Systematic position, composition, and origin of the Family Scombridae

A. F. Bannikov*

Institute of Palaeontology, USSR Academy of Sciences, Moscow

The suborder Scombroidei is considered as consisting of two superfamilies—Scombroidea (with only one family, Scombridae) and Trichiuroidea. Three subfamilies are distinguished within the family Scombridae: Scombrinae, Scomberomorinae, and Thunninae, and their characteristics and composition are described. Fossil as well as contemporary genera are included in the composition of the subfamilies. It is suggested that the family Scombridae is descended from Cretaceous carangid fishes.

Authors of all classifications of bony fishes have placed mackerels in the suborder Scombroidei of the order Perciformes. However, there is to date no consensus regarding the composition of the suborder Scombroidei. Regan (1909) placed Scombridae in a suborder with Trichiuridae, Xiphiidae, and Luvaridae. Later (Regan, 1929), he placed the families Gempylidae and Trichiuridae in a separate suborder. In L. S. Berg's classification of fishes (1955), the suborder Scombroidei consists of two superfamilies: Scombroidea and Xiphioidea, while Trichiuroidei and Luvaroidea are placed in separate suborders. In the classification of T. S. Rass and G. U. Lindberg (1971), Scombridae is also combined with Xiphiidae. This is also the view of Gregory and Conrad

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(1937). Like Regan (1909), Greenwood et al. (1966) and Zharov, Karpechenko, and Martinsen (1961) placed the families Scombridae, Gempylidae, Trichiuridae, Xiphiidae, Istiophoridae, and Luvaridae together in the suborder Scombroidei. Gosline (1968) placed the last three families in the suborder Xiphioidei. Finally there exists a classification according to which the suborder Scombroidei consists of the family Scombridae alone, while Trichiuriformes and Xiphiidiformes are given the rank of suborders (*The Life of Animals*, 1971).

The main reasons for combining the families Xiphiidae, Istiophoridae, and Luvaridae in the same suborder as Scombridae [to these Berg (1955) also added the fossil families Palaeorhynchidae, Blochiidae, and Xiphiorhynchidae) were formulated by Regan (1903, 1909). Regan noted that in all those families the rays of the caudal fin with their bifurcated proximal ends completely cover the hypural plate, and that the upper rays "almost meet on the median line" of the hypurals with the lower rays. In addition, *Luvarus* is close to Scombridae in the ossification of the rings of the sclera and in the wide opercular bones (Regan, 1903). Regan (1909) considered the rostral structure in fish of the families Xiphiidae and Istiophoridae a morphological extrapolation of the type characteristic of Scombridae (coracoid, non-extensible premaxillaries). All these morphological characters are explained by Gosline (1968) as an adaptation of large, fast-swimming fishes to hydrodynamic requirements. On the other hand, Gosline noted that Scombridae are very different from Xiphiidae. While in the vertebral column of Xiphiidae, Istiophoridae, and Luvaridae the number of vertebrae (23-26) is typical of generalized percoids, in that of Scombridae there are 31 or more. Unlike the Scombridae, in the above group the position of the pectoral fins is more ventral, the pelvic fins either have a reduced number of rays or are lacking, and the dorsal fin begins above the tip of the head, not behind it. Specialization of the caudal skeleton is also different in Xiphiidae and Scombridae. Thus Gosline (1968) shows conclusively that fishes of the families Istiophoridae, Xiphiidae, and Luvaridae are not a "highly specialized final stage of the Scombriformes" as suggested by Gregory and Conrad (1937), and they are not even closely related to Scombridae.

Scombridae were less often combined with Trichiuridae than with Xiphoriidae, even though possible links between Scombridae and Trichiuridae were not denied. It was noted that as regards many basic characters the least specialized trichiuroids of the family Gempylidae and the Scombridae are very similar. For example, a number of characteristic features of Gempylidae (elongated vertebrae, large teeth, bifurcated lateral line, etc.) are present in the genus *Grammatorcynus* of the Scombridae (Matsubara and Iwai, 1958). On the other hand *Ruvettus*, a member of Gempylidae, shows a certain similarity to the Scombridae (moderately elongated body, small number of vertebrae, presence of additional small fins, large 6-rayed pelvic fins).

