The Paleontology of Billfish—The State of the Art

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ABSTRACT

The major osteological features are described for living billfishes. All billfish remains are reviewed critically and some questionable forms are placed in Xiphioidei Incertae Sedis (uncertain status). The remaining xiphioids are placed into three families: Istiophoridae, Xiphiidae, and Xiphiorhynchidae. A new undescribed xiphiid from Mississippi shows that the billfish lineages must have diverged prior to the Eocene. Areas of research are suggested that will help place the paleontological studies on a more secure foundation.

Although billfish fossils have been known for over 130 yr (Agassiz, 1838), Regan (1909) and Berg (1940) have been the only ones to summarize the paleontological knowledge of this important group. This paper reviews all fossil groups that are generally considered to be billfish and separates the questionable from the unquestionable forms. In order to put the paleontological and phylogenetic discussion on a firm foundation, I have summarized some of the major osteological features. In addition, I have pointed out some areas of research that will aid future paleontological studies.

OSTEOLOGICAL INFORMATION

Since crania, rostra, and vertebrae are the most common billfish structures found in the fossil record, the following review of recent osteology will emphasize them.

Various authors (Gregory and Conrad, 1937; Nakamura, 1938; Nakamura, Iwai, and Matsubara, 1968; Ovchinnikov, 1970) have shown that the rostra, skull, and vertebrae differ greatly between the Xiphiidae (swordfish), on the one hand, and the Istiophoridae (marlin, sailfish, and spearfish), on the other hand. In general, the skeleton is lighter and less ossified in the Xiphiidae than in the Istiophoridae. The swordfish (Fig. 1) has a flattened rostrum, a short occipital region of the skull, and a one-piece lower jaw without a symphyseal joint. The istiophorids (Fig. 2) have a rounded rostrum, a comparatively longer occipital region, and a lower jaw with a predentary bone and a symphyseal joint. The vertebrae (Fig. 3) of the swordfish (when compared with the istiophorids) lack the overlapping processes, the centra are more cube-like than elongate, and the caudal skeleton (Fig. 4) has more separate bones (Fierstine and Applegate, 1968; Fierstine and Walters, 1968).

Comparative osteology has been little help in distinguishing between the various members of the family Istiophoridae. *Tetrapturus* and *Istiophorus* have 12 + 12 = 24 vertebrae and *Makaira* has 11 + 13 = 24 vertebrae. Since only isolated vertebrae have been found in the fossil record for istiophorids, this vertebral difference has not been useful to paleontologists. In general, there is generic similarity in bone morphology. In *Makaira* the bones are usually more massive than the other genera and the vertebral centra are much wider anteriorly (Fig. 5) than posteriorly (Nakamura et al, 1968).

The bones of the branchial apparatus and limb girdles have been studied by Nakamura (1938) and Nakamura et al (1968), and they have very briefly discussed the similarities and differences between the various species. These studies will prove useful when complete fossil skulls of istiophorids are found or when individual bones are recognized.

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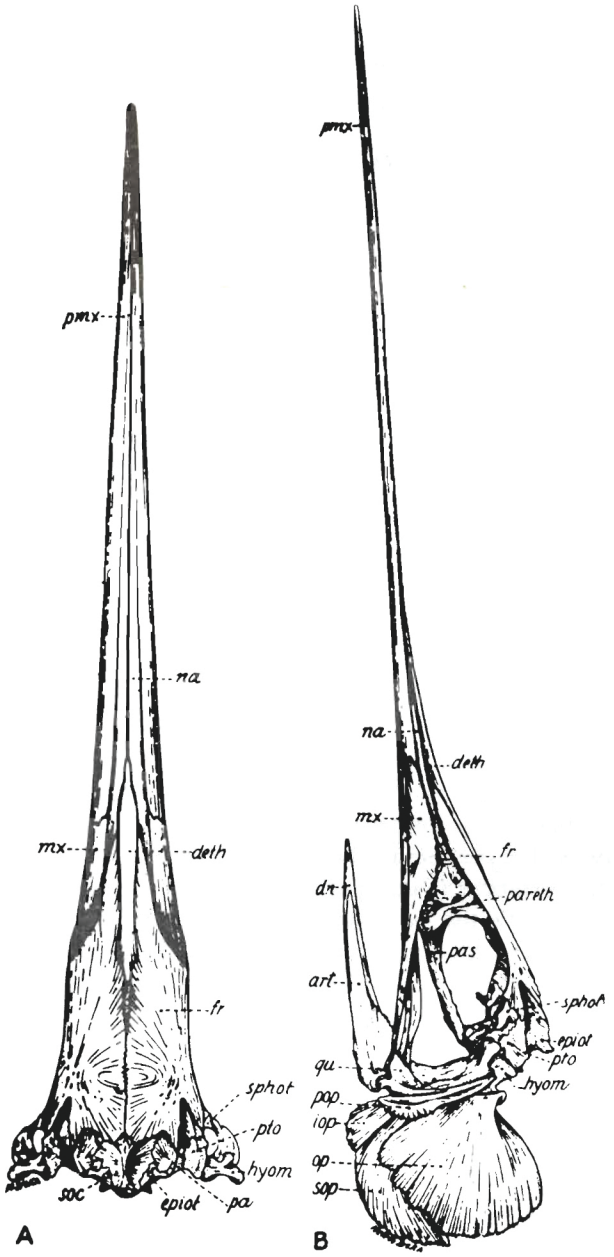


Figure 1.—Swordfish *(Xiphias gladius)* skull. **A.** Dorsal view. **B.** Lateral view. (From Gregory and Conrad, 1937.)

