphology is unlike any known species of extinct or extant billfish. Because most early workers placed fossil billfish of disparate morphologies in *Istiophorus*, Fierstine (2001b) renamed the specimen "*Istiophorus solidus*" to recognize its importance without establishing a new genus.

Istiophorus is monotypic [*I. platypterus* (Shaw and Nodder, 1792)] and has been found in deposits of late Miocene (Virginia), early Pliocene (North Carolina), and late Pliocene (California) age (Gottfried, 1982; Fierstine, 1998, 2001b). Although extant *I. platypterus* is readily identified by the sail-like first dorsal fin and the elongate pelvic fins (Nakamura, 1985), these characters are unknown in fossil sailfish. Two maxillae and five rostra of *I. platypterus* were identified in deposits at Lee Creek Mine (Yorktown Formation, early Pliocene, NC) (Fierstine, 2001b) and Gottfried (1982) identi-

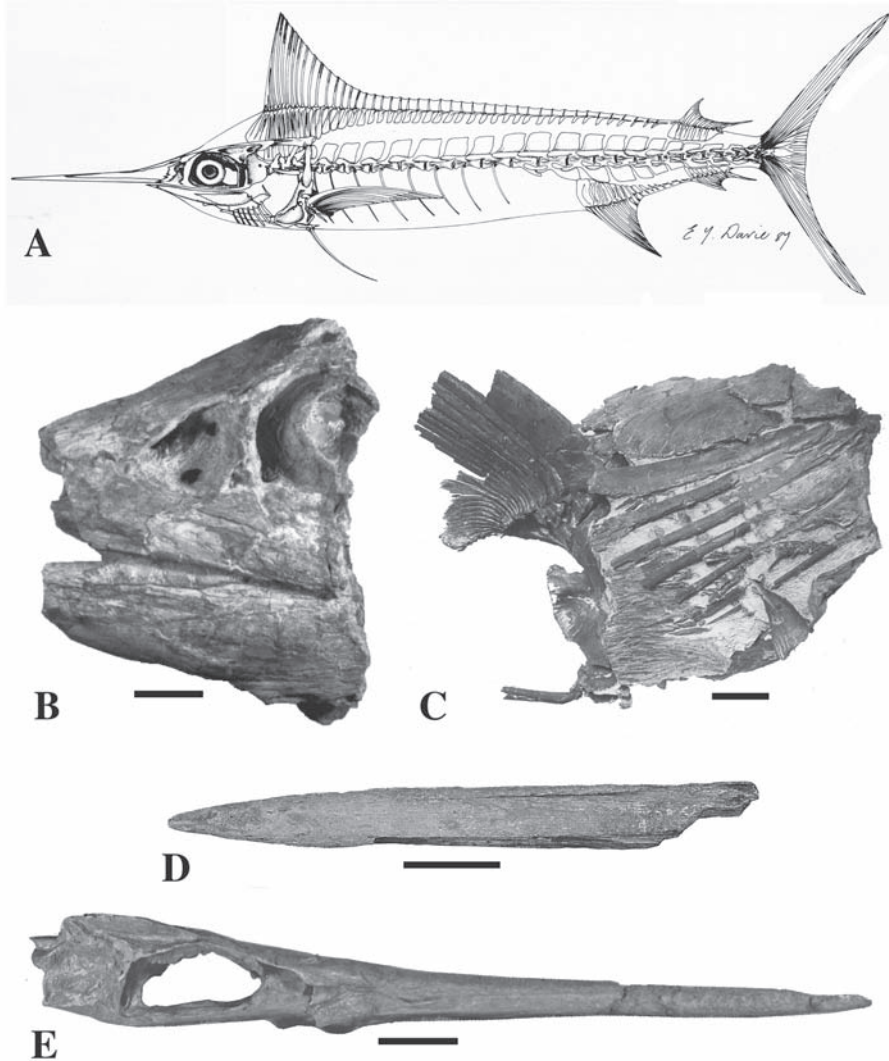


Figure 7. *Makaira* Lacépède, 1802. (A) Skeletal reconstruction of *M. nigricans* Lacépède, 1802, (from Davie, 1990). (B) Partial skull of *M. nigricans*, (IGM 7889), Trinidad Formation, late Miocene to late Pliocene, Baja California Sur, Mexico, left lateral view. (C) Right ventro-lateral view of the throat region (with pectoral and pelvic fins) of *M. indica* (Cuvier, 1832), (no museum number), (?)Cabatuan Formation, early Pleistocene, Northwest Central Luzon, Philippines. (D) Dorsal view of the rostrum of *Istiophorus calvertensis* Berry, 1917, holotype (USNM 9344), Eastover Formation, late Miocene, Virginia, U.S.A. (E) Right lateral view of the neurocranium and rostrum of *M. panamensis* Fierstine, 1978, holotype (USNM 181710), Chagres Sandstone, Late Miocene, Panama. Scale equals 5 cm (B–D), 10 cm (E).

fied a single, incomplete trunk vertebra from the San Diego Formation (late Pliocene, CA) as *I. platypterus*. There are two records of sailfish-like specimens. *Istiophorus* cf. *I. platypterus* was identified at Lee Creek Mine from one rostrum and one hypural, and *I. calvertensis* Berry, 1917, a distal rostrum (Fig. 7D), collected in the Eastover Formation (late Miocene, VA), was reidentified as *Istiophorus* cf. *I. platypterus* (Fierstine, 1998; 2001b).

