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Phylogeny and Larval Morphology of Pleuronectiform Fishes

(Psettodidae, Citharidae, Paralichthyidae and Bothidae)

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PHYLOGENY AND LARVAL MORPHOLOGY OF PLEURONECTIFORM FISHES (PSETTODIDAE, CITHARIDAE, PARALICHTHYIDAE AND BOTHIDAE)

BY

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by
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Abstract

The relationship between larval morphology and phylogeny in left eyed flounders was studied based on two points, ontogeny and phylogeny, and larval characters and classification. Facts observed in ontogeny seem to suggest phylogeny on some characters such as the urohyal bone, pelvic bone, caudal skeleton and on the caudal rays. On the other hand, remarkable correlations were found at the subfamily and family level between larval characters, such as condition of body, metamorphic size, origin of dorsal fin, presence of elongate dorsal fin rays, the posterior process of the pelvic bone, and presence of spines on the head, and classification; therefore, these larval characters were considered to have phylogenetic significance.

1. Introduction

Phylogeny is based on the theory of evolution and any taxonomic classification scheme originates from phylogenetic studies. But it is impossible to prove phylogeny experimentally. Therefore, phylogeny must be established using all the information available from such allied areas as paleontology, comparative morphology, comparative genetics, etc. The resultant classification scheme will be more reliable when data from such allied studies do not contradict each other.

Understanding of the phylogeny of fishes has been based on comparative morphology and paleontology, etc. Recently, a large number of researchers have studied the relationships between phylogeny and larval characters in the early developmental stages, in addition to the karyotypes or biochemical methods of analysis. When one tries to presume a phyletic relationship in a group of fishes, the phyletic significance of different characters, which have been obtained mainly from fossils and studies of comparative morphology, are evaluated. Those characters in which direction of evolution can be determined are utilized as phyletic characters and results from each of these characters are combined in order to hypothesize phyletic relationships. Researchers engaged in this type of study are greatly interested in how these phyletic characters change during early development and how these characters correspond to early developmental stages, and they are trying to obtain clues from them to study phylogeny.

This paper discusses how evolutionary trends of phyletic characters, obtained from comparative anatomy of various families of left eyed flounders, correspond to the early developmental stages of a specimen. It also attempts to elucidate the relationship between larval characters and phylogeny, although insufficient phyletic analyses have been conducted.

2. Classification

Before discussing the relationship between larval characters and phylogeny, it is necessary to review the history of classification of left eyed flounders based on characters obtained from comparative anatomy. Left eyed flounders are characterized by having both eyes on the left side of the body, and are generally represented by Paralichthyidae and Bothidae. In this paper Psettodidae and Citharidae are also included in this group of fishes.

Hubbs (1945) divided the group into four families, Psettodidae, Citharidae, Scophthalmidae and Bothidae according to their external morphology. Amaoka (1969) compared the skeletal anatomy of these families, except Scophthalmidae, utilizing some 50 characters. These characters included differences in location of various bones of the anterior and posterior cranium, condition of the branchial arch, the caudal skeleton and centra, development of the pelvic bone and urohyal, symmetry of the pelvic fins, number of the caudal fin rays and infraorbital bones, presence or absence of the first neural spine, and intermuscular bones, etc. Amaoka (1969) also postulated the significance of these structures among families, subfamilies and genera. The analysis of these characters according to trends in teleostean evolution revealed that the group may be classified into four families, i.e. Psettodidae, Citharidae, Paralichthyidae and Bothidae. Two subfamilies, Taeniopsettinae and Bothinae, are established under Bothidae (Fig. 1). This classification is shown below:

- Pleuronectiformes
  - Psettodidae
    - *Psettodes*
- Pleuronectoidei
  - Citharidae
    - Citharinae
      - *Citharoides*
    - Brachypleurinae
      - *Lepidoblepharon*, *Brachypleura*
  - Paralichthyidae
    - *Paralichthys*, *Pseudorhombus*, *Tarphops*, *Syacium*, *Cyclopsetta*, *Ancylopsetta*, etc., about 16 genera.
  - Bothidae
    - Taeniopsettinae
      - *Taeniopsetta*, *Engyophrys*, *Trichopsetta*
    - Bothinae
      - *Engyprosopon*, *Crossorhombus*, *Psettina*, *Laeops*, *Chascanopsetta*, etc., about 17 genera.

Among the above four families, Psettodidae is the most primitive in every character, followed by Citharidae and Paralichthyidae. Bothidae was found to be the most specialized.

3. Phylogeny and Ontogeny

There are still many unknown points on how phyletic characters, as described above, correspond to the early developmental stages since not enough data are available yet. Even so, there are data which suggest phyletic development in the urohyal, pelvic bone, pelvic fin, caudal skeleton, myorhabdoi, and the first neural spine of certain species of Paralichthyidae and Bothidae.

(1) Urohyal and Pelvic Bone

The urohyal is located at the isthmus of a fish and it is rectangular in shape in Psettodidae, but is somewhat expanded posteriorly or curved downward like a fish hook at the posterior end in the Citharidae. The lower portion of the urohyal extends forward in Paralichthyidae whereas in Bothidae it is much longer than the upper portion and it extends even further forward (Fig. 2).

The process of change in shape of the urohyal into a hook-shape or, forward movement of the lower, bent portion, is observed in the ontogeny of Engyophrys senta (Taeniopsettinae) as described by Hensley (1977) e.g., Fig. 3. The bone is fan-shaped in a larva 5.4 mm long, and an indication of change into a hook-shape is observed when the fish becomes 16.5 mm long. The bottom portion of the bone extends anteriorly in a 38.7 mm larva. This change correlates well with phylogenic development.

In Psettodidae, the pelvic bone, which supports the pelvic fin, is situated somewhat horizontally and posteriorly of the cleithrum; only the anterior portion of the pelvic bone touches the cleithrum. In Citharidae the pelvic bone is almost vertical and the anterior portion is located underneath the cleithrum. In this family, as well as in Psettodidae, the pelvic fins are symmetrical. In Paralichthyidae, a cartilagenous process develops at the ventral-anterior edge of the left pelvic bone. This process extends somewhat anteriorly and the left pelvic fin rays are more anterior relative to the cleithrum than in Psettodidae and Citharidae. In Bothidae, the pelvic rays are even further ahead of the cleithrum and in Taeniopsettinae the first ray only is forward of the cleithrum. In Bothidae the cartilagenous portion of the pelvic bone is longer, extends forward of the cleithrum, and articulates with the lower portion of the urohyal. A gap at the fourth ray is found in both the left and right pelvic fins, which are extremely asymmetrical (Fig. 2).

