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(Gyorui chigyo no keishutsu to keito, saba-kei gyorui)

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By

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Abstract

Larval characters and phylogenetic relationships were studied at the generic level in scombroid fishes belonging to the families Scombridae and Istiophoridae. Some larval characters (morphology of the head, etc.) seem to significantly reflect the phylogeny of the fish group.

1. Introduction

The families Scombridae, Istiophoridae, Xiphiidae, Gempylidae, and Trichiuridae are included in the scombroid fishes and the phylogenetic relationships among each family is hypothesized following Matsubara (1963).

Scombrid fishes first appeared in the Lower Eocene period. The ancestor forms (fossils) of Istiophoridae and Xiphiidae which appeared in the same period are considered to be a highly specialized group situated at the top of the evolutionary process while scombrid fishes are thought to be a relatively lower group which branched off during the evolutionary process.

On the other hand, families Gempylidae and Trichiuridae are thought to be a specially degenerative group morphologically. These fishes branched off from the trunk of the evolutionary tree where scomberomorine fishes (which belong to the group of scombrid fishes) are located. They migrated from a near-shore habitat to a mid-water habitat where adaptation to a new environment created a tendency of elongation of body and degeneration of caudal fin structure. It is assumed that such degeneration progressed from Gempylidae to the Trichiuridae fishes.

Although the habitat of scombrid fishes and billfishes is principally in the offshore surface layers, it varies from the nearshore region to the pelagic region, or in between these regions. Therefore, scombrid fishes are considered to be a derived and well differentiated group whose habitat ranges from shallow to mid-water.

The larval morphology of these scombroid fishes is shown in Figure 1. Although they show diverse larval forms, the large head, large mouth cleft and eye diamter, presence of spines on the head (preopercular spines, etc.), and posterior migration of the anus (the anus is located in the anterior region of the body in the beginning of post-larval period and it migrates posteriorly in the space to the anal fin which appears at the regular position) are common characteristics (Uchida 1963). The reason for extreme development of pigment spots in larvae of Xiphiidae and Istiophoridae compared to larvae of other scombroid families is due to their adaptation to near surface pelagic waters during both day and night; such pigment is not thought to be related to phylogeny.

Concerning larval morphology and phylogeny, a process of differentiation from some groups of scombroid fishes passing from Gempylidae to Trichiuridae is known to be repeated during the course of ontogenesis (Uchida 1964). That is, Gempylidae and Trichiuridae, adults of which possess an extremely elongate body, have larvae which possess a large head with a well developed preopercular bone and spinated anterior dorsal fin. But, as metamorphosis continues, the spines degenerate, and the body becomes elongate during later stages of ontogeny. The temporarily developed caudal fin in the larvae of *Eupleurogrammus muticus* is known to degenerate almost totally in the adult form. Not many examples of repeated metamorphosis, as described above, have been observed in fish groups other than in scombroid fishes.

Larval characters have yielded no clues as to the relationships between scombrid and istiophorid fishes. As mentioned before, perhaps they took separate pathways of differentiation in the process evolution.

Next, larval characters and phylogeny at the generic level will be discussed for these groups of fishes.

2. Larval characters and phylogeny of scombrid fishes

Fifteen genera are known to belong to the family Scombridae. Their relationships, shown in Figure 2, is based on results of a detailed taxonomic study (Collette and Chao 1975). *Gasterochisma* and Scombrini and Scomberomorini are considered to be more primitive than either Sardini or Thunnini, based on the structure of the caudal vertebrae.

The larval characteristics and phylogeny of 12 of 15 genera were examined (all but *Gasterochisma*, *Orcynopsis* and *Cybriosarda*, for which larval characters are not known).

Larval morphology of several genera is shown in Figure 3. The character of head spination in larvae is compared among the 12 genera (refer to Figure 2), and the result is shown in Table 1.

A common larval character, lack of head spination, is seen clearly in Scombrini (*Scomber* and *Rastelliger*). In Thunnini (*Auxis*, *Euthynnus*, *Katsuwonus* and *Thunnus*), all genera have also common characteristics of spination. Opposed to this, in Scomberomorini, three genera (*Grammatorcynus*, *Scomberomorus*, and *Acanthocybium*) have little common head-spine occurrences and in Sardini, *Sarda* and *Gymnosarda* do not share common characters with *Allothunnus* (Okiyama and Ueyanagi 1977).

Based on the above, studies were continued, because larval characters may reflect well on phylogeny (Okiyama and Ueyanagi, unpublished). Following the method of Ebeling and Weed (1973), 13 larval characters, including the above three, were chosen and were divided into three levels according to degree of development, numbered according to the level (1, 2, 3), and analyzed numerically. These 13 characters are listed below. Based on the assumption that *Scomber* is the most primitive, it was numbered as (1). The 13 characters considered are: 1) supraoccipital crest; 2) size of head; 3) length of intestine; 4) length of snout; 5) premaxillary teeth; 6) upper and lower jaw length; 7) preopercular spine; 8) supraorbital serration; 9) pterotic spine; 10) cartilage of the lower jaw tip; 11) dorsal pigmentation; 12) pigmentation on the abdominal side of the tail; and 13) number of myomeres. A comparison of these characters between the 12 genera are shown in Tables 2 and 3. From the total values shown in Table 2 and indicated relationship presented in Table 3 (where the values are high between the two genera), the 12 genera are grouped as follows:

Scomber, *Rastelliger*	Group A
Grammatorcynus	Group B
Allothunnus, *Auxis*, *Euthynnus*, *Katsuwonus*, *Thunnus*	Group C
Scomberomorus, *Acanthocybium*, *Sarda*, *Gymnosarda*	Group D

Fairly good correspondence is found between the groups of genera based on larval characters and according to relationships based on adult morphology (Figure 2). The problem with those that do not correspond, based on larval characters, include these possibilities: 1) that *Grammatorcynus* is located in a significantly independent position from _Scomberomorus_; 2) that _Allothunnus_ might be closer to _Thunnus_ than to _Sarda_; 3) there is a close relationship of _Scomberomorus_ and _Sarda_.