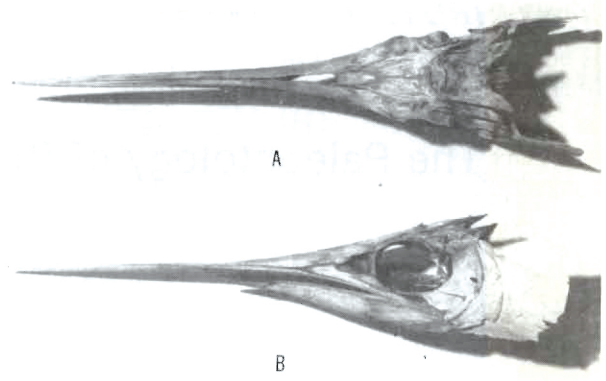


Figure 2.—Striped marlin *(Tetrapturus audax)* skull. **A.** Dorsal view. **B.** Lateral view.

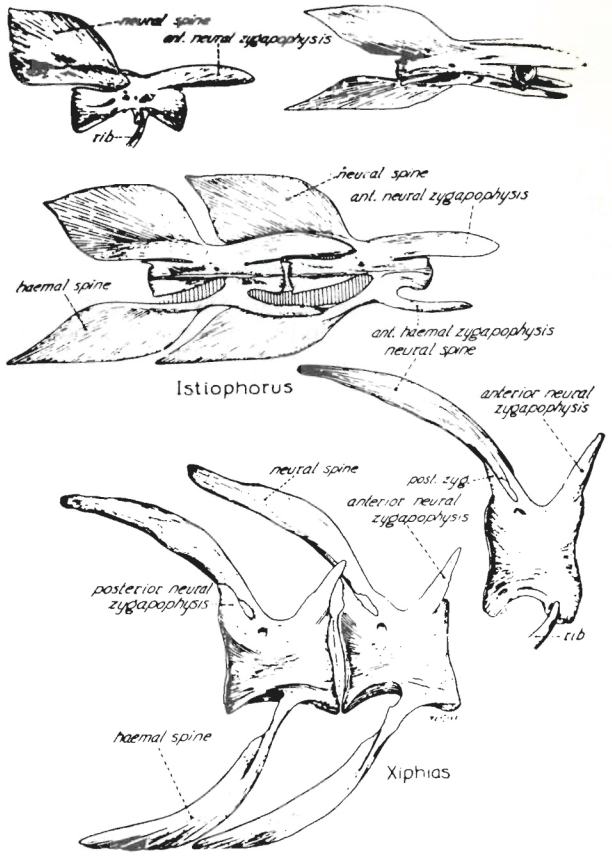


Figure 3.—Trunk vertebrae of billfish. (From Gregory and Conrad, 1937.)

REVIEW OF THE FOSSIL RECORD

Generally, taxonomists (Berg, 1940; Regan, 1909; and Romer, 1966) recognize five billfish families: Blochiidae, Istiophoridae, Paleorhynchidae, Xiphiidae, and Xiphiorhynchidae. I will use these families as a starting point for the following discussion. I agree with Gosline (1968, 1971) that these families should be placed in their own suborder, the Xiphioidei, within the Order Perciformes. I have neglected to include the family Luvaridae within the Xiphioidei because I do not believe it belongs there (it has a peculiar vertebral column and no rostrum) and because it has no fossil record.

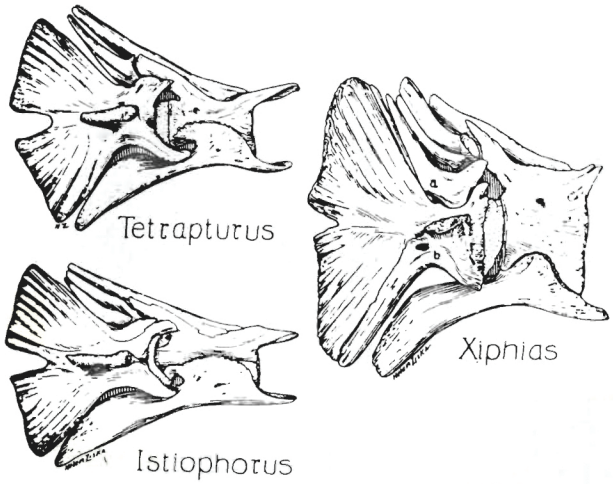


Figure 4.—Caudal skeletons of billfish. (From Gregory and Conrad, 1937.)

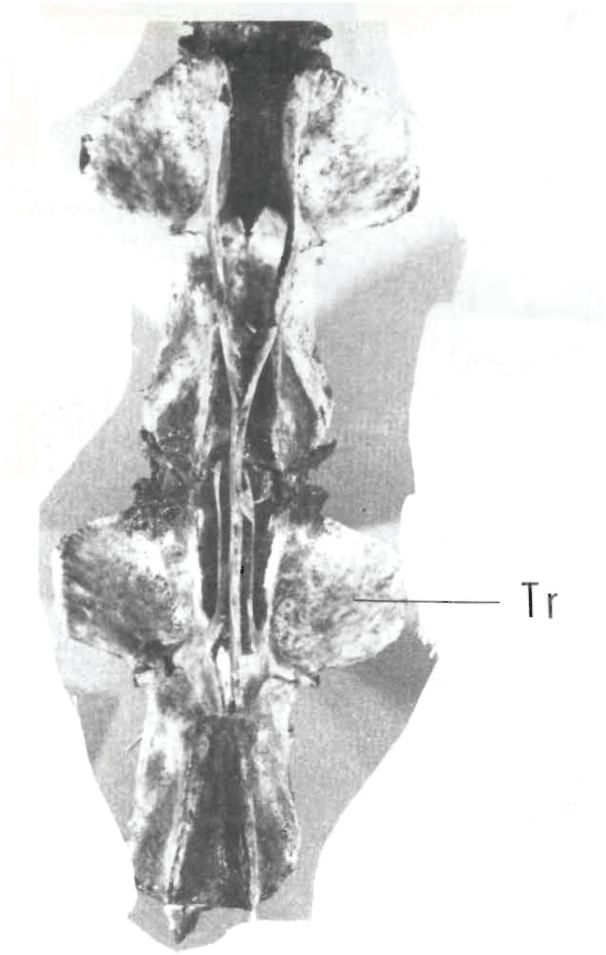


Figure 5.—Two successive caudal vertebrae from a black marlin *(Makaira indica)* showing the transverse flanges (Tr) that project from each centrum.

