BILLFISH REMAINS FROM SOUTHERN CALIFORNIA WITH REMARKS ON THE IMPORTANCE OF THE PREDENTARY BONE

HARRY L. FIERSTINE
California State Polytechnic College
San Luis Obispo and Research Associate
Los Angeles County Museum of Natural History

and

SHELTON P. APPLEGATE
Division of Vertebrate Paleontology
Los Angeles County Museum of Natural History

INTRODUCTION

Fossil fishes of the family Istiophoridae (Marlins, Sailfishes, and Spearfishes, have never been reported from the western United States and have rarely been recorded from North America (Berry, 1917; Eastman, 1917; Leidy, 1885; Leriche, 1942; Woodward, 1901). Billfish remains should be expected in southern California, since the extensive marine Tertiary deposits commonly yield fishes (carangids (David, 1943) and scombrids (Fierstine, in manuscript) that probably inhabited the same environment as the billfishes themselves.

Recently one of us (S.A.) collected or obtained billfish specimens from various fossil localities in southern California. One of the fossils, the predentary bone, was found to be such a peculiar osteological feature that a discussion of its taxonomic and biological implications was warranted.

MATERIALS AND METHODS

The fossil specimens are housed in the Division of Vertebrate Paleontology, Los Angeles County Museum of Natural History (LACM). All but one specimen is figured and the data for each specimen is given in the figure legend or in text. Table 1 lists the recent material examined in this study and the pertinent information for each specimen. The following scientific names are used in this paper:

Swordfish	*Xiphias gladius* Linnaeus
Shortbill spearfish	*Tetrapturus angustirostris* Tanaka
Longbill spearfish	*Tetrapturus pfluegeri* Robins and deSylva
Mediterranean spearfish	*Tetrapturus belone* Rafinesque

Striped marlin	*Tetrapturus audax* Phillipi
White marlin	*Tetrapturus albidus* Poey
White marlin	*Makaira indica* (Cuvier)
Black marlin	*Makaira nigricans* Lacepede
Blue marlin	*Istiophorus gladius* (Bloch)
Pacific sailfish	

The authority for these names are Howard and Ueyanagi (1965), Merrett and Thorp (1965), and Robins and deSylva (1960, 1963).

LOCALITIES:
Sharktooth Hill, Kern County, California, LACM loc. 1625, SW¼ of the SW¼, Sect. 25, T 28S, R 28E, Oil Center Quandrangle, U. S. G. S. 1954; near LACM loc. 1623, Middle Miocene.

El Toro, Orange Co., California, LACM loc. 1945, 1¼ miles SW of the town of El Toro, Sect. 34, T 6S, R 8 W, San Juan Capistrano Quadrangle, U. S. G. S., 1942; Upper Miocene.

Earl Calhoun Hill no. 2, Orange County, California, LACM loc. 65119. Sect. 34, T 6S, R 8W, San Juan Capistrano Quadrangle, U. S. G. S., 1942; further east than loc. 1945, Upper Miocene.

Newport Beach, Orange County, California, LACM loc. 6732, sand quarry near Palisades Road, Back Bay; Tustin Quadrangle, U. S. G. S. 1950, Late Pleistocene.

SYSTEMATIC DESCRIPTIONS

Order Perciformes
Suborder Xiphioidei
Family Istiophoridae
Istiophorid g. indet.
Figure 1A

Description: A nearly complete 67.5 mm long second abdominal vertebra (LACM 17695) was collected by Mr. Richard Bishop at LACM loc. 1625, Middle Miocene, Sharktooth Hill, Kern County California. The anterior end of the centrum measures 44.5 mm high and 40 mm wide; the posterior end of the centrum measures 44.1 mm high and 41 mm wide. The minimum width of the centrum is 21.5 mm.

A nearly complete anterior caudal vertebra (LACM 17049) which measures 227 mm long between the anterior edge of the zygapophysis and the posterior edge of the neural spine was collected by Mr. and Mrs. Lawrence McCain at LACM loc. 6732, Late Pleistocene, Newport