Concerning the taxonomic position of _Allothunnus_, which lacks a subcutaneous vessel, the presence of which is a characteristic of Thunnini, is the reason why _Allothunnus_ cannot be classified in Thunnini. On the other hand, the prootic pit on the cranium, which is a characteristic of Thunnini, but not of Sardini, is clearly found in _Allothunnus_, (Collette and Chao 1975). It casts some doubt whether or not _Allothunnus_ is close to Sardini. Larval characters discussed may indicate that _Allothunus_ is closer to Thunnini than Sardini, in addition the pattern of red pigment (which will be discussed in the last portion of this report) is similar between _Thunnus_ and _Allothunnus_ (Figure 7).

Concerning the relationships between _Scomberomorini_ and _Sardini_, four genera belonging to these tribes were grouped together, based on larval characters. However, it would be premature to assume a close relationship between them. Group D is the most highly specialized based on larval characters (Table 2), but the similarity among genera within the group is lower than other groups (Table 3). Based on adult taxonomy, the _Sarda_, _Gymnosarda_ group and the _Scomberomorus_, _Acanthocybium_ group are considered to be obviously different tribes (Figure 2), and it is known that _Gymnosarda_ and _Acanthocybium_ are morphologically different from other genera in the tribes (Collette and Chao 1975). Based on the above discussion, the classification of Group D, based on larval characters, cannot be considered appropriate. The reason why it leads to this classification seems to be due to the many specialized larval characters present in the four genera. Also, *Gymnosarda* and *Acanthocybium* are separated and placed in a specialized group distinct from *Sarda* and *Scomberomorus*, respectively. Larvae of *Acanthocybium* lack the supraoccipital crest which characterizes *Scomberomorus* and possesses specialized features such as elongation of viscera or elongation of upper and lower jaws. *Gymnosarda* has fewer myomeres (number of vertebrae) than *Sarda*, and the elongation of the upper and lower jaw, as found in *Acanthocybium*, is extremely specialized (Figure 3). The tendency toward such an enlargement of jaws in these genera is thought to be a specialization in larval morphology which does not always indicate phyletic relationships between the two genera. The reason why these parallel specializations appear is not clear, but the genera *Acanthocybium* and *Gymnosarda* each contain only one species; their distribution reaches to the pelagic region which differs from their close relatives found near-shore, and therefore these specializations are considered common for both genera.

Also it is known that the horizontal stripe of pigment, a larval characteristic in *Sarda*, also appears in *Gymnosarda*. This character is thought to be one indication of a close relationship between the two genera (Okiyama and Ueyanagi 1977).

The relationship of the number of vertebrae (abdominal and caudal) is considered to be a powerful method of studying relationships and phylogeny, and therefore various genera in Scombridae were analyzed for this relationship (Figure 4). Due to the large numbers of species and wide distribution of vertebral numbers in *Sarda* and *Scomberomorus*, their range of vertebral numbers are shown within the dotted lines. From the relationships observed between the number of abdominal vertebrae (AV) and caudal vertebrae (CV) in each genus, two series of relationships are considered. One is a series in which the number of vertebrae increases in the order of AV<CV, AV=CV, and AV>CV. This corresponds to Scombrini, Thunnini and Sardini, respectively (for groups A, B, C, and D). The other series has AV<CV with a wide distribution in number of vertebrae; this group includes Scomberomorini. In this latter group, *Acanthocybium* is very peculiar with a large increase in number of vertebrae and with AV=CV as an exception. Also, concerning the relationships of *Grammatorcynus* and *Scomberomorus*, which were previously discussed based on larval characters, it should be pointed out that the former has far fewer vertebrae which distinguishes it from *Scomberomorus*.

Based on the relationships of the number of vertebrae, discussed above, it is suggested that *Scomberomorus* has become evolutionarily differentiated from other genera in Scombridae. Unique larval characters such as the supraoccipital crest that is present only in this genus among the scombrids supports this hypothesis.

3. Larval characters and phylogeny of istiophorid fishes

The family Istiophoridae contains three genera and 11 species as discussed below.

In *Istiophorus*, there are two species distributed in the Indo-Pacific region and in the Atlantic Ocean. In *Tetrapturus*, there are six species: *T. angustirostrus* and *T. audax* in the Indo-Pacific region, *T. belone* in the Mediterranean Sea, and *T. pfluegeri*, *T. albidus* and *T. georgei* in the Atlantic Ocean.

In the genus *Makaira*, *M. mazara* occurs in the Indo-Pacific region, *M. nigricans* in the Atlantic Ocean and *M. indica* is distributed in the Indo-Pacific region.

