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THE OSTEOLOGY AND RELATIONSHIPS OF THE WAHOO (*ACANTHOCYBIUM SOLANDRI*), A SCOMBROID FISH[1]

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INTRODUCTION

During a recent study of the comparative osteology of the swordfish and the sailfish (Gregory and Conrad, 1937), the problem of the evolution of the Xiphiiformes arose. The literature abounds with suggestions that *Acanthocybium* forms a link between the Scombridae and the xiphiiform fishes. Therefore, we were particularly desirous of procuring an *Acanthocybium* for study. Extended correspondence, however, failed to produce the desired specimen.

In July, 1937, the American Museum–Lerner Bimini Expedition went to the Bahama Islands to secure anatomical and body-form data on the blue marlin. While there, Mr. Erl Roman, of Miami, Florida, caught and presented to the expedition a fine specimen of the much-

[1] Results of the Michael Lerner Ichthyological Expeditions, No. 15.

coveted wahoo (*Acanthocybium solandri*). Detailed measurements of this specimen in the flesh have been published (Conrad and La Monte, 1937). The skeleton has been mounted and has been placed in the study collection of the Department of Ichthyology.

OSTEOLOGY

The snout region of the skull of *Acanthocybium* was figured by Regan (1909), Starks (1910) published valuable notes on the skull and first three vertebrae, Eastman (1914) copied Regan's figure, and Kishinouye (1923) figured the axial skeleton and neurocranium. Kishinouye's figures, while beautifully drawn, are unfortunately so small that many of the details of structure are lost. Nor does he discuss specifically the skeleton of *Acanthocybium.* Thus it seems justifiable to present several new and more detailed drawings of both the skull and the vertebral column. These new drawings are the work of Mrs. Helen Ziska.

The skeleton of *Acanthocybium* (Fig. 1) is particularly notable among the Scombridae for its long skull, which is about one fourth of the standard body length, and its long, many segmented vertebral column.

SKULL

Neurocranium

OLFACTORY REGION.—The dorsal surface of the mesethmoid (Fig. 2, *deth*) of *Acanthocybium* lies slightly below the horizontal plane of the roofing bones of the skull and is slightly overlapped above by the frontals (*fr*). Its condition is essentially like that found in *Scomber*, *Thunnus*, and other Scombridae.

Lateral to the mesethmoid and dorsal to the narial opening is the nasal bone (*na*). In dorsal aspect the nasal of *Acanthocybium* is roughly triangular with the apex directed posteriorly and the base forward. The frontal overlaps the mesial border of the nasal for almost its entire length. The nasal bone of the wahoo is such a dense and stoutly developed element that no trace of the supraorbital canal is evident when the bone is held to the light. *Scomber* has a very different nasal than that of *Acanthocybium*, because in the former the nasals are long and narrow "like a tall and slender S" (Allis, 1903) and project far in front of the mesethmoid. With respect to the nasals, *Acanthocybium* resembles its close relative, *Scomberomorus*, which has similar large triangular-shaped nasal bones.

The parethmoids (Fig. 3, *pareth*) of *Acanthocybium* are well-de-

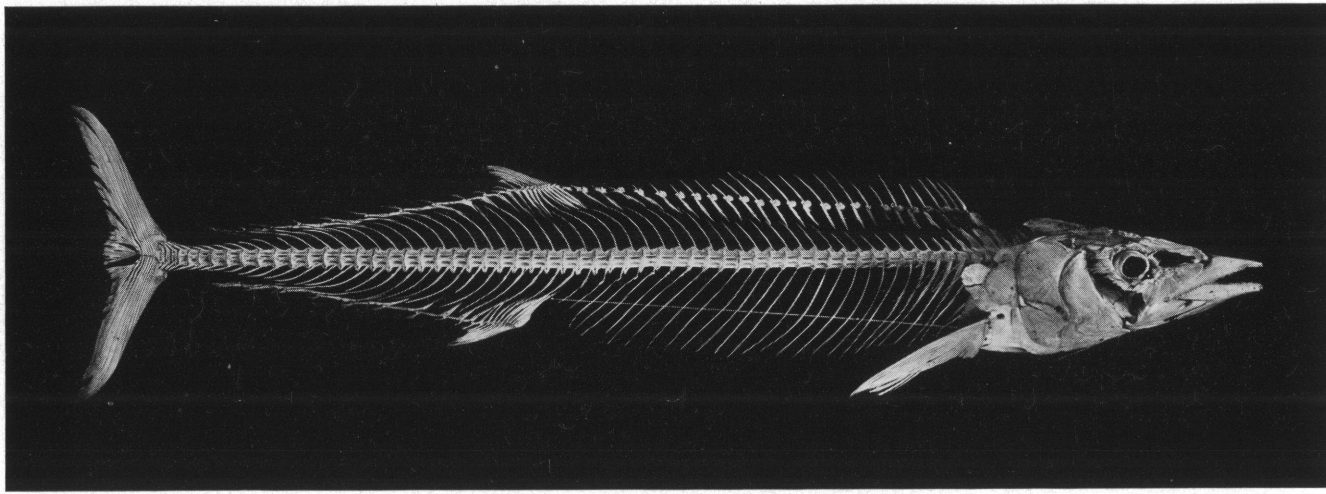

Fig. 1. Skeleton of wahoo (*Acanthocybium solandri*).

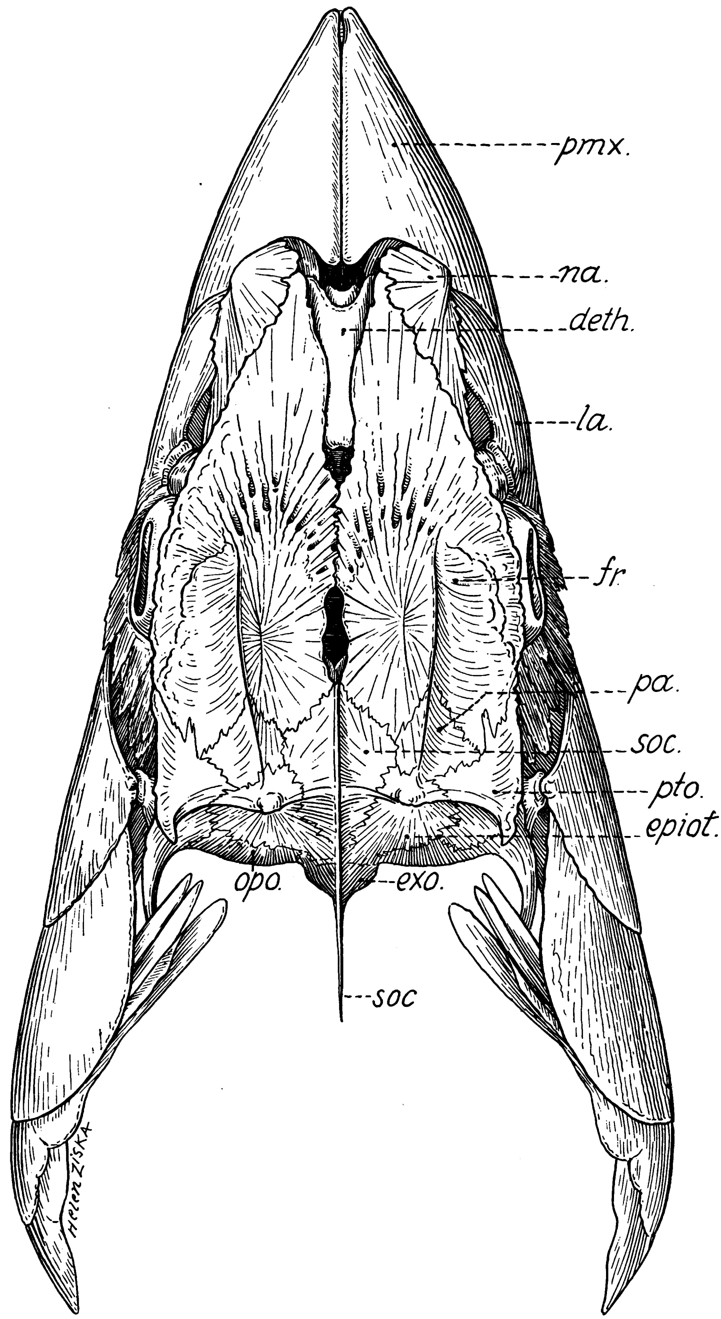

Fig. 2. Skull of *Acanthocybium*. Dorsal view.