The Blochiidae contains two distinct fossil forms, *Blochius longirostris* and what I call the "*Cylindracanthus* group". Complete skeletons of *Blochius* (Fig. 6) have been found in the Lower Eocene deposits of Monte Bolca, Italy. The skeletons are about 1 m long and exhibit many billfish characters such as: a round and elongate rostrum, a low vertebral number, elongate vertebrae, and a deeply forked caudal fin. To the best of my knowledge no one has critically studied *Blochius* since Woodward (1901) published his catalogue of fossil fishes.

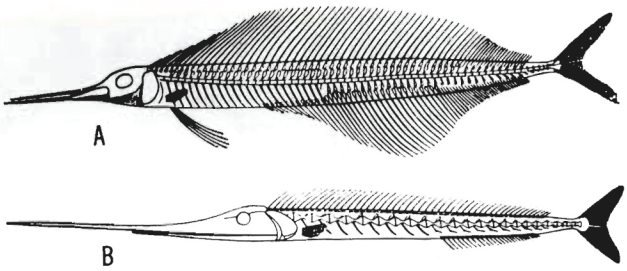


Figure 6.—**A.** Reconstruction of *Paleorhynchus glarisianus*. **B.** Reconstruction of *Blochius longirostris*. (From Gregory and Conrad, 1937; after Woodward, 1901.)

The "*Cylindracanthus* group" (*Aglyptorhynchus, Congorhynchus, Cylindracanthus, Glyptorhynchus, Hemirhabdorhynchus*, etc.) are all known by small, cylindrical, elongate structures (Fig. 7) that are thought to be rostral fragments of a *Blochius*-like fish (Carter, 1927). A few vertebrae have been attributed to the "*Cylindracanthus* group" because they were found associated with the rostra (Leriche, 1910), but the evidence that they belong to the "*Cylindracanthus* group" is simply circumstantial.

In order to tidy up the billfish classification, I have chosen (Fierstine and Applegate, in press) to put the "*Cylindracanthus* group" and *Blochius* into the Xiphioidei Incertae Sedis. Although the establishment of a category with uncertain affinities avoids the responsibility of making a precise taxonomic decision, it emphasizes our lack of knowledge of its members.

The Istiophoridae contains the living genera *Istiophorus, Makaira,* and *Tetrapturus,* and the fossil genera *Brachyrhynchus,* and possibly *Acestrus*. *Acestrus* (Fig. 8) is only known from the Early Eocene and the remains consist of the posterior part of skulls. Casier (1966) felt that these crania belonged to a billfish, but he also noted the similarity to the extinct scombrid, *Scombrinus*. The cranial fragments of *Acestrus* are quite small, only 50-60 mm

