

A Paleontological Review of Three Billfish Families (Istiophoridae, Xiphiidae, and Xiphiorhynchidae)

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In 1974, I summarized the osteological and paleontological knowledge of billfishes and suggested some areas of research to aid future paleontological studies (Fierstine 1974). My suggestions included: (1) a comparative osteological study, especially of the rostrum, in order to obtain more accurate identifications of fossilized material; (2) a functional study of the feeding mechanism, in order to explain observed interfamilial differences in the skull; (3) a functional study of the locomotor apparatus in order to elucidate inter- and intrafamilial differences in vertebrae, body shape and fin morphology, and (4) a more thorough study of those extinct families (Blochiidae and Paleorhynchidae) and genera (*Acestrus* and *Brachyrhynchus*) having uncertain affinities to other billfishes.

Since 1974, some of the foregoing items, as well as some not listed, have been studied with varying degrees of thoroughness. In the most comprehensive treatise, Schultz (1987) investigated all extant and extinct billfishes and developed a new taxonomic arrangement and evolutionary scheme based primarily on structure of the rostrum. The present study reviews the published accounts, presents some new information, and summarizes the relevant osteological and current paleontological knowledge of three billfish families (Istiophoridae, Xiphiidae, and Xiphiorhynchidae).

Systematics of Recent Forms

Although Schultz (1987) rearranged the extant billfishes into three families (Istiophoridae, Tetrapturidae, and Xiphiidae) and six genera (*Istiophorus*, *Makaira*, *Marlina*, *Pseudohistiophorus*, *Tetrapturus*, and *Xiphias*), I will follow

the taxonomic nomenclature of Nakamura (1983), with the exception that I agree with Robins and de Sylva (1960) that both the sailfish and blue marlin exist as single world-wide species, and not as separate Atlantic Ocean and Pacific Ocean forms.

Family Xiphiidae

Xiphias Linnaeus

Xiphias gladius Linnaeus, 1758 —
Swordfish

Family Istiophoridae

Istiophorus Lacépède

Istiophorus platypterus (Shaw and
Nodder, 1792) — Sailfish

Makaira Lacépède

Makaira indica (Cuvier, 1832) — Black
marlin

Makaira nigricans Lacépède, 1802 —
Blue marlin

Tetrapturus Rafinesque

Tetrapturus albidus Poey, 1860 —
White marlin

Tetrapturus angustirostris Tanaka, 1915
— Shortbill spearfish

Tetrapturus audax (Philippi, 1887) —
Striped marlin

Tetrapturus belone Rafinesque, 1810 —
Mediterranean spearfish

Tetrapturus georgei Lowe, 1840 —
Roundscale spearfish

Tetrapturus pfluegeri Robins and de
Sylva, 1963 — Longbill spearfish

Relevant Osteology of Recent Forms

Skull

General account and terminology. I will follow the lead of other billfish scientists (e.g., Nakamura

1983) and use the osteological terminology of Gregory (1933) and Gregory and Conrad (1937) where possible even though it may not conform to modern comparative developmental studies (Jollie 1986). Myer et al (in press) and Schultz (1987) independently discovered that the istiophorid rostrum contained a new paired element, the prenasal, which had mistakenly been considered part of the premaxillary bone by other workers.

Rostrum. The rostrum (or bill) is defined as that part of the snout which extends anteriorly from the anterior border of the bony orbit to terminate in a projection beyond the lower jaw (Fierstine 1978). The Istiophoridae and Xiphiidae have rostra with different morphologies.

The swordfish bill is flattened in cross-section, lacks denticles in the adult (Carter 1919), and usually contains a longitudinal series of central chambers (Poplin 1975, 1976; Poplin et al 1976; Schultz 1987) that demonstrate considerable intraspecific variation. In an X-ray examination of 39 rostra, I found 24 with chambers running the entire length of the rostrum, five with chambers only in the distal one-half, seven with chambers only in the distal one-fourth, and three with no chambers. There is a minor controversy over which bones form the swordfish rostrum. Gregory and Conrad (1937) discussed the problem and concluded that the distal three-fourths is primarily composed of premaxillae with paired nasals on the dorsal surface. The proximal one-fourth is composed of the dermethmoid, frontals, maxillaries, lateral ethmoids, and vomer. After dissecting a juvenile swordfish, Conrad (1937) concluded that the true nasal is "a minute but well-formed bony element lying dorsad to the narial openings" and the bones that Gregory and Conrad (1937) called nasals were just parts of the premaxillae. To the best of my knowledge, all subsequent workers (Nakamura 1983; Poplin et al 1976; Schultz 1987), except Johnson (1986), have followed Gregory and Conrad (1937) and, not Conrad (1937). If most authors are correct, then *X. gladius* lacks the prenasal bones found in istiophorids. However, if Conrad (1937) and Johnson (1986) are correct, then it is possible that the bones they called parts of the premaxillae, and that others called nasals, are really prenasals. This matter needs to be resolved.