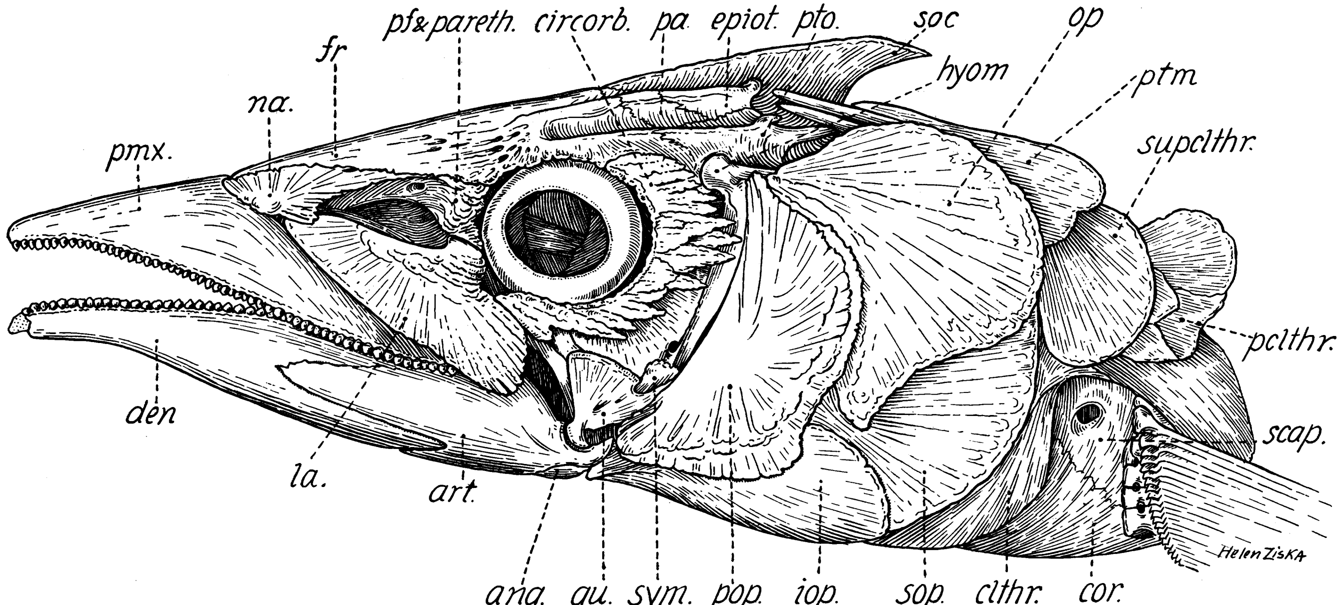

Fig. 3. Skull of *Acanthocybium*. Lateral view.

veloped cellular oil reservoirs which form the anterior margins of the orbits and the posterior and mesial walls of the nasal cavity. On the dorsal surface the parethmoids contact the nasals anteriorly and the frontals posteriorly while medially both contact the mesethmoid. The surface of the parethmoid which lines the nasal cavity is smooth and very unlike the spongy, cellular surface seen in the xiphiiform fishes.

ORBITAL REGION.—In common with most scombroid fishes *Acanthocybium* has a solid, heavy sclerotic case which consists of an anterior half and a posterior half. This sclerotic case, according to Starks (1910), is thicker and more dense than that of any other genus of scombroids.

A constant feature of the Scombridae is the large, much sculptured lacrymal bone (*la*). The large lacrymal of *Acanthocybium* is directed upward and forward, covering completely the maxilla (Fig. 4, *mx*) and supramaxilla (Fig. 4, *smx*). The lacrymal extends forward to lie ventral to the curved anterior end of the palatine (Fig. 5, *pal*) as in *Scomber*. At this same locus the antero-dorsal corner of the lacrymal has a concave, rolled border which fits mesial to the lateral angle of the base of the nasal "triangle." Lateral and dorsal to the palatal process of the parethmoid is the articulation for the lacrymal. Immediately below this articulation with the parethmoid a small hook on the lacrymal overlaps the anterior end of the supramaxilla.

As in *Scomber* and *Scomberomorus* the suborbital bones (*circorb*) posterior to the lacrymal are so mingled with the thick scales surrounding the orbit as to make it impossible to distinguish them. One of the suborbitals, however, is developed into a flange-like bone which projects into the orbit at the postero-inferior part of the ring. The lateral border of the bone bears the circumorbital canal while the mesial flange-like portion follows the contours of the sclerotic case. According to Starks (1910) *Scomberomorus* also possesses such a "suborbital shelf."

The frontals of *Acanthocybium*, with their conspicuous radiating growth lines, form the largest part of the dorsum of the neurocranium. The frontals are pointed anteriorly and diverge to expose the mesethmoid as in *Scomber*. Between the frontals are large fontanelles. One of these fontanelles runs forward about an inch and a half from the fronto-supraoccipital suture. A second starts about three quarters of an inch behind the posterior border of the mesethmoid and extends the remainder of the anterior length of the frontals. The failure of the frontals to close over the entire length of their contact seems to be a typical scombroid aberration (cf. *Scomber*, *Sarda*, *Thunnus*, *Istiophorus*, *Xiphias*, etc.). From the posterior surface of the parethmoid to the sphenotic (*sphot*) the frontal forms the dorsal border of the orbit. Posteriorly the frontals contact on the dorsal surface, the supraoccipital (*soc*), the parietals (*pa*), the pterotics (*pto*), and sphenotics; on the ventral surface, the sphenotics and alisphenoids.

The orbitosphenoid is lacking in *Acanthocybium*, as in *Scomber*.

"In *Scomberomorus*," says Starks (1910), "the brain chamber is open widely between the alisphenoids, while in this genus [*Acanthocybium*] the alisphenoids nearly meet at their middle and almost divide the opening into two parts." Laterally the alisphenoids contact the frontals and sphenotics and posteriorly abut against the proötics.

OTIC REGION.—In *Acanthocybium* and other Scombridae the opisthotics (*opo*) are not fused with the exoccipitals (*exo*). The condition of the opisthotic, according to Starks (1910), presents a character by which the Scombrinae can be separated from the remainder of the Scombridae. In the Scombrinae (*Scomber*, *Rastrelliger*) the opisthotic is situated on the lower surface of the cranium and is not interposed between the exoccipital and the pterotic. In the other Scombridae, including *Acanthocybium*, the opisthotic may be seen on both the dorsal and ventral surfaces of the cranium and on the lower surface it separates the pterotic from the exoccipital.

The pterotic of *Acanthocybium* ends posteriorly in a sharp spine as in *Scomber* and *Sarda*, but unlike *Scomberomorus* in which the posterior end of the pterotic is truncate.

The epiotic (*epiot*) of *Acanthocybium* is bounded on the dorsal surface of the skull by the parietal, the supraoccipital, the exoccipital and the pterotic. In *Scomber* there is a cartilage (see Allis, 1903, Fig. 5) which lies at the center of a ring of bones composed of epiotic, parietal, and pterotic. In *Acanthocybium*, *Thunnus*, and other scombroid genera, this cartilage is almost completely ossified.

The supraoccipital is in contact with the frontals anteriorly, thus separating the parietals from each other. The condition is therefore like that found in *Scomber* and other Scombridae.

BASICRANIAL REGION.—Due to the investing bones present on the mounted skull no observations of the basioccipital or parasphenoid were possible.

The basisphenoid seems to be very similar to the type found in *Scomber*.

Branchiocranium

OROMANDIBULAR REGION.—The premaxillae (*pmx*) of *Acanthocybium* are large and pointed anteriorly, both the ascending and particularly the

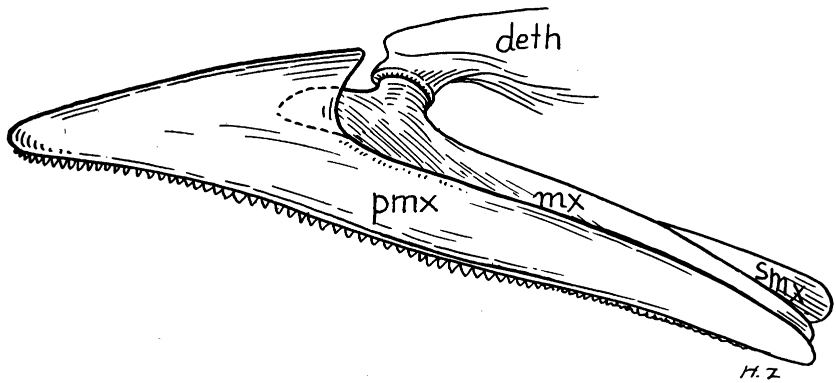

Fig. 4. Diagram showing the relation of the secondary upper jaw to the mesethmoid.

descending rami are exceedingly robust. Completely excluded from the gape is the maxilla which reaches from the posterior tip of the premaxilla anteriorly to form a bearing surface upon which the premaxilla rides. The maxilla itself is articulated with the ethmo-vomer block while the premaxilla is held away from the mesethmoid (Fig. 4). This articulation of the secondary upper jaw is essentially the same as that

