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THE COMPARATIVE OSTEOLOGY OF THE SWORDFISH (*XIPHIAS*) AND THE SAILFISH (*ISTIOPHORUS*)

BY WILLIAM K. GREGORY AND G. MILES CONRAD

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INTRODUCTION

Two complete skeletons and one immense skull of *Xiphias gladius* were secured near Louisburg, Nova Scotia, by the Michael Lerner Cape Breton Expedition of The American Museum of Natural History in July and August, 1936. One of these skeletons has been mounted for exhibition in the Museum's Hall of Fishes, while the other skeleton and skull have been deposited in the study collection of the Department of Ichthyology. A life-sized model (Fig. 1) of a North Atlantic record fish, weighing 601 pounds, caught by Mr. Lerner, was made by Al Pflueger of Miami, Florida, and has been placed on exhibition. Casts of this fish were made while it was still fresh and color notes were taken by Mr. Ludwig Ferraglio of the Museum's Department of Preparation.

Unlike most scombriforms, which are brilliantly colored, the color of the swordfish is a nearly uniform, dull muddy purple on the back and fins, the belly being a dirty white and the flanks bronze. Conceivably this dull color may have concealing value for the fish as it seeks its prey.

The swordfish follow the mackerel northward in July and August. Our party, however, did not find mackerel remains in their stomachs. We did find that the stomachs contained herring in abundance. Dr. C. J. Fish, the oceanographer, who has given close attention to the move-

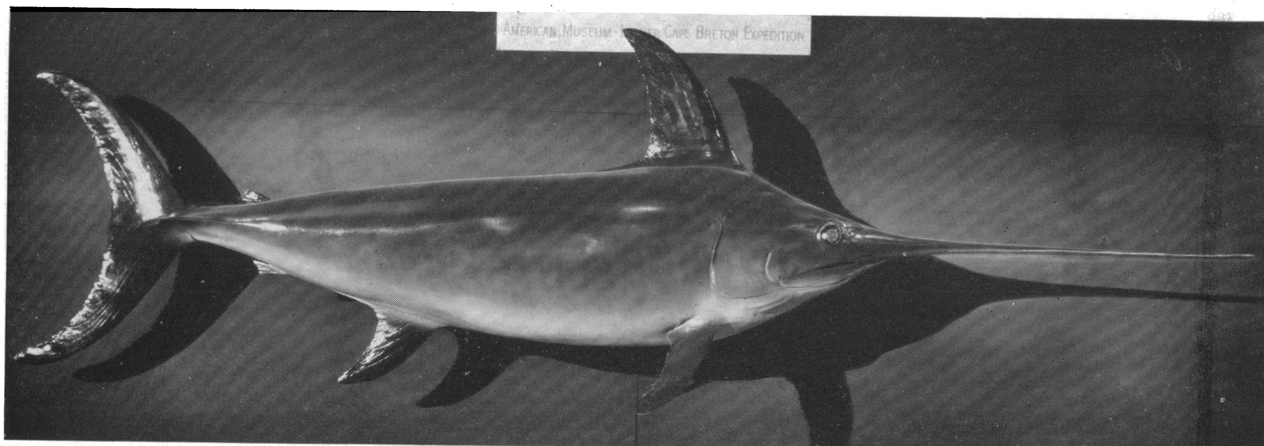

Fig. 1. Life-size model of swordfish.

ments of plankton and plankton-feeders, tells us he suspects that the herring feed at night when the plankton is near the surface and that the swordfish with their very large eyes see the phosphorescent glow caused by the movements of the herring in water containing light-producing organisms.

TABLE I.—Swordfish Measurements (in inches), Louisburg, July 21–Aug. 6, 1936

Total length, tip sword to notch caudal	106.5	111	113	140.5 (est. 143.3)	151	141
Tip sword to eye	39	40	40.5	43 (est. 46)	55	46
Head without snout	13	—	14	17.5	18	17
Eye	3	—	3	4	4	4
Base to notch caudal	6	—	7	—	9	
Lower jaw projects beyond eye	5.75	—	6	—	7	
Tip lower jaw to angle gape	9.5	—	—	—	$13\frac{1}{2}$	
Tip lower jaw to angle gape groove	10.75	—	—	—	$15\frac{1}{4}$	
Tip mandible to vent	—	—	—	62	$57\frac{3}{4}$	$55\frac{1}{2}$
Depth body at dorsal axil	18	—	16.5	—	33	32
Thickness at dorsal axil	11	—	—	—		
Dorsal origin to tip	17	18	16.5	24	$18\frac{1}{2}$	
Pectoral	14.25	11.5	17	20	16	
Anal	7.5	—	11	—	$15\frac{1}{2}$	
Caudal lobe	22	22.5	22	27.5	$26\frac{1}{2}$	
Caudal spread	31	32	32	43	$37\frac{1}{2}$	
Origin to tip lower lobe second dorsal	3.5	—	—	—	$4\frac{1}{2}$	
Origin to tip lower lobe second anal	3.5	—	—	—	$4\frac{1}{2}$	
Length dorsal keel	7				$8\frac{1}{4}$	
Depth dorsal keel	3				5	
Weight	225 lb. (est. total)	—	—	520 lb. (dressed net)	601 lb.	535 lb.

The expedition observed nothing contradictory to the common belief (Bigelow and Welsh, 1925, p. 242) that the swordfish pursues the herring, mackerel and cuttle-fishes and with sharp swings to the right and left strikes them with its sword and either cuts or stuns them. It certainly often swallows them whole, as noted by Raven and La Monte (1937) but some were found in the swordfish stomach with broken backs.

According to the fishermen the swordfish are ordinarily rather sluggish fish which cruise slowly at the surface, often with the dorsal fin cutting the water like a shark's. When harpooned, however, they develop great speed. Bigelow and Welsh (1925, p. 226) say that sometimes when struck the swordfish "sound with such speed and force as to drive the sword into the bottom" and come up with the mud still sticking to the sword. It has long been known that sometimes they drive the sword "right through the planking of a fishing vessel" (*ibid.*).

BODY-FORM AND FINS

The preceding notes suggest the reason for the streamlined torpedo-like body (Fig. 2). The greatest cross-section is just behind the dorsal fin and is an oval. There is a general parallelism with the mackerel sharks (*Isurus*, etc.) and especially with the ichthyosaurs.

The principal measurements of the fish from which the model was made were:

Total weight	601 lbs.
Length to notch of caudal fin (Pu)	151″
Greatest depth of body behind first dorsal	33″
Height of dorsal fin	$18^1/_2$″
Caudal spread (tt′)	$37^1/_3$″

More detailed measurements, made by J. T. Nichols, are given in Table I.

An analysis of the body forms and fins of *Xiphias*, *Makaira* and *Istiophorus* by means of their inscribed rectilinear figures, as first used by Gregory (1928*a*, 1928*b*), reveals the following facts.

Xiphias gladius.—The body of *Xiphias* is dolichosomatic if the sword is included (since the vertical diameter is less that 1/5 length Pp), but if the sword is not included, the body is mesosomatic, for the vertical diameter is then greater that 1/5 of P′p. The head length is nearly one-half of the total length and may be considered macrocephalic. The forehead is flat to slightly concave and the entering angle is low.