In contrast, the istiophorid bill has paired prenasal bones (Fig. 1), is rounded in cross-section, lacks any central chambers, and denticles adorn its ventral and generally its dorsal surfaces. The

three istiophorid genera can be distinguished by the shape of their rostra at the rostral mid-point (Fig. 2). The distribution of denticles (Table 1) and relative size of the paired nutrient canals show interspecific patterns.

Schultz (1987) noticed that the denticles along the ventral midline of the rostrum of the shortbill spearfish and Mediterranean spearfish are not housed in alveoli and detach when the rostra are prepared into skeletons. He separated all spearfishes (*T. angustirostris*, *T. belone*, *T. georgei*, and *T. pfluegeri*) from the other billfishes primarily on the basis of the edentulous zone. There was no mention of intraspecific or interspecific variation of the character.

Poplin et al (1976) described the microscopic anatomy of the swordfish rostrum. It is composed superficially of a thin layer of acellular primary bone that has the appearance of dentine. The superficial layer is underlain by acellular vascular bone containing secondary osteons (Haversian units) which are arranged into large bundles in the deeper regions (center) of the sword. There are no comparable histological studies of istiophorid rostra.

Lower jaw. With the exception of mentioning the presence or absence of the prementary bone, there are no published studies of other features of the lower jaw. The istiophorids have a stout mandible that is composed of the prementary, dentary, and articular bones. There is a well-developed intermandibular joint and each mandible has a strong cone-shaped quadrate-articular joint. In contrast, the swordfish has a much weaker lower jaw with no prementary bone or intermandibular joint. It has a rather simple quadrate-articular articulation.

Intrafamilial variation is unknown. The observation, however, that the shortbill spearfish has its prementary bone reduced to a tooth patch (Fierstine and Applegate 1968), is incorrect because the observation was based on an ab-

Table 1. Relative length of denticulated area on dorsum of rostrum of five species of extant billfishes. Relative length was determined by dividing the length of the denticulated zone by *L* (see Fig. 2 legend for definition).

Species	Number studied (N)	Average relative length of denticulated area	Range of relative length
<i>Makaira nigricans</i>	8	.02	.00-.03
<i>Makaira indica</i>	4	.05	.04-.07
<i>Tetrapturus audax</i>	6	.12	.03-.19
<i>Istiophorus platypterus</i>	4	.34	.08-.63
<i>Tetrapturus albidus</i>	9	.75	.57-.78

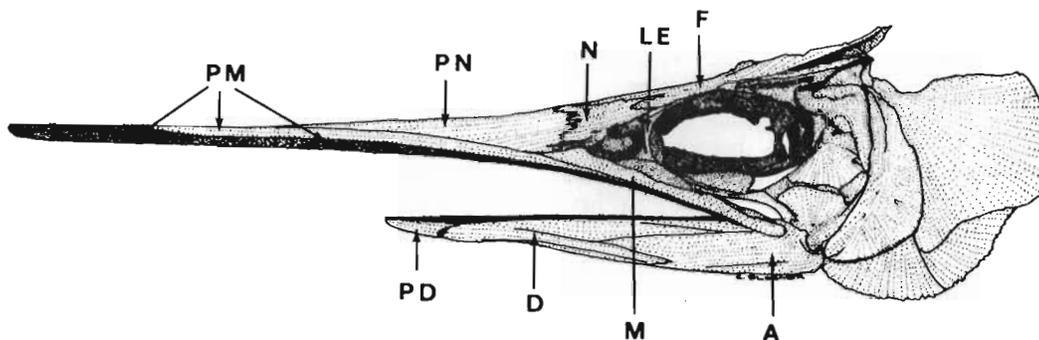


Figure 1. Skull and lower jaw of a blue marlin (*Makaira nigricans* Lacépède, 1802), left lateral view. Composite illustration by Charles Bloomer primarily from a 43.3 kg (95.5 lb) ♀ caught off Kailua-Kona, HI. Bones labeled as follows: Articular (A), Dentary (D), Frontal (F), Lateral ethmoid (LE), Maxillary (M), Nasal (N), Prementary (PD), Premaxillary (PM), Prenasal (PN).