Ontogenetic changes including forward displacement and bilateral asymmetry of pelvic bones is observed in development of the urohyal of Engyophrys senta (Hensley 1977) as shown in Figure 3. In a larva 5.4 mm long, the pelvic bone lies somewhat horizontally and touches only the posterior portion of the cleithrum. This condition is quite similar to that in Psettodidae. In a 16.5 mm larva, the pelvic bones become asymmetrical and are oriented more vertically with their anterior portion located directly below the cleithrum. This is similar to the condition in Paralichthyidae. In a 38.7 mm larva, the pelvic bones become extremely asymmetrical and the first ray on the left pelvic bone is in front of the first ray on the right pelvic bone. The tip of the pelvic bone extends over the lower edge of the cleithrum. This condition is found in the adult form of Taeniopsettidae. The forward displacement of the urohyal, pelvic bone, and pelvic fin rays is thought to have developed in a close relation with symmetrization of the dorsal fin with them (Amaoka 1972). Left eyed flounders are characterized by the unique way they swim and their fins (anal and pelvic fins), which are symmetrical to the dorsal fin, seem to function most effectively in swimming. Thus, along with the forward displacement of the dorsal fin, the pelvic fins and skeletal structure supporting the pelvic fins, are considered to have caused the forward movement of these bones.

Developmental changes found in the urohyal, pelvic bones, and pelvic fins in Engyophrys senta (Bothidae: Taeniopsettinae) indicate phylogenetic relationships among families and subfamilies.

(2) Caudal Skeleton

Recently the caudal skeleton has been recognized as an important character in phyletic classification. Psettodidae has five hypurals, one epural, one urodermal and a stegural; the first preural centrum and ural centra 1 and 2 do not fuse to the hypural nor does the second preural centrum fuse to the neural spine or the haemal spine (Fig. 4). Although in Citharidae the second preural centrum fuses with the neural spine, and the stegural is extremely degenerated, this family basically is at the same level as Psettodidae. Paralichthys, in family Paralichthyidae, possesses one epural and a stegural, but hypurals 1 and 2 are fused, hypural 3 is fused with hypural 4, and hypural 5 fuses with the urodermal. Also, preural centrum 1, and ural centra 1 and 2, are fused with hypurals 3 and 4, and the second preural centrum, with the neural spine and the haemal spine thereof, are fused together indicating a more advanced stage. Among the Paralichthyidae the stegural disappears in Pseudorhombus, and the epural is fused completely with the fifth hypural and the urodermal. All species belonging to Bothidae are exactly at the same level as Pseudorhombus (Fig. 4).

In the caudal skeleton of teleosts, various bones comprising the skeleton show a tendency to disappear and fuse in the course of evolution (Gosline 1961). Thus, the evolutionary process in left eyed flounders is conceived from primitive to advanced as: Psettodidae → Citharidae → Paralichthyidae (Paralichthys) → Paralichthyidae (Pseudorhombus) → Bothidae. In addition, left eyed flounders are characterized specifically by redivision and vertical symmetrization of the parhypural and hypurals (Paralichthys, Pseudorhombus, Engyprosopon, etc.). The former (redivision of hypurals) is considered to be a specific character observed in this fish group and assumed to be secondary evolution. On the other hand, the latter (vertical symmetrization) is presumed to develop as a result of its unique swimming method (Amaoka 1969).

Concerning ontogenetic changes in the caudal skeleton, there are detailed reports on Trichopsetta ventralis and Engyophrys senta, in family Taeniopsettinae (Futch 1977; Hensley 1977). Their research indicated fusion of preural centrum 1 and the ural centra with hypurals 3 and 4, and fusion of the epural with hypural 5; additionally preural centrum 2 fuses with the associated neural and haemal spines. The vertical symmetrization of the caudal skeleton was recognized clearly and it was considered to suggest the phyletic flow discussed above (Fig. 5). However, in these two species, hypurals 1 and 2 as well as 3 and 4 are already fused to each other at the earliest developmental stage, and the urodermal and the stegural were not present. This remains as a problem for future researchers, as it may indicate a limitation in the relation between ontogeny and phylogeny.

Next, let us refer to a work of Okiyama (1974) on the redivision of the hypurals. He observed the early developmental stages of the caudal skeleton in Paralichthys olivaceus, Pseudorhombus pentophthalmus, and Tarphops oligolepis and discovered that the hypurals and the parhypural appear in a form of a board in the larval stage and later become finely divided (Fig. 6). Okiyama believed that these findings support the phylogenetic theory suggested by Amaoka that this character was a secondarily derived occurrence (Amaoka 1969).

(3) The Number of Caudal Fin Rays

In Psettodidae there are five unbranched fin rays dorsally, 15 branched fin rays in the middle, and four unbranched fin rays ventrally, making a total of 24 rays (5+15+4=24). In Citharidae, the count is 4+15+4=23 or 4+13+4=21, in Paralichthyidae 3+13+2=18 or 2+13+2=17, and in Bothidae it is from 2+13+2=17 to 4+9+4=17. It is generally known that caudal fin rays decrease in number during the course of evolution. Likewise, in these families, a tendency toward a decrease in number of both branched and unbranched fin rays was observed from highest to lowest in number in the order of: Psettodidae → Citharidae → Paralichthyidae → Bothidae (Fig. 7).

Okiyama (1974) reported that during the early developmental stages of P. olivaceus, one small spur of a caudal fin ray appears at the lower end of the caudal fin, in addition to 18 fin rays; this small spur gradually becomes fused with the adjacent fin ray during the juvenile stage. This evidence is considered to indicate a tendency toward a decrease in the number of caudal fin rays during the course of evolution in these families.

(4) Intermuscular Bones

These small needle like bones are located along the myomeres of the lateral muscle of the body; they consist of four parts: upper myorhabdoi, epimeral, hypomeral and lower myorhabdoi (Fig. 8). These bones are present in all species belonging to the family Bothidae, but are not found in the other three families. They are found in certain orders of teleosts considered to be primitive such as Clupeiformes and Anguilliformes. Although left eyed flounders are considered a specialized group among teleosts, the presence of these bones in Bothidae may sugggest that the derivation of left eyed flounders dates from a much earlier period.

Ontogenetically, however, these bones are not present in the larval stage, but appear in the juvenile stage (Hensley 1977). This fact therefore suggests that the character is not a primitive, but a derived condition. It also leads to the conclusion that these bones are not analagous to the intermuscular bones observed in the lower Teleostei. Therefore, all phyletic characters in Bothidae, are considered to be derived and the ontogenetic finding of this character indicates that bothids are the most specialized group in the left eyed flounders. There is only one example of ontogenetic observation on these bones, so it will be necessary to increase the number of actual observations in order to confirm the accuracy of this hypothesis.

(5) First Neural Spine

The first vertebra in Bothidae possesses a neural arch but lacks a neural spine, while in other families both a neural arch and nerual spine are clearly found (Fig. 9). This lack of a neural spine also suggests that the Bothidae is extremely specialized compared to other families.

Hensley (1977) reported that this first neural spine does not exist from the beginning of development in larvae of E. senta (Bothidae). On the other hand, this spine was recognized in the ontogenesis of Paralichthys, family Paralichthyidae (Okiyama 1974). Regarding this character, no definite change was observed which might suggest any links between ontogeny and phylogeny.