The caudal fin is hypermacrocercal, the maximum spread (tt′) being about 1 1/2 times (ad + av). The spread of the caudal exceeds that of the mackerel sharks in proportion to the rest of the body (cf. *Lamna*). The caudal fin may be termed leptopygidial (delicate peduncle) for pd + pv is less that 1/4 (ad + av).

The dorsal fin is greater than 3/4 the body depth and may be called altiradial. It is situated very far forward, immediately above the pectoral fins and but a little way in front of the center of gravity of the entire fish. Probably the forward position and great height are advantageous not only in keeping the swordfish on a straight course but also in facilitat-

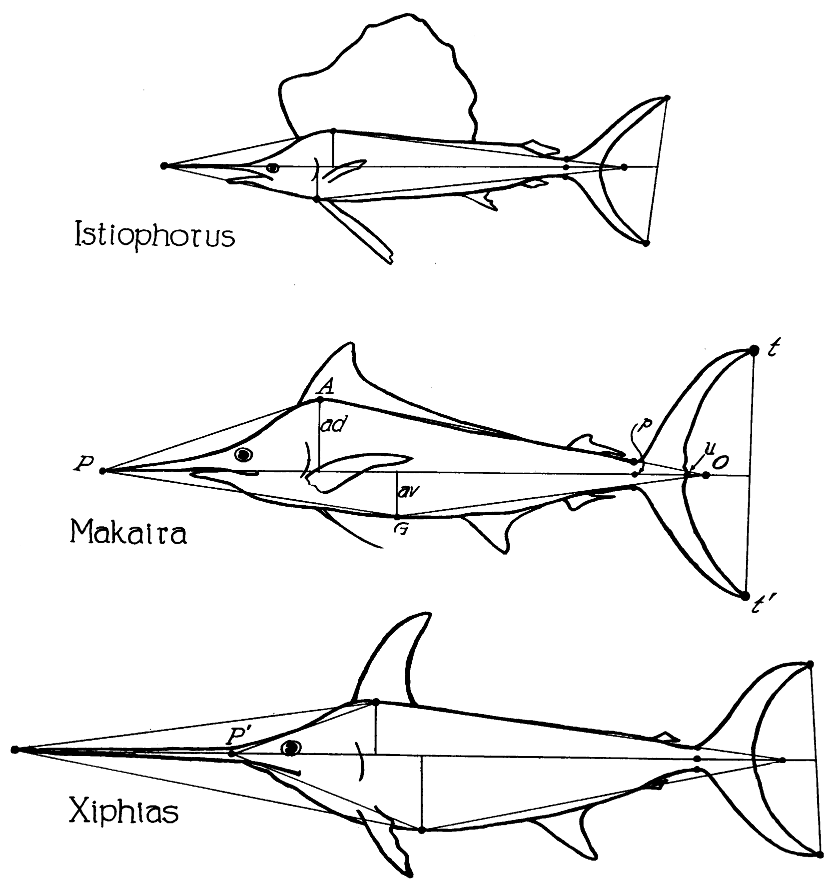

Fig. 2. Body-forms of swordfish, marlin and sailfish.

ing quick turning of the head. During lateral strokes of the sword the dorsal fin would probably be nearly stationary except for the free margin, but the side swing of the sword could be checked by sudden stiffening of the body and fins. If the swordfish were attacked by a large shark (as recorded by Bigelow and Welsh, p. 226), or by a killer whale, a direct ramming action of the sword might be useful. From the large size and protruding position of the eyes it is not improbable that the thrusts and sweeps of the sword may be closely regulated by the varying angles and distances of the opposite eyes with reference to the moving prey. In any event we may be sure that the dorsal, pectoral and anal fins are important factors in quick maneuvering. Moreover, if the fish were cruising slowly at the surface, the protruding dorsal fin might well transmit the thrusts of the surface ripples and thus act as a wind-vane. Then if the fish swam into the wind it might be more likely to encounter shoals of plankton drifting before the wind with their accompanying herring and other fish.

Here is a possible explanation of the protrusion of the dorsal fin above the surface in sharks, sailfishes, marlins and swordfishes. Unfortunately the literature of fishing, so far as we have been able to examine it, affords only the fact that swordfishes do cruise slowly at the surface. When they get near to a school of small fish they may sound and then rise through the school "striking right and left with their swords and then turning to gobble the dead or mangled fish" (Bigelow and Welch, *op. cit.*, p. 225). We may be sure that the enormous eyes play a chief part in directing the sword play.

The large erect dorsal is also necessary in order to meet the thrusts of the enormous caudal fin. The soft dorsal, originally elongate, is now nearly absent except for a small vestigial posterior dorsal.

The anal fin, which is relatively large and conspicuous, doubtless cooperates with the anterior dorsal in steering, rising and falling. The posterior portion of the anal is vestigial.

The pectoral fins are of a fair size, inserted low.

The pelvic fins are lacking in *Xiphias*.

"*Makaira ampla.*"—The body of *Makaira*, including the sword, is mesosomatic, for the body depth is greater than 1/5 of the length. The head is macrocephalic but is considerably shorter than that of *Xiphias*. The entering angle is low.

The caudal fin is more than twice the depth of the body and thus is definitely hypermacrocercal. Its spread, however, exceeds that of the tail in *Xiphias*. The caudal peduncle is about 1/5 of the body depth and is called leptopygidial.

The dorsal fin is altiradial but is somewhat less tall than that of *Xiphias*. It extends posteriorly quite far and is followed by the fairly well-developed posterior dorsal.

The anal fin, both anterior and posterior portions, is quite well developed.

The pectorals are inserted low and are comparable to those of *Xiphias.* Long and slender pelvic fins are present.

Istiophorus maguirei.—The body depth of *Istiophorus* is less than 1/6 of its length and the form is consequently dolichosomatic. The head is macrocephalic, proportionately much as in *Makaira.*

The caudal fin is hypermacrocercal, for tt′ is greater than twice the body depth. This caudal is the largest proportionately in our series. The caudal peduncle of *Istiophorus* is nomopygidial.

The dorsal fin is more than 1 3/4 of the body depth and is thus superaltiradial. The posterior dorsal is well developed but in contrast to the sail is negligible. This immense anterior dorsal fin is the most conspicuous feature of *Istiophorus.*

The pectoral fins are small and the pelvics are fairly well developed and long.

The body-forms and fins of these three genera may be summarized as follows:

	Xiphias	*Makaira*	*Istiophorus*
Body-form	Dolichosomatic	Mesosomatic	Dolichosomatic
Head	Macrocephalic	Macrocephalic	Macrocephalic
Caudal fin	Hypermacrocercal	Hypermacrocercal	Hypermacrocercal
Caudal peduncle	Leptopygidial	Leptopygidial	Nomopygidial
Dorsal fin	Altiradial	Altiradial	Superaltiradial
Pelvics	Absent	Present	Present

At first sight one would be inclined to consider the marked general resemblance between the swordfish and the marlins as an evidence of fairly close relationship, but it is more probable that these two groups, the Xiphiidae and the Istiophoridae, are merely parallel families of scombriform fishes which were already well separated from each other in Upper Eocene or Lower Oligocene times.

As we shall see later, it is probable that in both families the dorsal fin originally extended nearly the whole length of the body, from the occiput to the caudal peduncle. In the true sailfishes (*Istiophorus*) the anterior part of the dorsal has become excessively large; in the marlins there has probably been a secondary reduction of this fin except at the anterior end. In the swordfish line only the anterior part became excessively elongate, the posterior part greatly reduced.