Makaira belgicus (Leriche, 1926) (middle Miocene, Belgium) is a distal rostral fragment, and is the oldest known species of the genus. Schultz (1987) gave the age of the specimen as late Miocene, but I have been unable to corroborate his decision. It is very similar morphologically to the rostra of extant *M. nigricans* and of *M. nigricans* from Lee Creek Mine, except for the position of the nutrient canals within the rostrum (Fierstine, 2001b). *Makaira courcelli* (Arambourg, 1927) (early Pliocene, Algeria) consists of two rostra and several rostral fragments. Because the internal anatomy of the rostra is unknown (specimens have never been sectioned or CT scanned), it is difficult to make a meaningful comparison with other fossil and extant istiophorids (Fierstine, 2001b). *Makaira panamensis* Fierstine, 1978 (late Miocene or early Pliocene, Panama) was described from a large neurocranium with a poorly preserved rostrum attached (Fig. 7E). The rostrum was too badly crushed to provide useful comparative data. *Makaira teretirostris* (van Beneden, 1871) (?middle Miocene, Belgium) is a large, distal rostral fragment with paired nutrient canals and prenasal bones. The original description of the specimen was based on a cast and an artist's drawing, and disposition of the specimen itself is unknown. Schultz (1987) gave the type locality as southern France and age as Pliocene. Without more morphological information, Fierstine (2001b) was unable to make an accurate comparison with rostra of other extinct and extant billfishes. *Makaira purdyi* Fierstine, 1999b (early Pliocene, North Carolina) was identified from a single distal rostrum. It is morphologically distinct from any extant or extinct istiophorid by having the following combination of characters: (1) premaxillae are short and stout with denticles covering at least the distal one-half of its dorsal surface; (2) at the distal one-fourth of the length of the rostrum, the cross-section is nearly round (Fierstine, 2001b).

There are three fossil records of black marlin [*Makaira indica* (Cuvier, 1832)] or black marlin-like (*Makaira* cf. *M. indica*) specimens. The oldest record of *M. indica* is from Lee Creek Mine (early Pliocene), an identification based on four predentaries and two scapulae (Fierstine, 2001b). In this case, the identifications based on predentaries are flimsy evidence, but the scapulae are quite characteristic of black marlin, with each having a narrow, flat articular surface for the first pectoral fin ray (Wapenaar and Talbot, 1964). A nearly complete head (including pectoral and pelvic girdles and fins) of *M. indica* (Fig. 7C) was collected from the ?Cabatuan Formation (early Pleistocene), Luzon, Philippines (Fierstine and Welton, 1983). *Makaira* cf. *M. indica* was identified at Lee Creek Mine on the basis of a single, partial scapula.

Blue marlin (*Makaira nigricans* Lacépède, 1802) or blue marlin-like specimens are the most common fossils of the Istiophoridae. The earliest records are from the late Miocene where *M. nigricans* was identified in three deposits in southern California (Fierstine, 2001b), and *M. cf. M. nigricans* was identified in the Eastover Formation, Virginia (Fierstine, 1998), the Gatún Formation, Panama (Fierstine, 1999a), and the Pietra Leccese, Italy (Carnevale et al, 2002). The southern California specimens were originally identified as *Makaira* sp. (Fierstine and Applegate, 1968; Fierstine and Welton, 1988), but were re-identified by Fierstine (2001b) after more skeletal material of extant istiophorids became available. A large skull (Fig. 7B) and several rostra of blue marlin have been recovered from the Trinidad Formation, Baja California Sur, Mexico (late Miocene to Late Pliocene) (Fierstine et al., 2001). *Makaira nigricans* was the fossil istiophorid most commonly recovered at Lee Creek Mine (early Pliocene) (Fierstine, 2001b), where out of over 500 istiophorid specimens examined, 38 of them were rostra of *M. nigricans*. Besides the late Miocene specimens noted above,

31 specimens (mostly vertebrae) of *M. cf. M. nigricans* were identified at Lee Creek Mine (Fierstine, 2001b).

Schultz (1996) identified two rostral fragments from the early Pliocene, Spain, and Fierstine (2001b) identified five rostra and six other elements from Lee Creek Mine as *Makaira* sp. Four small, hourglass-shaped vertebrae from the London Clay (early Eocene), England were identified as *Makaira* sp. (Monsch, 2005). I question Monsch's identification because vertebrae are difficult to identify to genus or species, their morphology is unlike any istiophorid vertebra I have ever examined, and the age of the deposit is 20–30 Ma older than previously known for any other istiophorid.

The only records of the genus *Tetrapturus* are from Lee Creek Mine where Fierstine (2001b) identified 14 non-rostral elements as white marlin, *T. albidus* Poey, 1860 and two maxillae as white marlin-like, *T. cf. T. albidus*. He had reservations about recognizing these specimens as *T. albidus* because identifications were based on poorly preserved material.

Sometimes there are conflicting views on the depositional environment of strata containing fossil istiophorids. For example, Kimmel and Purdy (1984) concluded that the Eastover Formation represents a nearshore, shallow, cool-temperate environment, based on bottom fish, whereas Ward and Blackwelder (1980) concluded that the formation represented an open, pelagic, warm-temperate environment based on mollusks. There are other examples in the literature (Fierstine and Welton, 1988; Fierstine, 1998).