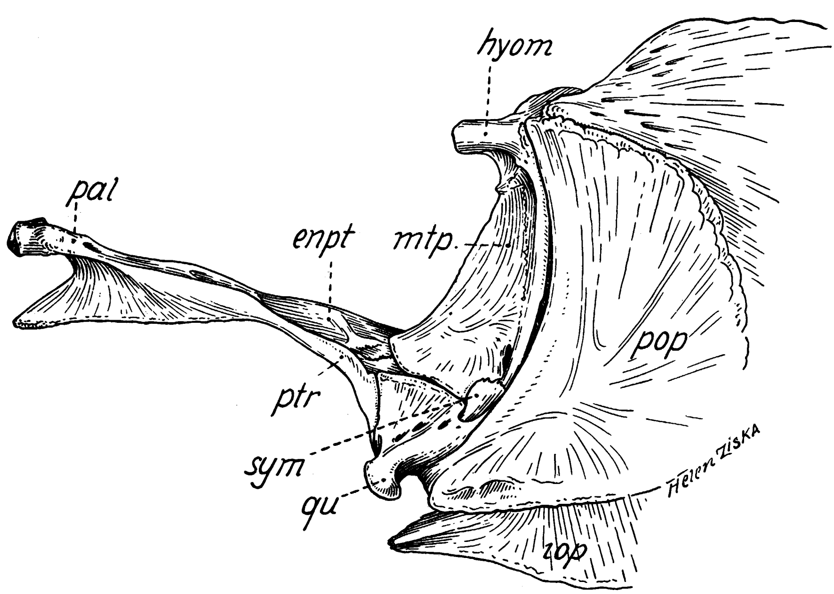

Fig. 5. Primary upper jaw of *Acanthocybium*, with associated structures.

found in *Scomber*. The posterior end of the maxilla is surmounted by a fairly large supramaxillary bone. In lateral view the entire maxilla and supramaxilla are hidden by the large lacrymal.

That long pointed premaxillae are thought to be so characteristic of the genus *Acanthocybium* is an unfortunate illusion. Proportionate measurements of the length of the premaxillae show that if the dorsal length of the skull (from anterior tip of premaxillae to posterior tip of supraoccipital crest) is considered as 1.0, the length of the premaxillae anterior to the dermethmoid will be:

Scomber...............0.23
Acanthocybium.........0.24

The palatine runs forward and hooks over the anterior end of the maxilla immediately ventral to the nasal. Along the ventral edge of the palatine there is a rather stout vertical lamina armed with very fine, minute, sharp teeth on its ventral surface. Posteriorly the palatine articulates with the entopterygoid (Fig. 5, *enpt*) and the pterygoid (*ptr*).

The pterygoid continues posteriorly to make a generous articulation in the form of a —< with the metapterygoid (*mtp*) and the quadrate (*qu*). The lower arm of the —< abuts against the entire length of the anterior edge of the quadrate, while the upper arm runs mesially to form a beveled, interdigitating articulation with the mesial surface of the metapterygoid.

The entopterygoid is a large thin bone that may be described in the words of Allis' (1903) description of *Scomber* as "shaped something like the bowl of a spoon." Anteriorly the entopterygoid is overlapped dorsally by the palatine. Along its lateral border it contacts the leg of the pterygoid Y. Its mesial and posterior edges are free from contacts.

The metapterygoid of *Acanthocybium* articulates with the hyomandibular (*hyom*) along its entire posterior and dorsal edge. Its anterior border lies free. At its ventral end it has a broad contact with the quadrate. Mesially the metapterygoid wraps a process around the column-like shaft of the hyomandibular.

The quadrate has the form of an equilateral triangle. The base of this triangle abuts against the ventral border of the metapterygoid. The apex of the quadrate triangle forms the articulation for the mandible.

The primary upper jaw of *Acanthocybium* is so close in morphology to that of *Scomber* as described and figured by Allis (1903) that one is hard put to find other than slight proportional differences between them.

The mandible of *Acanthocybium* is so very similar to that of *Scomber* that Allis' description of the mackerel mandible will apply almost word for word. *Acanthocybium* is said by Starks (1916) to possess a sesamoid articular bone. The entire dorsal border of the dentary (*den*) is armed with sharp, compressed, minutely serrated teeth. At the symphysis the two dentaries are tied together by a cap of cartilage. The symphysis of *Scomber* has no interdentary cartilage.

HYOID REGION.—The hyomandibular articulates with the neurocranium by means of two facets, one on the postero-inferior face of the sphenotic and the other on the ventral surface of the pterotic. Just ventral to the pterotic facet an articular process is developed into which the cup-shaped articulation of the opercular fits. Ventrally the hyomandibular abuts against the symplectic (*sym*), which is directed antero-ventrally, and the interhyal which is oriented along the axis of the hyomandibular shaft.

The symplectic of *Acanthocybium* is shorter and heavier than that of *Scomber*, but otherwise is essentially the same as in other Scombridae.

The interhyal articulates with the ceratohyal just above the process on the latter which articulates with a cup-like bearing on the interoperculum (*iop*). This well-developed bony cup on the mesial surface of the interoperculum which receives the articular facet of the ceratohyal is not present in *Scomber*.

The remainder of the hyoid arch of *Acanthocybium*, the hypohyal and basihyal, is not dissimilar to the conditions found in *Scomber*.

With the exception of the interoperculum mentioned above the opercular bones of *Acanthocybium* differ so little from those of *Scomber* that detailed description is unnecessary.

PECTORAL GIRDLE

The post-temporal (*ptm*) of *Acanthocybium* is a fairly stout bone connecting the pectoral girdle to the neurocranium. At its anterior end are three well-defined branches—dorsal, ventral, and median. The dorsal fork which rests on the epiotic lies in a horizontal plane and is deeply concave dorsally. The median fork lies in a vertical plane and its anterior end is made up of several spicule-like processes. The short, stout, ventral branch is directed antero-ventrally from the body of the bone. With regard to the post-temporal, according to Kishinouye, *Acanthocybium* resembles the Scombrinae more than the other Scombridae in the possession of this median branch.

There was no indication of the scale bone in our specimen of *Acanthocybium.* This bone which carries the lateral line canal on to the head is variably present in other groups of fishes, so that, while *Scomber* may possess one it is not strange that it is missing in the wahoo.

The supracleithrum (*supclthr*) is a more or less elliptically shaped bone which articulates at its dorsal end with the mesial surface of the post-temporal. Ventrally it overlaps the cleithrum (*clthr*). The anterior edge is quite thick while the posterior half of the bone is paper thin. Feebly attached to the posterior border of the supracleithrum are several very thin ossifications which apparently are postcleithra (*pclthr*).

The cleithrum is a large ∽-shaped bone in lateral view. The posterior curve bends ventrally and bears at its extremity two postcleithral bones (not figured, hidden by pectoral fin). The anterior curve is smoother and lies just mesial to the suboperculum (*sop*). The posterior arc is flat and |-shaped in section whereas the anterior portion is folded upon itself so as to be ∩-shaped in section. The lateral wing of this ∩ is wider than the mesial wing, but is parallel to it for its entire length as in other Cybiidae.[1] In the Thunnidae, on the other hand, this lateral wing is at a right angle to the mesial wing.

The coracoid (*cor*) is articulated antero-dorsally with the cleithrum and dorso-posteriorly with the scapula (*scap*). The coracoid overlaps anteriorly the lateral surface of the mesial wing of the cleithrum. A large foramen is left between its dorsal articulation with the cleithrum and the antero-ventral overlap of the coracoid on the cleithrum. This foramen is large, according to Kishinouye, in both *Acanthocybium* and *Gymnosarda* while in *Cybium* (*Scomberomorus*) and *Sarda* it is small.

Pelvic Girdle

The pelvic girdle of *Acanthocybium* is moderately developed and resembles the condition described by Kishinouye (1923) as typical for the Cybiidae.

Vertebral Column

The vertebral column of the Scombridae, like that of many teleosts, may be divided conveniently into several regions. The average form of each region differs considerably from the average form of any other region. At the extremities of each region there is a gradual transition

[1] The Cybiidae is a family of Scombriformes erected by Kishinouye in 1915.

from one form to the other. There are six such regions in *Acanthocybium* which may be described as follows (see also Table II):

1.—The post-cranial vertebrae characterized by stout neural arches and spines.

2.—The "mesabdominals" follow the post-cranials, bear ribs, but do not possess haemal arches.

3.—The posterior abdominals have closed haemal arches and bear ribs.

4.—The anterior caudals resemble greatly the posterior abdominals except that thay have lost the ribs and have developed haemal spines.

5.—In the "tail segment" the vertebrae have their neural and haemal spines entering into the support of the caudal fin.

6.—The hypural complex is an almost symmetrical fan which receives the rays of the caudal fin.

This basic plan of vertebral form is to be found in *Scomber* which has 31 vertebrae; in *Cybium* (*Scomberomorus*) *koreanum* which has 46; and in *Acanthocybium*, with its vertebral formula of 23–33 + 31–34 = 54–66.

That these rather closely related genera, with a common plan of backbone, differ so widely in vertebral counts substantiates Ford's (1937) observation that too great a dependence upon "number of vertebrae" will often separate backbones which are obviously similar in form.