Based on the taxonomic study of adult fishes, *Istiophorus*, *Tetrapturus*, and *Makaira* were formerly placed in different subfamilies based on the vertebral formula (former two genera have 12+12, the latter 11+13) - and they are thought to be apart phylogenetically. Their relationship based on larval characters and phylogeny were examined as follows (Ueyanagi 1963).

The elongate upper jaw, a characteristic of istiophorid fishes, is also found in the fossil fish, *Palaeorhynchus*, which is thought to be the ancestral form; hence, the elongate upper jaw may indicate phyletic meaning. When this character is examined during the larval period, clear differences were observed (e.g., longer in *Istiophorus* and *Tetrapturus*, and shorter in *Makaira*) as are shown in Figure 5. The change of snout/body length through ontogenesis, including the larval period, is shown in Figure 6. The values are very high in young stages in both *Istiophorus* and *Tetrapturus*, but on the contrary the value is extremely low in *Makaira*. Attention also should be paid to *T. angustirostris* in which the adult possesses an especially short snout among the species in the genus; the elongation of the snout is most significant in the larval period. In the case of *T. audax*, however, the snout/body length value is not so high among *Tetrapturus*, and it is thought to be rather intermediate between *Makaira* type and *Tetrapturus* type. The pattern of morphological change in snout length through ontogeny in various genera corresponds with the classification based on the taxonomic study of adult fishes and is thought to reflect phylogeny among the genera of istiophorid fishes.

4. Conclusion

As discussed above, some larval characters are thought to reflect the phylogeny of scombrid and istiophorid fishes.

Nevertheless there are other larval characters of these fishes which do not have special phyletic significance but are developed in order to adapt the larvae to conditions in the larval period. These two types of characters must exist overlapping each other. To distinguish each of these kinds of larval characters is not an easy task. Thus it is possible to have dealt with the latter kind of characters and neglected the former characters in the previous discussion.

The character which will be discussed here was not listed in Tables 2 and 3 because of uncertainty of its presence in all 12 genera of Scombridae. But this can be considered to be a former type of character (Ueyanagi 1966). As shown in figure 7, the pattern of red pigment appearing on the lateral side of the larvae is the same in Auxis, Euthynnus and Katsuwonus. The pattern of red pigment spots appear in one row with the position slightly away from the abdominal region in these genera, but in Thunnus red pigment spots appear on the lateral side of the tail in three rows (in some species the pigment does not appear on the dorsal area, and pigment is limited to two rows). From the same pattern found in Auxis, Euthynnus, and Katsuwonus (which are considered to be closely related in Thunnini), it is thought that this character has phyletic significance. Based on this assumption, the same red pigment spot formation which is found in Allothunnus and in Thunnus (Figure 7) may indicate a close relationship between them.

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Table 1. Comparison of head characteristics in scombrid fish larvae.

	Condition of spination		
	preopercular bone	supraorbital serration	pterotic bone
Scombrini			
Scomber	-	-	-
Rastrelliger	-	-	-
Scomberomorini			
Grammatorcynus	+	-	-
Scomberomorus	+	±	±
Acanthocybium	+	-	+
Sardini			
Sarda	+	+	+
Gymnosarda	+	+	+
Allothunnus	+	-	-
Thunnini			
Auxis	+	-	+
Euthynnus	+	-	+
Katsuwonus	+	-	+
Thunnus	+	-	+

Table 2. Comparison of larval characters in 12 genera of Scombridae (Part 1).

Larval character / Genera	Larval characters and levels of development 1	2	3	4	5	6	7	8	9	10	11	12	13	Total
Scomber	1	1	1	1	1	1	1	1	1	1	1	1	1	13
Rastrelliger	1	1	1	1	1	1	1	1	1	1	1	1	1	13
Grammatorcynus	1	3	1	2	1	1	3	1	1	1	1	1	1	18
Scomberomorus	3	3	1	3	2	2	3	2	2	2	1	1	3	28
Acanthocybium	1	3	3	3	2	3	3	1	3	3	3	1	3	32
Sarda	1	3	1	3	2	2	3	3	3	1	3	1	3	29
Gymnosarda	1	3	1	3	3	3	3	3	3	3	3	3	2	34
Allothunnus	1	3	1	2	2	1	3	1	1	1	3	3	2	24
Auxis	1	3	1	2	2	1	3	1	3	1	3	1	2	24
Euthynnus	1	3	1	2	2	1	3	1	3	1	3	1	2	24
Katsuwonus	1	3	1	2	2	1	3	1	3	1	3	1	2	24
Thunnus	1	3	1	2	2	1	3	1	3	1	3	2	2	25

Numbers in the table (1, 2, 3, etc.) indicate levels of development in 13 larval characters (Okiyama and Ueyanagi, In press).

Table 3. Comparison of larval characters in 12 genera of Scombridae (Part II).

Genera	S	R	G	Sc	A	Sa	Gy	Ao	Au	E	K	T
Scomber (S)	13	-	-	-	-	-	-	-	-	-	-	-
Rastrelliger (R)	13	13	-	-	-	-	-	-	-	-	-	-
Grammatorcynus (G)	10	10	13	-	-	-	-	-	-	-	-	-
Scomberomorus (Sc)	3	3	5	13	-	-	-	-	-	-	-	-
Acanthocybium (A)	3	3	5	6	13	-	-	-	-	-	-	-
Sarda (Sa)	4	4	6	8	9	13	-	-	-	-	-	-
Gymnosarda (Gy)	2	2	4	4	8	8	13	-	-	-	-	-
Allothunus (Ao)	6	6	9	4	6	7	7	13	-	-	-	-
Auxis (Au)	6	6	9	5	8	9	7	11	13	-	-	-
Euthynnus (E)	6	6	9	5	8	9	7	11	13	13	-	-
Katsuwonus (K)	6	6	9	5	8	9	7	11	13	13	13	-
Thunnus (T)	5	5	8	4	7	8	7	11	12	12	12	13

Numbers in the table, based on Table 2, indicate numbers of same level of development of larval characters between genera (Okiyama and Ueyanagi, In press).