4. Larval Characters and Classification

In larval fish, transitory characters such as spines on the head, elongated fin rays, projecting eyes or intestines often appear which are not found in adults. Such temporary larval characters are also found in larvae of left eyed flounders. Examples are the elongate dorsal fin rays and pelvic bone, and the presence of spines on the head, shoulder girdle, pelvic girdle and opercle. In addition to these characters, others related to metamorphosis (e.g., migration of eye) which are specific to these fishes make larval features much more complicated. In the present study, I examined how these characters correspond to the phyletic classification of adult forms, assuming all these characters to be larval characters. Larval characters are known for few species of left eyed flounders so inadequate data are available. Discussion here is concentrated on two families which include relatively large numbers of known larval forms, i.e. Paralichthyidae and Bothidae.

(1) Body Condition

There is a detailed report on larvae of three genera and three species in Paralichthyidae, _Paralichthys olivaceus_, _Pseudorhombus pentophthalmus_, and _Tarphops oligolepis_, from Japan (Okiyama 1974). These larvae generally possess a more or less thick body which is opaque. This trait was also pointed out by Futch (1977) and it seems to be found also in other species of this family (genera _Syacium_, _Ancylopsetta_, _Cyclopsetta_, etc.). On the other hand, larvae of about 20 species of Bothidae are known (e.g., _Arnoglossus tenuis_, _Psettina iijimae_, _Laeops kitaharae_, _Chascanopsetta lugubris_). The body in these species is extremely thin and transparent, so much so that the vertebrae and internal organs may be clearly observed in live specimens.

(2) Body Length at Metamorphosis

Left eyed flounders, unlike other types of fish, undergo a unique migration of the eye during metamorphosis (the right eye migrates to the left side of the body and becomes situated above the left eye). Body lengths of larvae during eye migration varies greatly among species (Table 1). The body length during eye migration is about 14.4 mm in _Hippoglossina oblonga_ which is a larger size than most other species in Paralichthyidae. The only exception was found in genus _Monolene_. This native American species is now classified under Paralichthyidae because of insufficient study on the details of adult skeletal structure. However, the placement of _Monolene_ in Paralichthyidae is questionable based on larval characters discussed below. Also, from recent analysis of certain characters of the skeleton, it is assumed that this genus can be classified under Bothidae instead of Paralichthyidae (Futch 1977; Hensley 1977; pers. comm. E. H. Ahlstrom). As for Bothidae, on the other hand, an extremely wide variety of body lengths during eye migration is found among different species. Sizes range from 15.0 mm in _Crossorhombus kobensis_ (this particular specimen was at a very early stage and the metamorphic body length is presumed to be fairly large) to 120 mm or greater in _Chascanopsetta lugubris_. However, larvae of Paralichthyidae in which eye migration occurs at 14.4 mm or less, can be clearly distinguished from those of Bothidae because such eye migration occurs at lengths greater than 15.0 mm.

Differences in body length at metamorphosis in these families may be related to the length of the planktonic period. It is known that larvae of left eyed flounders have a planktonic life until the period of eye migration and that they shift to a benthic life during or after the migration of eye is completed. Moreover, whereas larvae of Paralichthyidae are more often collected along the coast, larvae of Bothidae are caught by plankton nets in offshore areas and even oceanic areas. It is therefore concluded that bothids have a relatively longer planktonic period than the paralichthyids. The fact that the larval size at metamorphosis becomes larger in more presumably advanced bothids may be signifcant similar to the elongate dorsal fin, as discussed later, in terms of adaptation to the planktonic life. Similar features appear in leptocephalous larvae of anguillids and elopids and, together with adaptation to planktonic life, are considered phylogenetically significant (Greenwood et al. 1966). This same argument can be applied to left eyed flounders.

(3) Origin of the Dorsal Fin

The position where the dorsal fin originates varies in adult left eyed flounders and variation in position of origin is much more significant in larvae. In paralichthyid larvae such as Paralichthys and Pseudorhombus, the dorsal fin originates at the posterior of the eye (Fig. 10, A, B, D) whereas it originates above the eye in Syacium and Anclyopsetta (Fig. 10, C, E). In Bothidae the dorsal fin originates at the anterior of the eye (Fig. 10 G, Fig. 11). The origin of the dorsal fin is quite interesting, particularly in its relation to different phases of eye migration. In paralichtyid larvae, the right eye migrates anterior to the dorsal fin and the dorsal fin grows forward thereafter. In Bothidae, as was observed in Laeops kitaharae, Arnoglossus japonicus, and Taeniopsetta ocellata, the right eye migrates through "the slit," at the original point of the dorsal fin, which extends anterior to the eye as shown in Figure 10 H (Amaoka 1970, 1972, 1973). This character can be used to distinguish Paralichthyidae from Bothidae.

(4) Elongate Dorsal Fin Rays

The elongate anterior dorsal fin rays in larvae of left eyed flounders have long been known. It was observed in left eyed flounders that these fin rays are differentiated earlier than other rays and they continue to become elongate but eventually disappear during the late metamorphic stage (Okiyama 1967). Generally, elongate fin rays are thicker than the other rays and have membranes at the distal region. Sometimes the anterior ray is extremely long, as in A. japonicus, which is characterized by seven membrane projections. On the other hand, the second ray is only slightly longer than the other rays in Taeniopsetta ocellata (Fig. 10, 11). The numbers of elongate fin rays also vary widely in different genera. In this section, the relevance of the numbers of elongate dorsal fin rays to classification is discussed (Table 1).

The number of elongate dorsal fin rays observed in larvae of Paralichthyidae varies from zero to nine. Generally there are more than three elongate dorsal fin rays except in Monolene and Etropus. It is disputable whether Monolene is correctly classified in this family as discussed above in the section on body length. Further research may be necessary to determine the taxonomical position of Etropus. On the other hand, only the second ray is elongate in larvae of Bothidae. These differences in the number of elongate dorsal fin rays at the anterior of the dorsal fin, enable bothid families to be classified into two groups. Elongate dorsal fin rays in larvae have generally been considered as an apparatus which is adapted to the planktonic period in various fish groups which are phyletically distinct (Uchida 1937). But Okiyama (1967) suggested the phyletic significance of this apparatus based on the consistency of its appearance in Pleuronectiformes.

The elongate dorsal fin rays may well be considered as a character which is indicative of phyletic relationships because of the difference in the number of such rays between Paralichthyidae and Bothidae and particularly for their consistency in number and position in Bothidae.

(5) Posterior Process of the Pelvic Bone

The lower part of the pelvic bone is bifurcated antero-posteriorly with the anterior portion supporting the rays. The posterior process in the adult has a short projection, but it is elongate in larvae. In larvae of Paralichthyidae, the posterior process is relatively short, ending far anterior to the anus. The posterior process is long in Bothidae, extending posteriorly along the intestine and liver. These organs protrude outwardly and reach the anus in _L. kitaharae_ and _C. lugubris_ (Fig. 11, D, G). This posterior process is present until shortly before metamorphosis but degenerates during late metamorphosis and remains only as a short projection.

The length of the posterior process is closely related to the condition of viscera, such as the outward protruding liver and intestine, and this projection seems to function as protection for the viscera. Since these characters clearly differ in bothids and paralichthyids, they may be closely related to phylogeny.