The skull of the least specialized Scombridae (subfamily Scombrinae) is very similar to that of trichiuroids, even such specialized genera as *Lepidopus* (Starks 1911), is far more similar than to that of the tuna. Gregory (1933) noted that the trichiuroid skull (*Prometichthys*, *Lepidopus*) is a modification of the skull of *Scomber*: it is as narrow in the occipital, interorbital, and ethmoid regions, but noticeably more elongated. The supraoccipital and parietal crests are similarly developed in *Scomber* and *Lepidopus*, and consequently also the supratemporal recesses. The median crest on the frontals is absent in both genera, and the nasal bones are small and thin. The most distinct difference in the structure of the calvaria in the two genera is the strongly elongated ethmoid region and frontals of *Lepidopus* (Fig. 1).

A close look at the caudal skeleton of *Aphanopus*, a specialized genus of Trichiuridae, shows clearly its considerable similarity to that of Scombridae (Fig. 2a). As in the latter, in *Aphanopus* the hypurals are fused with the supporting bodies into a symmetrical plate. Like mackerels (Scomberomorinae; Fig. 3a), *Aphanopus* has a hypural diastema and a rudimentary neural spine on the second.

However, even those researchers who combined Trichiuridae and Scombridae in one suborder noted the different evolutionary tendencies of these two groups (Gosline, 1968). In the process of evolution, Trichiuroidea acquired a very long taeniate body, up to 160 vertebrae, and large teeth, the front ones being transformed into fangs; their pectoral fins are ventrally oriented, while the pelvic and caudal fins are frequently reduced or absent. Thus Trichiuridae are comparatively slow swimming semi-deepwater predators. Scombridae, on the other hand, evolved through adaptation towards active predation in near-surface waters, and as a result, the mobile tuna has a compact, streamlined body with a thick caudal fin, normally developed pelvic fins, and a highly developed circulatory system.

From the above, it would appear that the classification proposed by Gosline (1968) is the most correct. Gosline combined the families Scombridae, Gempylidae, Trichiuridae, and Scombrolabracidae in the suborder Scombroidei; this is evidently correct, because the kinship between Scombridae and Trichiuridae is indisputable. At the same time, taking into account the distinctive evolutionary tendency of this group, Gosline elevated the family Scombridae as a superfamily Scombroidea.

The family Scombridae was first defined by Regan (1909) in approximately its present composition. Starks (1910) distinguished five subfamilies within the family Scombridae: Scombrinae, Scomberomorinae, Acanthocybiinae, Sardinae, and Thunninae. In 1923 a monograph appeared in which the Japanese scientist Kishinouye divided the family Scombridae into 4 families (Scombridae, Cybildae, Thunnidae, Katsuwonidae), the last two being placed in a special order "Plecostei". Kishinouye contrasted this order with the order "Teleostei" (all other bony fishes) with its single suborder Acanthopterygii. The reason advanced for this peculiar division of Thunnidae (Kishinouye, 1923) was the discovery that the circulatory system of tunas and skipjack tunas differs significantly in development from that of all other fishes. This is associated with their higher body temperature and their active movement. In fact Thunnidae have more blood, more blood vessels, and a larger heart, while leaf-shaped vascular plexuses have developed in the lateral muscles, accounting for the dark-red, almost black color of the parts of the lateral muscle located either side of the vertebral column, under the "corset". The inner side of the liver or haemal canal also carries distinctive vascular plexuses (Kishinouye, 1923; Gibbs and Collette, 1966). As is known, the blood temperature of Thunnidae is above sea temperature, this temperature difference amounting under some conditions to as much as 9-10°. The extreme view, recognizing Thunnidae as a separate order, is based on specialization of individual organs and, as a number of authors have shown (Soldatov and Lindberg, 1930; Fraser-Brunner, 1950; Svetovidov, 1964) excessive significance is attributed to isolated anatomic details, especially the deep-seated "red muscles" of Thunnidae which are derivatives of the superficial red muscles of other Teleostei (Zharov, 1967).

Fig. 1. Calvaria of contemporary Scombroidei: a) *Scomber scombrus*, b) *Lepidopus caudatus* (after Gregory, 1933). epo – epiotic, exo – exoccipital, fr – frontal, meth – mesethmoid, na – nasal, par – parietal, pareth – parethmoid, pto – pterotic, soc – supraoccipital, spho – sphenotic, v – vomer.