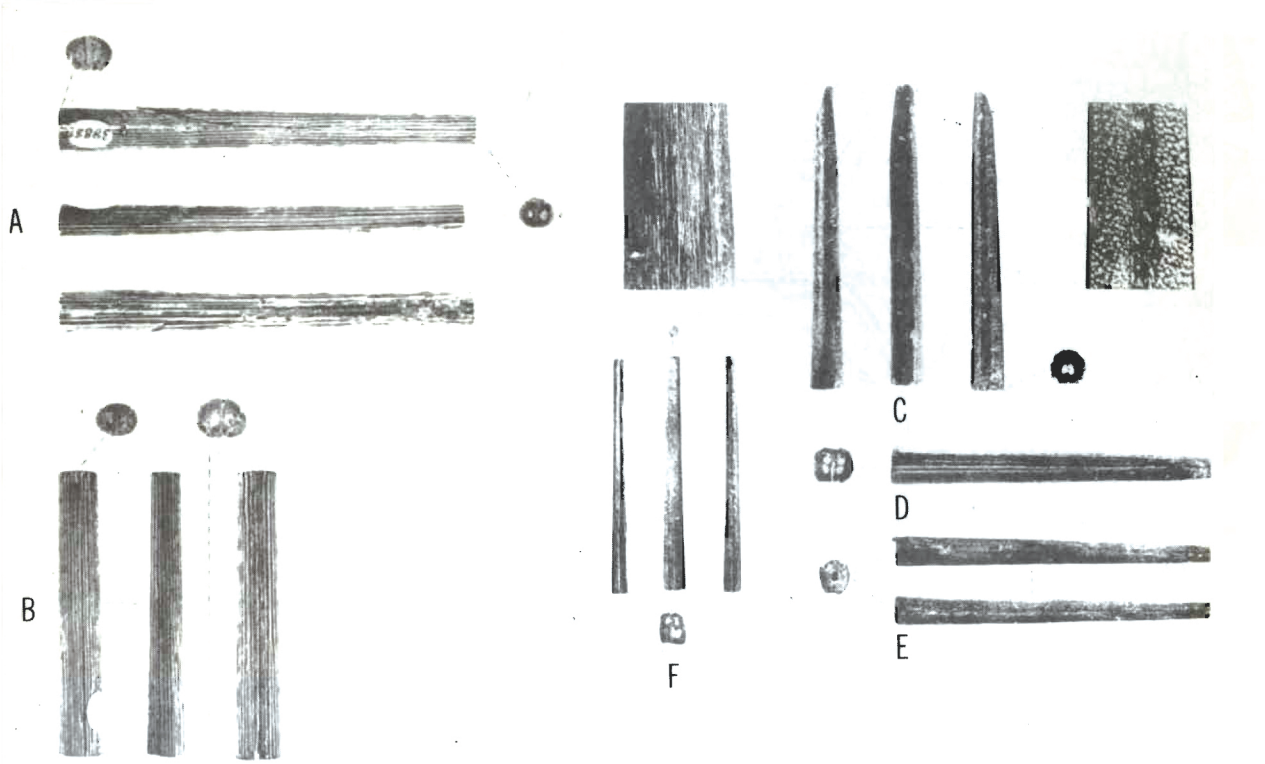


Figure 7.—Rostra of the "*Cylindracanthus* group" **A, B.** *Cylindracanthus rectus*. **C, D, E.** *Aglyptorhynchus venablesi* **F.** *Aglyptorhynchus sulcatus*. (From Casier, 1966.)

in length. It is possible that these small skulls belong to one of the small spearfishes. Three species of *Brachyrhynchus* have been described from rostra found in the Eocene of Belgium and the Pliocene of Italy. Woodward (1901) thought that *Brachyrhynchus* was probably identical with *Istiophorus*. Based upon the figures that I have seen, I agree that *Brachyrhynchus* belongs to an extant genus of the Istiophoridae.

Most paleontologists (Woodward, 1901; Leriche, 1910; Casier, 1966) seem to have lumped all living istiophorid species into a single genus *(Istiophorus* or *Tetrapturus)* and to the best of my knowledge, Fierstine and Applegate (1968) have been the only paleontologists to try to place the fossils into one or more of the three extant genera. Our attempt was not too fruitful because of the lack of comparative osteological studies on the living forms. Nevertheless, we recognized a predentary bone and a rostrum (Fig. 9) from the Miocene of California as belonging to *Makaira* sp. The identifications were based on the fact that these structures were much larger and more massive than the similar structures in *Istiophorus* and *Tetrapturus*.

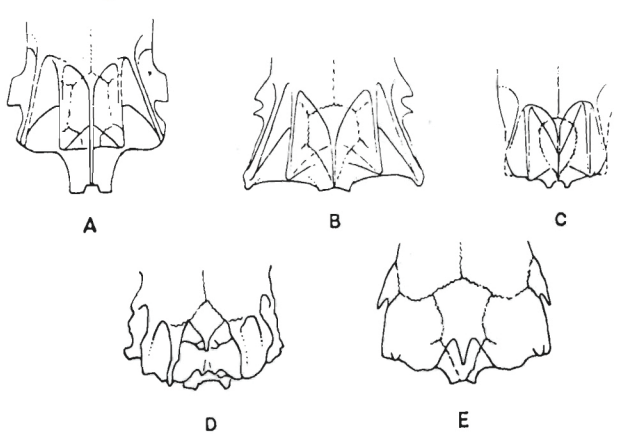
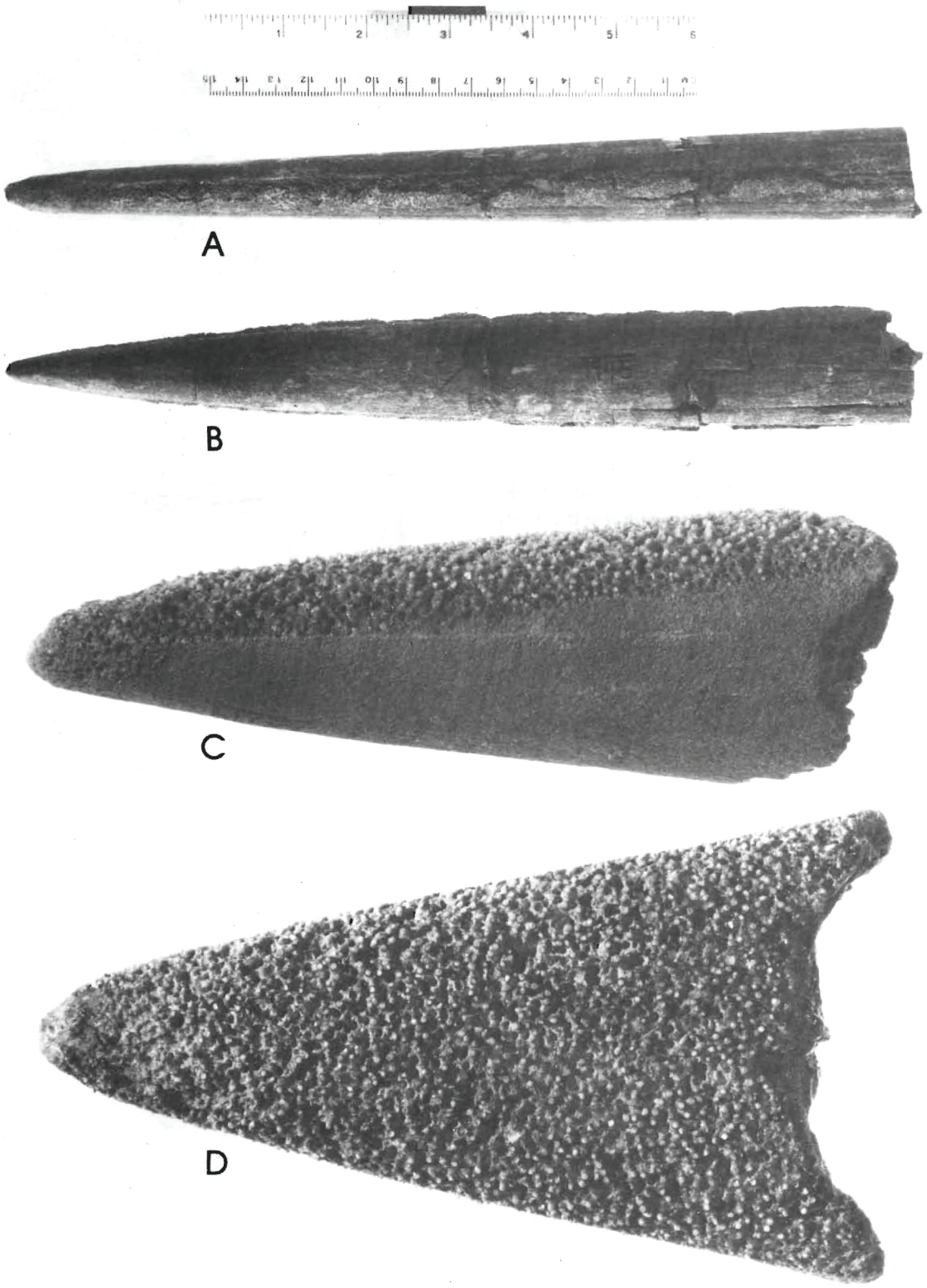