(6) Spines

It is known that unique spines appear temporarily on the cranium or preopercle during the larval stage in a relatively large number of species of fishes. In left eyed flounders, these spines also appear on the preopercle, cranium, urohyal, cleithrum and posterior process of the pelvic bone (Fig. 12); their appearance varies among subfamilies and families (Table 1).

Spines on the preopercular bone appear in every paralichthyid genus except _Monolene_ and _Citharichthys_ (the former, as discussed above, seems to fall under Bothidae; as for larvae of the latter genus, further review is necessary). On the other hand, these spines never appear in the opercular region in Bothidae. Spines on the sphenotic bone are situated above the eye and appear in many species of Paralichthyidae, although there are some species which have no spines. Absolutely no sphenotic spines are found in Bothidae.

Epiotic spines, situated posteriorly above the eye, are found only in larvae of Taeniopsettinae. None are found in Paralichthyidae and Bothinae.

The urohyal is situated anterior to, and above, the pelvic fin and in some species supports many spines at the edge of abdomen. These spines are found in all species in the subfamily Taeniopsettinae but are, with the exception of some species, usually absent in Paralichthyidae and Bothinae.

During the larval stage the cleithrum is exposed at the lower portion of the pectoral fin base and small spines are present at the rear edge in some species. These spines appear in all species of Taeniopsettinae but only in some species of Bothinae.

We previously discussed the shape of the posterior process of the pelvic bone. The spines on the pelvic bone are found at the edge of the posterior process in some species. These spines are found in all species of Taeniopsettinae, but are absent in all Paralichthyidae and most Bothinae.

Although insufficient phyletic analysis has been done on the position of these spines, their phyletic significance should be noted because of the stability of its appearance at the family and subfamily level. An interesting issue related to this point is that three genera in Taeniopsettinae were formerly classified under Paralichthyidae. Recently, however, these genera were transferred to Bothidae as a separate subfamily because of their adult skeletal structure and larval characteristics (Amaoka 1969; Futch 1977; Hensley 1977). It may also be pointed out that transfer of the genus Monolene to Bothidae, instead of Paralichthyidae, may be appropriate (Futch 1977; Hensley 1977). This author strongly supports the view that the presence of spines in left eyed flounders are characteristics which reflect phyletic relationships among families and subfamilies, based on the appearance of the spines in Monolene and Taeniopsettinae.

5. Conclusion

The ontogeny of phyletic characters insofar as the characters which have been studied are concerned, is considered to indicate phylogeny, and can be an effective method to understand the relationship of families. But some of the characters which disappear during phylogenesis could not be found during ontogenesis. This remains as a theme for future research but it may be limited as a method for obtaining clues to phylogeny based on ontogeny.

A remarkable correlation was found at the level of family and subfamily between larval characters and the classification of left eyed flounders (Table 2). The elongate dorsal fin rays, long posterior process of the pelvic bone, large sized larvae, etc. are larval characters which have been interpreted as an ecological adaptation for planktonic life, while a series of numerous spines frequently found on the head may be a character adapted for protection of head (Kyle 1913; Uchida 1937; Amaoka 1973). The appearance of these larval characters, however, has a strong correlation with, and high stability in, the classification system.

These findings may suggest that though phyletic evaluation on larval characters has been insufficiently carried out, the larval characters discussed in this paper have phyletic significance and that they have either developed or degenerated in close relation with the ecological adaptation to planktonic life or protection.

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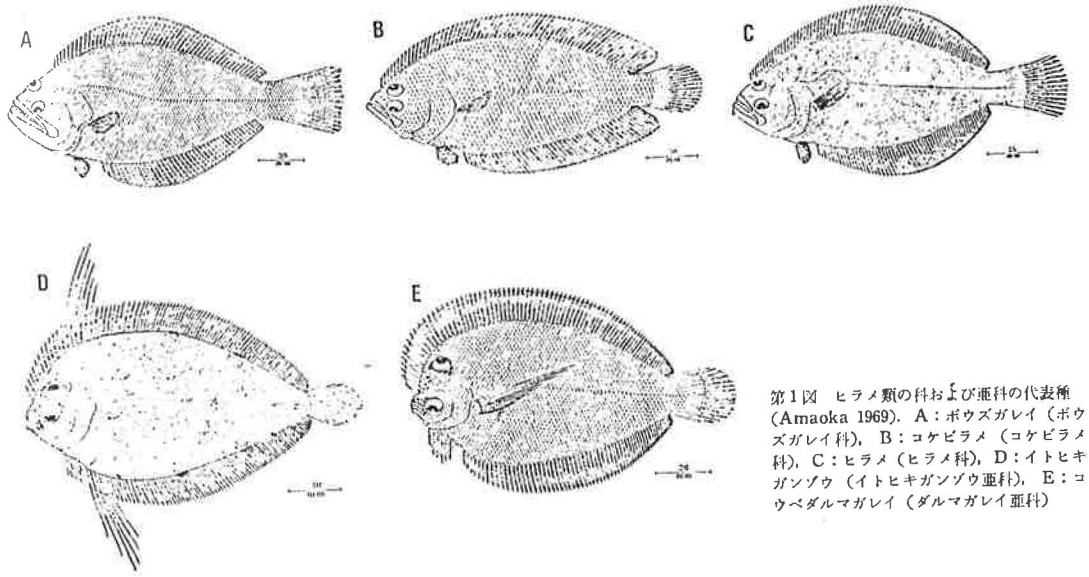
Table 1. Metamorphic body lengths, number of elongate dorsal rays and presence or absence of spines in larvae of Paralichthyidae and Bothidae. Abbreviations are the same as Fig. 12.

Family subfamily genus	Number of spines	Metamorphic body length	Number of elongate dorsal rays	Spines PS	 SS	 ES	 US	 CS	 BS
Paralichthyidae									
Paralichthys	2	13.3,9.5<12.1	4 - 5	+	+	-	-	-	-
Pseudorhombus	2	10.1,9.2<10.1	3 - 7	+	+	-	-	-	-
Tarphops	1	9.2	6	+	-	-	-	-	-
Syacium	1	8.2<13.0	5	+	+	-	-	-	-
Anchlopsetta	1	8.2	8	+	+	-	-	-	-
Hippoglossina	1	13.0<14.4	6 - 7	+	-	-	-	-	-
Cyclopsetta	1	12.9<14.0	9	+	+	-	-	-	-
Etropus	1	10.0<12.0	0 - 1	+	-	-	-	-	-
Citharichthys	1	14.0	3	-	-	-	-	-	-
Monolene	1	30.0	1	-	-	-	-	-	-
Bothidae									
Taeniopsettinae									
Taeniopsetta	1	59.0<60.0	1	-	-	+	+	+	+
Engyophrys	1	18.9<19.6	1	-	-	+	+	+	+
Trichopsetta	1	28.5<35.7	1	-	-	+	+	+	+
Bothinae									
Engyprosopon	2	16.7<;18.4<	1	-	-	-	+	+,-	+
Crossorhombus	3	15.0<,19.0<,20.0<	1	-	-	-	+,-	+,-	+
Psettina	4	16.7<,17.2<,18.1<,19.1<	1	-	-	-	+,-	-	+,-
Bothus	2	29<38.5,30<40	1	-	-	-	-	-	-
Arnoglossus	3	21.6<,30.5<46	1	-	-	-	-	-	-
Laeops	3	51<,70.5<,79<84	1	-	-	-	-	-	-
Neolaeops	1	91<	1	-	-	-	-	-	-
Chascanopsetta	2	78<,120<126	1	-	-	-	-	-	-

Table 2. Summary of relationships between larval characters and classification system in Paralichthyidae and Bothidae. () indicates a condition found only in some species.