Fig. 2. Caudal skeleton of contemporary Perciformes: a) *Aphanopus carbo*, family Trichiuridae (after Monad, 1968); b) *Trachurus trachurus*, family Carangidae. dh – hypural diastema, e – epural, cp – preural center, h – hypural, hap – haemapophysis, nap – neurapophysis, ph – parhypural.

Fig. 3. Caudal skeleton of Scombridae: a – *Scomberomorus maculatus* (after Monod, 1968), contemporary; b – *Scomber japonicus* (after Monod, 1968), contemporary; c – *Sarda vara* Bannikov, Caucasus, Lower Oligocene; d – *Auxis thazard*, contemporary. Keyed as in Fig. 2.

Even though the separation of tuna from other Scombridae is not justified, many ichthyologists have accepted Kishinouye's classification (1923) almost without modification. Berg (1955), for example, divided scombrids into the families Scombridae and Cybiidae within the superfamily Scombroidea of the suborder Scombroidei, recognizing the order Thunniformes with one family (Thunnidae) and two subfamilies (Thunninae and Auxidinae).

Many authors who have combined Thunnidae and Scombridae in one suborder nonetheless included other families—Scombridae, Cybiidae, Thunnidae (Casier, 1966; Zharov, 1967; Monod, 1968; and others). But the division into families has no firm foundation, since between genera there are no sharp morphological differences which would justify their division into such larger groups (Fraser-Brunner, 1950; Svetovidov, 1964).

Fraser-Brunner (1950) showed that the similarity between all Scombridae is very considerable and extends to a number of important anatomical and morphological characters. He placed all scombrids in one family with two subfamilies: Gastrochismatinae and Scombrinae. Later Matsubara (1955) recognized the subfamilies Thunninae, Katsuwoninae, Auxiinae, Scombrinae, and Scomberomorinae. Lindberg (1971) distinguished 4 subfamilies within the family Scombridae: Scombrinae, Sardinae, Acanthocybiinae, and Gasterochisminae.

From a study of fossil material, I am convinced that the unification of scombrid fishes into one family is correct. The study of the probable phylogenetic links allows us to suppose that the most natural subdivision of the family Scombridae is into 3 subfamilies: Scombrinae, Scomberomorinae, and Thunninae, corresponding to the three phylogenetic branches of Scombridae distinguishable as early as the Paleocene. The first members of the subfamilies Scombrinae (genus *Scombrosarda*) and Thunninae (genus *Paleothunnus*) are known from the Upper Paleocene of Turkmenia (Danil'chenko, 1968; Bannikov, 1978). The oldest genera of mackerels were found in the Paleocene deposits of equatorial Africa: *Landanichthys* and *Scomberomorus* (Dartevelle and Casier, 1949). It is quite unnecessary to create tribes within the Scombridae as some authors have done (Collette and Chao, 1975; Devaraj, 1975), because these tribes are equivalent to subfamilies.

In fishes of the subfamily Scombrinae there are 31 vertebrae in the vertebral column. The vertebrae are elongated, the last 4 to 5 trunk vertebrae are provided with thin, short parapophyses. The frontals and the ethmoidal region of the skull are narrow. The circumorbital ring of the suborbital bones is complete. As a rule the teeth are small and conical, except in the genus

*Grammatorcynus*. Scales cover the entire body, without enlarging strongly in the region of the pectoral fins. The first dorsal fin is high, either joined to, or separated from the second dorsal fin. The caudal fin is forked. The caudal peduncle has no median keel (except in the genus *Grammatorcynus*). In the caudal skeleton of fishes of the subfamily Scombrinae the hypaxial and epaxial hypurals are not fused, but divided by a cleft. The second preural vertebra has no neural spine (Fig. 3b). It has two epurals. There is a hypural diastema. The stegural is not separated from the body of the first preural vertebra. The subfamily Scombrinae includes three contemporary genera: *Scomber*, *Rastrelliger*, and *Grammatorcynus*, and one fossil genus, *Scombrosarda*.*