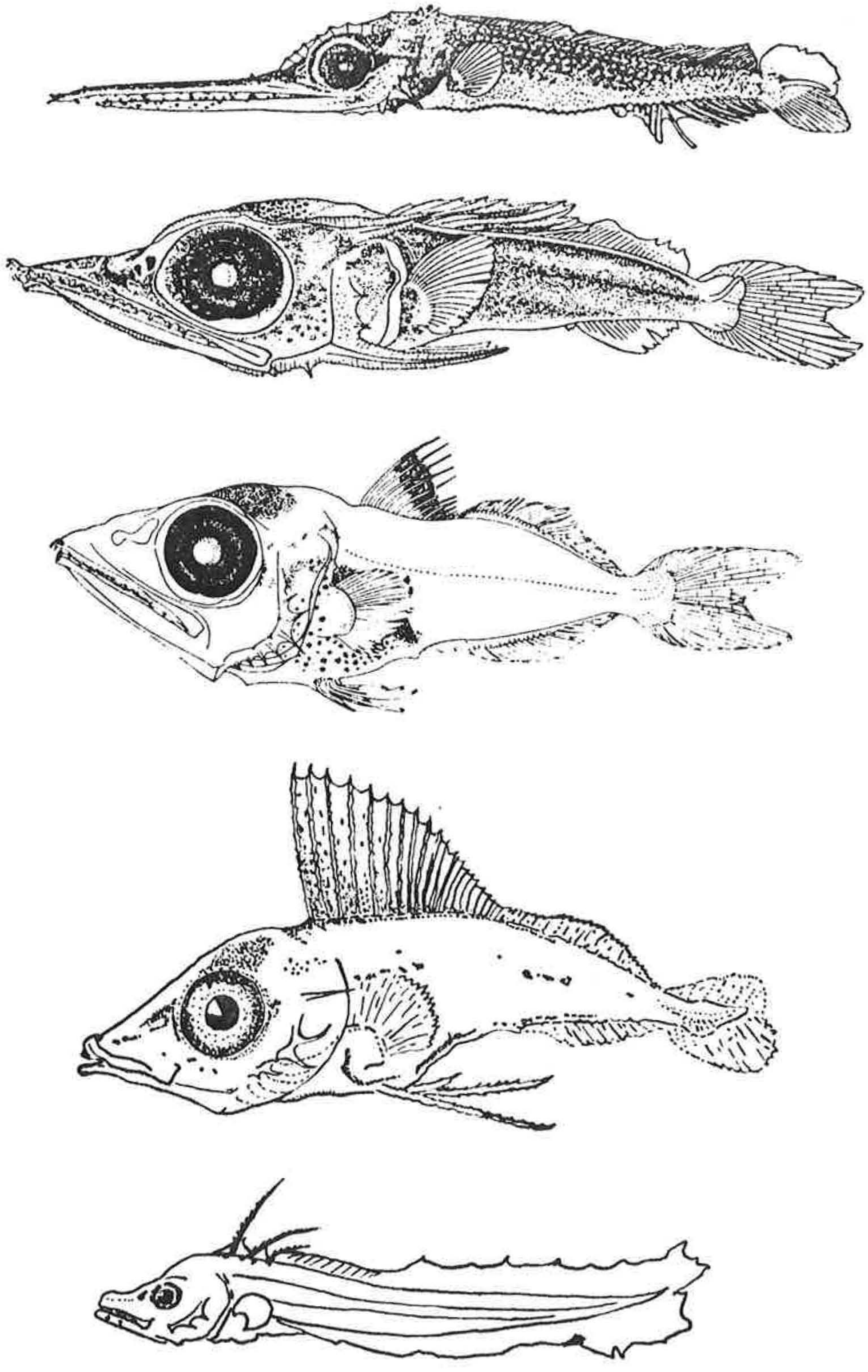

Fig. 1. Scombroid fish larval morphology. From top, *Xiphias gladius*, 11 mm (Yabe et al. 1959)[1/]; *Tetrapturus audax*, 11.6 mm (Ueyanagi 1959)[1/]; *Thunnus alalunga*, 10.1 mm (Ueyanagi 1969)[1/]; *Gempylus serpens*, 6.9 mm (adapted from Voss 1954)[1/]; *Trichiurus lepturus*, 7.4 mm (adapted from Uchida 1966)[1/].

1/ [Ed note: Not listed in literature cited of original article.]