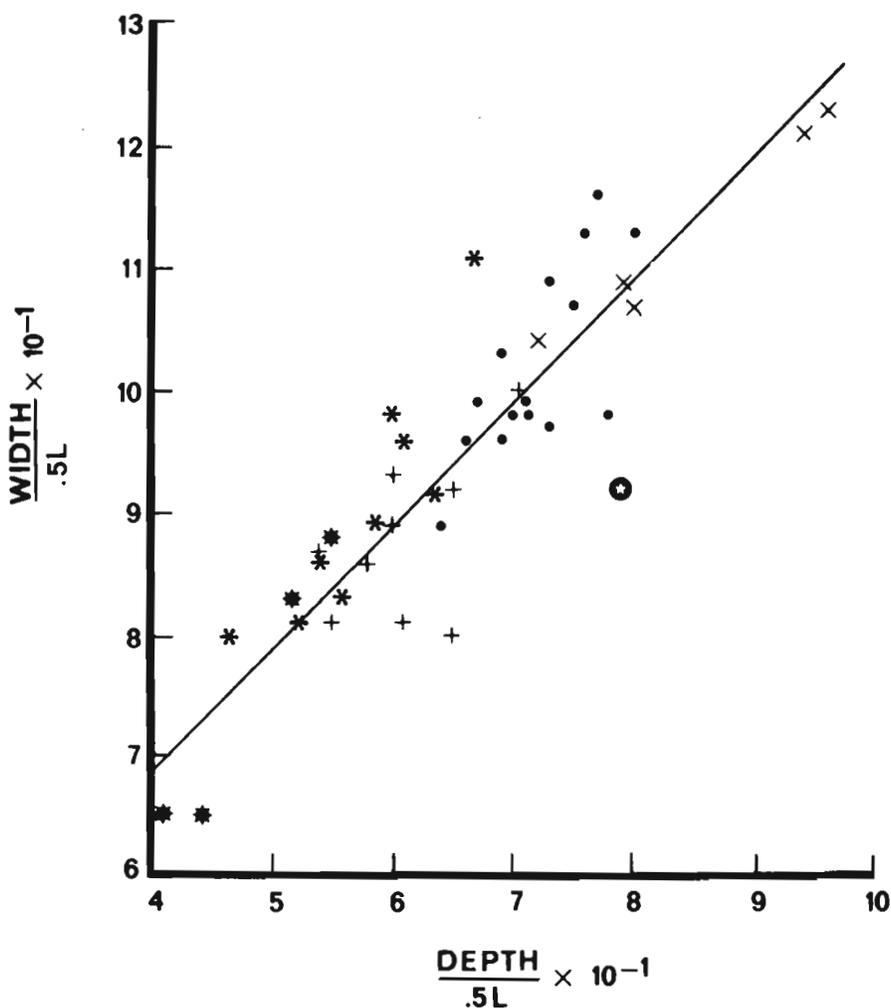


Figure 2. Simple regression of depth (D) and width (W) of 43 rostra measured at mid-rostrum length (.5L) for six species of billfishes. Rostrum length (L) was determined by measuring the straight-line distance from the distal tip to the anterior orbital margin of the lateral ethmoid. *Istiophorus platypterus* (*), n=4; *Makaira indica* (x), n=5; *M. nigricans* (●), n=15; *M. panamensis* (⊙), n=1; *Tetrapturus albidus* (*), n=9; *T. audax* (+), n=9.

normal specimen. Additional specimens have a small, well-developed prementary bone and a lower jaw with an intermandibular joint.

Other skull bones. Billfishes differ in the proportions of their skulls. For example, the Xiphiidae have a short post-orbital region and a longer rostrum, whereas the Istiophoridae have a comparatively longer post-orbital region and shorter rostrum (Ovchinnikov 1970). In the Istiophoridae, the cranium becomes stouter and wider with body length (Nakamura 1983). *Makaira* has the widest and most massive cranium and *Istiophorus* and *Tetrapturus* have more moderate-sized crania.

Vertebrae. Vertebral counts and shape differ between the Xiphiidae and Istiophoridae, and *Makaira* has enlarged transverse processes (apophyses) on its centra which are lacking in other istiophorid genera (Nakamura 1983). There are only a few other studies of vertebral morphology and variation.