Mackerels (subfamily Scomberomorinae) have 32-64 vertebrae in the vertebral column. The vertebrae are foreshortened, about half of the posterior trunk vertebrae are provided with parapophyses. The frontals and ethmoidal region are moderately dilated. The ring of the suborbital bones is incomplete. The teeth are large, conical or laterally compressed. The body is completely covered in small scales, the "corset" of enlarged scales in the region of the pectoral girdle is either weakly expressed or absent. The first dorsal fin is extended, but short, close to the second. The caudal fin is crescent-shaped or of similar form. The median keel on the caudal peduncle is developed, but has no bony body. In the caudal skeleton of mackerels the hypurals and the bodies supporting them are fused into a symmetrical plate with the hypural diastema on the posterior end. The second preural vertebra has a short rudimentary neural process (Fig. 3a). There are 2 epurals and a stegural. The subfamily Scomberomorinae consists of two contemporary genera,

* The diagnosis and composition of the subfamilies follow Fraser-Brunner (1950), recognizing 12 contemporary genera of Scombridae (excluding *Gasterochisma*). Some problematic fossil scombrid genera (*Aridodus* White, *Boscombrus* David, *Miothunnus* Denis, *Seombridarum* Koken, etc.) are not included in the composition of subfamilies because they have been described from few remains and their position is unclear.

*Scomberomorus* and *Acanthocybium*, and 8 fossil genera, *Aramiehthys*, *Eocoelopoma*, *Landanichthys*, *Neoeybium*, *Seombramphodon*, *Scombrinus*, *Sphyraenodus*, and *Wetherellus*.

The Thunnidae (subfamily Thunninae) have between 35 and 54 vertebrae in the vertebral column. The vertebrae are subquadrate in projection, approximately half the posterior trunk vertebrae have extended parapophyses. The frontals are strongly dilated, sometimes with openings on the boundary with the parietals and the supraoccipital. The parethmoids are broad. The circumorbital ring of the suborbital bones is incomplete. The teeth are conical, small (except in the genus *Sarda*). The "corset" is developed in all genera, behind it the body is bare or covered in small scales. The first dorsal fin is high, close to the second (except in the genus *Auxis*). The caudal fin is crescent-shaped. The median keel is well developed. The caudal skeleton of tuna, like that of mackerels, has a single hypural plate, but without a hypural diastema. A neural spine of normal size is present on the second preural vertebra (Fig. 3c, d). There is no epural. There is a stegural. The subfamily Thunninae has 10 genera: contemporary genera *Allothunnus, Auxis, Futhynnus, Gymnosarda, Orcynopsis, Sarda, Thunnus*[*]; and 3 fossil genera *Ocystias, Palaeothunnus, Woodwardella*.

I do not agree with Zharov (1967), who divided tuna fishes into 2 families, Thunnidae and Sardidae. The table drawn up by that author shows that all the characters of these families overlap.

As regards the contemporary genus *Gasterochisma*, which has 45 vertebrae in the vertebral column and large scales on the body, its classification as a special subfamily within the family

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[*] Some authors (Gibbs and Collette, 1966) also recognize the existence of the contemporary genera *Katsuwonus* and *Cybiosarda*.

Scombridae by some authors (Fraser-Brunner, 1950; Lindberg, 1971) would appear doubtful. In the first place there is to date no fossil material that would permit clarification of the relationships of *Gasterochisma*. Secondly Gosline's studies (1968) have shown that this genus is as similar to Bramidae as to Scombridae, as a result of which he concludes that if *Gasterochisma* is a scombrid fish, then it deviates strongly. Therefore this genus, of uncertain systematic position, is not included among the Scombridae in this paper.

Opinions about the origins of the family Scombridae vary. The view that the origins of Scombridae may be connected with the percoid family Carangidae is the most widespread (Starks, 1909, 1911; Nikol'skiy, 1954). Gregory (1933) concluded, on the basis of a comparative study of contemporary Scombridae and Carangidae, that Scombridae represent progressive and highly specialized descendants of a Cretaceous member of the family Carangidae. Casier (1966), who studied the extensive material on the ichthyofauna from the lower Eocene of London clays, does not disagree with this. Some authors have even combined the Carangidae and Scombridae in a single category of "percomorph" fishes (Jordan and Evermann 1896; Fowler, 1936).