SKELETON

It seemed very desirable that the osteology of such an interesting form as *Xiphias* be described for it is so primitive geologically and yet so specialized structurally. However, it was not until after we had drawn our figures of the various elements of the skeleton that we found Cuvier and Valenciennes' (1831) beautiful figures of the skull of *Xiphias* and the skeleton of *Tetrapturus*. While their figures can scarcely be improved upon, we feel that a comparative discussion of the skeletons of *Istiophorus* and *Xiphias* is not uncalled for, because it may serve to bring out the significance of the habitus divergences of these two families, the Xiphiidae and the Istiophoridae (Table II). The literature of the Xiphiiformes deals chiefly with the taxonomy and problems of distribution of the group but there are numerous papers to be found that touch upon the osteology. Cuvier and Valenciennes (1831) give descriptions of the osteology of *Xiphias, Tetrapturus* and *Istiophorus*, but do not figure the latter; Brühl (1847) figures the skull and part of the vertebral column of *Tetrapturus* and a dorsal view of the skull of *Xiphias;* Knox (1870) describes briefly a few skeletal details of *Istiophorus* and figures the first three abdominal vertebrae and the dorsal fin rays with their corresponding interneurals; Lütken (1877) figures the entire skelton of *Tetrapturus;* Goode (1883) figures the skeletons of *Xiphias*, *Istiophorus* and *Tetrapturus;* Regan (1909) illustrates a structural series with diagrams of the rostral region in several scombroids, including *Istiophorus* and *Xiphias;* and finally, Gregory (1933) figures the neurocranium of *Istiophorus.*

The drawings are the work of Mrs. Helen Ziska and the photographs were taken by the Museum's photographic department.

The skeleton of *Xiphias* as mounted (Fig. 3) is particularly notable for its relatively stout column with but few segments. The stout block-like centra are necessary to meet the powerful thrust of the large tail and the adverse leverage brought about by the long rostrum. Also remarkable are the shortness and poor development of the ribs. The loss of pelvic fins was noted above but here we see that pelvic bones are lacking as well.

THE VERTEBRAL COLUMN.—Taking into consideration the close parallelism of the Xiphiiformes, it is of particular interest to note the striking heritage differences between *Xiphias* and *Istiophorus* as displayed in the vertebral column.

Comparison of the two skeletons reveals a strong anteroposterior emphasis of the centra and their processes in *Istiophorus* and a moderate dorsoventral growth in *Xiphias.* Cuvier and Valenciennes (1831) and

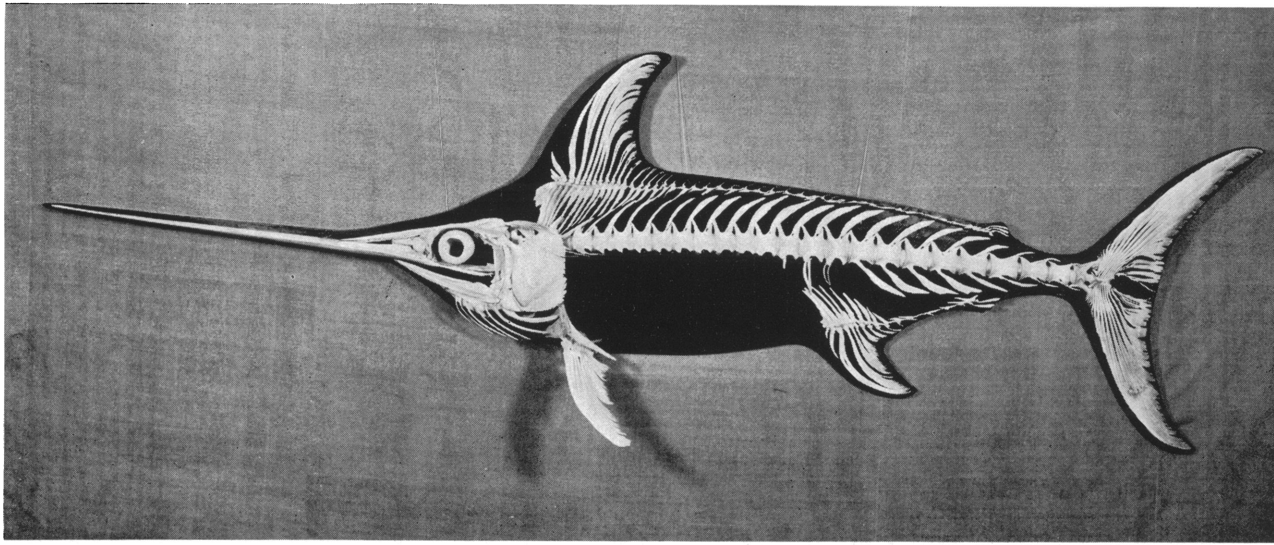

Fig. 3. Skeleton of swordfish.

Brühl (1847) figure the vertebral column of the marlin, *Tetrapturus*, which agrees perfectly with that of *Istiophorus*, so that further discussion of the column of the sailfish will apply also to that of *Tetrapturus*.

A vertebral count gives *Xiphias* fifteen pre-caudals and eleven caudals, including the tail centrum, to make a total of twenty-six vertebrae. The specimen of *Istiophorus* which was available for our study had twelve pre-caudal and twelve caudal vertebrae, making a total of twenty-four. In *Istiophorus* prominent anterior neural zygapophyses form a slot into which the flattened, laminated and expanded neural spines fit (Fig. 4). The anterior zygapophyses overlap about two-thirds of the preceding neural spine in the anterior pre-caudals and increase in relative length as they pass rearward until in the posterior pre-caudals the zygapophysis is projected beyond the point at which the neural spine of the preceding vertebra arises. This forms a very rigid spinal column and seems to permit free movement in only the dorso-ventral plane. The posterior neural zygapophyses are barely produced. The ribs articulate with the centra in front of slightly produced transverse processes.

Contrasted with these unusual specializations of the sailfish are the conservative, more generalized conditions found in the swordfish. The centra of *Xiphias* (Fig. 4) have a cuboid appearance as compared with the elongate, rather hour-glass shape of those in the sailfish. The neural spines of *Xiphias* are not expanded and are well produced dorsally. The anterior neural zygapophyses spring obliquely upward rather than horizontally forward as they do in *Istiophorus*, and overlap slightly the neural spines of the preceding vertebrae. The overlap of the neural spine by the following anterior zygapophysis seems to be characteristic of the Xiphiiformes, for Kishinouye's (1923) figures of mackerel and tuna skeletons do not show this condition. The posterior neural zygapophyses of *Xiphias* are strongly produced and, in marked contrast to *Istiophorus*, are almost as long as the anterior zygapophyses. The ribs of the swordfish are inserted on short, stubby transverse processes. As noted above, the number of pre-caudal vertebrae is markedly different in the two genera.