Most often, there are no conflicting views. Based on geological evidence, Gibson (1983) concluded that zone 1 of the Yorktown Formation at Lee Creek Mine (early Pliocene) was deposited at water depths of 80–100 m, a conclusion that was basically in agreement with Purdy et al. (2001). The black marlin bearing strata of the Cabatuan Formation (early Pleistocene, Philippines) was deposited in water slightly deeper than 300 m (Fierstine and Welton, 1983), and the istiophorid bearing strata of the Trinidad Formation (late Miocene–late Pliocene, Baja California Sur) was deposited far offshore at a water depth of at least 100 m (Fierstine et al., 2001).

HABITAT PREFERENCES AND DISTRIBUTIONAL PATTERNS

Fierstine (1998, 2001b) hypothesized that fossil istiophorid billfishes had ecological preferences and distributional patterns similar to extant istiophorids, a hypothesis based on the assumption that fossil and extant istiophorids were similar physiologically. This hypothesis has tacitly been extended to include fossil and extant *Xiphias* (Fierstine and Starnes, 2005). Although the hypothesis sounds reasonable, there is no way to prove it, and if there is conflicting evidence, one tends to choose the evidence that supports the hypothesis. As noted above, sometimes there are conflicting data as to the depositional environments of strata that contain billfishes, so the paleontologist often chooses the environment that is similar to the habitat of extant billfishes (i.e., oceanic with a water depth of at least 100 m). For example, Fierstine and Weems (2004) reported that *X. rotundus* in the Chandler Bridge Formation (late Oligocene, South Carolina), a shallow, lagoonal habitat, grew to become giant fish, probably over 5–6 m in total length. Fish of this size would not normally inhabit shallow water. Fierstine and Starnes (2005) tried to explain the presence of *X. eocaenicus*, another supposed giant oceanic fish, in two middle Eocene shallow water deposits and concluded that because they are remains of rostra, the specimens were either

transported into shallow water by ocean currents, as stomach contents if specimens were eroded, as remains of a stranded individual, or as remains of an animal (e.g., a whale) that had been impaled previously in deeper water.

Distributional patterns of fossil billfishes are explained in much the same way as ecological preferences, that is they are based on (biased by?) the distributions of extant billfishes. For example, the presence of *M. indica* at Lee Creek Mine (early Pliocene, North Carolina) was explained as having migrated from the Pacific Ocean via the Panama Seaway rather than around the Cape of Good Hope from the Indian Ocean (Fierstine, 2001b). On the other hand, Fierstine (2001a) explained the presence of *Aglyptorhynchus* in the eastern Pacific Ocean as having migrated in the opposite direction, i.e., from the Atlantic Ocean via the Panama Seaway rather than a transpacific migration from the Tethys Sea. Carnevale et al. (2002) explained the presence of *M. cf. M. nigricans* in the Mediterranean Sea during the late Miocene (blue marlin are absent from the Mediterranean today) by the billfish migrating from the Indian Ocean via the narrow, soon-to-be closed Tethys Seaway or possibly from the Atlantic Ocean via a shallow portal in Spain or a shallow corridor in Morocco.

Not all distribution patterns are hypothetical. For example, there are three records of the genus *Makaira* from late Miocene deposits of southern California (Fierstine and Applegate, 1968; Fierstine and Welton, 1988; Fierstine, 2001b). Although there are published records of extant *M. nigricans* as far as 35°N in the eastern Pacific Ocean (Nakamura, 1985), extant blue marlin are considered rare off southern California today (Eschmeyer et al., 1983). Thus, the fossil record of *M. nigricans* provides evidence that the coastal paleoclimate of southern California was warmer than at present (Fierstine and Welton, 1988).

LOSS OF JAWS OF EQUAL LENGTH IN EXTANT BILLFISHES

Is there a functional explanation for extant billfishes having their rostra extend well beyond their lower jaws, whereas most extinct billfish genera (e.g., *Aglyptorhynchus*, *Palaeorhynchus*, *Xiphiorhynchus*) have upper and lower jaws of equal length? Based on the knowledge that modern billfishes sometimes use their rostrum for defense and food capture (Frazier et al., 1994), if jaws of equal length were used to impale prey or a predator, both jaws would probably be closed or nearly closed during the act of stabbing. After the initial thrust, the billfish would need to withdraw its jaws from the object fairly quickly in order to pass water over its gills for respiration. Withdrawal from small prey would probably not be a problem, but withdrawal from large predators (e.g., sharks or other billfishes) could be difficult. It is well known that sometimes healthy istiophorid billfishes are captured with foreshortened bills (Frazier et al., 1994) and that sometimes sharks and billfishes have been captured with one or more bills impaled in their body (Fierstine, 1997; Fierstine et al., 1997). Thus, withdrawal can be difficult with only a rostrum, but the extinct billfish would need to withdraw both jaws. Istiophorids can remain healthy with a foreshortened rostrum (they are not regenerated), but if the loss included a foreshortened lower jaw as well, I doubt it would be able to continue to capture prey and would starve. Thus, a billfish having an elongate rostrum and shorter lower jaw is probably better adapted for impaling prey and predator than jaws of equal length. This argument might not hold for *Xiphias*, because to the best of my knowledge, no swordfish has been caught with a foreshortened rostrum, even though numerous objects (e.g., deep

