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Development of Median and Paired Fin Skeleton of *Paralichthys olivaceus* (Pleuronectiformes: Paralichthyidae)

Eduardo F. Balart

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Abstract Development of median and paired fins and their supports are described for *Paralichthys olivaceus*, giving details on origin, shape, ossification and meristic counts. All fin supports begin to form through cartilage in the following sequence: pectoral (2.62 mm SL), dorsal (4.60 mm SL), caudal (5.55 mm SL), anal (5.95 mm SL) and pelvic fin support (8.57 mm SL). Completion and partial ossification of fin structures are already present by the 40th day after hatching (ca. 16 mm SL), after eye migration. This study shows how developmental osteology may clarify identification and terminology of fish bones (e.g., caudal skeleton). Comparisons with other species belonging to Pleuronectiformes elucidate basic pattern of fin formation within the order, and depict interesting departures which may be of taxonomic and/or systematic utility.

Paralichthys olivaceus is one of the most exploited flounder in Japanese waters probably because its abundance close to shore. Actually this species is also the subject of extensive artificial propagation. Despite the increase in fundamental knowledge about this flounder (e.g., Okiyama, 1967; Tsuruta and Omori, 1976; Minami, 1982; Kuwahara and Suzuki, 1982), information on osseous structure is scarce and incomplete (Amaoka, 1969), and as far as could be determined only Okiyama's studies (1967; 1974) contribute to knowledge on osteological development. Studies on the osteological development provides various information about functional aspects of larval survival as well as providing a potential tool for taxonomic and systematic works (Dunn, 1983).

This paper deals with the development of median and paired fins and their support of *Paralichthys olivaceus* giving details on their origin, shape, ossification and meristic counts.

Materials and methods

A total of 164 specimens of *Paralichthys olivaceus* was used in this study. Of them, 154 were laboratory-reared and ranged from 2.62 to 17.43 mm in standard length (SL) 0–42 days after hatching (a. h.). Specimens were reared at the Japan Sea Farming Association, Miyako Station (Iwate Prefecture), and Kyoto University, Maizuru Fisheries Research Station (Kyoto Prefecture). Fourteen wild-caught specimens ranging from 38.90 to 107.15 mm SL (locality unknown), were kindly supplied by Dr. T. Minami. Reared specimens were preserved in either 5% buffered formalin or Bouins solution, whilst wild specimens were fixed in 10% formalin. Clearing and staining were done by Dingerkus and Uhler's (1977) method. However, specimens fixed in Bouins were greately decalycified, and were therefore used only for cartilage observations. Since formalin even at as low a concentration as 5% decalcifies bone, it may be presumed ossification took place a little before that stated in this work.

Observations and drawings were made with a Wild M5 and Nikon SMZ10 stereoscopic microscope with the aid of camera lucida. Measurements of smaller specimens were made with a Nikon V20 profile projector associated to a Nikon SMZ6F digital counter, and by a calibrated ocular micrometer attached to a microscope. Larger specimens were measured with a Kanol dial caliper. Fin rays and pterygiophores were counted regardless of their degree of development; counts on paired fins included both sides.

Results

Caudal fin skeleton. The caudal fin complex (Fig. 1I) is integrated by 2 preural centra; a detached autogenous parhypural; a broad ventral hypural plate (H 1+2) articulated to 1st preural centrum; a broad dorsal hypural plate (H 3+4)