The vertebral column of *Acanthocybium* is the longest to be found among the Scombridae. Such a many segmented column may indicate that the wahoo has a more sinuous locomotor habitus than is to be found among the Scombridae generally.

Abdominal Vertebrae

The abdominal vertebrae of *Acanthocybium* (Fig. 6) are quite variable in their form. The first vertebra bears no rib, but the second bears both a pleural and an epipleural rib. The epipleurals are found articulated to the head of the broad pleural rib on all of the anterior vertebrae from the second to the tenth inclusive. "In this respect," according to Starks (1910), "*Acanthocybium* differs from all of the other genera, as in the others all of the epipleurals are on the centra."

All of the abdominals bear more or less strongly developed anterior and posterior neural zygapophyses. The anterior neural zygapophysis is peculiarly developed with a tiny slot (Fig. 6, "x") into which fits the posterior zygapophysis of the preceding vertebra. This interlocking arrangement is not of the same design as that in *Istiophorus* (see Gregory and Conrad, 1937, p. 10), for in the latter the right and left anterior zygapophyses together form a slot into which fits the neural spine of the vertebra in front. Thus a similar mechanical effect, the strengthen-

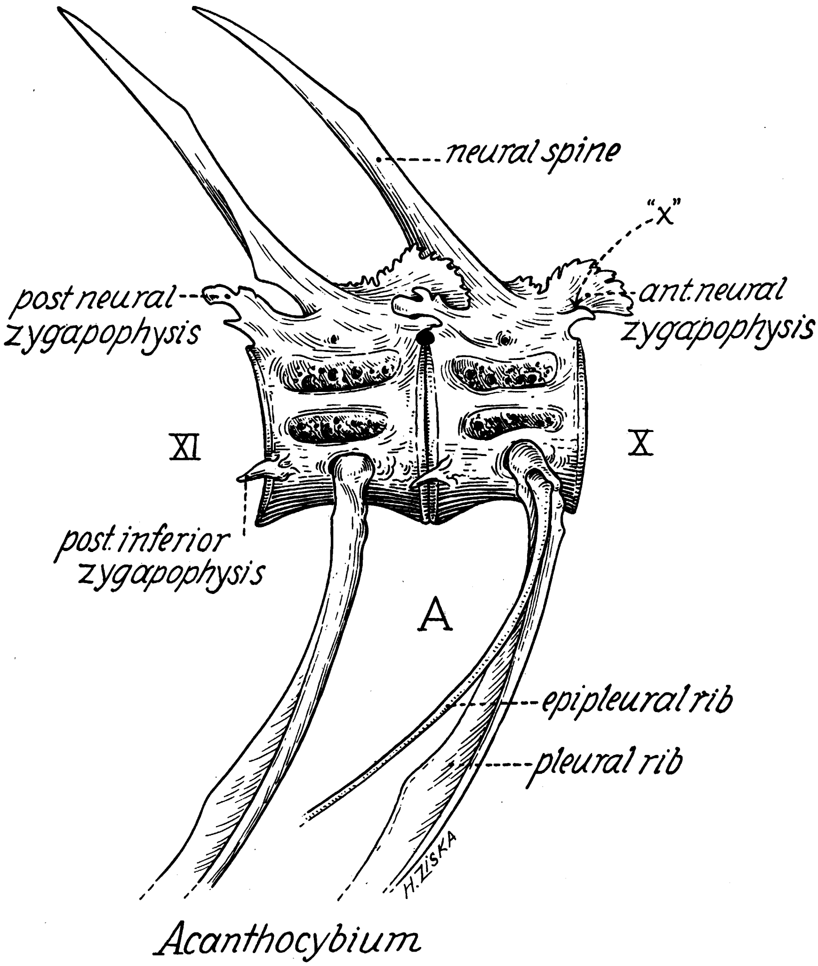

Fig. 6. Abdominal vertebrae of *Acanthocybium.*

ing of the column, is arrived at by different means in these two scombroid genera.

A postero-inferior zygapophysis is developed in *Acanthocybium.* The eighth vertebra is the first one on which such a perceptible haemal zygapophysis is noticed. This posterior haemal zygapophysis arises from the bony septum between the ventral and median lateral fossae of the centrum in the anterior abdominals, but as the centra deepen and the ventral fossae become more pronounced the posterior haemal zygapophyses move to the ventral border of the ventral fossa. In the more anterior abdominals this zygapophysis may serve to stiffen the column.

The neural spine of the first vertebra is not attached (*autogenous*) to its centrum. The neural arches and spines of the first five or six vertebrae are stoutly developed with an antero-posterior emphasis. The neural spine of the seventh is perceptibly the shortest of those on the abdominal vertebrae and from this point until a peak is reached on the 37th vertebra, under the second dorsal fin, they become progressively longer.

Haemal parapophyses are sufficiently developed to be first noticed on the sixteenth vertebra. From that point backward they become increasingly long until, on the twenty-seventh vertebra, they meet in the mid-ventral position to form a closed haemal arch. The next five vertebrae (27th to 31st, inclusive), although bearing true haemal arches are to be considered as abdominals for they all bear pleural ribs.

The abdominal centra of *Acanthocybium* are "square" and heavily sculptured with deep fossae in lateral aspect. The more anterior abdominals have but two deep fossae—a dorsal and a median—dorsal to the rib facet. In the posterior abdominals as the parapophyses approach the antero-ventral border of the centra a ventral fossa is developed. The remainder of the centra are characterized by these three deep lateral fossae until on the fifty-sixth vertebra of the caudal series the median fossa is swamped out. In the possession of three lateral fossae per centrum *Acanthocybium* differs from all other Scombridae except *Cybium* (*Scomberomorus*) *koreanum*. Kishinouye's figure of *Cybium* (*Scomberomorus*) *chinense* shows incipient median fossae in the caudal vertebrae.

Caudal Vertebrae

The anterior caudal vertebrae of *Acanthocybium* (Fig. 7) are very similar to the most posterior abdominals, except that the haemal arch develops a spine and the ribs and rib facets are eliminated.

The arrangement of the neural zygapophyses is exactly as in the abdominal vertebrae.

There are stoutly developed anterior and posterior haemal zygapophyses which oppose each other but do not overlap. There is no slot-like mechanism devised to stiffen the ventral side of the column.

More posteriorly, the fifty-seventh vertebra (Fig. 8A), presents a much modified condition. Here the dorsal and ventral fossae are very deep pits, while the median fossa is becoming eliminated. The entire surface of the centrum is covered with the most intricate filigree work which may serve to lighten the structure while preserving its strength. In common with all the scombroids the neural and haemal spines and arches of *Acanthocybium* are noticeably flattened down in the "peduncle" region. This has resulted in the loss of both the posterior neural and haemal zygapophyses, while anteriorly the neural and haemal zygapophyses have been much reduced. The lateral ridges are not expanded to form bony lateral keels in the peduncle region as in the tunas.

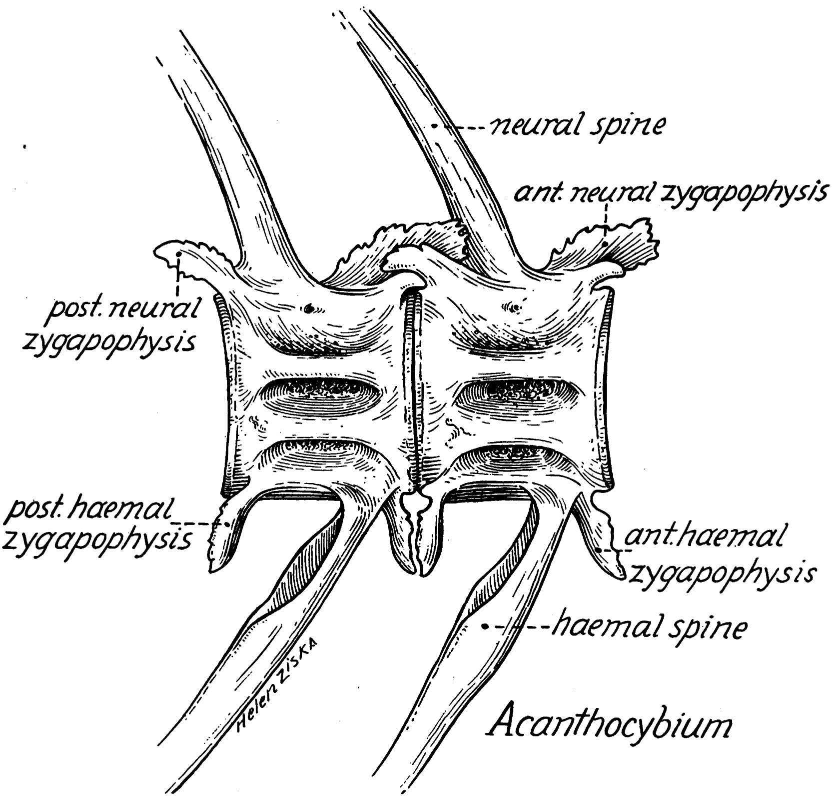

Fig. 7. Caudal vertebrae of *Acanthocybium*

Hypural Complex

The nomenclature of the description that follows is based upon the system suggested by Whitehouse (1910).