Gottfried (1982) noted that intervertebral foramina were positioned more anteriorly in *Makaira* than in *Istiophorus* and *Tetrapturus*, and that the posterior zygapophyses originated more posteriorly on the centrum in *Istiophorus* than in the other istiophorids. Using the 14th vertebra, Nakamura (1983) noted that *Makaira* has wide and high (more or less square) neural spines, whereas *Istiophorus* has rather low, more narrow, triangular neural spines. *Tetrapturus* is more or less intermediate. The ratio of centrum length to width of the 6th vertebra of a black marlin, blue marlin, sailfish and striped marlin differs among genera (Fierstine and Welton 1988). The sailfish has the slimmest centrum, the black marlin and blue marlin the most robust, and the striped marlin's centrum is intermediate in proportion.

The structure of the hypural complex differs between the Istiophoridae and Xiphiidae (Gregory and Conrad 1937; Fierstine and Walters 1968; Collette et al 1984; Potthoff and Kelley 1982; Potthoff et al 1986; Johnson 1986). Similarities include three epurals, one uroneural, and a deep posterior notch between the upper and lower hypural plates. Differences include fusion of the parahypural with the hypural plate in istiophorids, whereas the parahypural is autogenous in *Xiphias*. The uroneural remains free from the 5th hypural in *Xiphias* while istiophorids lack a 5th hypural element.

Fins and fin supports. The black marlin is the only istiophorid with a pectoral fin that cannot be folded back against its body in the adult

(Nakamura 1983). The surface of the scapula that articulates with the large first pectoral ray is flat in the black marlin, whereas the same surface in other istiophorids is round (Wapenaar and Talbot 1964). Fierstine and Welton (1983) noted that the articular surface of the first pectoral ray of the black marlin was about half the size of the same surface on a similar-sized blue marlin.

The swordfish lacks pelvic fins and pelvic girdles (basipterygia), whereas istiophorids have well-developed girdles with reduced number of rays.

Potthoff and Kelley (1982), Collette et al (1984), and Potthoff et al (1986) studied the early osteological development of the median fin supports in the swordfish and sailfish. Since these studies have few descriptions of adult structures, they have limited application to paleontology when most specimens consist of isolated rostral fragments and vertebrae.

Fossil Record

Identification

Schultz (1987) proposed a classification scheme of extant and extinct billfishes that differs significantly from the scheme accepted by other modern workers (Collette et al 1984, Fierstine 1978, Johnson 1986, Myer et al in press, Nakamura 1983). His osteological observations were based upon limited material: a skull preparation of a Mediterranean spearfish, and one rostrum each of a blue marlin, sailfish, swordfish, and striped marlin. Therefore, the distinguishing characters he proposed lacked an understanding of interspecific or intraspecific variation. Most of his knowledge of the fossil specimens came from a thorough review of the literature, but not from actual specimens. Since I lack confidence in his data, I can not accept his classification of taxonomic groups and lineages.

Istiophoridae. Fierstine (1978) reviewed all fossil istiophorids known at the time. Most descriptions were based upon single isolated rostra or vertebrae; all were described from Eocene, Miocene, Pliocene, and Pleistocene deposits, and few were compared with recent skeletal material. Early workers (see references in Fierstine 1978 and Schultz 1987) generally placed specimens into new or existing fossil species of *Istiophorus*, except for Van Beneden (1871) who erected a new genus, *Brachyrhynchus*. Although Fierstine (1978) questioned the accuracy of these early identifications, he took the conservative approach and made no attempt to

re-identify or reclassify them.

The systematic studies of the recent Istiophoridae by Robins and deSylva (1960 and 1963), Nakamura et al (1968) and Nakamura (1983) provided a firm basis and reference point for modern paleoichthyological investigations. Most fossil specimens are similar or identical to recent specimens. Barbolani (1910) foreshadowed this interpretation when he placed *Brachyrhynchus*, plus some new specimens, into the living *Istiophorus herschelii* (Gray, 1838) which was synonymized with the blue marlin (*Makaira nigricans* Lacépède, 1902) by Nakamura et al (1968).

The only fossil record of a sailfish is based on a single, fragmentary vertebra from the Upper Pliocene San Diego Formation (Gottfried 1982). The fossil vertebra was compared to vertebrae from only one or possibly two extant sailfish specimens, and was found similar. Although the identification may be correct, it should be re-studied by comparing it to a larger series of specimens from several billfish species.