The caudal vertebrae of *Istiophorus* add to their firmly jointed dorsal side an haemal arch, which is practically an upside-down version of the neural arch (Fig. 4). With the exception of the first caudal vertebra, which has no anterior haemal zygapophysis, the remaining caudals have a pair of anterior haemal zygapophyses which together form a slot for the haemal spines of the preceding vertebrae. Among the other scombroids such a tendency is noted in *Auxis*. These anterior haemal zygapophy-

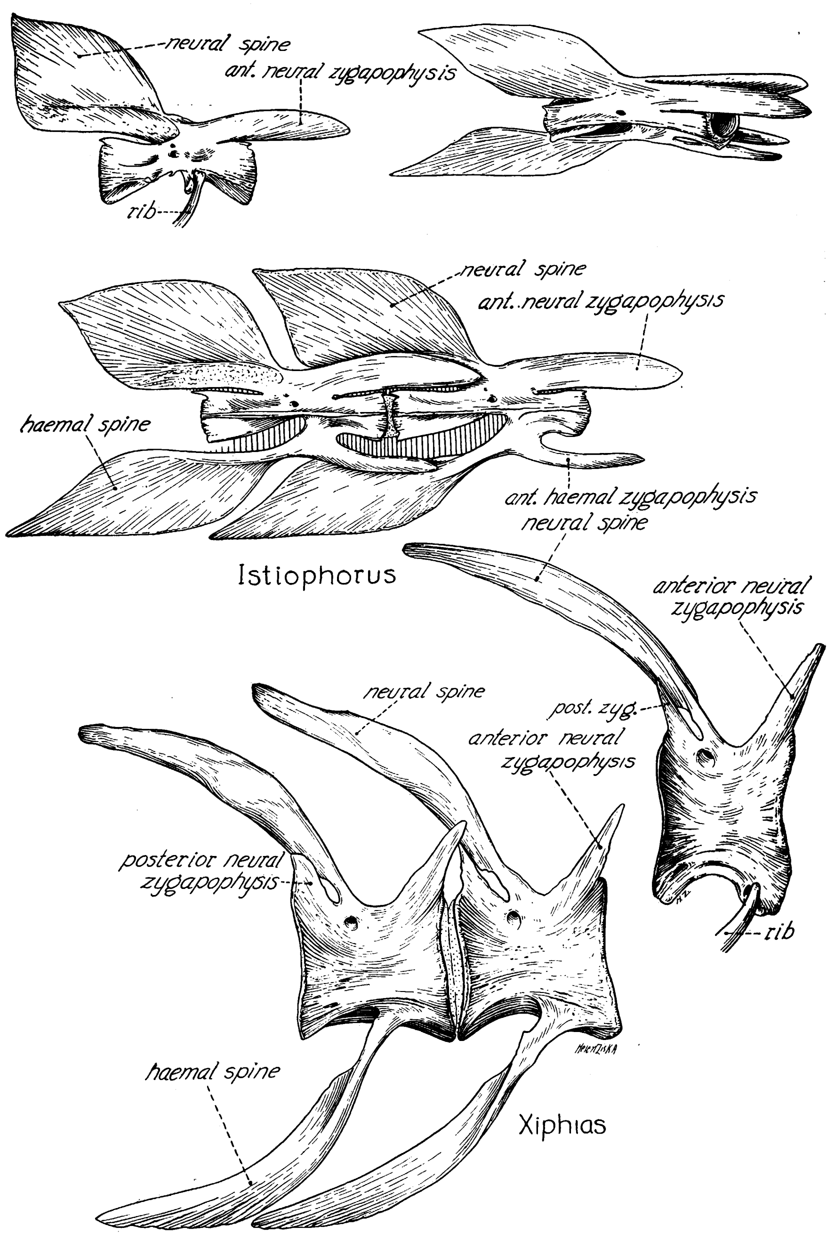

Fig. 4. Abdominal and anterior caudal vertebrae of *Xiphias* and *Istiophorus.*

ses are not as long as their corresponding neural elements, but add appreciably to the lateral stiffening of the column. This mutual dovetailing of the vertebrae results in an almost complete elimination of lateral movement of one segment upon the other and probably favors use of the entire column as a spring under tension in the horizontal plane. It may perhaps be due to this peculiar spring-like character of the backbone that sailfishes are able to "walk on their tails," that is, to shoot out of the water and propel themselves forward for a short distance by strong movements of the caudal fin against the water.

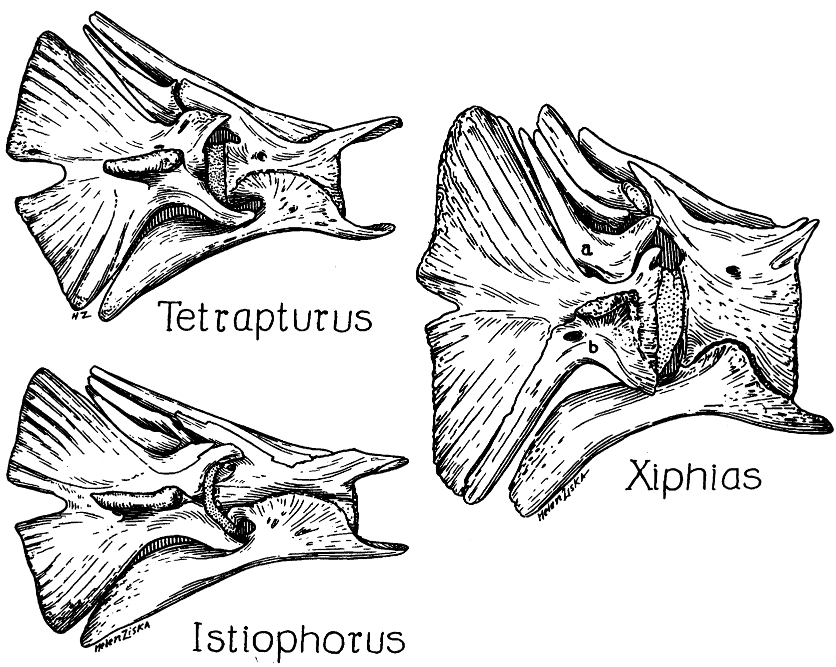

Fig. 5. Hypural fan and supporting elements.

In *Xiphias* the caudal vertebrae become slightly longer than deep, but the neural spines continue as in the pre-caudals, becoming smaller toward the tail. The anterior and posterior neural zygapophyses grade off posteriorly in keeping with the neural spines. Ventrally haemal arches are present and, like the neural spines, the haemal spines are not expanded. The anterior and posterior haemal zygapophyses are very slightly produced. The vertebrae of *Xiphias* seem to be movable on each other in both the dorsoventral and lateral directions.

HYPURALS.—The tail complex (Fig. 5) of *Xiphias gladius* seems to be more closely associated with the condition in the Istiophoridae than with any of the other groups of mackerel-like fishes. Allowing for the general anteroposterior emphasis of the post-cranial skeleton in the sailfish, the tail vertebrae and the arrangement of the hypurals are very similar in the two families. Two free hypurals (Fig. 5, *a*, *b*) are noted in *Xiphias*, but evidence of their fusion with the other hypurals may be seen in *Istiophorus*. *Tetrapturus* carries this fusion still further. The Istiophoridae have the lateral hypural crest very well developed, whereas that of *Xiphias*, while prominent enough, is much less so. Study of Kishinouye's (1923) plates shows an almost complete lack of a deep notch in the posterior hypural complex of the other scombroid fishes but this notch is quite prominent in the Xiphiiformes.