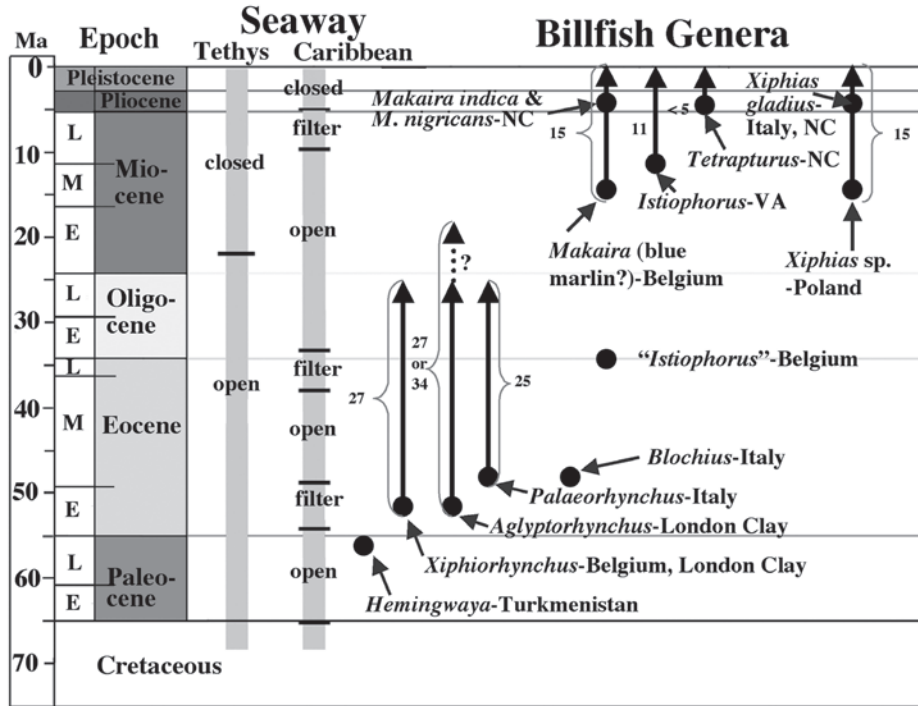


Figure 8. First appearance and last appearance of various genera of billfish in relation to the geologic time scale (Gradstein et al., 2004) and evolution of the Caribbean (Ituralde-Vinent, 2003) and Tethys (Rögl, 1998) seaways during the Cenozoic. Modified from Dickson and Graham (2004).

sea submersibles, marine turtles, whales) have been found with broken swordfish bills impaled in them (Frazier et al., 1994). However, the swordfish tends to slash its prey, not impale them (Scott and Tibbo, 1968), thus use of its bill for impalement may only be a desperate act of defense or an error in judging distance when feeding under floating or slow moving objects (Frazier et al., 1994).

CONCLUSIONS AND FUTURE DIRECTIONS OF RESEARCH

There are five families of fossil and extant billfishes (six if you believe the subfamilies Xiphiinae and Xiphiorhynchidae deserve family status) (Fig. 8). Hemingwayidae from the late Paleocene of Turkmenistan, is the oldest billfish family. The first appearance (FA) of each of the families occurred in the region of the Tethys Sea (or Paratethys), except for the subfamily Xiphiinae that first appeared in the western North Atlantic Ocean. Two of the families (Hemingwayidae and Blochiidae) have never been found outside their type locality and chronostratigraphic unit. Three genera, *Aglyptorhynchus*, *Palaeorhynchus*, and *Xiphiorhynchus* were in existence for approximately 27 Ma, i.e., the time that elapsed between their FA and last appearance (LA). The times between the FA and present for the extant genera *Istiophorus*, *Makaira*, *Tetrapturus*, and *Xiphias* are 11 Ma, 15 Ma, < 5 Ma, and < 15 Ma, respectively.

There is at least a 5 Ma gap in the fossil record between the FA of all extant billfish genera (excluding the questionable "*Istiophorus solidus*") and the LA of any extinct billfish genus. There is a gap of 10 Ma between the LA of the Xiphiorhynchinae and

the FA of the Xiphiinae. If the two subfamilies are truly sister taxa, then you would expect them to overlap or be continuous. Greater scrutiny of museum collections from the early and middle Miocene (e.g., Astoria Formation, Oregon, U.S.A.; Calvert and Choptank formations, eastern U.S.A.) should help complete our knowledge of the paleohistory of the Istiophoridae and Xiphiidae.

There are numerous other areas of fruitful and pending research. The study of the fairly complete head of a *Xiphiorhynchus*-like billfish from the Austrian Oligocene that is being completed by Fierstine and Pfeil (2002) will provide details about the subfamily heretofore unknown. The analysis of the fish fauna of the Ashley and Chandler Bridge formations, South Carolina, as reported by Fierstine and Weems (2004), will elucidate the morphology of the lower jaw and vertebrae of *Aglyptorhynchus*. Finally, a detailed cladistical analysis of both extinct and extant billfishes using both morphological and molecular data should provide meaningful phylogenetic relationships between the Scombroidei and Xiphiodei and within the Xiphiodei.

ACKNOWLEDGMENTS

This review would not have been possible without the vision of amateur collectors and the assistance of professionals at museums and universities who allowed me to examine specimens in their custody. These individuals were identified in my previous publications and for the sake of brevity they will not be acknowledged again here. B. Collette and an anonymous reviewer suggested important changes to the paper to make it more accurate and readable. A. Fierstine deserves special recognition for her continued support and encouragement of my research interests.