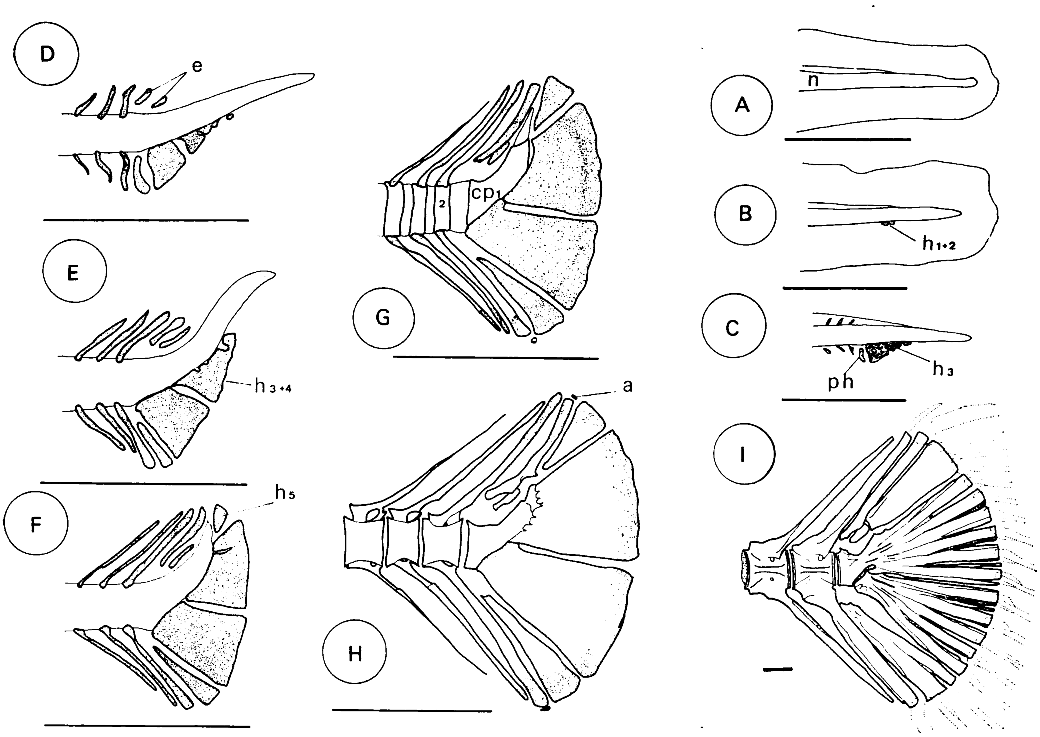

Fig. 1. Development of caudal fin support in *Paralichthys olivaceus*. A, 4.87 mm SL; B, 5.55 mm SL; C, 6.98 mm SL; D, 7.60 mm SL; E, 8.31 mm SL; F, 9.37 mm SL; G, 11.13 mm SL; H, 16.51 mm SL; I, 86.45mm SL. a, accesory cartilage; cp 1–2, preural centra 1–2; e, epural; h, hypural; n, notochord; ph, parhypural. Stippled areas show cartilage. Open areas show developing ossification except notochord. Scales indicate 1 mm.

fused to the tip of 1st preural centrum; an autogenous 5th hypural (H 5) having proximal end very close to 2nd epural; 2 epurals of contrasting size, being the anteriormost elongated whilst the posterior epural is very reduced; usually 13 branched rays supported by hypural pieces and 4 unbranched but segmented rays in addition to an unsegmented spur raylet located in both, dorsal and ventral sides. Total ray number, however, can range from 18 to 19 (Table 1) following 1+2+13+2+1 or 1+2+13+1+1 caudal formula (dorsal spur+unbranched + branched + unbranched + ventral spur). Multiple and somewhat deep scissures are present on distal margin of parhypural and hypural pieces. Developmental evidence assures *P. olivaceus* lacks uroneurals as well as ural centra which are never observed.

Caudal fin complex develops among 17 day old specimens (5.55–6.12 mm SL). Two small cartilage buds appear ventral to the unflexed notochord which probably correspond to 1st and 2nd hypurals (Fig. 1B). By 21 day a. h. the parhypural is already detached from the notochord (Fig. 1C). Smaller specimens, i.e., 6.76 mm SL, exhibits hypural 1 and 2 well fused to each other as well as a small cartilage protruding posteriorly. Larger specimens, in contrast, have a somewhat enlarged dorsal hypural plate and also develop neural and haemal arches belonging to the future preural centrum 2. By 24 day a. h. (7.35–7.63 mm SL) 2 cartilaginous epurals of nearly equal size appear. The dorsal hypural plate still remains incomplete. Among larger specimens, i.e. 7.60 mm SL, an early notochord flexion is observed (Fig. 1D), though it also occurs early in larger specimens (over 8 mm SL) belonging to younger batches (i.e., 20 days old). The notochord flexion is associated to its own distal regression. Thus, by 9.37 mm SL (25 days old) hypural 5 develops at the tip of notochord (Fig. 1F). The anteriormost epural