SHOULDER-GIRDLE.—Just as there is a tendency toward an anteroposterior emphasis in the axial skeleton of the Istiophoridae, there is also such a trend in the shoulder-girdle. The posterior angle of the cleithrum is extended somewhat more in *Istiophorus* than in *Xiphias*. The anterior border of the coracoid grows forward until it touches the cleithrum in *Istiophorus*, but not in the swordfish. In cross section the supracleithrum of the sailfish would be a much flattened oval with the greatest diameter lying along the anteroposterior plane, while in the swordfish the cross section would be roughly circular. The posttemporal of *Istiophorus* is incipiently three-pronged as in percoid fishes, while that of *Xiphias* is definitely two-pronged.

PELVIC GIRDLE.—There is no trace of pelvic bones or fin in *Xiphias*, while in *Istiophorus* these elements are well developed.

SKULL.—The skull of *Xiphias gladius* (Fig. 6) is approximately seven times as long as it is deep, whereas that of *Istiophorus* is about six times as long as deep. The long "broadsword" of *Xiphias* and the more delicate "rapier" of *Istiophorus* are the dominant and conspicuous features of the two skulls.

Throughout the scombroid series the suborbital bones are rather weak and in *Xiphias* the reduction is almost complete. Although they were lost in our specimen, Cuvier and Valenciennes (1831) figure them as a row of thirteen minute bones not articulated with each other but extending from the sphenotic process to the base of the parethmoid. Goode's (1883) figure of *Xiphias* does not include these suborbitals. In *Istiophorus* the suborbitals, while reduced from the primitive condition (as seen in *Scomber*), are relatively much larger than those of *Xiphias*. As a substitute for the lack of protection afforded the eye by the sub-

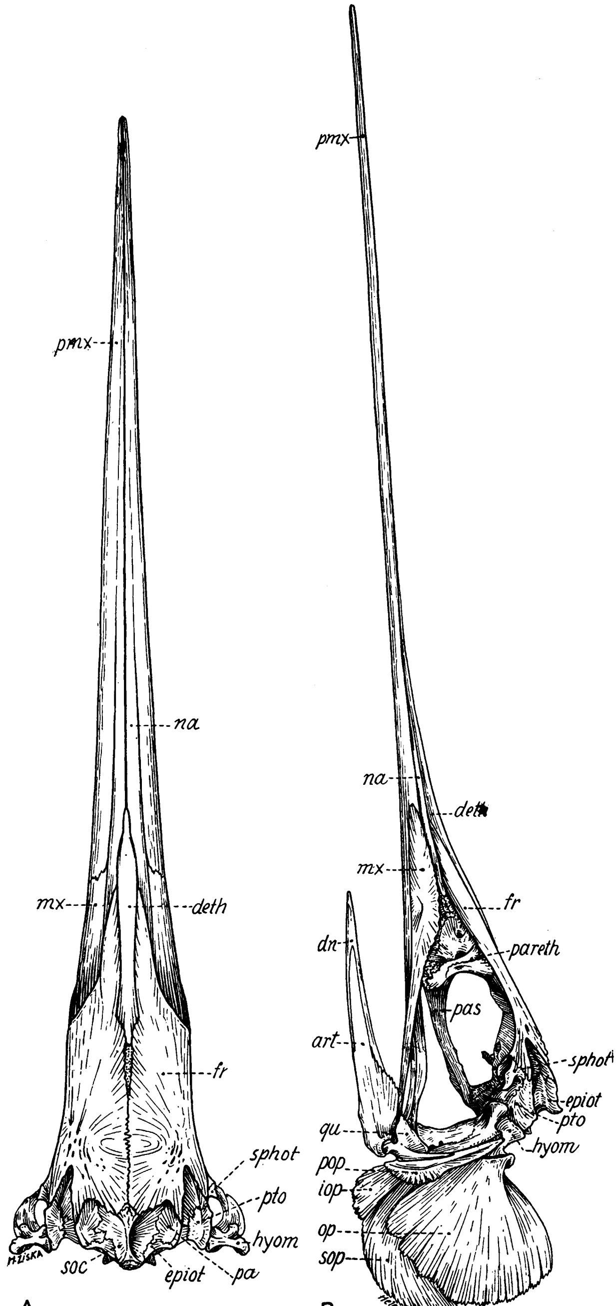

Fig. 6. Skull of *Xiphias*. A, dorsal; B, left lateral view.

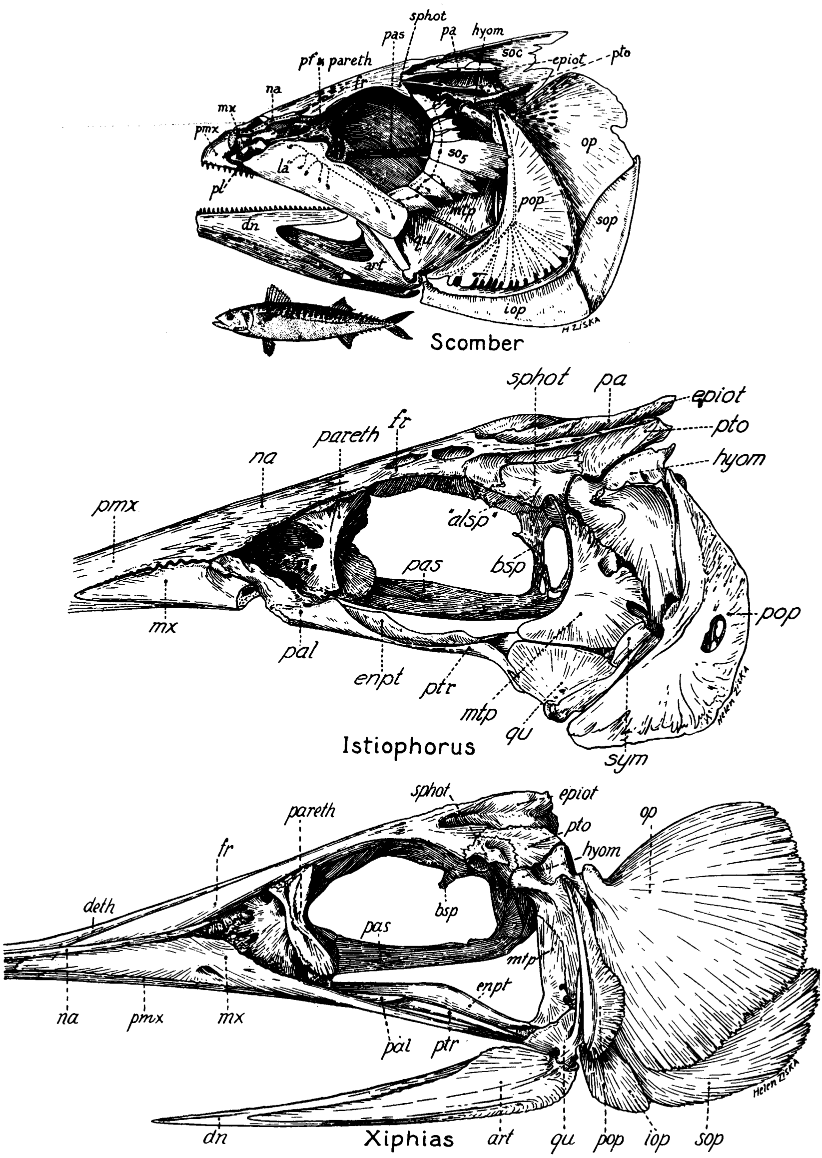

Fig. 7. Skulls of *Scomber*, *Istiophorus* and *Xiphias*, lateral views. *Scomber* after Allis (1903).