The genus *Makaira* is represented in the geological record from the Middle Miocene to present (Table 2). With the exception of the Lee Creek, Pungo River, and Italian specimens, each discovery probably represents a single individual. Six species of *Makaira* have been recognized as fossils, the extant black marlin and blue marlin, and four extinct species, *M. belgicus* (Leriche, 1926), *M. calvertensis* (Berry, 1917), *M. courcelli* (Arambourg, 1927), and *M. panamensis* Fierstine, 1978. Leriche (1926) described *M. belgicus* from a partial rostrum and abdominal vertebra, and Arambourg (1927) described *M. courcelli* from a partial rostrum. These two species probably belong to the genus *Makaira*, but their incomplete condition makes it difficult to confirm or reject their specific identification.

Myer et al (in press) believe that only *M. calvertensis* is present in the very large Lee Creek billfish assemblage, but I think critical review would probably synonymize *M. calvertensis* with the blue marlin, and would find black marlin present as well (see paleozoogeographic discussion below).

There are no known fossil specimens of the genus *Tetrapturus*.

Xiphiidae. Fossil swordfish are rare, with most specimens coming from the Italian Pliocene. Several rostral fragments that were originally named *X. delfortrieri* Lawley (1876), were redescribed and renamed *X. gladius* var. *delfortriei* by Santucci (1923). Recently, Sorbini (1987) discovered a nearly complete 135-cm-long swordfish in the Middle Pliocene Marecchia River ichthyofauna. The specimen is figured but not described. In the only other positive fossil record of the family, Poplin (1975) described a rostral fragment of a swordfish from the subrecent (Neolithic) of southern France.

Other fossil records of *Xiphias* are erroneous or questionable. *Xiphias rupeliensis* Leriche, 1908, was described from several vertebrae and an articular bone from the Middle Oligocene of Belgium (Leriche 1908, 1926). The vertebrae are similar enough to *Xiphiorhynchus kimblalocki* Fierstine and Applegate, 1974, that *Xiphias rupeliensis* is probably a xiphiorhynchid rather than a xiphiid. Eastman (1917) described a rather massive, isolated caudal vertebra from the Eocene of South Carolina as *Xiphias* (?) sp., but it lacks one of the diagnostic features of an xiphiid hypural, namely that the parahypural is not autonomous but, rather, is fused to the hypural fan. Fierstine (1974) and Fierstine and Applegate (1974) thought they had found the rostrum of a new genus of Eocene swordfish, but histological examination revealed that the

Table 2. Distribution of fossil marlins of the genus *Makaira*.

Species	Age	Formation	Locality	References
<i>M. indica</i>	Early Pleistocene	?Cabatuan	Luzon, Philippines	Fierstine and Welton (1983)
<i>M. nigricans</i>	Pliocene	?	Italy	Barbaloni (1910)
<i>M. calvertensis</i>	Early Pliocene	Yorktown	Lee Creek, North Carolina, U.S.A.	Meyer <i>et al.</i> (in press)
<i>Makaira</i> sp.	Latest Miocene	San Mateo	Oceanside, California, U.S.A.	Fierstine and Welton (1988)
<i>M. courcelli</i>	Latest Miocene	?	Oran, Algeria	Arambourg (1927)
<i>Makaira</i> sp.	Late Miocene	Monterey	El Toro, California, U.S.A.	Fierstine and Applegate (1968)
<i>M. panamensis</i>	Late Miocene	Chagres S.S.	Panama	Fierstine (1978)
<i>M. belgicus</i>	Middle Miocene	?	Belgium	Leriche 1926)
<i>M. calvertensis</i>	Middle Miocene	Pungo River	Lee Creek, North Carolina, U.S.A.	Meyer <i>et al.</i> (in press)

rostrum was composed of calcified cartilage and more properly belonged to a sawfish (Pristiidae) or saw shark (Pristiophoridae).

A segment of an articulated vertebral column with partial dorsal and anal fins, from the Middle Miocene of Poland, was identified as belonging to a young specimen of *Xiphias* sp. (Jerzemska 1962). Comparing this account with Gregory and Conrad (1937) and Potthoff and Kelley (1982), I believe that the vertebrae in the Polish specimen are too numerous and have the incorrect morphology to have anything to do with *Xiphias*.