Figure 8.—Diagrams of the occipital region of several scombroids and xiphioids. **A.** *Wetherellus*. **B.** *Scombrinus*. **C.** *Acestrus* sp. **D.** *Acestrus ornatus*. **E.** *Xiphiorhynchus*. (From Casier, 1966.)

Figure 9.— *Makaira* sp. from the middle Miocene of California. Rostrum, lateral view (**A**) and dorsal view (**B**). Predentary, lateral view (**C**) and dorsal view (**D**). (In part from Fierstine and Applegate, 1968.)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The Paleorhynchidae (Fig. 6) comprises five genera *(Enniskillenus, Homorhynchus, Hemirhynchus, Paleorhynchus,* and *Pseudotetrapturus)* that are found from the Eocene to the Oligocene of Europe. One species, *Pseudotetrapturus luteus,* reaches up to 4 m in length (Danil'chenko, 1960), although other species usually are no longer than 1 m in length. Their vertebral count varies from 45 to 60. According to Danil'chenko (1960), *P. luteus* resembles *Tetrapturus* in dimensions and body form and in the structure of the elongated snout, but it differs from *Tetrapturus* in the far greater number of vertebrae, the much longer lower jaw, the more dorsal position of the pectoral fins, and the presence of large scales. Since I feel that the resemblances to the istiophorids are probably a result of convergence, I choose to put them in the Xiphioidei Incertae Sedis.

The family Xiphiorhynchidae is known from five species found in the Eocene of Africa, America, and Europe. The original description was from cranial fragments and subsequently various rostra were thought to be conspecific with the cranial fragments (Woodward, 1901). The crania (Fig. 10) are similar in proportions to those found in the Istiophoridae. Recently the Los Angeles County Museum of Natural History was given a large rostrum and two associated vertebrae (Figs. 11, 12) which belong to a new species of *Xiphiorhynchus* (Fierstine and Applegate, in press). One vertebra, an abdominal, is similar in size and shape to an abdominal vertebra of a black marlin *(Makaira indica),* whereas the other vertebra, a caudal, is similar in shape to that of a swordfish. Both vertebrae are strongly ossified like

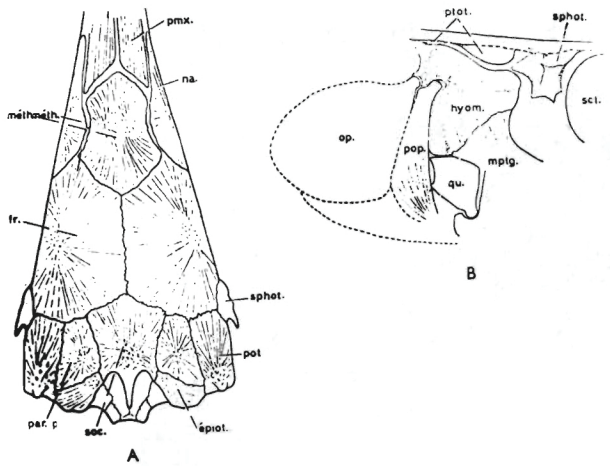


Figure 10.—Semidiagrammatic reconstruction of *Xiphiorhynchus priscus.* **A.** Dorsal view of skull. **B.** Lateral view of opercular region. (From Casier, 1966.)