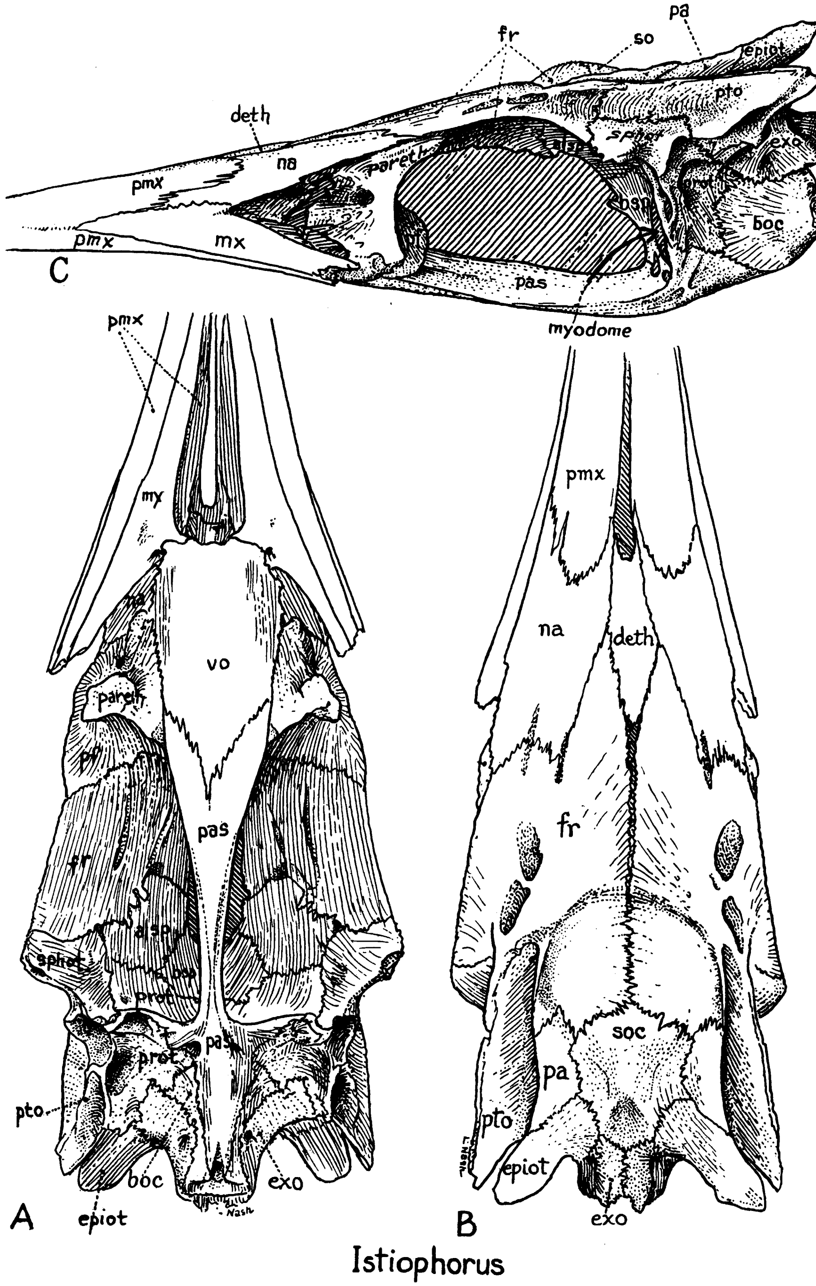

Fig. 8. Skull of *Istiophorus*. A, under side; B, top; C, left side. After Gregory (1933).

orbitals, a heavy, solid sclerotic ring is developed in *Xiphias* (Fig. 3), *Istiophorus* and probably in the other Xiphiiformes.

The metapterygoid (Fig. 7), which is broad and quite prominently separate in *Istiophorus*, becomes narrow and closely articulated to the hyomandibular in *Xiphias*. The symplectic is well developed and normal in position in *Istiophorus*, but in *Xiphias* it is so well articulated to the quadrate as to give the appearance of being fused to it. The quadrate of the swordfish presents in side view the typical equilateral triangular shape, whereas in the sailfish it becomes expanded anteriorly, along with the lower border of the metapterygoid, to form a more or less quadrilateral outline. The significance of these differences is discussed below (p. 20).

In both *Istiophorus* and *Xiphias* the parasphenoid (Fig. 8) flares abruptly to meet the broad and prominent vomer. In the sailfish the basisphenoid bone (Figs. 7, 8) is a well-developed Y-shaped bone, the leg of which articulates with the parasphenoid. Although Cuvier and Valenciennes (1831) state, "Je ne trouve pas de sphénoïde antérieur dans mes squelettes," we find that in the swordfish (*Xiphias*) the characteristic Y-shaped basisphenoid is formed but, unlike that of *Istiophorus*, the leg of the Y does not reach ventrally far enough to articulate with the parasphenoid (Fig. 7).

The form and sculpture of the parethmoids in both of these genera is very similar to that of *Scomber*, the typically primitive scombriform fish.

The well-developed opercular series of bones of *Xiphias* (Fig. 7) have their posterior edges serrated and are rather similar in pattern to those of the sailfish. Their large size in relation to the rest of the skull is a scombriform heritage and is probably, according to Gregory (1933, p. 309), "conditioned . . . by the voluminous development of the branchial apparatus."

In 1909, Regan figured a structural series of scombriform rostra, starting with *Acanthocybium*, passing through *Istiophorus* and *Xiphias*, and culminating in the Eocene *Xiphiorhynchus*. Of this series we have had only two for study, *Istiophorus* and *Xiphias*. After long study of the formation of the sword in *Istiophorus* it became more and more apparent that certain of the elements had been wrongly homologized by Regan. In *Istiophorus* what he has called the frontal is really a separate bone (Figs. 7, 8) lying anterior to the frontal and dorsad to the nasal opening. This "frontal" of Regan has been rightly called nasal by Gregory (1933, p. 317, Fig. 197). What then is the element labelled "nasal" by Regan? The maxillae do not form a part of the dorsum of the sword for they lie lateral and posterior to the premaxillaries. Gregory (1933) labelled the element ventral to the nasal cavity as the lacrymal. However, it now appears possible that the lacrymal has become fused to the maxilla, for the mesial portion of this bone is certainly the seat for the characteristic anterior hook of the palatine over the maxilla (Fig. 9). In addition, the mesial ventral surface of this lacrymo-maxillary element abuts directly on to the vomer as does a typical maxilla. With the maxilla and nasal accounted for, we still lack a homologue for the greater portion of the sword. We believe that the element labelled "nasal" by Regan in *Istiophorus* is nothing more than the ascending branch of the premaxilla, so that the sword is made up entirely of the premaxillae in the sailfish.