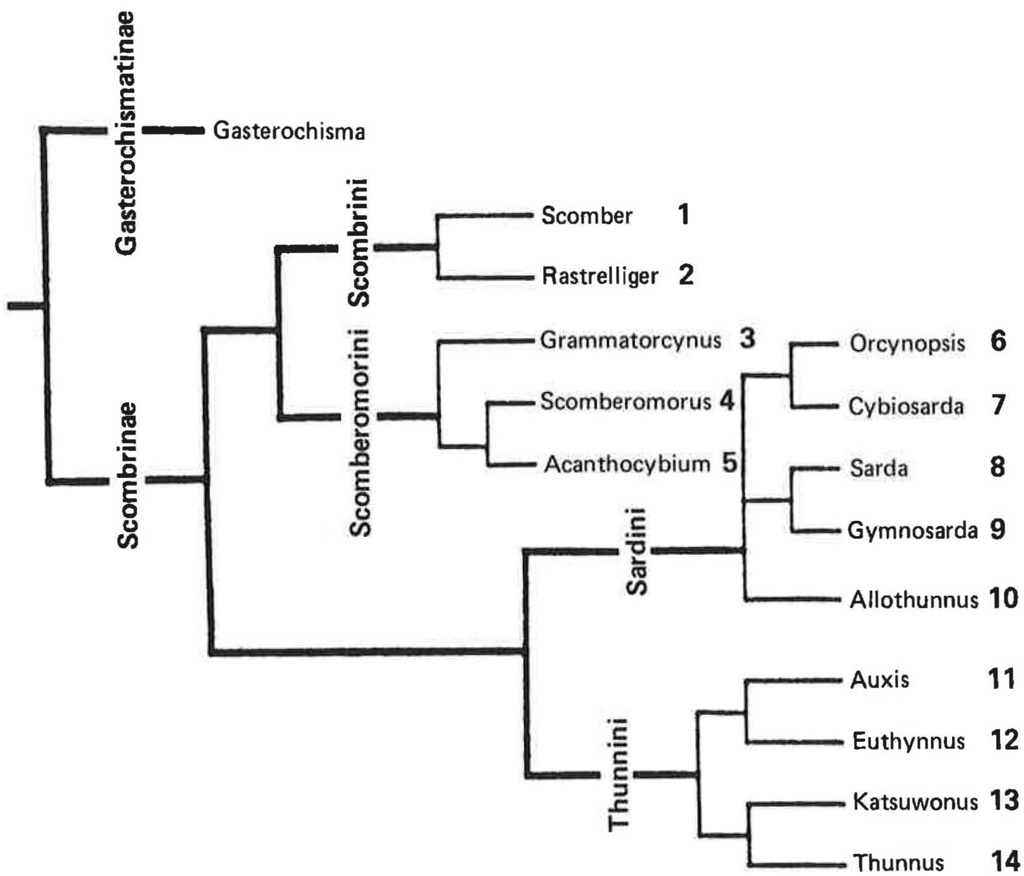

Fig. 2. Relationship among scombrid fish (Scombridae) - subfamilies, tribes, genera. (Collette and Chao 1975).