The last four vertebrae (58th to 61st, inclusive) preceding the hypural fan (62) enter into the support of the caudal fin. The neural spines of the 58th, 59th, 60th, and 61st form a series of epurals. Between the epurals and the hypurals is a group of three autogenous dorsal caudal radials (Fig. 8B). The hypural fan of the 62nd vertebra is spread symmetrically both dorsally and ventrally. The haemal spines of the vertebrae 58th to 61st, inclusive, all serve to help support the caudal fin so may be considered as hypurals.

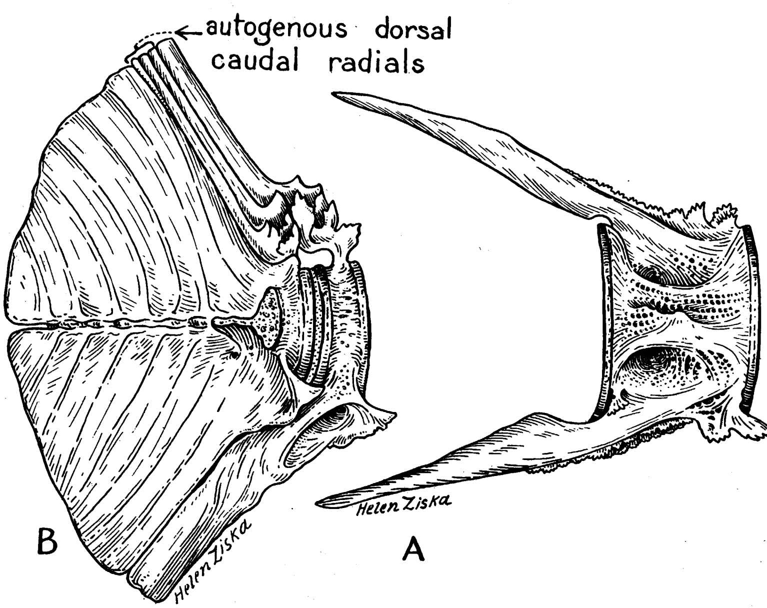

Fig. 8. *Acanthocybium:* A, 57th vertebrae; B, hypural complex.

In form and arrangement the hypural complex of *Acanthocybium* resembles that of *Cybium* (*Scomberomorus*) more than it does the primitive *Scomber*. However, the hypurals arising from the penultimate and antepenultimate vertebrae of *Cybium* (*Scomberomorus*) *chinense*, from Kishinouye's (1923) figures, seem to be autogenous whereas in *Acanthocybium* the hypurals are fused to their respective vertebrae. In *Gymnosarda*, on the other hand, the ventral elements are fused with their respective vertebrae and are thus true hypurals. There are several dorsal caudal radials present in *Cybium* (*Scomberomorus*), but none in *Gymnosarda*. While the posterior notch in the hypural fan is prominent in *Cybium* (*Scomberomorus*) and not so marked in *Acanthocybium* the general form of the fan is not dissimilar.

In *Scomber scombrus*, according to Ford's (1937) figure, the hypurals of the penultimate and the antepenultimate vertebrae are autogenous. The shape of the fan is much less symmetrical than in *Acanthocybium* or *Cybium* (*Scomberomorus*). There is a well-defined epural appressed but not fused to the dorsal hypural. There is no evidence of this in either *Acanthocybium* or *Cybium* (*Scomberomorus*) in which the hypurals are separated from the epurals by dorsal caudal radials.

Gill (1863), Lütken (1880), Jordan and Evermann (1896), and many other authors have concurred in placing the wahoo, *Acanthocybium solandri*, among the Scombridae as understood in the broad sense. Starks (1910) published a phylogenetic tree which shows *Acanthocybium* as an offshoot of *Scomberomorus* (*Cybium*). Kishinouye (1923) placed *Acanthocybium* in his family Cybiidae which includes the genera often known as Spanish and King mackerels. Most authors, however, sink Kishinouye's Cybiidae in the Scombridae.

Study of the osteology of *Acanthocybium* seems to indicate that these previous authors have been correct in considering it to be an aberrant but definite member of the Scombridae.

RELATIONSHIPS WITH THE XIPHIIFORMES

Does the genus *Acanthocybium* form a connecting link between the Scombridae and the Xiphiiformes? Such a belief is implied by the following statements of Lütken, Jordan and Evermann, Starks, and Kishinouye.

Lütken (1880), as translated by Bean in Goode's 'Materials for a history of the swordfishes' (1883), makes the following statement:

> Despite certain analogies between *Xiphias* and *Histiophorus* at their appearance from the egg, there are very considerable differences between them in their very first conduct—differences which show well enough that the separation between these two genera is rather wide. To this result one must come also by comparison of the bony structure of a *Histiophorus* or a *Tetrapturus* with that of a *Xiphias*. The closest generically of the *Histophori*, especially of the *Terapturi*, we will in a later section, find in the genus *Acanthocybium*, which presents decided resemblances. If these show nothing more than a very close relationship, they at any rate unite the tie too firmly for one to regard the Xiphioids as other than a subsection of the great mackerel family.

In a French résumé of his article, 'Spolia Atlantica. . . . ,' Lütken has the following to say about *Acanthocybium:*

> That *Acanthocybium* is the Thynnoid form most nearly approaching the swordfish is shown by the peculiar modification of the branchiae and the prolongation of the intermaxillaries [premaxillaries], which, if more developed, would become the short rostrum of *Tetrapturus belone*. The genus thus acquires peculiar importance

from a systematic point of view; and a detailed investigation of the still unknown structure of its skeleton would be especially desirable.

Jordan and Evermann (1896) in their 'Fishes of North and Middle America' make the statements below:

> This remarkable genus [*Acanthocybium*] indicates a long step from *Scomberomorus* toward the type of the swordfishes.
>
> This group [Istiophoridae] represents a younger stage in the development of *Xiphias*, and is intermediate between the latter and the scombroid stock, from which both are derived. The gaps are wide in the series *Scomberomorus, Acanthocybium, Istiophorus, Tetrapturus, Xiphias,* but the natural sequence seems evident.

Starks (1910) in his paper on the 'Osteology and mutual relationships of the fishes belonging to the family Scombridae,' says:

> *Acanthocybium* naturally comes next to *Scomberomorus* though . . . . . it certainly does not deserve a position so close to *Scomber*. It shows, as was long ago pointed out, an apparent divergence toward the swordfishes.

Kishinouye, more recently (1923), says:

> This family [Cybiidae] is related on one hand to the Xiphiidae in the reticulate gills, absence of gill-rakers, small narrow scales, etc. through the genus *Acanthocybium*. . . . .

Later in the same paper under the generic description he says:

> This genus [*Acanthocybium*] comprises a rather aberrant form, more or less related to the Xiphiidae.

Despite this belief that *Acanthocybium* points the way to the Xiphiiformes, none of the authors quoted have gone so far as to remove this genus from the Scombridae (in the broad sense) and place it with either the Istiophoridae or Xiphiidae. That it is an aberrant side branch of the Scombriformes is unquestioned, but it seems extremely doubtful that it diverges from the Scombridae in the direction of the Xiphiiformes.

Nevertheless an extended comparison of *Acanthocybium* with the xiphiiform genera will either substantiate or eliminate the concept expressed by the several authors above.

Body and Fin Form

The bases upon which the wahoo (*Acanthocybium solandri*) has been so continuously linked with the Xiphiiformes are but vaguely suggested in the literature examined. Its elongate body; its long dorsal fin; the prominent beak; all these features, coupled with the peculiar modification of the branchii in *Acanthocybium* and *Xiphias*, as alluded to by Lütken (1880), have probably given rise to this opinion.