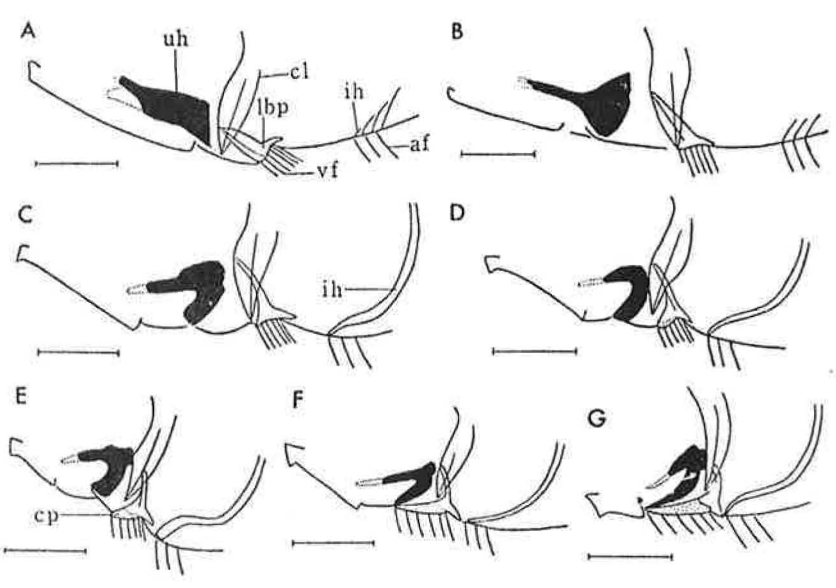
Family	Paralichthyidae		Bothidae	
subfamily		Taeniopsettinae		Bothinae
Metamorphic body length	less than 14.4 mm		more than 15 mm	
Body	thick and opaque		thin and clear	
Position where dorsal fin originates	posterior or above the eye		anterior to the eye	
Number of elongate dorsal rays	3-9		1	
Posterior process of pelvic bone	ends far anterior to anus		reaches to or near anus	
Preopercular spines	present		none	
Sphenotic spines	present (none)		none	
Epiotic spines	none	present		none
Spines on urohyal	none	present		none (present)
Spines on cleithrum	none	present		none (present)
Spines on posterior process of pelvic bone	none	present		none (present)



第1図　ヒラメ類の科および亜科の代表種 (Amaoka 1969). A：ボウズガレイ（ボウズガレイ科), B：コケビラメ（コケビラメ科), C：ヒラメ（ヒラメ科), D：イトヒキガンゾウ（イトヒキガンゾウ亜科), E：コウベダルマガレイ（ダルマガレイ亜科)

Fig. 1 Representative species belonging to families and subfamilies of left eyed flounders (Amaoka 1969).

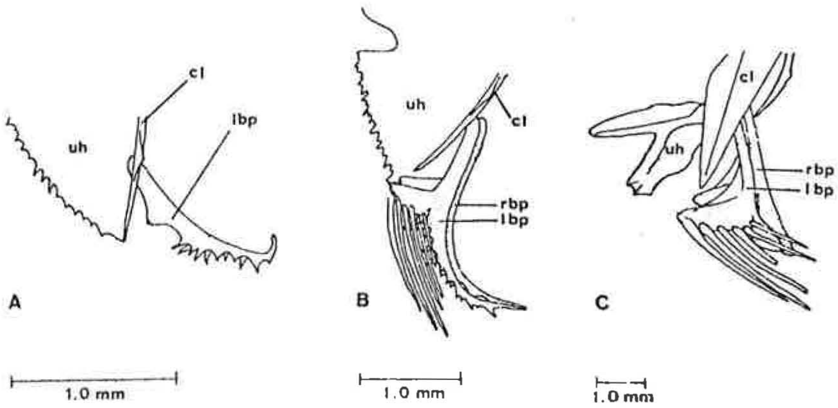
A. *Psettodes erumei* (Psettotidae); B. *Citharoides macrolepidotus* (Citharidae); C. *Paralichthys olivaceus* (Paralichthyidae); D. *Taeniopsetta ocellata* (Taeniopsettinae); and E. *Crossorhombus kobensis* (Bothidae).



第2図　ヒラメ類の尾舌骨(uh)，鎖骨(cl)，左側腰骨(lbp)，腹鰭(vf)，第1血管間棘（ih）および臀鰭（af）の関係の7型（Amaoka 1969, 1972）．A：ボウズガレイ，B：*Brachypleura novaezeelandiae*，C：コケビラメ，D：ヒラメ　E：イトヒキガンゾウ，F：ナンヨウダルマ，G：ホシダルマガレイ

Fig. 2 Relations among urohyal (uh); cleithrum (cl); left pelvic bone (lbp); pelvic fin (vf); 1st haemal spine (ih); and anal fin (af) in seven genera of left eyed flounders (Amaoka 1969, 1972).

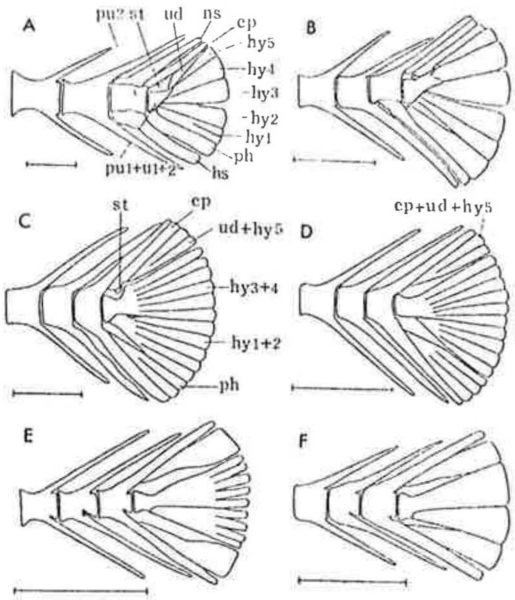
A. P. erumei; B. Branchypleura novaezeelandiae; C. C. macrolepidotus; D. P. olivaceus; E. C. kobensis; F. Arnoglossus polyspilus; and G. Bothus myriaster.



第3図　*Engyophrys senta*（イトヒキガンゾウ亜科）の尾舌骨，鎖骨，腰骨および腹鰭の初期発生（Hensley 1977）．A：体長5.4mm，B：16.5mm，C：38.7mm，rbp：右側腰骨，他の略号は第2図と同じ

Fig. 3 Changes in urohyal, cleithrum, pelvic bone, and pelvic fin during early developmental stages in Engyophrys senta (Taeniopsettinae), after Hensley (1977).