LITERATURE CITED

- Agassiz, L. 1833–44. Recherches sur les poissons fossiles. Histoire de l'Ordre des Ganoïdes. 2: 255–257, plate 44, 3 figures; 5: 1–222. Neuchatel.
- Arambourg, C. 1927. Les Poissons fossiles d'Oran. Matériaux pour la Carte géologiques de l'Algérie, Série 1, Paleontologie 6: 1–298.
- _____. 1967. Résultats scientifiques de la mission C. Arambourg en Syrie et en Iran (1938–1939). II. Les Poissons Oligocènes de l'Iran. Notes et Mém. sur le Moyen-Orient, Mus. Natn. Hist. Nat. Paris. 8: 9–247.
- Bannikov, A. F. 1993. A new species of the genus *Palaeorhynchus* (Perciformes, Palaeorhynchidae) from the Upper Eocene in the Northern Caucasus. J. Ichthyol. 33: 50–56.
- van Beneden, P. J. 1871. Recherches sur quelques poissons fossiles de Belgique. Bull. Acad. Royale de Belgique, 2nd série, 31: 493–518.
- _____. 1873. Notice sur un nouveau poisson du terrain Bruxellien. Bull. Acad. Roy. Belgique, 2nd série, 35: 255–259.
- Berry, E. W. 1917. A sailfish from the Virginia Miocene. Am. J. Sci. 43: 461–464.
- Blainville (Ducrotay de), H. M. 1818. Poissons fossiles. Nouveau dictionnaire d'Histoire Naturelle, appliqué aux Arts, -à l'Agriculture, à l'Economie rurale et domestique, à la Médecine, etc. 27: 310–395.
- Breard, S. Q., Jr. 1991. Paleoecology of a late Eocene (Bartonian) vertebrate fauna, Moodys Branch Formation, Techeva Creek, Mississippi. Trans. Gulf Coast Assoc. Geol. Soc. 41: 43–55.
- Carnavale, G., C. Sorbini, W. Landini, and A. Varola. 2002. *Makaira* cf. *M. nigricans* Lacépède, 1902 (Teleostei: Perciformes: Istiophoridae) from the Pietra Leccese, Late Miocene, Apulia, Southern Italy. Palaeontograph. Italica 88: 63–75.
- Casier, E. 1966. Faune ichthyologique du London Clay. London, British Museum (Nat. Hist.), 2 vols. 496 p., 68 pls.

- Collette, B. B., J. R. McDowell, and J. Graves. 2006. Phylogeny of recent billfishes (Xiphoidei). *Bull. Mar. Sci.* 79: 455–468.
- Cope, E. D. 1869. Descriptions of some extinct fishes previously unknown. *Proc. Boston Soc. Nat. Hist.* 12: 310–317.
- Cuvier, G. 1832. *Tetrapturus indicus* in G. Cuvier and A. Valenciennes, eds. *Histoire Naturelles Poissons* 8: 554–626.
- Daniilchenko, P. G. 1960. Bony fishes of the Maikop Deposits of the Caucasus. (Originally in Russian, translated by A. Mercado, Israel Program for Scientific Translations, Jerusalem, 1967). *Trudy Paleo. Inst. Akad. Nauk SSSR* 78: 1–248.
- Darteville, E. and E. Casier. 1949. Les poissons fossils du Bas-Congo et des regions voisines. (Deuxième Partie). *Ann. Mus. Roy. Congo Belge, Series A*, 2: 201–256.
- Davenport, D., J. R. Johnson, and J. Timbrook. 1993. The Chumash and the swordfish. *Antiquity* 67: 257–272.
- Davie, P. S. 1990. Pacific marlins: anatomy and physiology. Massey University Press, Palmerston North, New Zealand. 88 p.
- Dickson, K. A. and J. B. Graham. 2004. Evolution and consequences of endothermy in fishes. *Physiol. Biochem. Zool.* 77: 998–1018.
- Eastman, C. R. 1911. Catalog of fishes in the Carnegie Museum. Part 1. Fishes from the Upper Eocene of Monte Bolca. *Mem. Carnegie Mus., Pittsburgh* 4: 349–391.
- Eschmeyer, W. N., E. S. Herald, and H. Hammann. 1983. A field guide to Pacific coast fishes of North America from the Gulf of Alaska to Baja California. Houghton Mifflin Company, Boston. 336 p.
- Fierstine, H. L. 1974. The paleontology of billfish—the state of the art. Pages 34–44 in R. S. Shomura and F. Williams, eds. *Proc. Int. Billfish Symposium, Kailua-Kona, Hawaii*, 9–12 August 1972. Part 2. Contributed Papers. NOAA Tech. Rept. NMFS (Nat. Mar. Fish. Serv.) Spec. Sci. Rept. 675 p.
- _____. 1978. A new marlin, *Makaira panamensis*, from the Late Miocene of Panama. *Copeia* 1978: 1–11.
- _____. 1990. A paleontological review of three billfish families (Istiophoridae, Xiphiidae, and Xiphiorhynchidae). Pages 11–19 in R. H. Stroud, ed. *Planning the future of billfishes. Part 2. Contributed papers. Proc. 2nd Int. Billfish Symp., Kailua-Kona, Hawaii*, August 1–5, 1988.
- _____. 1997. An Atlantic Blue Marlin, *Makaira nigricans*, impaled by two species of billfishes (Teleostei: Istiophoridae). *Bull. Mar. Sci.* 61: 495–499.
- _____. 1998. *Makaira* sp. cf. *M. nigricans* Lacépède, 1802 (Teleostei: Perciformes: Istiophoridae) from the Eastover Formation, Late Miocene, Virginia, and a reexamination of *Istiophorus calvertensis* Berry, 1917. *J. Vert. Paleo.* 18: 30–42.
- _____. 1999a. *Makaira* sp. cf. *M. nigricans* Lacépède, 1802 (Teleostei: Perciformes: Istiophoridae) from the Late Miocene, Panama, and its probable use of the Panama Seaway. *J. Vert. Paleo.* 19: 430–437.
- _____. 1999b. A new shortbilled marlin of the genus *Makaira*, from the Yorktown Formation (Early Pliocene), eastern North Carolina at Lee Creek Mine, USA. *Tertiary Res.* 19: 71–77.
- _____. 2001a. A new *Aglyptorhynchus* (Perciformes: Scombroidei: †Blochiidae) from the Late Oligocene of Oregon. *J. Vert. Paleo.* 21: 24–33.
- _____. 2001b. Analysis and new records of billfish (Teleostei: Perciformes: Istiophoridae) from the Yorktown Formation, Early Pliocene of eastern North Carolina at Lee Creek Mine. Pages 21–69 in C. E. Ray and D. J. Bohaska, eds. *Geology and paleontology of the Lee Creek Mine, North Carolina, III. Smith. Contrib. Paleobiol.* 90.
- _____. 2005. A new *Aglyptorhynchus* (Perciformes: Scombroidei) from the Lincoln Creek Formation (late Oligocene, Washington, U.S.A.). *J. Vert. Paleo.* 25: 288–299.
- _____ and S. P. Applegate. 1968. Billfish remains from southern California with remarks on the importance of the prementary bone. *Bull. Southern California Acad. Sci.* 67: 29–39.