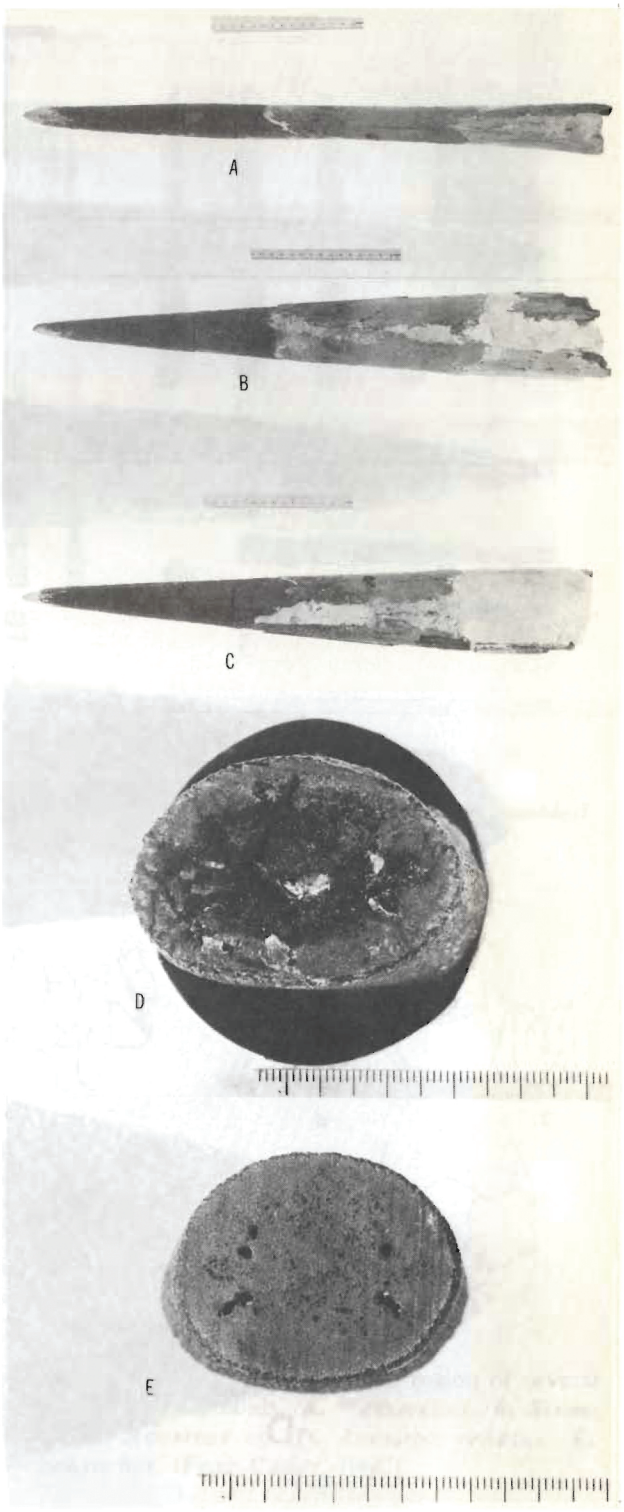
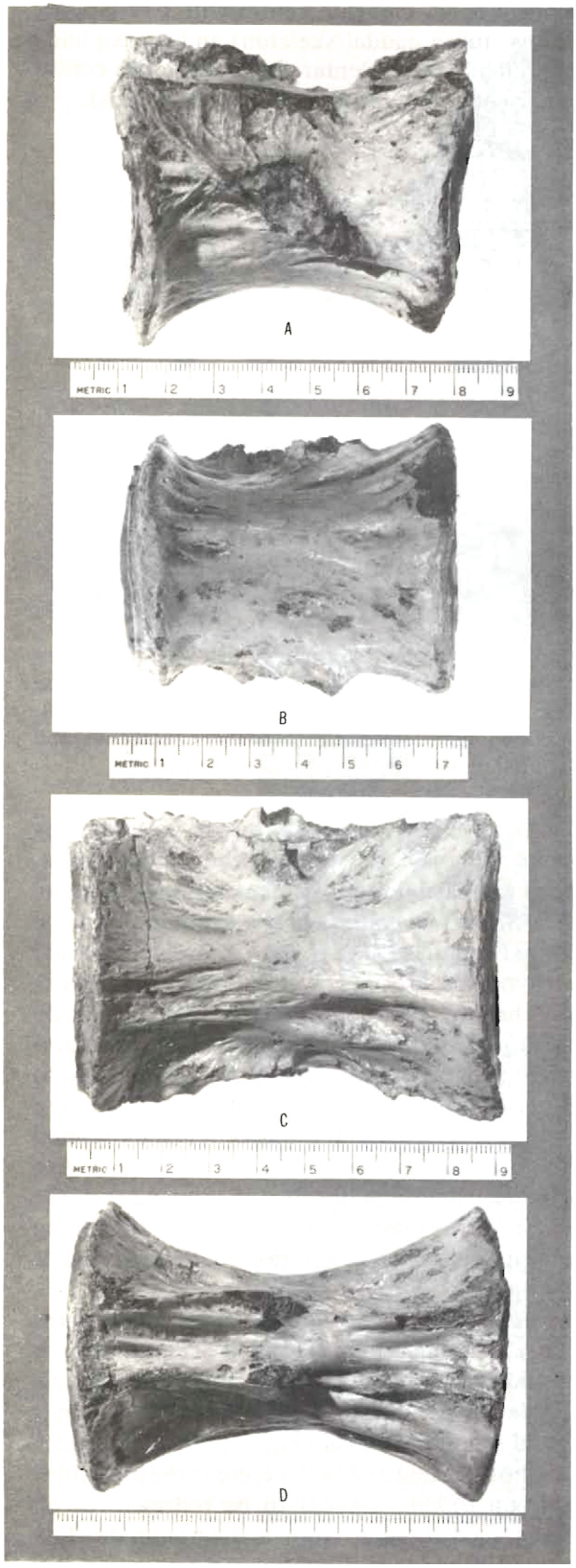


Figure 11.—Rostrum of *Xiphiorhynchus* sp. from the Eocene of Mississippi. **A.** Lateral view. **B.** Dorsal view. **C.** Ventral view. **D.** Cross-section taken 220 mm from distal tip. **E.** Cross-section taken 170 mm from distal tip.



those of the Istiophoridae. The large rostrum is similar in size and shape to that of the genus *Makaira* except that it is more flattened at its base. In cross-section, the xiphiorhynchid bill (Fig. 11) has a central longitudinal nutrient canal as well as two or more pairs of lateral nutrient canals. Istiophorids have only one pair of lateral longitudinal canals and lack a central canal. Xiphiids have a central longitudinal canal with only one pair of lateral canals. In short, this new species of *Xiphiorhynchus* seems to be intermediate to both the Istiophoridae and the Xiphiidae.