A. Body length 5.4 mm; B. 16.5 mm; C. 38.7 mm.
rbp: right pelvic bone.
Other abbreviations are the same as in Fig. 2.

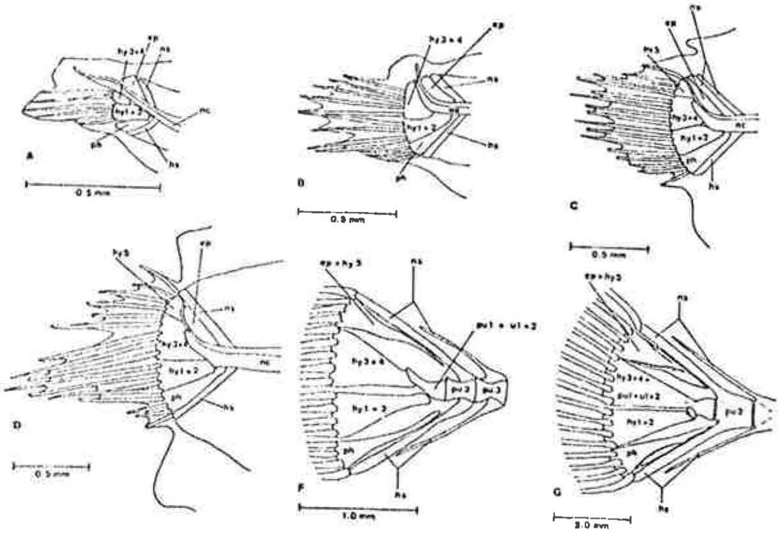


第4図　ヒラメ類の尾鰭骨格の6型．A：ボウズガレイ，B：コケビラメ，C：ヒラメ，D：ヘラガンゾウ（ヒラメ科），E：カネコダルマ(ダルマガレイ科)，F：モンダルマ（ダルマガレイ科）．pu：尾鰭椎前椎骨，u：尾鰭椎骨，st：翼尾骨，ud：尾皮骨，ep：上尾軸骨，hy：下尾軸骨，ph：準下尾軸骨，ns：神経棘，hs：血管棘．＋記号はゆ合した状態を示す

Fig. 4 Six types of caudal skeletal structures in left eyed flounders.

A. *P. erumei* (Psettodidae); B. *C. macrolepidotus* (Citharidae); C. *P. olivaceus* (Paralichthyidae); D. *Pseudorhombus oculocirris* (Paralichthyidae); E. *C. kanekonis* (Bothidae); F. *Bothus mancus* (Bothidae).

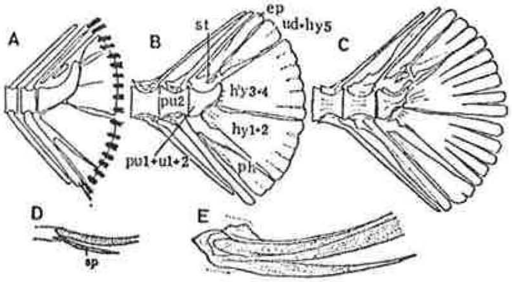
pu: preural centrum; u: ural centrum; st: stegural; ud: urodermal; ep:epural; ph: parhypural; ns: neural spine; hs: haemal spine; +: indicates fusion of the bones.



第5図 *Engyophrys senta* の尾鰭骨格の初期発生（Hensley 1977）A：体長 4.6mm，B：5.5mm，C：7.0mm，D：7.6mm，E：15.3mm，F：45.7mm，nc：脊索，他の略号は第4図と同じ

Fig. 5 Changes in caudal skeletal structure during early developmental stages in E. senta (Hensley 1977).

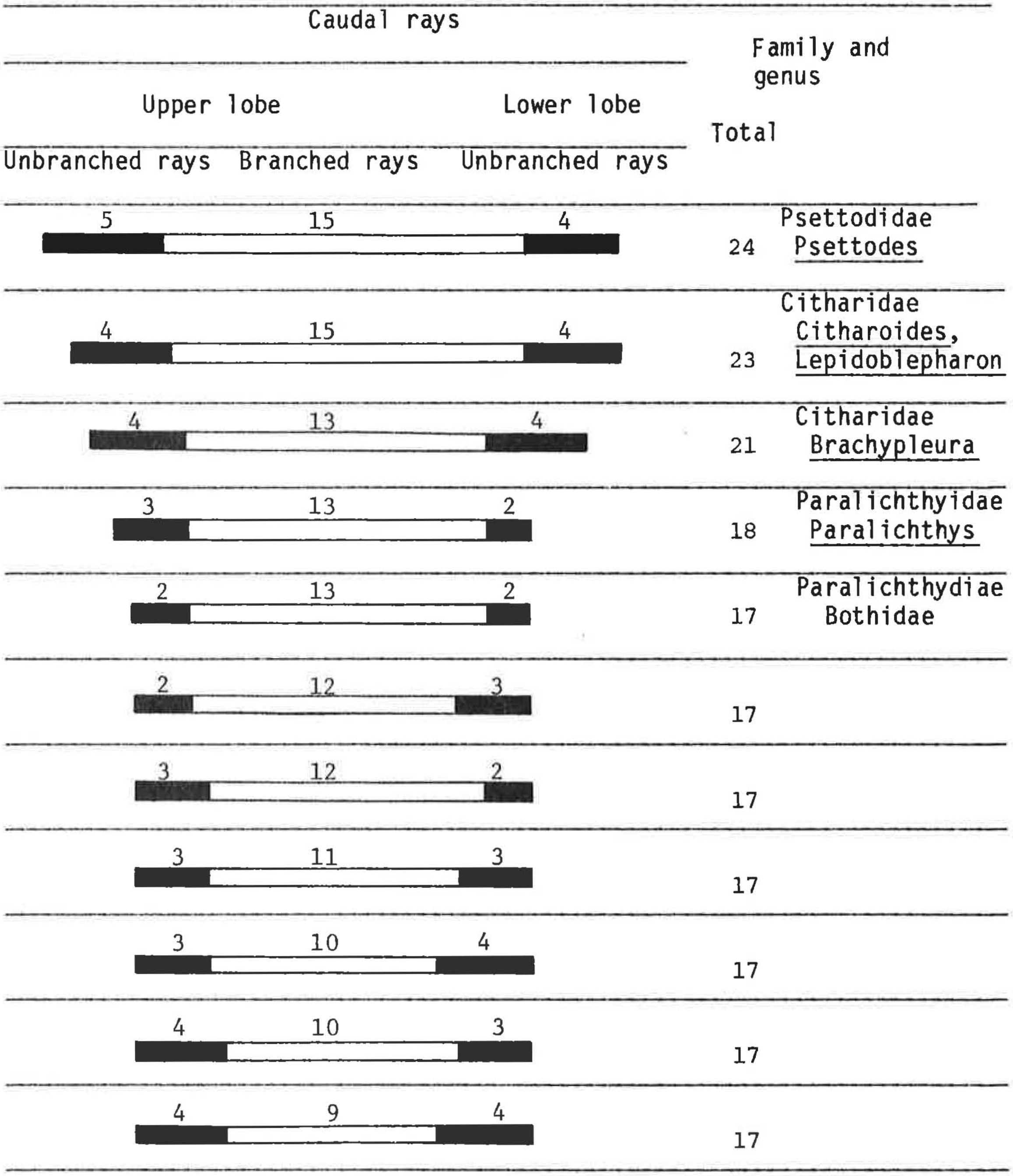
A. Body length 4.6 mm; B. 5.5 mm; C. 7.0 mm; D. 7.6 mm; E. 15.3 mm; F. 45.7 mm.
nc: nothchord.
Other abbreviations are the same as in Fig. 2.