- _____ and _____. 1974. *Xiphiorhynchus kimblalocki*, a new billfish from the Eocene of Mississippi with remarks on the systematics of xiphioid fishes. *Bull. Southern California Acad. Sci.* 73: 14–22.
- _____ and K. A. Monsch. 2002. Redescription and phylogenetic relationships of the Family Blochiidae (Perciformes: Scombroidei), middle Eocene, Monte Bolca, Italy. *Miscellanea Paleontologica, Studi e Ricerche sui Giacimenti Terziari di Bolca, Mus. Civico Storia Nat. Verona* 9: 121–163.
- _____ and F. Pfeil. 2002. A new species of xiphiorhynchid billfish (Perciformes: Scombroidei) from the Austrian Alps (early Oligocene). *J. Vert. Paleo.* 22 (3, Supplement): 53A.
- _____ and J. E. Starnes. 2005. *Xiphiorhynchus* cf. *X. eocaenicus* (Woodward, 1901), (Scombroidei: Xiphiidae: Xiphiorhynchinae) from the Middle Eocene of Mississippi, the first transatlantic distribution of a species of *Xiphiorhynchus*. *J. Vert. Paleo.* 25: 280–287.
- _____ and R. E. Weems. 2004. A fine catch of billfish from the Oligocene of South Carolina. *J. Vert. Paleo.* 24(3, supplement): 57A.
- _____ and B. J. Welton. 1983. A black marlin, *Makaira indica*, from the early Pleistocene of the Philippines and the zoogeography of istiophorid fishes. *Bull. Mar. Sci.* 33: 718–728.
- _____ and _____. 1988. A late Miocene marlin, *Makaira* sp. (Perciformes, Osteichthyes) from San Diego County, California, U.S.A. *Tertiary Res.* 10: 13–19.
- _____, G. M. Cailliet, and J. A. Neer. 1997. Shortfin Mako, *Isurus oxyrinchus*, impaled by Blue Marlin, *Makaira nigricans* (Teleostei: Istiophoridae). *Bull. Southern California Acad. Sci.* 96: 117–121.
- _____, S. P. Applegate, G. González-Barba, T. Schwennicke, and L. Espinosa-Arubarrena. 2001. A fossil blue marlin (*Makaira nigricans* Lacépède) from the middle facies of the Trinidad Formation (upper Miocene to upper Pliocene), San José del Cabo Basin, Baja California Sur, México. *Bull. Southern California Acad. Sci.* 100: 59–73.
- Frazier J. G., H. L. Fierstine, S. C. Beavers, F. Achaval, H. Suganuma, R. L. Pitman, Y. Yamaguchi, and M. A. Prigioni. 1994. Impalement of marine turtles (Reptilia: Cheloniidae and Dermochelyidae) by billfishes (Osteichthyes: Istiophoridae and Xiphiidae). *Environ. Bio. Fishes* 39: 85–96.
- Gibson, T. G. 1983. Stratigraphy of Miocene through Lower Pleistocene Strata of the United States Central Atlantic Coastal Plain. Pages 35–80 in C. E. Ray, ed. *Geology and paleontology of the Lee Creek Mine, North Carolina*, I. Smith. *Contrib. Paleobiol.* 53.
- Gosline, W. A. 1968. The Suborders of Perciform Fishes. *Proc. U. S. Nat. Mus.* 126: 1–78.
- Gottfried, M. D. 1982. A Pliocene sailfish *Istiophorus platypterus* (Shaw and Nodder, 1791) from southern California. *J. Vert. Paleo.* 2: 151–153.
- Gradstein, F. M., J. G. Ogg, and A. G. Smith. 2004. *A geologic time scale 2004*. Cambridge University Press, Cambridge, United Kingdom. 589 p.
- Gregory, W. K. and G. M. Conrad. 1937. The comparative osteology of the swordfish (*Xiphias*) and the sailfish (*Istiophorus*). *Am. Nov.* 952: 1–25.
- Iturralde-Vinent, M. A. 2003. A brief account of the evolution of the Caribbean Seaway: Jurassic to Present. Pages 386–396 in D. R. Prothero, L. C. Ivany, and E. A. Nesbitt, eds. *From greenhouse to icehouse, the marine Eocene-Oligocene transition*, Columbia University Press, New York.
- Jermanska, A. 1962. Fossil bony fishes from the Miocene of Upper Silesia, Poland. *Acta Palaeontol. Polonica* 7: 235–247.
- Johnson, J. R. 1993. The swordfish in Chumash Prehistory. *Alolkoy* 1993(summer): 97.
- Kimmel, P. G. and R. Purdy. 1984. Fossil fish of the Calvert and Eastover formations. Pages 205–209 in L. W. Ward and K. Krafft, eds. *Stratigraphy and paleontology of the outcropping Tertiary Beds in the Pamunkey River Region, Central Virginia Coastal Plain*. Guidebook for Atlantic Coastal Plain Geological Association 1984 field trip; Atlantic Coastal Plain Geological Association.
- King, C. 1981. The stratigraphy of the London Clay and associated deposits. *Tertiary Res., Spec. Papers* 9: 1–158.