The Xiphiidae has a poor fossil record and this may be due to the poor ossification of its bones. Leriche (1910) identified one caudal vertebra from the Oligocene of Belgium as *Xiphias rupelensis* and it is similar to the hypural plate of *Xiphias gladius*. Most references to fossil Xiphiidae refer to the "*Cylindracanthus* group" or to the Istiophoridae. Recently Shelton Applegate of the Los Angeles County Museum of Natural History found a rostrum in the Eocene of Mississippi. It is 750 mm long, is depressed, and has a cross section at its base similar to a double-bladed axe. Distally the sharp lateral edges become blunt and the edge has a scalloped margin. Although the rostrum is unique, I strongly feel that it belongs to an yet unknown xiphiid.

In summary then, the classification of billfish should be:

ORDER PERCIFORMES
SUBORDER XIPHIOIDEI
FAMILY ISTIOPHORIDAE (? *Acestrus, Brachyrhynchus, Istiophorus, Makaira, Tetrapturus*)
FAMILY XIPHIORHYNCHIDAE (*Xiphiorhynchus*)
FAMILY XIPHIIDAE (*Xiphias*, and undescribed Eocene genus)
XIPHIOIDEI INCERTAE SEDIS
FAMILY PALEORHYNCHIDAE (*Eniskillenus, Hemirhynchus, Homorhynchus, Paleorhynchus, Pseudotetrapturus*)
FAMILY BLOCHIIDAE (*Blochius*, ? "*Cylindracanthus* group")

Figure 12.—Two vertebrae of *Xiphiorhynchus* sp. from the Eocene of Mississippi. **A.** Lateral view of abdominal vertebra. **B.** Ventral view of abdominal vertebra. **C.** Lateral view of caudal vertebra. **D.** Ventral view of caudal vertebra.

At this time it is difficult to propose any phylogenetic scheme. Evidence seems to suggest that at least three billfish groups had differentiated and were living contemporaneously during the Eocene. Members of the recent genera were living in Miocene seas and they may be conspecific with those that are alive today. Whatever form was the common ancestor to the istiophorid and xiphiid lineages had to be in existence prior to the Eocene.

AREAS OF RESEARCH

Comparative osteological studies on recent billfish are needed in order to reasonably evaluate the fossil forms. Good osteological collections are rare because museums and universities lack the necessary storage space; thus they usually avoid the preparation of large skeletons. Therefore, my first suggestion would be for more skeletons. A study of the relative size and dimensions of the rostra and vertebrae would be very useful. Since these structures are usually found separate from the rest of the skeleton, simple comparative morphometric data would aid their identification. Even though paleontologists have placed importance on the histology of fossil bills, the placement and number of nutrient canals and the structure of the denticles are not known for many of the recent forms.

The functional anatomy of the feeding apparatus and the method of locomotion are not known. For example, the function of the predentary bone has been surmised (Fierstine and Applegate, 1968) and the role of the bill itself is just conjecture (Wisner, 1958; Tibbo, Day, and Doucet, 1961). The presence of the predentary bone may be an adaptive feature for large "slab-sided" fish with elongated upper or lower jaws. Aspidorhynchid holosteans (Fig. 13) have a predentary bone (Orlov, 1964; Zittel, 1932) and the extinct clupeiform suborder Saurodontoidei has an edentulous predentary which extends the lower jaw well beyond the upper (Bardack, 1965). Neither of these groups are thought to be directly related to each other or to the istiophorids (Greenwood, Rosen, Weitzman, and Myers, 1966; Gosline, 1968, 1971).

No one has reliably measured the swimming speed of a billfish or analyzed their swimming movements. It is fairly obvious that the size and behavior of these fish are difficult barriers, but they could be overcome. A better understanding of the feeding and locomotory apparatuses would help us explain the differences between the istiophorids (rounded bill, predentary bone, elongate centra with overlapping processes, fused caudal skeleton) and the xiphiids (depressed bill, no predentary bone, cube-like centra with no overlapping processes, no pelvic fins).

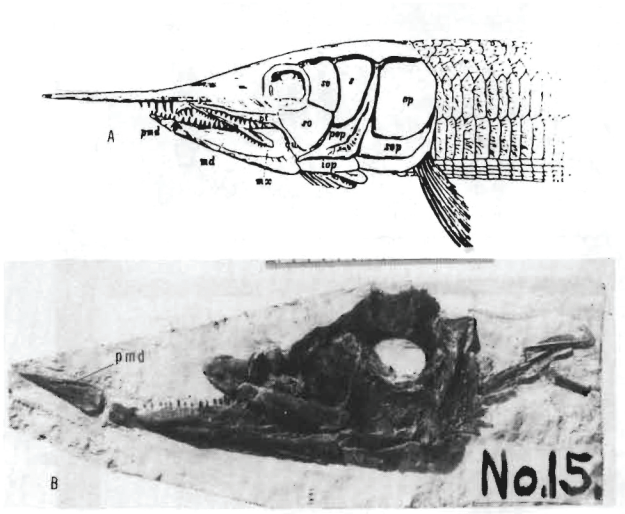
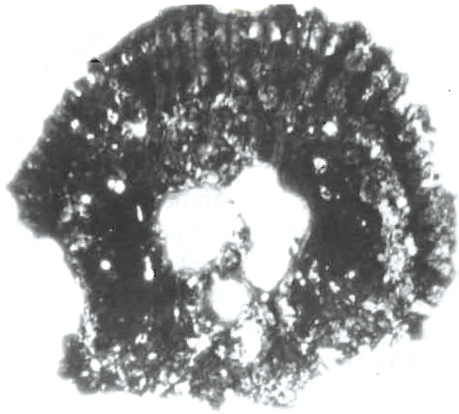


Figure 13.—Two other examples of fish with predentary (pmd) bone. **A.** *Aspidorhynchus acutirostris* from the Jurassic of Solenhofen, Germany. (From Zittel, 1932.) **B.** Unidentified saurodontid. Age (probably Cretaceous) and location unknown.