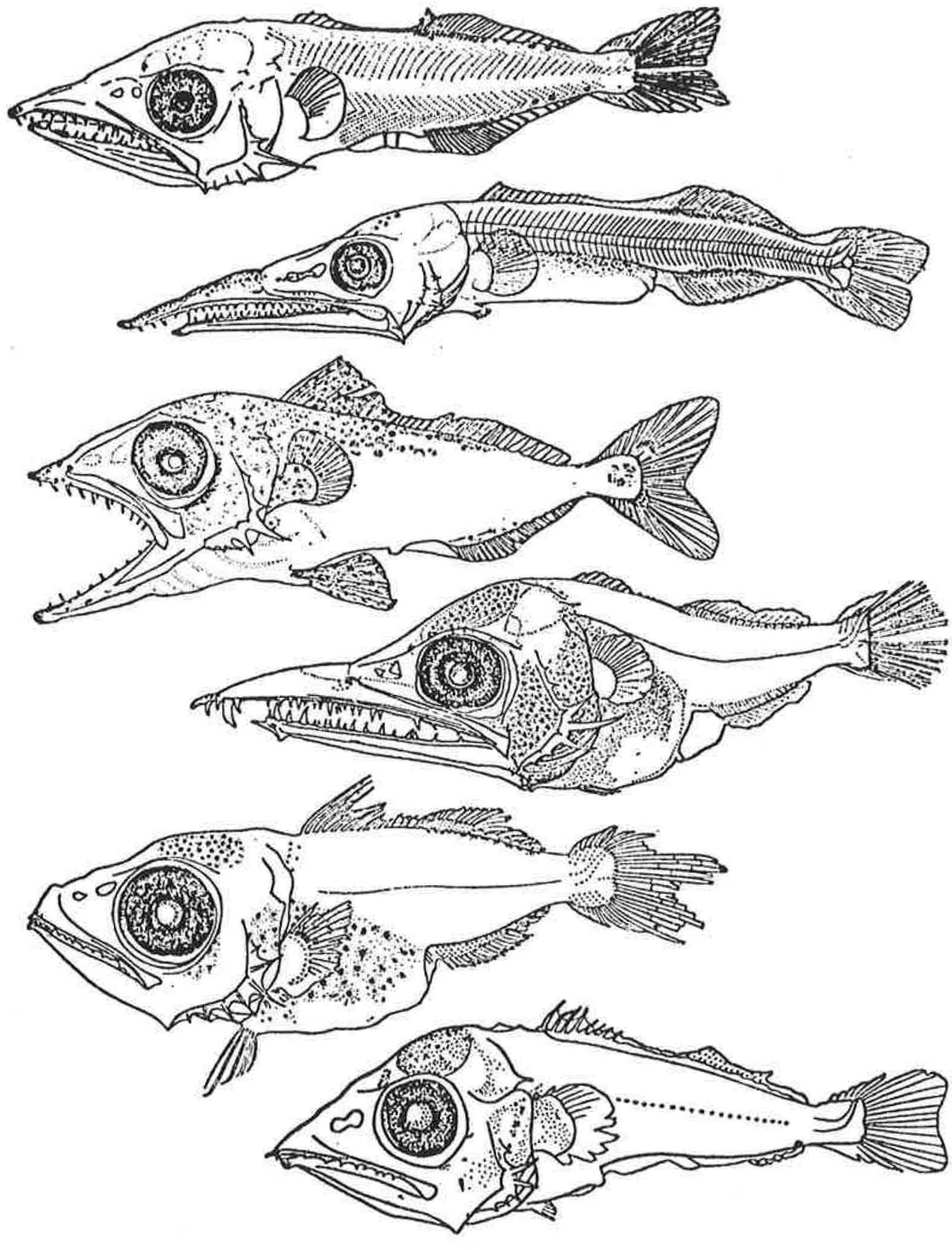

Fig. 3. Scombrid fish larval morphology (six species). From top *Scomberomorus cavalla* 10 mm (Wollam 1970)1/; *Acanthocybium solandri*, 10.7 mm (Matsumoto 1967)1/; *Sarda orientalis*. 16.7 mm (Pinkas 1961)1/; *Gymnosarda unicolor*, 9.06 mm (Okiyama and Ueyanagi 1977); *Allothunnus fallai*, 8.7 mm (Watanabe et al. 1966)1/; *Katsuwonus pelamis*, 7.8 mm (Nankai Reg. Fish. Res. Lab., 1964)1/.

1/ [Ed note: Not listed in literature cited of original article.]

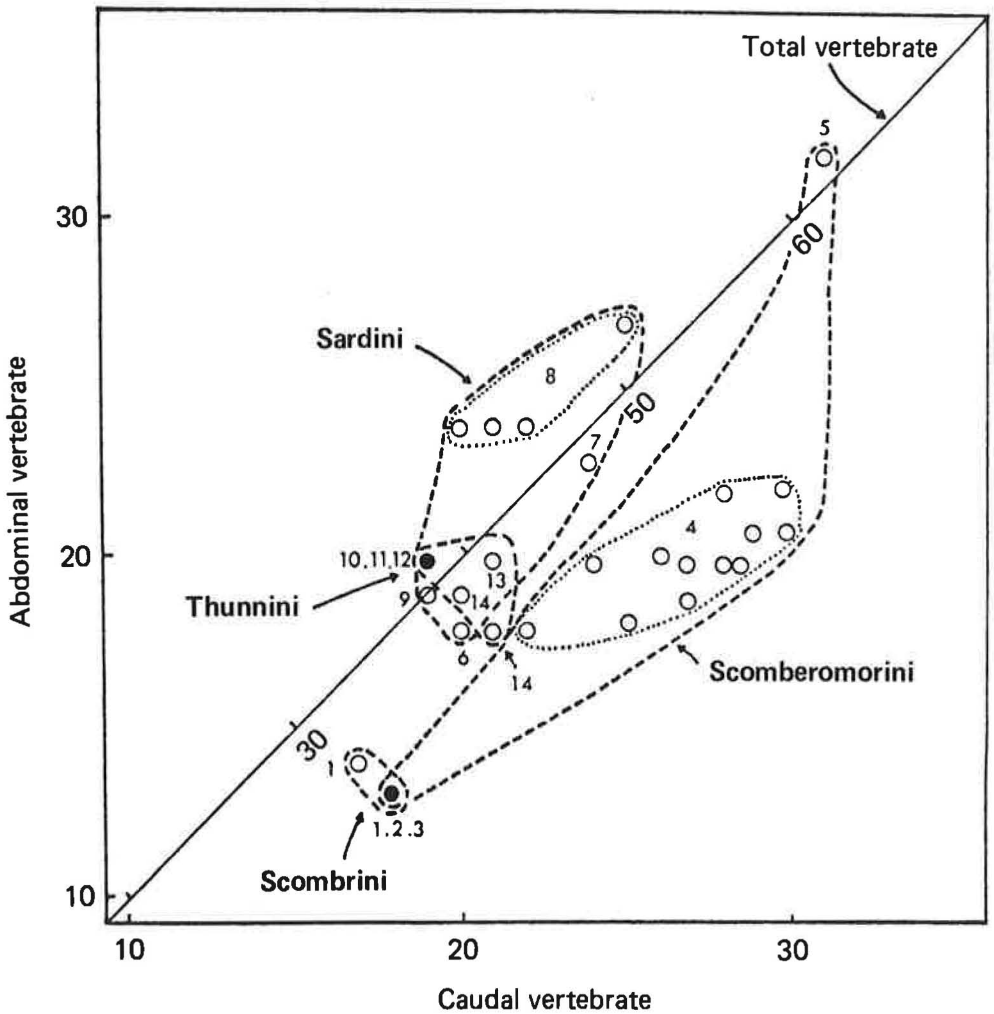

Fig. 4. Relationship of vertebrae numbers - abdominal vertebrae and caudal vertebrae - in Scombrid fish. Numbers attached to white circle are numbers of each genus (Refer to Table 2). Black circles show numbers of pleural genera which possess same numbers of vertebrae.