TABLE 1
GENERAL INFORMATION FOR RECENT SPECIMENS

Scientific Name	*Standard length (mm)*	*Locality*	*Material*	*Collection Number and/or Institution**
Xiphias gladius	?	?	axial skel.	UCLA
Xiphias gladius	?	?	caudal skel.	LACM
Xiphias gladius	?	?	lower jaw	LACM
Tetrapturus angustirostris		100 mi. E. Monterey, Calif.	head skel.	SIO 59-287-43A
Tetrapturus audax	est. 1900		axial skel.	UCLA S281
Tetrapturus audax	1933	off Baja Calif.	complete	CAS
Tetrapturus audax	?	Southern Calif.	head	Cerritos Coll.
Tetrapturus audax	?	off San Diego, Calif.	caudal skel.	LACM
Tetrapturus audax	?	?	axial skel.	SIO
Tetrapturus audax	?	off Southern Calif.	head	LACM
Tetrapturus audax	2,328	Rancho Buena Vista, Baja California del sur	caudal skel.	SLO (HLF No. 2)
Makaira holei Jordan and Evermann Holotype (= *T. audax*)	2,211	off Catalina Id., Calif.	mounted skin	CAS No. 610
Istiophorus gladius	2,250		axial skel.	UCLA S549
Istiophorus greyi Jordan and Evermann Holotype (= *I. gladius*)	2,808	Cape San Lucas, Baja, Calif.	mounted skin	LACM Accession No. 1497
Makaira marlina Jordan and Hill Holotype (= *Makaira indica*)	3,791	Cape San Lucas, Baja, California	mounted skin	LACM Accession No. 1497
Makaira indica	?	?	axial skel.	UCLA S551
Makaira nigricans	?	?Atlantic Ocean	mounted skin	LACM

*CAS = California Academy of Science
UCLA = University of California, Los Angeles, Ichthyological Collection
CC = Cerritos College, Norwalk, California, Biology Department
SIO = Scripps Institute of Oceanography, Ichthyological Collection
SLO = California State Polytechnic College, San Luis Obispo, Biology Department
LACM = Los Angeles County Museum of Natural History

Beach, Orange County, California. This was donated to the Los Angeles County Museum of Natural History. The centrum is 115 mm long and its minimum width is 36.5 mm; the dorsal extension of the neural spine is missing.

Discussion: The general shape of both vertebrae was similar to all the istiophorids studied except that the centrum of the abdominal vertebra was more constricted. Width to length ratios of the centrum (Table 2) only eliminated *M. indica* as a possible candidate. The large size of the caudal vertebra probably eliminates *T. audax* as a contender, however the lack of comparative material over various size ranges inhibits a precise identification.

TABLE 2

CENTRUM MEASUREMENTS OF THE 2ND ABDOMINAL VERTEBRA

Centrum Measurements (mm)

Species	Narrowest width	Maximum length	Width to length ratio
FOSSIL (LACM 17695)	21.5	67.5	.31
Pacific Sailfish (UCLA S549)	12.5	54.0	.23
Striped marlin (UCLA S281)	11.5	42.5	.27
Black marlin (UCLA S551)	37.0	59.5	.60

Makaira sp.
Figures 1A, 2A

Description: A 281 mm long bill fragment (LACM 17693) was found at LACM loc. 1945 and a complete 72.5 mm long predentary bone (LACM 16074) was collected at LACM loc. 65119. Both localities are Upper Miocene and the measurements for the two elements are given in Table 3.

The bill has two small nutrient canals exposed at the broken surface of the proximal (basal) end. The canals are small (4.6 mm by 2.5), closely set together (4 mm apart), and are acentrically located toward the ventral surface. Although there are only a few denticles preserved, it appears that only the ventral one-half bears denticles and that the dorsal