Xiphiorhynchidae. This monogeneric family (*Xiphiorhynchus* Van Beneden, 1871) contains five species [*X. aegypticus* Weiler, 1929, *X. elegans* Van Beneden, 1871, *X. kimblalocki* Fierstine and Applegate, 1974, *X. parvus* Casier, 1966, and *X. priscus* (Agassiz, 1839)], from the Eocene of either North Africa, western Europe, or eastern North America (see references in Fierstine and Applegate 1974, Schultz 1987) and one species (*X. hungaricus* Weiler, 1943) from the Middle Oligocene of southcentral Europe (Weiler 1943).

The rostra are round in cross-section, have denticles (exact pattern is unknown), are composed of acellular bone (Beltan 1976), and are distinguished from istiophorid bills by the presence of a large central canal and more than one pair of lateral nutrient canals, and probably by the absence of prenasal bones. The original descriptions *Xiphiorhynchus* were from cranial fragments that were presumed to have had rostra (Agassiz 1838). Woodward (1901), and most recently Casier (1966), considered some of the rostra and skulls conspecific, even though none were articulated together. Until a xiphiorhynchid skull is discovered with a rostrum, I lack confidence in their identification. In fact, since most species are known only from rostral fragments, I have little faith in the validity of the characters that distinguish the species.

Schultz (1987) described a new genus and species, *Thalattorhynchus austriacus*, Middle Miocene, Austria, from a distal rostral fragment. The distinguishing feature was a single, off-center, longitudinal canal that was observed by computerized tomography. No paired, lateral nutrient canals were visible. The specimen looks similar to most istiophorid rostral fragments, except for the single canal, which may be anomalous; therefore, I do not believe the specimen is a xiphiorhynchid.

Fierstine and Applegate (1974) concluded,

based on a description of *X. kimblalocki*, that xiphiorhynchids are intermediate to the Xiphiidae and Istiophoridae. The rostrum is broad at its base, similar to a swordfish, but it is round in the distal one-half, similar to the istiophorids. Both the swordfish and *Xiphiorhynchus* have a central canal in their rostra, while the istiophorids have only one pair of lateral canals. The abdominal vertebra of *X. kimblalocki* is similar to the shape of an anterior abdominal vertebra of the black marlin, whereas the caudal vertebra is similar to the shape of a swordfish caudal vertebra.

Paleozoogeography

Istiophoridae and Xiphiidae. According to Eschmeyer et al (1983), Nakamura (1983), and Robins et al (1986), istiophorid billfishes are generally distributed in tropical and warm temperate seas, whereas the swordfish is distributed world-wide in tropical (at mesopelagic depths), warm temperate, and cold temperate seas. Some istiophorid species are found world-wide, while others have a more restricted distribution. For example, the black marlin, shortbill spearfish, and striped marlin inhabit only the Pacific Ocean, with occasional strays into the southeastern Atlantic Ocean, whereas the longbill spearfish and white marlin are restricted to the Atlantic Ocean, with the latter occasionally found in the Mediterranean Sea.

Fossil discoveries of the Istiophoridae and Xiphiidae are generally found in deposits within the distributional range of the extant species, and their discoveries have neither raised nor solved any paleozoogeographic problems (Fierstine 1978; Fierstine and Welton 1983, 1988).

Recently, I have been studying the rostrum of a black marlin from the Middle Miocene of Panama. During the Middle Miocene there were no known geographic or ecological barriers in the region of the future Isthmus of Panama to impede the movement of the black marlin from the Pacific Ocean to the Atlantic Ocean (or vice versa). Gillette (1984) concluded there was a Tertiary Caribbean Faunal Province that extended from Ecuador through the Caribbean Sea to coastal North Carolina in the Atlantic Ocean. Most likely, the black marlin was part of that faunal province and reexamination of the numerous specimens of *M. calvertensis* from the Middle Miocene deposits, Lee Creek, North Carolina (Myer et al in press) will probably reveal that black marlin occurred in the Atlantic Ocean both

before and after the formation of the Panama land bridge. This early discovery weakens the hypothesis, "that the black marlin is a more recent derivative (than the blue marlin) that was unable to thrive in the Atlantic Ocean because of a temperature barrier" (Fierstine 1978), and fuels the controversy that the black marlin may be more generally present, especially in the south Atlantic Ocean, but lacks scientific confirmation.