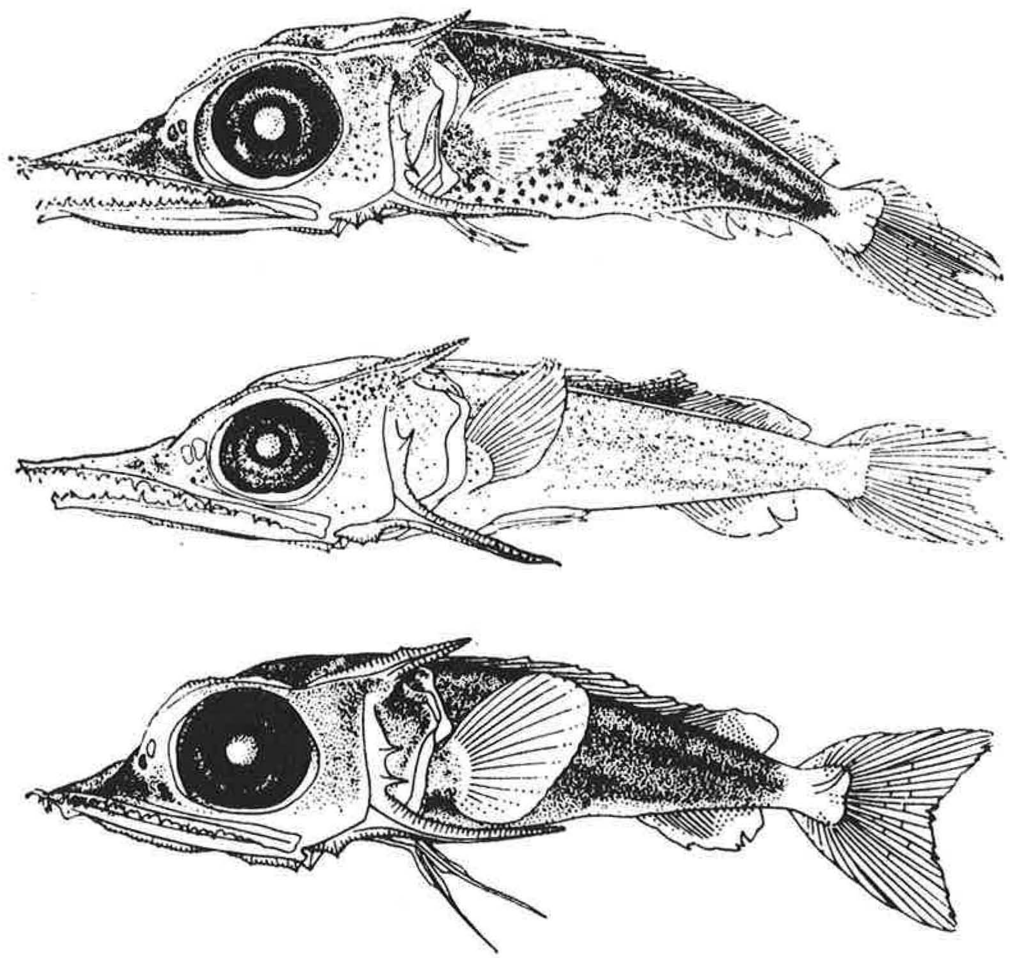

Fig. 5. Istiophorid larval morphology. From top Tetrapturus angustirostris (total length 15 mm), Istiophorus orientalis (15.4 mm), Makaira mazara (14.4 mm).