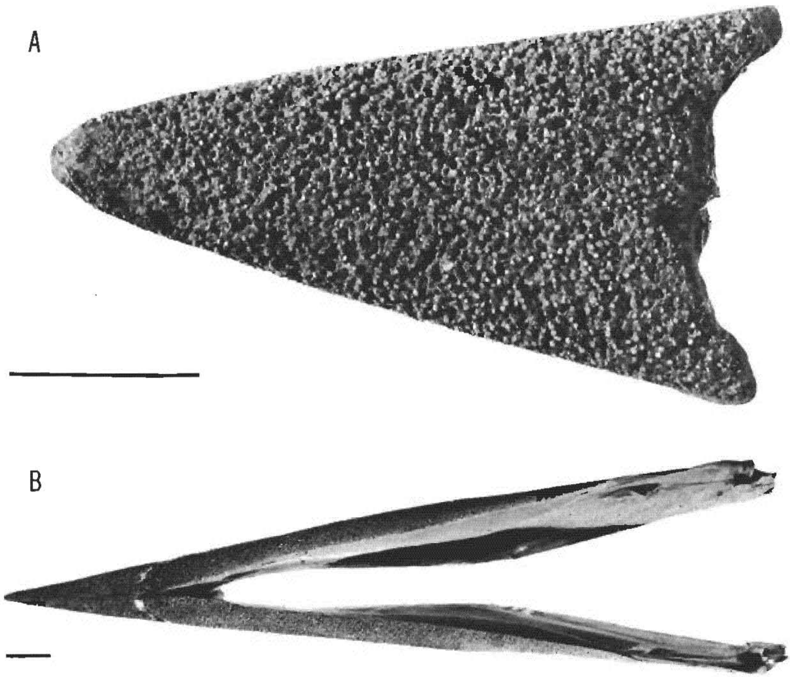

Figure 1. A. Istiophorid g. indet., second abdominal vertebra, LACM $\frac{1625}{17695}$, left lateral view. B. *Makaira* sp., bill fragment, LACM $\frac{1945}{17693}$, left lateral view.
A line two cm long is indicated for each specimen.

one-half is smooth. The proximal surface of the predentary bone is rugose and indicates a complicated articulation with the two dentary bones. The denticles are evenly distributed on the entire dorsal surface and extend to its widest point.

Discussion: The identification is based on size (Table 3) which compares poorly with the more slender-billed Pacific sailfish, shortbill spearfish, and striped marlin. The size of the fossil bill was minimal because of its lack of denticles and its worn condition. Since we assumed these species to be representative of the genera, *Tetrapturus* and *Istiophorus,* they were eliminated and only *Makaira* was left as a possible candidate. The elimination of *Istiophorus* on the basis of size is strengthened by the fact that the Holotype of *I. greyi* was once a record-size fish (Jordan and Evermann, 1926).

The bill is nearly identical in size and shape to one (Table 3) described as *Istiophorus calvertensis* Berry 1917 from the Calvert formation, Tar

Figure 2. A. *Makaira* sp., predentary bone, LACM $\frac{65119}{16074}$ dorsal view. B. *Tetrapturus audax*, dorsal view of lower jaw. The predentary bone became separated from the rest of the jaw during preparation and has been restored to its normal anatomical position. The denticular pattern would not normally be interrupted and its articulation with the dentary bones would not be obvious in this view.
A line two cm long is indicated for each specimen.

Bay, James River, Prince George County, Virginia, ?Miocene. It differs from *I. calvertensis* on the peripheral location and size of the nutrient canals. The denticles are missing on the Virginia specimen, however it probably also belongs to *Makaira*. In the recent specimens examined, the dorsal surface of the bill was smooth except in the Holotype of *I. greyi* where the distal one-half of the dorsal surface has small denticles.
Predentary bone discussion: The denticles of the fossil are evenly distributed on the dorsal surface, a feature that it shares with *I. greyi* (Holotype) and *T. audax*. It differs in this feature from *M. marlina* (Holotype) and *M. nigricans*) where the denticles do not extend across the entire dorsal surface at the basal (proximal) end.

A predentary bone is a rare element in the Teleostei. So far as known,

TABLE 3

Comparison of Bill and Predentary Proportions

		Bill (mm) (height/width)		Predentary (mm) (height/width)
Specimen	Base	Mid pt.	One cm from tip	Base
Fossil	*28*	*22.5*	*11.0*	--
(LACM 17693)	37	32.5	8.5	
Fossil	-	-	-	*25.5*
(LACM 16074)				43.9
Istiophorus	*26*	*23.5*	*18.5*+	--
calvertensis	36	33.0	28.0	
Makaira marlina	*49*	*35*	*11.0*	*34.0*
Type	70	46	10.5	38.5
Makaira nigricans	*25*	*19*	*7*	*23*
	36	27	8	44
Istiophorus greyi	*28*	*17*	*6.5*	*16*
Type	34	22	9.0	19
Tetrapturus audax	*22.0*	*15.0*	*5.2*	*15*
(LACM)	37.5	22.5	7.2	27

+ Measurement taken approximately 7.8 cm from tip.

it occurs only in the clupeiform extinct suborder Saurodontoidei (Berg, 1940) and in the perciform suborder Xiphioidei. It is edentulous in the saurodontoids and it extends the lower jaw well beyond the upper. The predentary in the xiphioids is restricted to the family Istiophoridae where it bears numerous denticles and the upper jaw or bill extends far anterior to the predentary bone.

The presence of the predentary bone in the saurodontoids is a widely known fact among paleoichthyologists (Bardack, 1965), however the presence of the bone in the Istiophoridae is not universally known. It is briefly mentioned by Regan (1909), Gregory and Conrad (1937 a), Conrad (1938), and Nakamura (1938), but no mention is made of this element in later anatomical or systematic accounts.