- Lacépède, B. G. E. 1801. Histoire naturelle des poissons. 3: 558.
 _____, 1802. Histoire naturelle des poissons. 4: 728.
- Landini, W. and L. Sorbini. 1996. Ecological and trophic relationships of Eocene Monte Bolca (Pesciara) fish fauna. Pages 105–112 in A. Cherchi, ed. Autoecology of selected fossil organisms: achievements and problems. Boll. Soc. Paleo. Italiana Spec 3.
- Lawley, R. 1876. Nuovi Studi sopra ai Pesci ed altri vertebrati fossili delle Colline Toscane. Firenze. 122 p.
- Leidy, J. 1856. Indications of twelve species of fossil fishes. Proc. Philadelphia Acad. Nat. Sci. 7: 395–397.
 _____. 1860. Description of vertebrate fossils. Pages 99–112 in F. S. Holmes, ed. (1858–1860), Post-Pleiocene fossils of South Carolina. Russel and Jones, Charleston.
- Leriche, M. 1909. Note Préliminaire sur des Poissons nouveaux de L'Oligocene belge. Bull. Soc. Belg. Géol., Paléo., Hydrol. Procés-Verbaux 22: 378–384.
 _____. 1926. Deux *Glyptorhynchus* nouveaux de Bruxellien (Eocene moyen) du Brabant. Ann. Soc. Roy. Zool. Belg. 56: 121–124.
- Linnaeus, C. 1758. Systema Naturae. 10th ed. 1: ii+824 p. Holmiae (=Stockholm), Sweden.
- Manning, E. M. 2003. The Eocene-Oligocene transition in marine vertebrates of the Gulf Coastal Plain. Pages 366–385 in D. R. Prothero, L. C. Ivany, and E. A. Nesbitt, eds. From greenhouse to icehouse, the marine Eocene-Oligocene transition. Columbia Univ. Press, New York.
- Monsch, K. A. 2000. The phylogeny of Scombroid fishes. Ph.D Diss. Univ. of Bristol, England. 2 vols. 272 p.
 _____. 2005. Revision of the Scombroid fishes from the Cenozoic of England. Trans. Roy. Soc. Edinburgh: Earth Sci. 95: 445–489.
 _____, H. L. Fierstine, and R. E. Weems. 2005. Taxonomic revision and stratigraphic provenance of *Histiophorus rotundus* Woodward 1901 (Teleostei, Perciformes). J. Vert. Paleo. 25: 274–279.
- Muizon, C. de and T. J. DeVries. 1985. Geology and paleontology of late Cenozoic marine deposits in the Sacaco area (Peru). Geolog. Rundschau 74: 547–563.
- Nakamura, I. 1985. An annotated and illustrated catalogue of marlins, sailfishes, spearfishes, and swordfishes known to date. FAO Fisheries Synopsis no. 125 5: 1–65.
- Nelson, J. S., E. J. Crossman, H. Espinosa-Pérez, L. T. Findley, C. R. Gilbert, R. N. Lea, and J. D. Williams. 2004. Common and scientific names of fishes from the United States, Canada, and Mexico. Am. Fish. Soc., Spec. Publ. 29, Bethesda.
- Pharisat, A. 1991. La Paleichthyofaune du Rupélien marin de Froidefontaine (Territoire de Belfort). Taxinomie et populations, genese du gisement implications paleobiographiques. Ann. Sci. Univ. Franche-Comte, Besancon, Géolog. 4: 13–97.
- Poey, F. 1860. Memorias sobre la historia natural de la isla de Cuba, acompañadas de sumarios latinos y extractos en francés, etc. La Habana, Cuba. 2: 97–336
- Poplin, F. 1975. Restes de rostre d'Espadon trouves dans un gisement néolithique de l'étang de Leucate (Aude). Bull. Soc. Préhist. Française, Études et Travaux 72: 69–70.
- Prokofiev, A. M. 2004. Caudal skeleton of the enigmatic Upper Paleocene xiphioid fish *Hemingwaya sarissa* Sytchevskaya and Prokofiev, 2002; a new interpretation, with some emendations to the diagnosis of the family (Teleostei: Xiphioidea: Hemingwayidae). Zoosystematica Rossica 13: 125–127.
- Prothero, D. R. 1994. The Eocene-Oligocene transition, paradise lost. Columbia Univ. Press, New York. 291 p.
- Purdy, R. W., V. P. Schneider, S. P. Applegate, J. H. McLellan, R. L. Meyer, and B. H. Slaughter. 2001. The Neogene sharks, rays, and bony fishes from Lee Creek Mine, Aurora, North Carolina. Pages 71–201 in C. E. Ray and D. J. Bohaska, eds. Geology and paleontology of the Lee Creek Mine, North Carolina III. Smith. Contr. Paleobiol. no. 90.
- Rafinesque, C. S. 1810. Caratteri di alcuni nuovi generi e nuove specie de animali e piante della Sicilia, con varie osservazioni sopra I medesimi. Salerno. 105 p.