The European fossil billfish need to be studied by someone who is familiar with the recent forms. There is no fossil group that does not need review. What is *Brachyrhynchus*? Is it a synonym of some recent istiophorid? Is *Acestrus* an istiophorid? Paleorhynchids are now well-known from Russia (Danil'chenko, 1960). Their large size and body shape may be adaptive features that result from convergence and are not a result of any relationship to the xiphioids. Since their upper and lower jaws are nearly equal in length, the paleorhynchids remind me of a huge needlefish (Order Beloniformes). Are the smaller paleorhynchids just the juveniles of the much larger *Pseudotetrapturus luteus*? If nothing else, the quality of the illustrations of *P. luteus* needs to be improved.

The study of *Blochius* would be especially rewarding. Of all the uncertain groups, it seems to be the most likely candidate to be included in the Xiphioidei proper. Dr. George Myers (pers. comm.) once told me that *Blochius* had a predentary bone. No mention is made of this structure in the literature. In addition *Blochius* needs to be redrawn, as all available figures stem from a diagrammatic line drawing in Woodward (1901).



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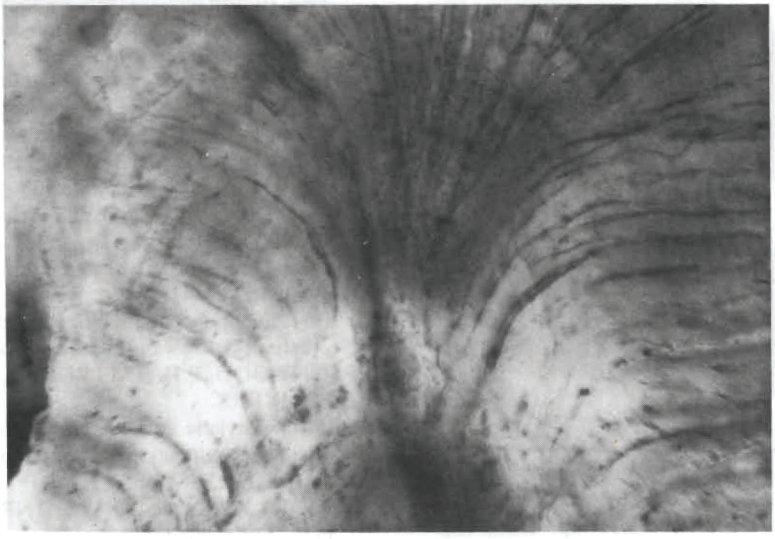

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Figure 14.—Cross-section of a rostrum of *Glyptorhynchus* sp. from the Miocene of California. **A.** Low power. **B.** Medium power. **C.** High power.

The "*Cylindracanthus* group" is currently in taxonomic chaos. Casier (1966) divided the group into two parts; he placed one group in the family Blochiidae of the Order Heteromi (=Notacanthiformes) and the other group in the family Xiphiidae of the Order Scombromorphi (=?Scombroidei). No explanation was given as to why there was a relationship to the Order Notacanthiformes. Carter (1927) showed that a *Cylindracanthus* rostrum was similar histologically to a bill fragment of *Blochius* and he also showed that it was similar to a spine of the living trunkfish, *Ostracion*. Does this mean that the *Cylindracanthus* structures are bills or spines? What other structures would have a similar histology? The microscopic interpretation is very equivocal. Carter (1927) stated that the *Cylindracanthus* rostrum was composed of dentine. Tor Orvig (pers. comm.) interpreted *Cylindracanthus* bills to be composed of acellular bone. Rainier Zangerl (pers. comm.) interpreted a photomicrograph (Fig. 14) of a ground thin section of a *Glyptorhynchus* rostrum as dentine whereas, Melvin Moss (pers. comm.) has suggested that the same structure is composed of acellular bone.

The rostra of the "*Cylindracanthus* group" are characterized by two or more rows of "alveoli" (Fig. 15) on one surface, the supposed ventral surface. The "alveoli" are thought to have contained denticles, but no tooth-like structures have ever been present. I personally think that most, if not all, of the "*Cylindracanthus* group" rostra will prove to be fin spines. These structures are too numerous and common in the fossil record for each to represent an individual fish.

Much of our lack of knowledge of fossil billfish stems from the paucity of comparative anatomical studies. Once this foundation is built there are many intriguing problems to solve in the fossil record. It is my hope that this paper has served as a stimulus for others to enter an uncrowded research field.

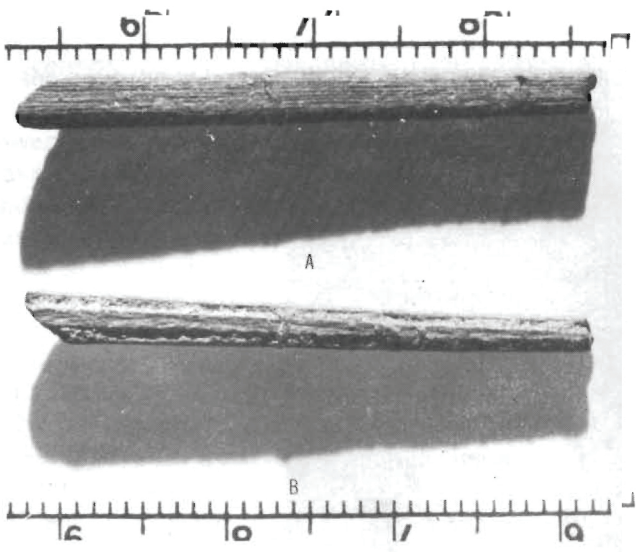

Figure 15.—Rostrum of *Glyptorhynchus* sp. from the Miocene of California. **A.** Lateral view. **B.** Ventral view showing two alveolar grooves.

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