A more detailed analysis of the body form fails to show how such an assumed relationship could exist. It is evident at once from figure 9

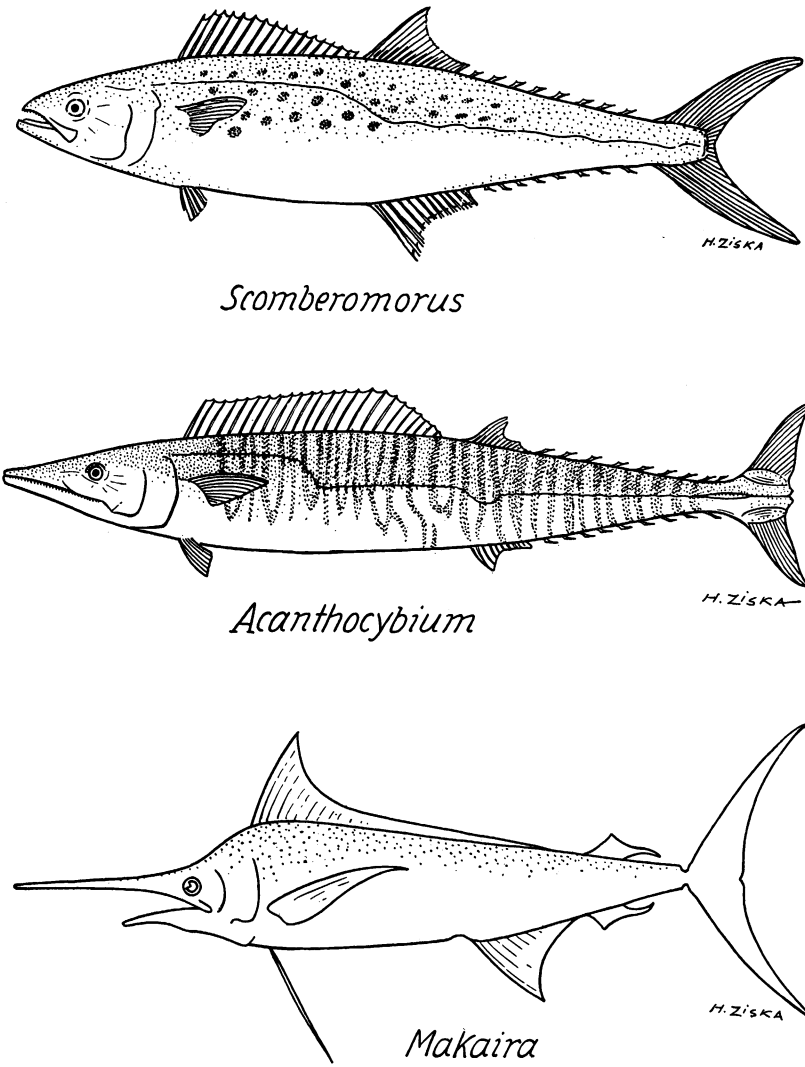

Fig. 9. Body forms of *Scomberomorus*, *Acanthocybium*, and *Makaira*.

that *Acanthocybium* more nearly resembles *Scomberomorus* than *Makaira*. The long, low first dorsal seen in *Acanthocybium* is noteworthy in the Scombridae, whereas in the Xiphiiformes there is a strong tendency to emphasize the anterior portion in the Istiophoridae and lose the posterior part in the Xiphiidae. The finlets of the second dorsal region which

TABLE I.—Comparison of the Body Forms of *Scomber*, *Scomberomorus*, *Acanthocybium*, and *Makaira*.

Indices	*Scomber colias*	*Scomberomorus maculatus*	*Acanthocybium solandri*	*Makaira nigricans ampla*
Body length $\frac{\text{length} \times 100}{\text{depth}}$	Mesosomatic 477%	Mesosomatic 463%	Dolichosomatic 652%	→ Dolichosomatic 631% Mesosomatic 453%
Body width $\frac{\text{width} \times 100}{\text{depth}}$	Mesothoracic 71%	Mesothoracic 50%	← Mesothoracic 68%	→ Mesothoracic 60% Stenothoracic 40%
Head length $\frac{\text{head length} \times 100}{\text{body length}}$	Nomocephalic 28%	Nomocephalic 23%	← Nomocephalic 24%	Macrocephalic 36%
Head depth $\frac{\text{head depth} \times 100}{\text{head length}}$	Mesocephalic 62%	Mesocephalic 64%	Platycephalic 48%	→ Platycephalic 29%
Head width $\frac{\text{head width} \times 100}{\text{head depth}}$	Mesocranial 65%	Mesocranial 67%	← Mesocranial 76%	→ Mesocranial 70%
Snout length $\frac{\text{snout length} \times 100}{\text{head length}}$	Nomorhynchal 31%	Nomorhynchal 40%	← Nomorhynchal 50%	Hypermacrorhynchal 66%
Upper jaw length $\frac{\text{upper jaw} \times 100}{\text{head length}}$	Mesognathic 38%	Macrognathic 57%	Mesognathic 49%	Macrognathic 78%
Eye $\frac{\text{eye length} \times 100}{\text{head length}}$	Mesophthalmic 22%	Microphthalmic 12%	← Microphthalmic 10%	→ Microphthalmic 6%
Gill chamber $\frac{\text{length preop. to operc.} \times 100}{\text{head depth}}$	Mesocameral 51%	Mesocameral 47%	← Mesocameral 54%	→ Mesocameral 64%
Peduncle vertical $\frac{\text{min. depth peduncle} \times 100}{\text{body depth}}$	Leptopygidial 15%	Leptopygidial 19%	← Leptopygidial 21%	→ Leptopygidial 19%

Peduncle width $\frac{\text{peduncle width} \times 100}{\text{peduncle depth}}$	Eurypygidial 96%	Eurypygidial 157%	←	Eurypygidial 104%	→	Eurypygidial 80% ±
First dorsal length $\frac{\text{fin length} \times 100}{\text{body length}}$	Medibasic 16%	Longibasic 26%	←	Longibasic 33%	→	Longibasic 48%
First dorsal height $\frac{\text{fin height} \times 100}{\text{body depth}}$	Mediradial 60%	Breviradial 29%	←	Breviradial 21%		Altiradial 89%
Second dorsal length $\frac{\text{fin length} \times 100}{\text{body length}}$	Medibasic 28%	Longibasic 42%		Medibasic 30%		Perbrevibasic 4%
Second dorsal height $\frac{\text{fin height} \times 100}{\text{body depth}}$	Breviradial 25%	Mediradial 45%	←	Mediradial 35%		Breviradial 21%
Anal length $\frac{\text{fin length} \times 100}{\text{body length}}$	Medibasic 26%	Longibasic 40%		Medibasic 27%	→	Medibasic 23%
Anal height $\frac{\text{fin height} \times 100}{\text{body depth}}$	Breviradial 25%	Mediradial 49%	←	Mediradial 42%		Longiradial 78%
Pectoral fin length $\frac{\text{fin length} \times 100}{\text{body length}}$	Breviradial 11%	Breviradial 12%	←	Breviradial 11%		Mediradial 20%
Pelvic fin spread $\frac{\text{fin spread} \times 100}{\text{body length}}$	Parviareal 2.9%	Parviareal 4%	←	Parviareal 3%	→	Parviareal 0.4%
Pelvic fin length $\frac{\text{fin length} \times 100}{\text{body length}}$	Breviradial 9%	Breviradial 5%	←	Breviradial 3%		Mediradial 13%
Caudal fin length $\frac{\text{fin length} \times 100}{\text{max. spread caudal}}$	Brachycercal 140%	Brachycercal 22%	←	Brachycercal 34%	→	Brachycercal 20%
Caudal fin spread $\frac{\text{fin spread} \times 100}{\text{body depth}}$	Macrocercal 114%	Hypermacrocercal 167%	←	Hypermacrocercal 173%	→	Hypermacrocercal 217%

are so characteristic of the Scombridae are seen in *Acanthocybium*, but not in *Makaira*. The pelvic fins of both *Acanthocybium* and *Scomberomorus* are quite robust and apparently quite functional; in *Xiphias*, they are completely lost; and, in the Istiophoridae, they are so long and thin as to seem incapable of locomotor function. The caudal fin of *Acanthocybium* lacks the deep concavity of the Scombridae, in this regard resembling the typical *Makaira*. The most striking difference between *Acanthocybium* and the Xiphiiformes is the prominent beak of the latter. This last difference is, however, only one of degree, for the rostrum is merely an elongation of the premaxillaries.

Table I compares the body form details of *Scomberomorus*, and *Scomber*, representing the Scombridae; *Makaira nigricans ampla*, representing the Xiphiiformes; and *Acanthocybium solandri*. The table is based on material published by Conrad and La Monte (1937) and a series of unpublished measurements made by Dr. William K. Gregory on the Arcturus Expedition of the New York Zoological Society in 1925. The definitions of the body form terms are those given by Gregory (1928 *b*).

It will be seen from a study of Table I that *Acanthocybium* resembles *Scomberomorus* in seventeen characters and *Makaira* in thirteen. Ten of these characters are common to all three and are undoubtedly an indication of their mutual scombroid heritage. Thus, in head length, snout length, first and second dorsal fin height, anal fin height, and pectoral and pelvic fin length *Acanthocybium* resembles *Scomberomorus;* whereas in body length, head depth, and anal length the wahoo resembles *Makaira*.

The long sword of *Makaira* so prejudices the measurement of body length that comparisons with *Acanthocybium*, and other forms, are profoundly affected. Gregory and Conrad (1937) noted that if the sword was arbitrarily eliminated from consideration in *Xiphias* the body length was mesosomatic. Conrad and La Monte (1937) found that some of their *Makaira* were mesosomatic while others were dolichosomatic with the swords included; without the sword all were definitely mesosomatic. Thus, the fundamental mesosomy of the Xiphiiformes, a scombroid heritage, is masked by their prominent rostra.