- Rögl, F., 1998. Palaeogeographic considerations for Mediterranean and Parathethys Seaways (Oligocene to Miocene). *Ann. Naturhist. Mus. Wien, Serie A, für Mineral. und Petrograph., Geol. und Paläo., Anthro. und Prähist.* 99: 279–310.
- Sanders, A. E. 1980. Excavation of Oligocene marine fossil beds near Charleston, South Carolina. *Nat. Geograph. Soc. Res. Repts.* 12: 601–621.
- _____, 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. *U. S. Geol. Surv. Bull.* 1529-H: 105–124.
- Santucci, R. 1923. Nuovi studi sui pesci fossili della Liguria. *Boll. Soc. Geol. Italiana* 41: 195–213.
- Schneider, V. P. and H. L. Fierstine. 2004. Fossil tuna vertebrae punctured by istiophorid billfishes. *J. Vert. Paleo.* 24: 253–255.
- Schultz, O. 1987. Taxonomische Neugruppierung der Überfamilie Xiphoidea (Pisces, Osteichthyes). *Ann. Naturhist. Mus. Wien, Serie A, für Mineral. und Petrograph., Geol. und Paläo., Anthro. und Prähist.* 89: 95–202.
- _____. 1996. Der Erstnachweis eines Schwertfischverwandten aus dem Südostspanischen Pliozän: *Makaira* sp. (Istiophoridae, Xiphoidei, Osteichthyes). *Documenta Naturae* 106: 13–23.
- Scott, W. B. and S. N. Tibbo. 1968. Food and feeding habits of swordfish, *Xiphias gladius*, in the Western North Atlantic. *J. Fish. Res. Bd. Canada* 25: 903–972.
- Shaw, G. and F. P. Nodder. 1792. *Xiphias platypterus*: The broadfinned swordfish. *The Naturalist's Miscellany*, plate 88. 28 p.
- Sorbini, L. 1988. Biogeography and climatology of Pliocene and Messinian fossil fish of Eastern-Central Italy. *Boll. Mus. Civico Storia Nat. Verona* 14: 1–85.
- Stinton, F. C. 1966. Fish otoliths from the London Clay (appendix). Pages 404–464+plates in E. Casier, ed. *Faune ichthyologique du London Clay*. London, British Museum (Nat. Hist.), 2 vols.
- Sytchevskaya, E. K. and A. M. Prokofiev. 2002. First findings of Xiphoidea (Perciformes) in the Late Paleocene of Turkmenistan. *J. Ichthyol.* 42: 227–237.
- Taylor, J. 1978. Cenozoic. Pages 323–351 in W. S. Kerrow, ed. *The ecology of fossils, an illustrated guide*. MIT Press, Cambridge.
- Volta, G. S. 1796–1808. *Illiolitologia Veronese del Museo Bozziano ora annesso a quello del Conte Giovambattista Gazola e di altri gabinetti fossili veronesi con la versione latina*. Stamperia Guiliari, Verona, 323 p.
- Wapenaar, M. L. and F. H. Talbot. 1964. Note on the rigidity of the pectoral fin of *Makaira indica* (Cuvier). *Ann. South African Mus.* 48: 167–180.
- Ward, L. W. and B. W. Blackwelder. 1980. Stratigraphic revision of upper Miocene and lower Pliocene beds of the Chesapeake Group—Middle Atlantic Coastal Plain. *Bull. U. S. Geol. Surv.* 1482-D: 1–61.
- Weiler, W. 1929. *Ergebnisse der Forschungsreisen Prof. E. Stromers in den Wüsten Ägyptens. V. Tertiäre Wirbeltiere. 3. Die Mittel- und obereocäne Fischfauna Ägyptens mit besonderer Berücksichtigung der Teleostomie*. Abhand. Bayer. Akad. Wissen. Math.-Naturwissen. Abteilung Neu Folge 1: 1–57.
- _____. 1943. Ein Schwertfisch-Rostrum aus dem Mitteloligozän Ungarns. *Z. Deutsch. Geol. Gesellschaft* 95: 214–217.
- Woodward, A. S. 1901. *Catalogue of the fossil fishes in the British Museum (Natural History)*. 4: i-xxxix+1–636, 22 figs., 19 plates. British Museum (Nat. Hist.), London.
- de Zigno, A. 1887. Nuove Aggiunte alla Ittiofauna dell'Epoca Eocena del Veneto. *Memorie dell'Istituto Veneto di Scienze, Lettere ed Arti* 23: 1–24.

ADDRESS: (H.L.F.) *Biological Sciences Department, California Polytechnic State University, San Luis Obispo, California 93407-0401. E-mail: <hfiersti@calpoly.edu>*.