Regan (1909), on the other hand, considered that Scombridae are not related to Carangidae. This is also the view of Gosline (1968), who considers that the numerous morphological characters common to members of both families are the result of parallel development. To justify this point of view Gosline points out that in Carangidae the supraoccipital crest continues through the frontals to the ethmoid region, the interorbital commissure of the supraorbital canal of the seismosensory system is always complete and opens through the median aperture between the frontals in the middle of the crest, the circumorbital ring is always complete and consists of 5 suborbital bones.

Finally, Carangidae have 24-25 vertebrae in the vertebral column. At the same time, as Gosline (1968) notes, among Scombridae only the genera *Gasterochisma*, *Scomberomorus*, and *Acanthocybium* have a longitudinal median frontal crest, in others it is absent. Furthermore, in Scombridae the interorbital commissure of the supraorbital canal is always incomplete and does not open through an aperture between the frontals. The suborbital bones in Scombridae are variously modified or are completely absent, and there are no fewer than 31 vertebrae in the vertebral column. Gosline bases all his conclusions on contemporary material. As an example of less specialized percoids, close to the probable antecedents of Scombridae, Gosline cites Pomatomidae and Scombropidae, in which the anterior part of the calvaria is smooth, the interorbital commissure of the interorbital seismosensory canal incomplete and there are 26 vertebrae in the vertebral column.

Gosline's arguments seem less convincing than those of Starks (1911), who argued in favor of an affinity between Carangidae and Scombridae. Among the numerous morphological characters of the skull of Carangidae listed by Starks, only a few differ from those of Scombridae; for example the opisthotic does not extend to the dorsal side of the skull between the exoccipital and the pterotic as in the progressive Scombridae, and in Carangidae the premaxillary is often prominent. Other features of the skull of Carangidae mentioned by Starks (1911) are present to a greater or lesser degree in all or some Scombridae. Gregory (1933) noted that the low-bodied, elongated forms of Carangidae are closer to Scombridae than the deep-bodied ones. They have a wider operculum, a lower frontal crest, and the mouth is large with premaxillaries that do not protrude.

The structure of the postcranial skeleton of Scombridae and long-bodied Carangidae is also similar. If one considers the caudal skeleton of such contemporary Carangidae as *Trachurus* and *Decapterus*, its undoubted similarity to the caudal skeleton of the least-specialized Scombridae, members of the subfamily Scombrinae, becomes obvious; it consists of the same elements, differences being noticeable only in details of the structure (Figs. 2b and 3b). This is evidently an example of parallel development in the evolution of closely related groups. At the same time the caudal skeleton of fishes from the family Pomatomidae is very primitive; its elements do not fuse into a single hypural plate. Finally in Carangidae, as in Scombridae, the first spiny rays of the anal fin are separated from the soft part of the fin by a small space. Additional small fins (a basic character of Scombridae) are frequently also found in species of Carangidae.

It thus appears that the family Scombridae is descended from Cretaceous carangid fishes with an elongated body without bony plates along the sides, with a reduced frontal crest and a non-extensible premaxillary. All the features listed above are typical of the carangid genus *Archaeus*, known as early as the Upper Paleocene (Danil'chenko, 1968). It is quite possible that this genus and the oldest Scombridae had common or close ancestral forms. It should, undoubtedly, be borne in mind that unlike the hypothetical ancestor, the real ancestor frequently had characters—difficult to predict—showing inherent specialization (Tatarinov, 1972).

In the process of evolution, Scombridae acquired a large number of vertebrae, they lost the circumorbital ring of the suborbital bones (fully preserved only in fishes of the subfamily Scombrinae) and the median crest on the frontals (preserved in rudimentary form in several genera of the subfamily Scomberomorinae).

Key to subfamilies of the family Scombridae

1 (2). Well developed "corset". There is a bony keel on the caudal peduncle. No epurals or hypural diastema...............................Thunninae

2 (1).There is no distinct "corset" or bony median keel on the caudal peduncle. Epurals and a hypural diastema are present.

3 (4). Suborbital ring complete. Thirty-one vertebrae in vertebral column. Epaxial and hypaxial hypurals divided by a cleft...............Scombrinae

4 (3). Suborbital ring incomplete. More than 32 vertebrae in vertebral column. Hypurals merge into a single plate ...............Scomberomorinae

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