Just as the sword of the xiphiiform fishes influences the length classification, so does it influence the relative depth of the head. With the sword eliminated the depth of head in *Makaira* is mesocephalic as in *Scomberomorus* and other scombroids.

The long pointed snout is considered characteristic of *Acanthocybium*. However, as is shown above (p. 9), the premaxillaries are not inordinately long. Whence comes this appearance? In the first place, the head of *Acanthocybium* is very long (about one-fourth of the total body length), secondly, the head is very shallow, or platycephalic. Such a long and low head must give the impression of a sharply pointed snout. In contrast is *Scomberomorus* with its deeper, or mesocephalic, character. The snout of *Scomberomorus* is but moderately pointed and the entering angle is somewhat greater than in *Acanthocybium.*

This body form analysis suggests that *Acanthocybium,* although unique among Scombridae in its extreme length and shallow depth, is essentially one of the Scombridae and without affinities to the Xiphiiformes.

This extremely long, arrow-like body must be admirably streamlined for it has been recorded as traveling at a speed of 41 miles per hour (Howell, 1937), a speed far in excess of that of other fishes so measured.

Osteology

In the discussion below on the possible relationships of *Acanthocybium* to the Xiphiiformes as evidenced by its osteology, many references will be made to the conditions to be found in *Istiophorus* and *Xiphias.* In the interests of simplicity, however, as few details of xiphiiform osteology as possible will be mentioned. For further details the reader is referred to two recent papers in which observations on the osteology and relationships of *Xiphias* and *Istiophorus* were made (Gregory and Conrad, 1937; Conrad, 1937). It may be mentioned here, however, that the skeletons of all of the Istiophoridae (*Istiophorus, Makaira, Tetrapturus*) are essentially alike.

Skull

Any comparison of the skulls of various scombroids must take into account those resemblances which are the fundamental heritage of all members of the group. Regan (1909) listed the following characters, among others, as basic to all scombroids:

(1) Maxillaries more or less firmly attached to the non-protractile 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 osseous roof for the myodome.

Another common feature of all of the scombroids is the large size of the opercular bones.

As is indicated by the list of heritage characters above, the neurocrania of *Xiphias*, *Istiophorus*, and *Acanthocybium* are all very similar fundamentally. The arrangement of the crests is similar in all of them and differs only in proportions. The position of the nasal bone in *Acanthocybium* is more like that in *Istiophorus* than *Xiphias*. In *Istiophorus* and *Acanthocybium* the nasal is large and robust and receives some of the thrust of the upper jaw whereas in *Xiphias* the nasal is a very small vestige receiving no stresses or strains.

Lütken (see above, p. 17) suggested that *Acanthocybium* could be more readily compared with the Istiophoridae than with *Xiphias*. In the character of the suspensorium this is certainly true, for the anteroposterior dimension of the metapterygoid is similarly great in both *Istiophorus* and *Acanthocybium* while in *Xiphias* this same dimension is very much reduced. The symplectic is prominent in lateral view in both the wahoo and the sailfish, but is hidden from view by the quadrate in *Xiphias*. The quadrate of *Acanthocybium*, however, is of the primitive triangular type noted in *Scomber* and *Xiphias* with no evidence of the quadrilateral tendency seen in *Istiophorus*. The pterygoid of *Acanthocybium* has a firm and broad abutment against the entire anterior wall of the quadrate, even extending dorsad and mesially onto the metapterygoid. Such an extensively braced condition more nearly resembles the istiophorids than *Xiphias*, for in the latter only a point contact exists between the pterygoid and the most anterior angle of the "quadrate triangle." The entopterygoids of both *Acanthocybium* and *Istiophorus* are developed mesially into a rather broad plate, but in *Xiphias* the entopterygoid is quite narrow. The palatine of the wahoo is very much as in *Istiophorus* passing forward as it does to hook over the anterior end of the maxilla immediately beneath the nasals.

Of course the most striking specialization of both the Istiophoridae and the Xiphiidae is the possession of long, sword-like premaxillaries. Conrad (1937) showed that the swords of both families, while differing in details, are fundamentally alike for they consist chiefly of hypertrophied premaxillae. Regan (1909) implied by diagram that *Acanthocybium* was the primitive stage in the development of the rostrum. But certainly *Acanthocybium* is no nearer the condition in the Xiphiiformes than is *Scomber*. Either of these fishes could be the starting point of a structural series of scombriform rostra leading to the swordfishes, but it seems doubtful that *Acanthocybium* is a genetic precursor of any of the Xiphiiformes, either in this character or any other.

In *Xiphias* the articular is the dominant element of the mandible; in *Makaira* it is less so; while in *Scomber* and *Acanthocybium* both the dentary and the articular contribute more or less equal amounts. An angular bone is present in *Acanthocybium* which is visible in lateral view whereas the angulars of *Xiphias* and *Makaira* are almost completely mesial and cannot be seen in lateral aspect. As in *Acanthocybium*, a sesamoid articular bone is present in the xiphiiform fishes. The predentary bone which is present in the Istiophoridae is absent in both *Xiphias* and *Acanthocybium*.

The arrangement of the opercular bones of *Acanthocybium* differs considerably from those in either *Makaira* or *Xiphias*. The preoperculum is proportionately larger in the wahoo than in any of the Xiphiiformes. The preoperculum of *Acanthocybium* has a somewhat rectangular form, while that of *Makaira* or *Istiophorus* has a crescent shape. The preopercle of *Xiphias* has become so narrow antero-posteriorly as to be a relative sliver. The operculum of *Acanthocybium* seems nearer to that of *Makaira* than to *Xiphias*, for the antero-inferior corner is projected ventrally until it almost makes contact with the interoperculum, while in *Xiphias* the antero-inferior corner of the opercle is rounded and does not meet the interoperculum. The subopercula of the wahoo and *Scomber* are quite large and project dorsally farther than in the Xiphiiformes. The interoperculum of *Acanthocybium* with its marked antero-posterior elongation is similar to that of *Scomber*. This contrasts with the dorso-ventral emphasis of the interoperculum in the xiphiiform fishes.

Comparison of the skulls of *Acanthocybium*, *Istiophorus*, and *Xiphias* indicates that most of the specializations of the Xiphiiformes are in the secondary upper jaw and other differences were probably brought about to meet altered stresses developing with the evolution of the sword. However, the general similarity of the neurocrania reflects only a common scombroid heritage and does not provide a clue to the phylogeny of the Xiphiiformes.

Vertebral Column

Lütken (see above, p. 18), in considering the relationship of *Acanthocybium* with the Xiphiiformes, was sufficiently cautious to suggest that the post-cranial skeleton be studied before a final disposition of *Acanthocybium* was made. It is in the vertebral column (which Lütken apparently did not have) that the answer to the problem of the relationships of *Acanthocybium* seems to lie.

The vertebral column of *Acanthocybium* is long and many segmented, some individuals having as high as sixty-six vertebrae. *Xiphias* and *Istiophorus* have much shorter columns with fifteen precaudals and eleven caudals in the swordfish while the latter genus has twelve precaudals and twelve caudals to make a total of twenty-four. Thus, the recent Xiphiiformes have the least number of vertebrae of any of the scombroids, whereas *Acanthocybium* has the largest number among the members of the Scombridae. This is a quantitative contrast which is unfortunately broken down when *Palaeorhynchus*, a Lower Oligocene sailfish, is examined. *Palaeorhynchus* has about sixty vertebrae.

Light can be thrown on this problem of the relationships of *Acanthocybium* with the xiphiiform fishes only by an analysis of the qualitative characters of the individual vertebrae (Tables II, III, IV) for, as was pointed out above (p. 12), too great a dependence on vertebral counts may often separate backbones which are quite similar in morphology. In this case, however, it seems that not only are the counts dissimilar but also the morphology.

Under the discussion of the vertebral column of *Acanthocybium* we found that the column could be divided into six quite definite regions. Let us compare these regions in the wahoo with their homologues in the Xiphiiformes.

I.—The post-cranial vertebrae of *Acanthocybium* were characterized by stout neural arches and spines and were about six in number. In both *Xiphias* and *Istiophorus* the true post-cranials are only two in number. These post-cranials are so different in form from each other and from the remainder of the vertebrae as to give the appearance of a pseudo atlas and axis arrangement. The first vertebra in the Xiphiiformes articulates with the exoccipitals by means of two dorso-lateral facets. In *Istiophorus* and *Xiphias* the first post-cranial bears a rib whereas in *Acanthocybium* this is lacking. The neural arch is present in the first post-cranial of *Istiophorus*, but no spine is developed. There is an indication of a posterior neural zygapophysis in *Istiophorus*. In *Xiphias* a neural spine is present on the first post-cranial as well as a posterior neural zygapophysis. The second post-cranial of *Istiophorus* bears a pleural rib, has both an anterior and a posterior neural zygapophysis, but has no neural spine developed. In *Xiphias* the second post-cranial may be described in the same manner as for *Istiophorus*.