Xiphiorhynchidae. Xiphiorhynchids have been found only in Tertiary deposits associated with the north Atlantic Ocean and western Tethys Sea (or its remnant, the Mediterranean Sea). If xiphiorhynchids are the earliest known true billfishes (see discussion below), then the Atlantic Ocean and Tethys Sea are probably the center of origin for billfishes.

Evolutionary Discussion

Collette et al (1984) discussed the phylogenetic relationships of the six families and 44 genera of extant Scombroidei and concluded that the Istiophoridae and Xiphiidae are sister groups, and together are a sister group to the Scombridae. In a more extensive cladistic analysis, Johnson (1986) concluded that the billfishes (Istiophoridae and *Xiphias*) should be placed as separate tribes within the Scombridae, and together are a sister group to *Acanthocybium*. The last two groups share the feature of a horizontal, premaxillary beak in the larvae, which elongates in adult billfishes.

Although I do not believe that billfishes belong to the same family as mackerels and tunas, I am now persuaded by the argument that billfishes do not belong in their own separate suborder (Xiphioidae) and are related to the Scombridae. The similarities between billfishes and *Acanthocybium* is not a new idea and Johnson's novel presentation makes one look for evidence to support or reject his hypothesis. For example, does *Acanthocybium* have a prenasal bone? Does the istiophorid prenasal bone appear early or late in development? Does the swordfish rostrum have prenasal bones or is it composed primarily of premaxillae? If scombrids are more primitive than billfish, then are there fossil billfish having more than 24 vertebrae (or 26 in the swordfish) or fewer than three epurals? Johnson (1986) believes that a thorough study of the extinct family Paleorhynchidae may resolve some of these questions, but I doubt it. I concluded that paleorhynchids were probably not

true billfishes (Fierstine 1974) for the same reasons that Johnson found them a potential ancestor. Paleorhynchids have very elongated upper and lower jaws and numerous (45-60) vertebrae.

After extensive analysis, Nakamura (1983) believes that the shortbill spearfish is most similar to the ancestral billfish. Some of the features are: bill short and round, cranium fairly stout with a narrow parasphenoid and vomer, needle-like scales with few points, large slab-sided body, and triangular neural and haemal spines. His phylogenetic conclusions are weakened by his mixing of plesiomorphic and apomorphic characters.

No evidence has yet been presented to refute the hypothesis that the Xiphiorhynchidae are morphologically intermediate to the Istiophoridae and Xiphiidae (Fierstine and Applegate 1974) and may be closest to the scombrid-billfish connection postulated by Collette et al (1984) and Johnson (1986).

Summary

The paleontology and relevant osteology of adult billfishes are reviewed from the literature and unpublished studies. In the Istiophoridae, the premaxillary and prenasal bones form a rounded rostrum with denticles, the lower jaw has a prementary bone and well-developed intermandibular joint, and the elongated vertebrae form a rigid spinal column. Certain skull and vertebral proportions exhibit intergeneric differences, and the denticle pattern and relative size of the nutrient canals of the rostrum show interspecific differences.

All fossil istiophorids belong to one of five species of *Makaira*, with the exception of one vertebra specified as *Istiophorus*. There are no known fossil specimens of *Tetrapturus*. Istiophorids occur from the Middle Miocene to the present and have a zoogeographic distribution similar to extant species, except that *Makaira indica* may have been common in the western north Atlantic Ocean before the formation of the Isthmus of Panama. In the Xiphiidae, the rostrum is flat, is composed of acellular bone with secondary osteons, contains a variable number of central chambers, and lacks denticles in the adult. There is a controversy over which bones form the rostrum. It may be composed primarily of premaxillae, or premaxillae and nasals, or premaxillae and prenasals. The lower jaw lacks a prementary bone. The vertebrae are

cube-shaped and are not modified into a stiffened unit.

Disregarding identifications based on isolated vertebrae, the Xiphiidae is monotypic (*Xiphias gladius*) and has no fossil record before Pliocene times. The extinct Xiphiorhynchidae are characterized by a rounded rostrum with central chambers and denticles, and apparently without prenasal bones. The vertebrae are not formed into a stiffened unit. The family is monogeneric (*Xiphiorhynchus*) with six species, and is limited to Tertiary deposits (Eocene of Africa, Europe, and North America, and the Oligocene of Europe) associated with the north Atlantic Ocean and western Tethys Sea (or its remnant, the Mediterranean Sea). The Xiphiorhynchidae may be closest to the scombrid-billfish connection postulated by recent workers.

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