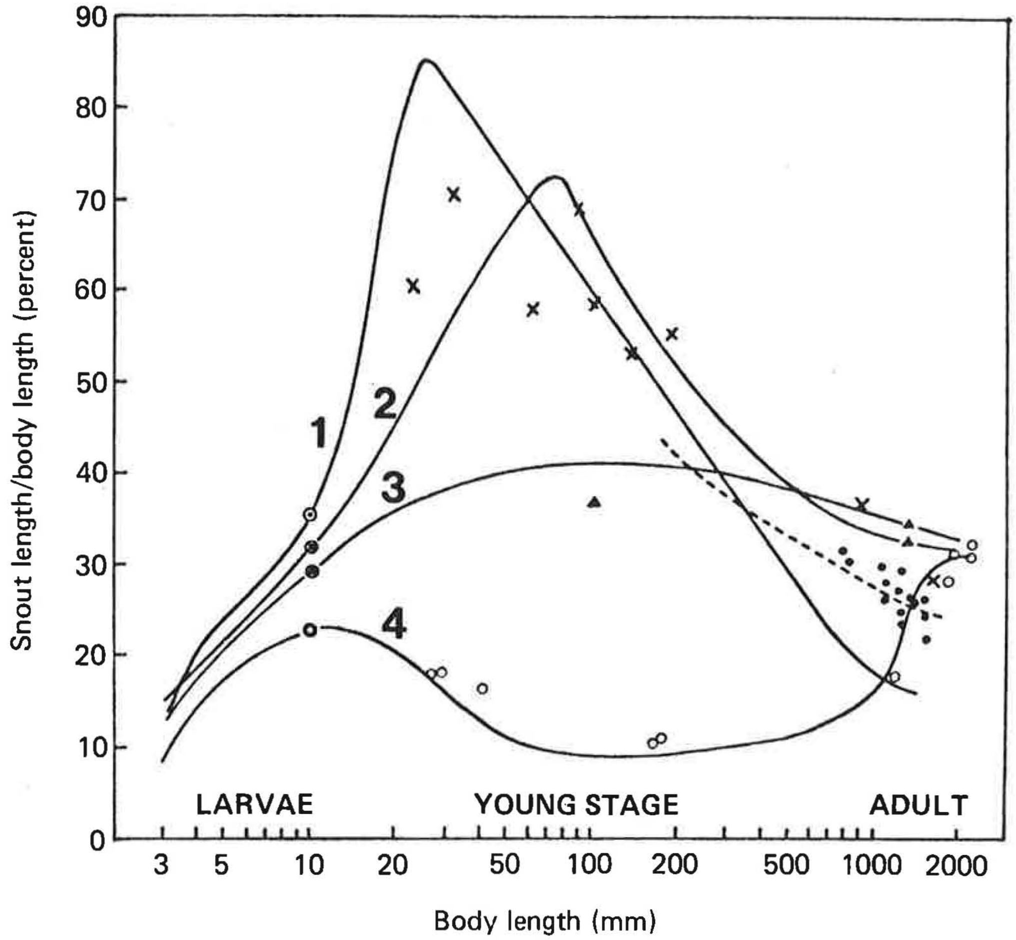

Fig. 6. Relationship of snout length to body length during growth. (Ueyanagi 1973). 1, 2, 3, 4 indicate T. angustirostris, I. orientalis, T. audax, M. mazara (Indo. Pacific). X's: Istiophorus in Atlantic, black circles: T. pfluegeri, black triangles: T. albidus, white circles: M. nigricans. Body length is the distance from the posterior margin of the orbit to the tip of center rays of the tail.

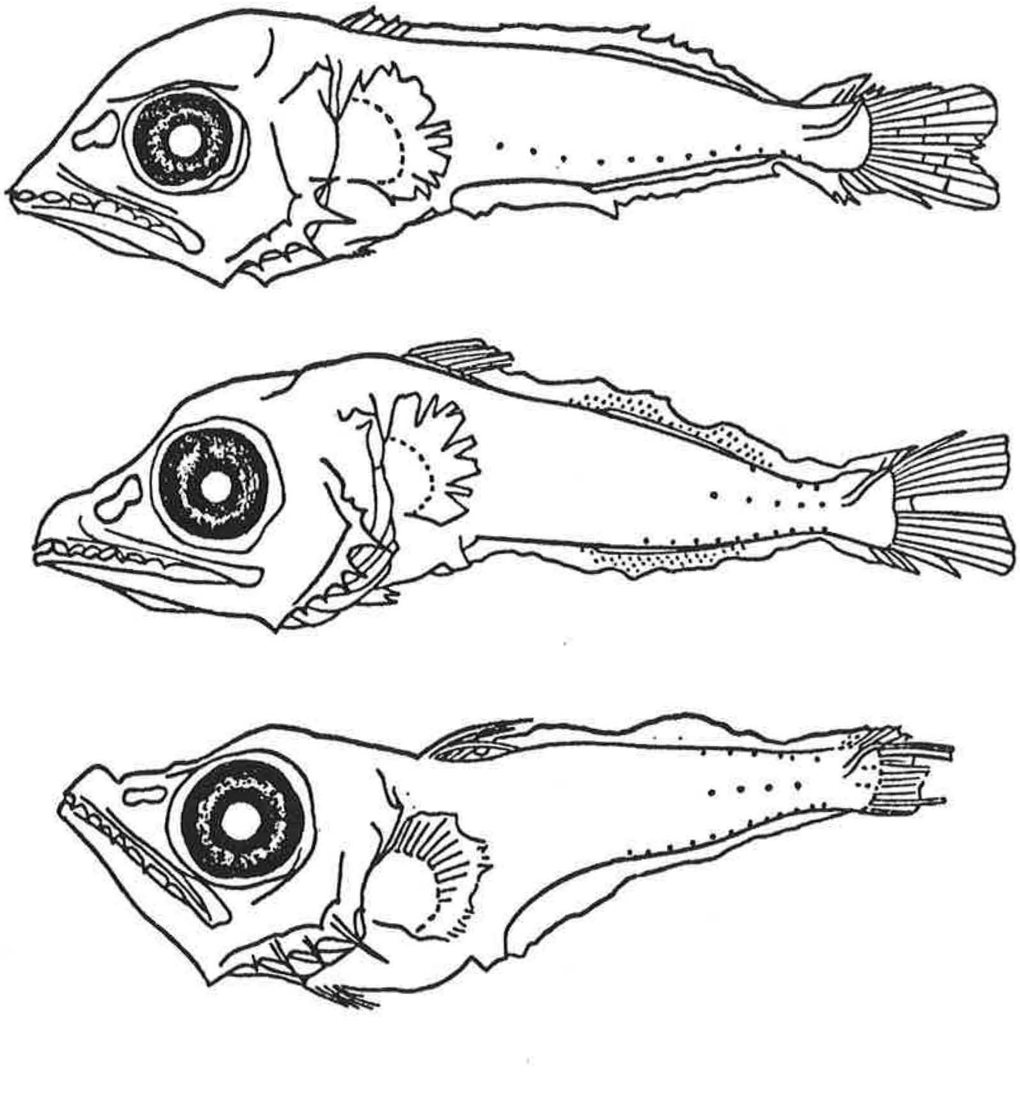

Fig. 7. Comparison of red pigment pattern formation in larval stage. From top Auxis, Thunnus, Allothunnus (Ueyanagi 1966).