第6図 ヒラメの尾鰭骨格（A～C）および尾鰭下端微少鰭条（D～E）の初期発生（沖山 1974）．AD：体長 11.7mm，B：32.0mm，CE：55.0mm，sp：微少鰭条，他の略号は第4図と同じ

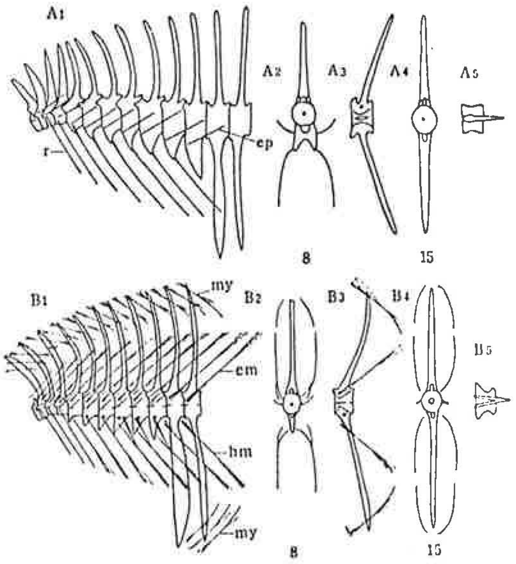
Fig. 6 Changes in caudal skeletal structure (A-C) and small spur of the caudal ray at the lower edge of caudal fin during early developmental stages in P. olivaceus (Okiyama 1974).

A,D: Body length 11.7 mm; B.: 32.0 mm; C,E: 55.0 mm;
SP: small spur of the caudal ray.
Other abbreviations are the same as in Fig. 2.



Caudal rays				
Upper lobe		Lower lobe	Total	Family and genus
Unbranched rays	Branched rays	Unbranched rays		
5	15	4	24	Psettodidae *Psettodes*
4	15	4	23	Citharidae *Citharoides*, *Lepidoblepharon*
4	13	4	21	Citharidae *Brachypleura*
3	13	2	18	Paralichthyidae *Paralichthys*
2	13	2	17	Paralichthydiae Bothidae
2	12	3	17	
3	12	2	17	
3	11	3	17	
3	10	4	17	
4	10	3	17	
4	9	4	17	

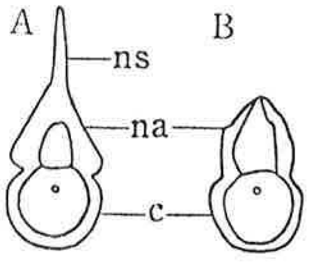
Figure 7. Change in number of caudal fin rays in left eyed flounders (Amoaka 1969, 1972).



第8図 ヒラメ類の前部中軸骨格とその附属骨格の2型（Amaoka 1969). A：ヒラメ, B：コウベダルマガレイ. A_2B_2：第8脊椎骨前面, A_3B_3：第15脊椎骨側面, A_4B_4：同前面, A_5B_5：同背面. ep：上肋骨, r：肋骨, my em hm：肉間骨群

Fig. 8 Two types of anterior axial skeletons and their accessory bones in left eyed flounders (Amaoka 1969).

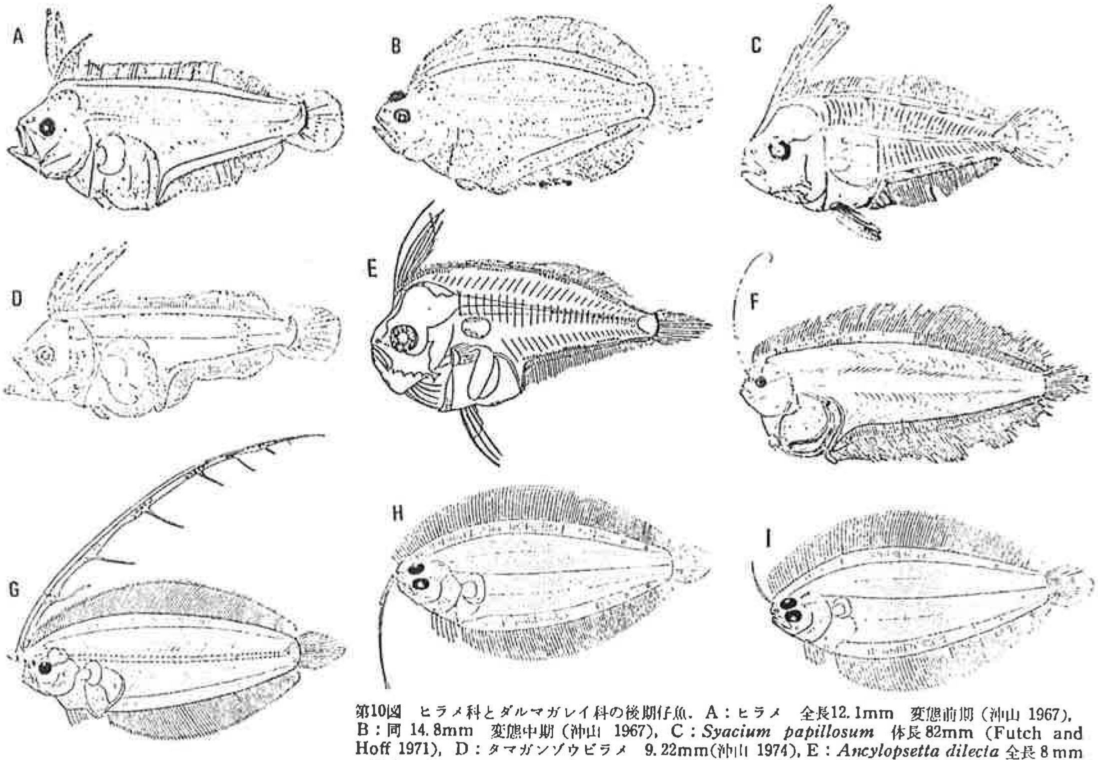
A. *P. olivaceus*; B. *C. kobensis*; A_2B_2: frontal view of 8th vertebra; A_3B_3: side view of 15th caudal vertebra; A_4B_4: anterior view of 15th caudal vertebra; A_5B_5: dorsal view of 15th caudal vertebra. ep: epipleural; r: rib; my: myorhabdoi; em: epimeral; hm: hypomeral bones.