The formation of the sword in *Xiphias*, however, still remains for consideration (Figs. 6, 7). There are two possibilities: either the sword may be made up as in the sailfish or it may be made up of other elements and merely parallel that of *Istiophorus*. If the nasals in *Xiphias* have been pushed forward and outward laterally by the forwardly expanding fron-

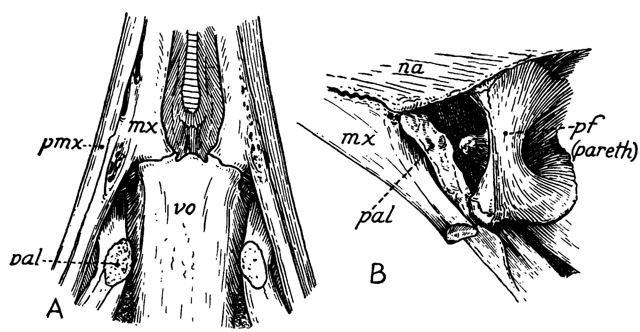

Fig. 9. *Istiophorus:* relations of maxilla to surrounding elements. A, palatal view; B, oblique left side view.

tals until they are now represented by a mere sliver situated above the narial cavity but covered dorsally by the overhanging frontals, then the elements of the sword may be homologized with those of *Istiophorus*. However, all the authorities who have concerned themselves with this problem (Cuvier and Valenciennes, 1831, Brühl, 1847, and Regan, 1909) name the dominant element of the *Xiphias* sword the nasal. Structurally this is the same element which we have identified in *Istiophorus* as the ascending ramus of the premaxilla.

The bone that we identify as nasal retains part of its primitive association with the narial cavity for it enters the cavity anteriorly. There is also no evidence of any other nasal elements. If therefore we are to homologize the elements of the sword with those of the sailfish, we must acknowledge its identity as the nasal. Thus in the sailfish (Fig. 8) the enlarged nasals form the main part of the broad roof of the skull above the narial cavity and they serve to stiffen the base of the sword on the dorsal surface, whereas in *Xiphias* (Fig. 6) the narrow nasals have grown forward along with the premaxillae, meeting in the mid-line on the dorsal surface of the sword itself in front of and laterally to the elongate dermethmoid. Apparently the entire rostrum of the swordfish must be stronger and better braced than that of the sailfish.

In both types the greatly enlarged and expanded ethmoid complex must play an important part in acting as a combined thrust block and buffer between the cranium and the ram. The ethmoid complex as a whole is nearly filled with a mass of thin spongy bone, the interior of which reminds one of a wasp's nest. The innumerable small cells seem to form a reservoir of oily substance, which in life is probaby enclosed in a continuous chamber under relatively high pressure. As seen from above, after the removal of the surrounding roofing bones the ethmoid complex would be roughly wedge-shaped, the point of the wedge being directed anteriorly. In *Istiophorus* the middle portion (mesethmoid, dermethmoid) ends in front and below in a Y-shaped column which rests firmly on the broadly expanded platform of the vomer. The broad rear of the wedge is formed by the paired parethmoids (Fig. 8) (prefrontals), which meet in the mid-line in front of the orbits, of which they form the front pillars; they rest below upon the vomer and palatines. Each one is pierced by the large olfactory foramen. In *Xiphias* the spongy mass is of great size but otherwise we detect no important difference from *Istiophorus* except that the mesethmoid is greatly prolonged in front and its spongy part more expanded.

The mandible of *Xiphias* (Fig. 7) is very short in proportion to the length of the skull and does not extend as far as the anterior edge of the maxilla. In *Istiophorus*, however, it extends relatively much farther forward, although it does not approach the tip of the rostrum. The lower jaw of the sailfish differs from that of *Xiphias* in having a predentary bone. Although Cuvier and Valenciennes do not figure a predentary bone in *Tetrapturus*, Regan lists it as one of the family characters of the Istiophoridae. Both *Xiphias* and *Istiophorus* possess a sesamoid articular bone on the mesial surface of the articular (Starks). Although the pattern of the lower jaw is very similar in both there is a marked dorsal convexity in that of *Istiophorus*.

The cranial vault in *Istiophorus* is wide transversely and shallow dorsoventrally. Its roof is formed by the frontals, sphenotics, pterotics, parietals, epiotics and supraoccipital, the latter extending far forward to meet the frontals. This roof is strongly built and braced to resist the posterodorsal stream of stresses from the rostrum; it also supports the strong suspensorium of the oralo-branchial complex. The sides of the cranial vault are formed chiefly by the "alisphenoids," proötics and opisthotic-exoccipitals. The latter in turn form a stiff secondary floor for the brain-stem and rest firmly on the very strong vertically deepened basioccipital. The proötics are continued ventrolaterally into large stiff buttresses, which in turn border the capacious chamber for the eye muscles, and are continuous below with ascending wings of the parasphenoid. Both the basioccipital and the proötic buttresses receive the posteroventral thrusts from the vertically arched and very stiff keel bone (parasphenoid), which also supports the slender stem of the basisphenoid. The keel bone, which is stiffened against buckling by its triangular midsection, thus transmits and distributes part of the backward thrusts from the rostrum as well as the forward thrusts from the vertebral column. The tripartite occipital condyles are very strongly braced to resist both fore-and-aft pressures and torsion.

In *Xiphias* the conditions of the cranium are nearly as described above except that the entire cranial vault is shorter anteroposteriorly and wider transversely, the lateral ventral buttresses of the proötics around the myodome have the anterior borders reflected and deficient toward the outer margins; the ventral stem of the basisphenoid is not ossified. On the roof of the occiput the narrow fossae for the mm. levator arcus palatini, dilatator operculi, levator operculi and trapezius are all relatively small.

The sphenotic and pterotic facets for the hyomandibular in *Istiophorus* are extended anteroposteriorly and the wide suspensorium is directed mostly downward. In *Xiphias* the pterotic facet is shorter and tilted backward and upward, so that the suspensorium is directed more backward; correlated features are the anteroposterior shortness of the metapterygoid, quadrate and preopercular, and the small size of the mandible in *Xiphias*.

We have examined the habitus features of the skulls of the sword-fish and the sailfish which separate them so distinctly from the remaining scombriform fishes. Where is the scombroid heritage? As a typical "primitive" of the group, *Scomber* (Figs. 7, 10) serves admirably. The dorsal aspect of the skull of *Scomber* shows the same occipital pattern of elements as in *Xiphias* or *Istiophorus*. The arrangement of the crests is similar in all, differing only in proportions. The relatively long premaxillaries are showing a tendency to extend themselves forward. The narrow finger-like nasals overlap the premaxillaries. With the forward growth of the premaxillaries the nasals are ready to follow in *Xiphias*, while in *Istiophorus* the nasals widen laterally but retain their primitive position as in *Scomber*.

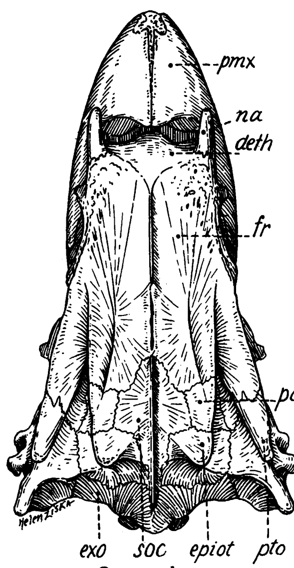

Fig. 10. *Scomber*, top view of skull.

In side view the skull of the mackerel (Fig. 7) differs markedly from *Xiphias* in the large size of the suborbitals. The lacrymal, plastered over the maxilla in *Scomber*, perhaps has become fused to it in *Xiphias*. The opercular series is large and dominant in both. The parethmoids are strikingly alike in all of these genera. The reduction of some of the elements in the Xiphiiformes, notably the pterygoids, is probably the result of altered stresses developing with the evolution of the sword.