The predentary bone is absent in *X. gladius* and all members of the family Scombridae. This element is neither discussed nor figured in the Gempylidae (Matsubara and Iwai, 1958) nor in the Trichiuridae (Tucker, 1956). The structure (Fig. 2B) is well-developed in *T. audax, M.*

indica, M. nigricans, and *I. gladius* (observation based on the Holotype *I. greyi*). In a single specimen of *T. angustirostris* the predentary is represented by a very small denticle-bearing bone at the mandibular symphysis.

The absence of a predentary bone *X. gladius* adds another difference (bill and body shape, fin structure, myology, squamation, vertebral number, and vertebral shape) to the xiphiid and istiophorid lineages. The observation that *T. audax* has a well-developed element and that *T. angustirostris* has a tiny one might have important taxonomic implications. However, until the presence or absence of a predentary bone is determined for *T. pfluegeri, T. belone,* and *T. albidus,* the exact taxonomic importance of this element will remain unknown.

The function of the bone has not passed the point of speculation. Bardack (oral presentation before the Society of Vertebrate Paleontology, November 15, 1966) thought that the edentulous predentary of the saurodontids may have created a water flow pattern that directly aided the fish to gather food. This function seems unlikely for the predentary of istiophorids. Their bone helps form the contour of the head, but the dentary bones themselves should be able to provide this function without invoking a separate bony element.

The long-billed forms have a thin mandibular symphysis in order to conform to a laminar head shape. Since movement of the lower jaws at the symphysis is important for expanding the orobranchial cavity (Schaeffer and Rosen, 1961), then a thin symphysis would make a weak joint. This joint could be strengthened if it were moved to a thicker part of the jaw through the development of a predentary bone. The reduction of the predentary in *T. angustirostris* may be a functional response to the shorter bill and mandibles. The carnivorous characins apparently strengthen their mandibular joint by developing an interlocking arrangement (Gregory and Conrad, 1937b). There is no symphyseal joint in the swordfish hence it probably differs from the istiophorids in its method of expanding its orobranchial cavity. However, the dried lower jaws seem to be thin and flexible and this flexibility may allow adduction of the mandibles.

The origin of the predentary bone is unknown. It is unlikely that the bones of saurodontids and istiophorids are homologous structures. According to Greenwood, *et al.* (1966) the Istiophoridae, a member of the Acanthopterygii, was derived from a Protocanthopterygian. This latter group seems to have no elements in the lower jaw anterior to the dentary bone (see Berg, 1940), therefore the istiophorid element is a neomorph. The saurodontids presumably belong to Greenwood *et al's* Osteoglossomorpha, a separate lineage from the Protocanthopterygii-

Acanthopterygii lineage. These two lines have their common ancestry in the pholidophoroid holosteans which also seem to lack elements in the lower jaw anterior to the dentary bone (see Berg, 1940). Thus, the saurodontoid predentary is also a neomorph and is not homologous with the istiophorid predentary bone.

SUMMARY

The Istiophoridae was represented in southern California during the Miocene and Pleistocene periods. Because of a paucity of fossil material and lack of comparative recent skeletons, exact identifications were impossible. A second abdominal vertebra and an anterior caudal vertebra were identified as istiophorid g. indet., and a bill and predentary bone were identified as *Makaira* sp. All fossil elements seemed to be quite similar to the same elements in living billfish.

The predentary bone of the Istiophoridae is a neomorph since it is not found in any ancestral or closely related teleost fish. Its large size in *Istiophorus gladius, Makaira nigricans, M. indica,* and *Tetrapturus audax* and its small size in *T. angustirostris* may have important systematic implications. It is absent in *Xiphias gladius*. It is suggested that because of the istiophorid head shape, the symphysis of the lower jaw is thin. Thus, the symphyseal joint would be weak during expansion and contraction of the orobranchial cavity except that the predentary bone functions to move the joint posteriorly to a thicker part of the jaw in order to strengthen the interdentary joint.

ACKNOWLEDGEMENTS

We wish to thank Dr. Boyd Walker (University of California, Los Angeles), Dr. Richard Rosenblatt (Scripps Institute of Oceanography), Mr. Jules Crane (Cerritos College and Mr. William Follett (California Academy of Science) for the use of specimens examined in the course of this study. Particular thanks goes to Dr. Vladimir Walters (University of California, Los Angeles) for his stimulating criticism of the function of the predentary bone. Dr. David H. Dunkle (U.S. National Museum) read the manuscript and offered comments.