II and III.—The remainder of the abdominal vertebrae of the Xiphiiformes cannot be divided into "mesabdominals" and posterior abdominals for they are all remarkably alike in form. None of the abdominal centra of either section of the Xiphiiformes possess the closed haemal arch which is so typical of the Scombridae. *Istiophorus* bears ribs on all abdominals and post-cranials, but in *Xiphias* ribs are borne only on the two post-cranials and on the first two and last three abdominal vertebrae. *Acanthocybium* bears ribs on all abdominals and on all post-cranials, but the first. However, no xiphiiform fish bears epipleural ribs, while they are present in most Scombridae, including *Acanthocybium*.

As noted above (p. 12) the interlocking of the vertebrae by means of the zygapophyses is seen to a marked degree in both *Acanthocybium* and *Istiophorus*, but the details of design are fundamentally different. *Xiphias* shows this interlocking only to a slight degree, but it is readily comparable to the system used in *Istiophorus*.

The most striking specialization in the column of *Istiophorus* (Gregory and Conrad, 1937, Fig. 4) is the large, antero-posteriorly developed, flange-like neural spines which are accompanied by long, thin, horizontally placed anterior neural zygapophyses. In *Xiphias* (Gregory and Conrad, 1937, Fig. 4) the neural spines are long and compressed slightly, while both anterior and posterior neural zygapophyses are well developed, but rise obliquely rather than horizontally from the centra. In *Acanthocybium* the neural spines are long and tapering to a point and the neural zygapophyses are moderately developed.

IV.—The caudal vertebrae of *Xiphias* and *Istiophorus* are quite uniform. However, in both of these xiphiiform types there is a more abrupt jump from the abdominals to the caudals than in *Acanthocybium*. This, of course, is because no haemal arches are formed in xiphiiform fishes until the caudal region starts.

In *Istiophorus* the haemal arch and spine is a counterpart of the neural elements—the same interlocking scheme being used. In *Xiphias*, while the haemal spines resemble the neural spines, the haemal zygapophyses are poorly developed in the caudal region. In *Acanthocybium* the neural elements are as in the abdominals, but the haemal zygapophyses, although very well developed, merely oppose each other and do not interlock.

The centra of *Acanthocybium* are "cuboid" and heavily sculptured by deep lateral fossae. The anterior abdominals have dorsal and median fossae and as one passes posteriorly a ventral fossa is added. The median fossa is eliminated in the posterior caudals. *Xiphias* likewise has a "cuboid" centrum in the abdominal region, with a tendency for the centra to lengthen in the caudal region. However, *Xiphias* shows none of the "sculpturing" seen in *Acanthocybium* and other Scombridae. In fact the surface is so plain and rather concave that one gets the impression of "degeneracy." As an opposite extreme the typical centrum in *Istiophorus* is long and hour-glass shaped with a certain amount of sculpturing.

V and VI.—The hypural complex remains to be discussed. Each of these forms has a homocercal tail, and in each the hypural fan which is the major support of that tail is almost perfectly symmetrical. As was noted above, the last five vertebrae (including the hypural fan) in *Acanthocybium* all enter into the support of the caudal fin, but in both *Xiphias* and *Istiophorus* only the last two vertebrae are concerned.

The vertebrae of the Xiphiiformes are of two definite types neither of which is comparable to those of *Acanthocybium.* Regan (1909) and Gregory and Conrad (1937) showed that the two modern families of swordfishes, the Xiphiidae and the Istiophoridae, may be traced back to the Eocene form *Blochius* and the Lower Oligocene *Palaeorhynchus,* respectively. Characteristic of the *Xiphias-Blochius* line are squarish, cuboid centra unrelieved by surface sculpturing, with short ribs, and with none of the antero-posterior emphasis seen in *Istiophorus.* The istiophorid-*Palaeorhynchus* line is characterized by an extreme antero-posterior development of the centra, neural, and haemal spines, and the zygapophyses. It was concluded that the xiphiiform fishes represented two distinct but parallel lines of scombroid evolution.

TABLE II.—A Synopsis of the Vertebral Column of *Acanthocybium solandri.*

Serial number of vertebrae	Characteristics
1	**Post-cranial.** Neural arch and spine autogenous but large.
2–6	**Post-cranial.** Neural spines robust, slightly laminated.
7–26	**Mesabdominals.** Neural spines round, tapering to a point. No haemal arches.
27–32	**Posterior abdominals.** Haemal arches with ribs, no spines.
33–57	**Caudals.** Haemal arches and spines.
58–60	**Tail segment.** Haemal and neural spines support caudal fin.
61	**Tail segment.** Neural spine autogenous.
	Three dorsal caudal radials between the 61st and 62nd vertebrae.
62	**Hypural fan.**

TABLE III.—A Synopsis of the Vertebral Column of *Istiophorus*.

Serial number of vertebrae	Characteristics
1	**Post-cranial.** Neural arch nearly fused over; no neural spine; no anterior neural zygapophysis.
2	**Post-cranial.** Neural arch not fused; no neural spine; anterior neural zygapophysis well developed. Neural arch not laminate.
3–4	**Abdominals.** Neural arches laminate, not fused into a spine.
5–12	**Abdominals.** Neural arches fused into a spine.
13	**Caudal.** Haemal arch and spine; no anterior haemal zygapophysis.
14–21	**Caudals.** As in 13th but with anterior haemal zygapophyses.
22	**Caudal.** Neural and haemal spines losing laminate character; haemal arch and spine autogenous.
23	**Tail segment.** Neural and haemal arches and spines autogenous.
	Two dorsal caudal radials between 23rd and 24th vertebrae.
24	**Hypural fan.**

TABLE IV.—A Synopsis of the Vertebral Column of *Xiphias gladius*

Serial number of vertebrae	Characteristics
1	**Post-cranial.** Neural arch not fused over (directed dorsally); no neural spine; no anterior neural zygapophysis; short centrum.
2	**Post-cranial.** Neural arch and anterior neural zygapophysis exceedingly robust; neural arch not fused; arch and zygapophysis rise obliquely anteriorly and posteriorly. Centrum longer than deep.
3–7 or 8	**Abdominals.** Neural arches and zygapophyses less robust but similar to 2nd; arches not fused into spine. Cuboid centra.
9–15	**Abdominals.** Neural arches fused to form spine. Cuboid centra.
16–24	**Caudals.** Haemal arches and spines developed. Spines become progressively shorter; centra progressively longer.
25	**Tail segment.** Neural and haemal spines and arches autogenous.
	Three dorsal and one ventral caudal radials interposed between 25th and 26th vertebrae.
26	**Hypural fan.**

Examination of these three columns—*Acanthocybium*, *Xiphias*, and *Istiophorus*—leaves one with the impression that we are dealing with very different forms (Tables II, III, IV). There is no doubt that *Acanthocybium* has definite affinities with the Scombridae for the form of the individual vertebra is of the scombrid type—more or less cuboid in shape, with well-marked lateral fossae, and, as in many mackerels and tunas, with the haemal arch developed over the posterior part of the abdominal cavity. All of these characters and more are lacking in the xiphiiform fishes.

SUMMARY

A study of the osteology of the highly specialized scombroid, *Acanthocybium solandri*, substantiates the work of previous authors in placing it in the family Scombridae.

Prolonged consideration of its alleged relationship to the xiphiiform fishes brings out the following points:

1.—*Acanthocybium* is unique among the Scombridae in its extremely long and shallow body which reflects externally its many segmented vertebral column. The Xiphiiformes, on the other hand, have a pseudo-dolichosomy which is brought about by the long sword alone, for they have the fewest number of vertebrae of any species in the order (with the exception of *Luvarus imperalus*).

2.—In quality of body form *Acanthocybium* is one of the Scombridae and is quite unlike the Xiphiiformes.

3.—Comparison of the skulls of *Acanthocybium*, *Istiophorus*, and *Xiphias* shows that the specializations seen in the Xiphiiformes are the result of altered stresses developing with the evolution of the sword.

4.—However, the sword may just as easily have arisen from the primitive *Scomber* as from *Acanthocybium*, for both have equally pronounced premaxillae.

5.—A common scombroid heritage is indicated by the general similarity of neurocrania in the three genera studied.

6.—The quality of the vertebral column as a whole is very different in all three genera (Tables II, III, IV).

7.—The individual vertebrae of the three types are so very different in form that it is evident that one is dealing with three divergent lines of scombroid evolution.

It is concluded, therefore, that the wahoo, *Acanthocybium solandri*, is an aberrant but true member of the Scombridae with no genetic relation or even parallelism to the Xiphiiformes. If descendants of an *Acanthocybium*-like ancestor are to be sought perhaps they may be found among the primitive cutlass-fishes, such as *Ruvettus*, which are characterized by many segmented columns.

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