CLASSIFICATION AND PHYLOGENY

The Xiphiidae and Istiophoridae, although generally parallel families with more or less divergent habitus details, are yet tied together in a

TABLE II.—Chief Differences in the Skeletons of the Swordfish, the Sailfish and the Mackerel

	Xiphias	*Istiophorus*	*Scomber*
SKULL			
Suborbitals	Minute; not articulated with each other	Fairly well developed; touching each other	Fairly well developed; touching each other
Metapterygoid	Closely articulated to hyomandibular	Separated by cartilage from hyomandibular	Separated from hyomandibular
Symplectic	Almost fused to quadrate	Normal, not fused to quadrate	Normal, not fused to quadrate
Quadrate	Triangular shape in side view	Quadrilateral in side view	Triangular shape in side view
Basisphenoid	Leg of "Y" does not articulate with parasphenoid	Does articulate with parasphenoid	Does articulate with parasphenoid
Nasals	Very narrow, prolonged on dorsum of sword	Broad, short; do not form part of sword	Small, projecting forward and slightly overlapping pmx.
Mesethmoid	Narrow, elongate	Short	Broad
MANDIBLE			
Pre-dentary bone	Not present	Present	Not present
SHOULDER-GIRDLE			
Posttemporal	Two-pronged	Incipiently three-pronged	Three-pronged
PELVIC GIRDLE	None	Well developed	Well developed
VERTEBRAL COLUMN			
Number of vertebrae			
Pre-caudals	15	12	14 (*japonicus*)[1]
Caudals	11	12	17 (*japonicus*)[1]
Shape of centra	Cube-like	Elongate; hour-glass shape	Elongate cube, with some of the hour-glass character[1]
Anterior neural zygapophyses	Placed obliquely; long	Horizontally placed, very long	Horizontally placed; fairly long[1]
Posterior neural zygapophyses	Strongly produced	Barely produced	Produced slightly[1]
Neural spines	Not expanded, produced dorsally	Laminated, expanded antero-posteriorly	Not expanded; produced dorsad[1]
Anterior haemal zygapophyses	Very slightly produced	Horizontal, quite long	Horizontally placed; quite long[1]
Posterior haemal zygapophyses	Very slightly produced	Not produced	Slightly produced[1]
Haemal spines	Not expanded	Laminated, expanded antero-posteriorly	Not expanded[1]

common scombroid heritage, which, as recognized by Regan (1909, p. 70), includes the following among other characters:

(1) Maxillaries more or less firmly attached to the nonprotractile premaxillaries which are typically produced and pointed anteriorly.
(2) Cranium with orbito-rostral portion elongate and postorbital portion abbreviate.
(3) Parietals separated by supraoccipital.
(4) No orbitosphenoid.
(5) Basisphenoid present.
(6) Proötics giving rise to an osseus roof for the myodome.
(7) Vertebral column of solid centra, which are coössified with the arches.

The generic "habitus" characters in the skeletons of *Xiphias*, *Istiophorus* and *Scomber* are set forth in Table II.

It has long been known that the swordfish (*Xiphias gladius*) is a highly specialized end-stage of the scombriform series. Cuvier and Valenciennes (1831) so considered it and Regan, more recently (1909), concurs by placing it in the division Xiphiiformes along with the living marlins and sailfishes (Istiophoridae) and three extinct families (Palaeorhynchidae, Blochiidae and Xiphiorhynchidae). All these families date back to Eocene times, while *Acestrus* (Xiphiidae) and *Xiphiorhynchus* are found in Lower Eocene deposits. The Scombridae also begin in the Lower Eocene, whereas the other scombroids do not appear until the Oligocene period. The fact that the structurally primitive family (Scombridae) and its highly specialized offshoots (Xiphiiformes) were living side by side in early Eocene times seems to indicate that the latter stemmed off from the scombrids in the Cretaceous.

The Eocene fish, *Palaeorhynchus*, with its high elongate dorsal, its neural and haemal spines with thin posterior laminar expansions and well-developed pelvic fins, seems to point the way toward the Istiophoridae. *Palaeorhynchus* must have its high number of vertebrae (from 50 to 60) reduced, however, before it attains the *Istiophorus* condition.

On the other hand, the Upper Eocene form *Blochius*, placed by Smith Woodward (1901) in the Blenniiformes but subsequently referred to the Xiphiiformes by Regan (1909), seems to be near the stem of the Xiphiidae. In its lack of pelvic fins and girdle, stout and few-segmented column, unexpanded neural and haemal spines and its short feeble ribs, *Blochius* compares quite favorably with *Xiphias*.

Gregory (1933) published a pictorial phylogeny of the scombriform fishes in which *Xiphias* was depicted as branching from the istiophorid line relatively late in the history of the group. From the evidence assem-

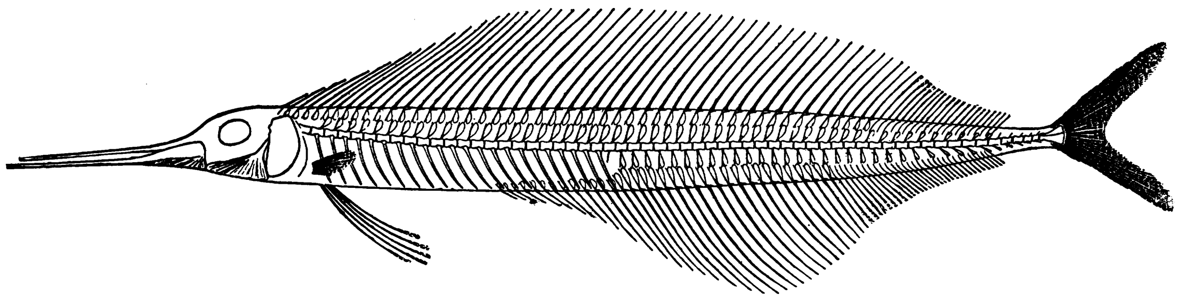

Fig. 11

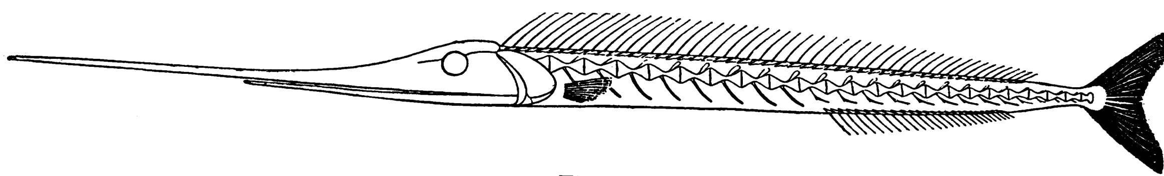

Fig. 12

Fig. 11. Reconstruction of the Lower Oligocene sailfish, *Palaeorhynchus glarisianus*. After Smith Woodward (1901). About 1/5 natural size.

Fig. 12. Reconstruction of the Lower Eocene swordfish, *Blochius longirostris*. After Smith Woodward (1901). About 1/6 natural size.

bled in this paper it appears, however, that the foregoing idea was probably incorrect and that we must adopt Regan's view (1909) that the Xiphiidae and Istiophoridae run back separately to basal Eocene times, parallel but distinct.

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