Special thanks is due to the administration and faculty of the California State Polytechnic College, San Luis Obispo for awarding one of us (HLF) a special research leave for the spring quarter, 1967 to participate in this research.

LITERATURE CITED

BARDACK, D.
1965. Anatomy and evolution of chirocentrid fishes. *Univ. Kansas Paleo. Contrib., Vertebrata*, Art. 10, 86 p.

BERG, L. S.
1940. Classification of fishes both recent and fossil. Ann Arbor, Michigan: Edward Bros., 517 p.

BERRY, E. W.
1917. A sailfish from the Virginia Miocene. *Amer. J. Sci.*, 43:461-464.

CONRAD, G. M.
1938. The osteology and relationships of the wahoo *(Acanthocybium solandri)*, a scombroid fish. *Amer. Mus. Novitates* (1000):1-32.

DAVID, L. R.
1943. Miocene fishes of southern California. *Geol. Soc. Amer.*, Special Pap. no. 43, 193 p.

EASTMAN, C. R.
1917. Fossil fishes in the collection of the United States National Museum. *Proc. U.S. Nat. Mus.*, 52:234-304.

GREENWOOD, P. H., D. E. ROSEN, S. H. WEITZMAN and G. S. MYERS
1966. Phyletic Studies of Teleostean fishes, with a provisional classification of living forms. *Bull. Amer. Mus. Nat. Hist.*, 131:339-456.

GREGORY, W. K. and G. CONRAD
1937a. The comparative osteology of the swordfish *(Xiphias)* and the Sailfish *(Istiophorus)*. *Amer. Mus. Novitates*, (952):1-25.
1937b. The structure and development of the complex symphyseal hinge-joint in the mandible of *Hydrocyon lineatus* Bleeker, a characin fish. Pro. Zool. Soc. London, p. 4, 975-984.

HOWARD, J. K. and S. UEYANAGI
1965. Distribution and relative abundance of Billfishes (Istiophoridae) of the Pacific Ocean. *Studies in Trop. Oceanogr. Miami* vol. 2, 134 p.

JORDAN, D. S. and B. W. EVERMANN
1926. A review of the giant mackerel-like fishes, tunnies, spearfishes and swordfishes. *Calif. Acad. Sci., Occ.* Pap., 12:1-113.

LEIDY, J.
1855. Indications of twelve species of fossil fishes. *Proc. Acad. Nat. Sci. Phil.* 7:395-397.

LERICHE, M.
1942. Contribution a l'etude des faunes ichthyologique marines des terrains Tertiaires de la plaine cotiere, Atlantique et du centre des Etats-Unis. Le synchronisme des formations tertiaires des deux cotes de l'Atlantique. Mem. Soc. Geol. France, n.s. 20:5-110.

MATSUBARA, K. and T. IWAI
1958. Anatomy and relationships of the Japanese fishes of the family Gempylidae. College of Agriculture, Kyoto University, Mem. Fish Series, Special No., June: 23-54.

MERRETT, N. R. and C. H. THORP
1965. A revised key to the scombroid fishes of East Africa with new observations on their biology. Ann. Mag. Nat. *Hist.*, 8:367-384.

NAKAMURA, H.
1938. Report of an investigation of the spearfishes of Formosan waters. Reports of the Taiwan Government — General Fishery Experiment Station. *U.S. Fish and Wildlife Serv. Spec. Sci.* Rept. (153):1-46.

REGAN. C. T.
1909. On the anatomy and classification of the scombroid fishes. Ann. Mag. Nat. Hist. 8:66-75.

ROBINS, C. R. and D. P. deSYLVA
1960. Description and relationships of the longbill spearfish, *Tetrapturus belone,* based on western north Atlantic specimens. *Bull. Mar. Sci. Gulf and Caribbean,* 10:383-413.

1963. A new Western Atlantic spearfish, *Tetrapturus pfluegeri,* with a redescription of the Mediterranean spearfish *Tetrapturus belone, Bull. Mar. Sci. Gulf and Caribbean,* 13:84-122.

SCHAEFFER, B. and D. E. ROSEN
1961. Major adaptive levels in the evolution of the actinopterygian feeding mechanism. *Am. Zoologist,* 1:187-204.

TUCKER, D. W.
1956. Studies on the trichiuroid fishes-3. A preliminary revision of the family Trichiuridae. *Bull. British* Mus. Nat. *Hist.,* Zool., 4:73-130.

WOODWARD, A. S.
1901. Catalogue of the fossil fishes in the British Museum (Natural History). Vol. 4, London. 636 p.

Accepted for publication December 18, 1967.