第9図 ヒラメ類の第1脊椎骨の2型（Amaoka 1969). A：コケビラメ, B：イトヒキガンゾウ. ns：神経棘, na：神経弓門, c：椎体

Fig. 9 Two types of first vertebra in left eyed flounders (Amaoka 1969).

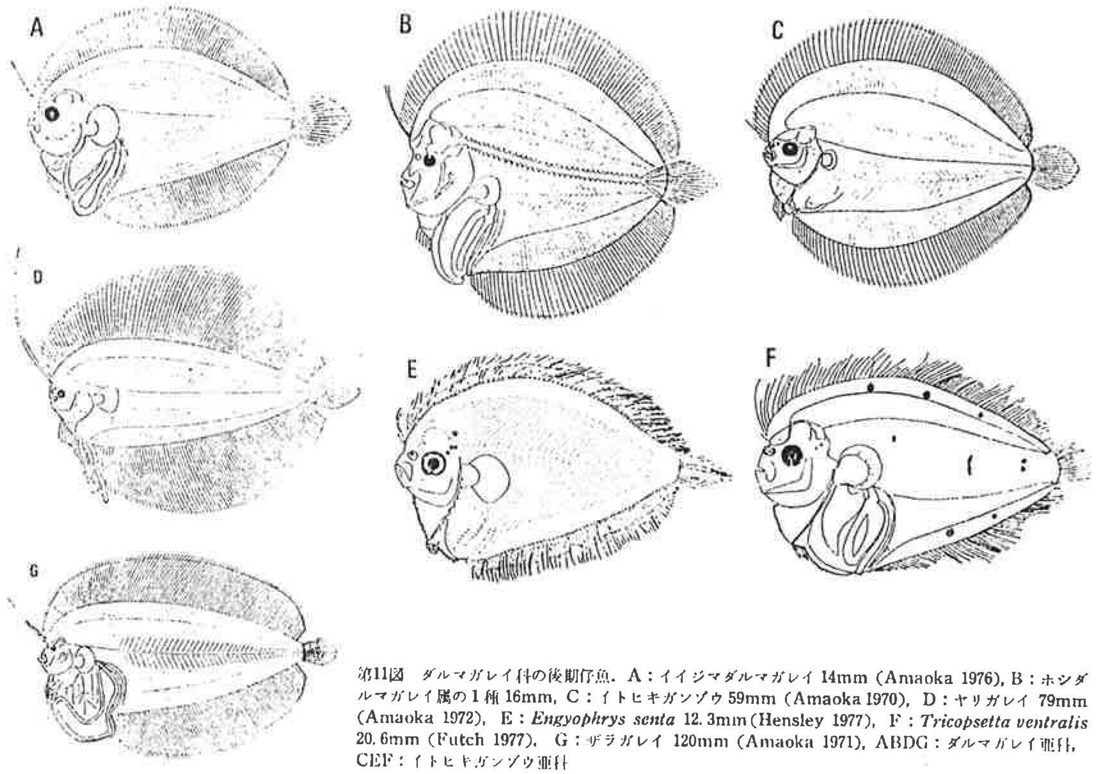
A. *C. macrolepidotus*; B. *T. ocellata*; ns: neural spine; na: neural arch; c: centrum.



第10図　ヒラメ科とダルマガレイ科の後期仔魚．A：ヒラメ　全長12.1mm　変態前期（沖山 1967），B：同 14.8mm　変態中期（沖山 1967），C：*Syacium papillosum* 体長82mm（Futch and Hoff 1971），D：タマガンゾウビラメ　9.22mm（沖山 1974），E：*Ancylopsetta dilecta* 全長8mm（Hsiao 1940），F：*Monolene sessilicauda* 29.5mm（Futch 1971），G：ニホンダルマガレイ 30.5mm　変態前期，H：同46.0mm　変態中期，I：同46.9mm　変態後期（Amaoka 1973）．A～F：ヒラメ科（Fの所属は疑問），G～I：ダルマガレイ科

Fig. 10 Postlarvae of Bothidae and Paralichthyidae.

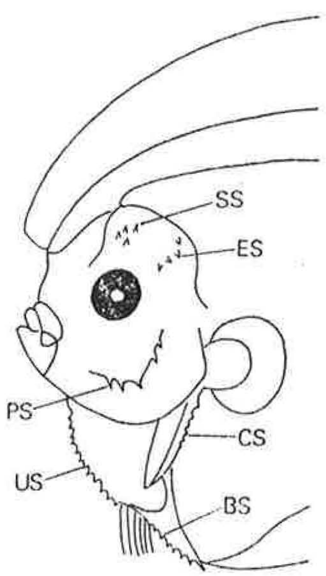
A. *P. olivaceus*, total length 12.1 mm, early metamorphic stage (Okiyama 1967); B: Same, 14.8 mm, middle metamorphic stage (Okiyama 1967); C. *Syacium papillosum*, body length 82 mm (Futch and Hoff 1971); D. *Pseudorhombus pentophthalmus*; body length 9.22 mm (Okiyama 1974); E. *Ancylopsetta dilecta*, total length 8 mm (Hsiao 1940); F. *Monolene sessilicauda*, 29.5 mm (Futch 1971); G: *Arnoglossus japonicus*, body length 30.5 mm, early metamorphic stage (Amaoka 1973); H. Same, 46.0 mm, middle metamorphic stage; I: Same, 46.9 mm, late metamorphic stage.
A-F: Paralichthyidae (F is questionable), G-I: Bothidae.



第11図　ダルマガレイ科の後期仔魚．A：イイジマダルマガレイ 14mm (Amaoka 1976), B：ホシダルマガレイ属の1種 16mm, C：イトヒキガンゾウ 59mm (Amaoka 1970), D：ヤリガレイ 79mm (Amaoka 1972), E：*Engyophrys senta* 12.3mm (Hensley 1977), F：*Tricopsetta ventralis* 20.6mm (Futch 1977), G：ザラガレイ 120mm (Amaoka 1971), ABDG：ダルマガレイ亜科, CEF：イトヒキガンゾウ亜科

Fig. 11 Postlarvae of Bothidae.

A. Psettina iijimae, body length 14 mm (Amaoka 1976); B. Bothus sp., body length 16 mm (Amaoka unpublished); C. T. ocellata, body length 59 mm (Amaoka 1970); D. Laeops kitaharae, body length 79 mm (Amaoka 1972); E. E. senta, body length 12.3 mm (Hensley 1977); F. Tricopsetta ventrails, body length 20.6 mm (Futch 1977); G. Chascanopsetta lugubris, body length 120 mm (Amaoka 1971).
A,B,D,G: Bothidae
C,E,F: Taeniopsettinae



第12図　ヒラメ類の仔魚に出現する棘の部位と名称．SS：楔耳骨棘，ES：上耳骨棘，PS：前鰓蓋骨棘，CS：鎖骨棘，US：尾舌骨棘，BS：腰骨後方突起棘

Fig. 12 Position and names of spines that appear in larvae of left eyed flounders.

ss: sphenotic spine; es: epiotic spine; ps: preopercular spine; cs: spine on cleithrum; us: spine on urohyal; and bs: spine of posterior process of pelvic bone.