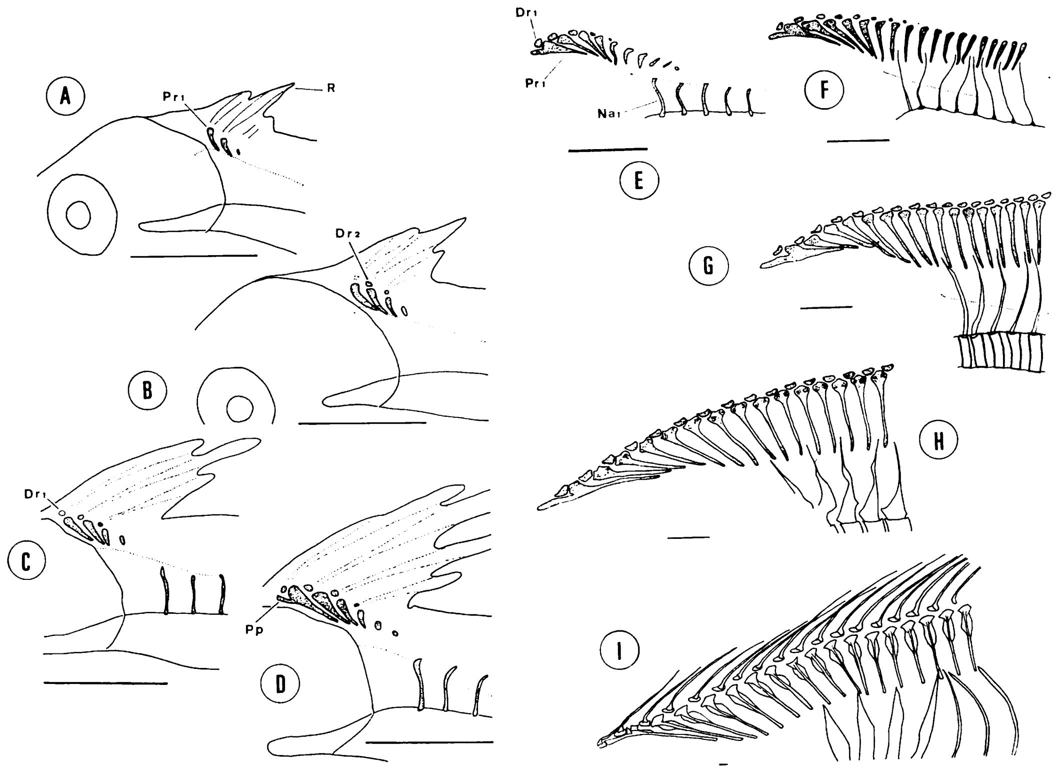

Fig. 2. Development of anterior part of dorsal fin support in *Paralichthys olivaceus*. A, 4.82 mm SL; B, 5.44 mm SL; C, 5.65 mm SL; D, 6.04 mm SL; E, 6.98 mm SL; F, 8.31 mm SL; G, 11.13 mm SL; H, 16.50 mm SL; I, 107.15 mm SL. Dr, distal radial; Na, neural arch; Pr, proximal radial; Pp, anterior process; R, elongated ray. Stippled areas show cartilage. Open areas show developing ossification. Scales indicate 0.5 mm.

looks already strikingly larger than the posterior one at this stage. By 30 days a. h. (9.55–12.08 mm SL) preural centrum 1 ossifies like preceeding centra (Fig. 1G). Hypural 5 looks like an enlarged triangular cartilage. A notochord remnant separates it from the epurals. The hypural ossification is evident at 40 day a. h. (Fig. 1H). This event seems to coincide with the fusion of hypural plate 3+4 to preural centrum 1, though the symphysial line is still apparent. The distal end of the hypurals and the anterior epural remain cartilaginous. Epural 2 looks very reduced and somewhat hidden by the 1st epural. Hypural 5 inserts between the 1st epural and the preceeding dorsal hypural plate. Ossification of the cartilaginous caudal support follows the formation pattern, that is, from the ventral hypural dorsad to the epurals. Scissures on the distal margin of the parhypural and hypural plates develop later after metamorphosis. A specimen 38.90 mm SL has 3 shallow scissures in each central plate, whereas by 86.45 mm SL they are multiple and deeper (Fig. 1I).

Caudal ray development is shown in Fig. 7. The rays appear prior to notochord flexion but unossified. The smallest specimen bearing rays (3 rays) is 5.89 mm SL (17 day old). Among 25 day old specimens (8.63–9.44 mm SL) a full complement of principal rays is present. Segmentation is evident before 8.15 mm SL and coincides with ray ossification. Ossification spreads out from mid-rays toward dorsal and ventral rays. Branching of rays starts by 40 days a. h., that is, just after metamorphosis. A 16.12 mm SL specimen has 9 branched rays whilst by 17.43 mm SL they totalled 11 in number. The ventral spur develops first, by 9.37 mm SL, whereas the dorsal spur appears

Table 1. Fin ray number of median and paired fins of some *Paralichthys olivaceus* juveniles.

SL (mm)	Dorsal			Anal			Caudal			Pelvic						Pectoral					
	T	BR	UBR	T	BR	UBR	T	BR	UBR	T		BR		UBR		T		BR		UBR	
										L	R	L	R	L	R	L	R	L	R	L	R
38.90	79	3	76	61	3	58	19	13	6	6	6	4	4	2	2	13	13	0	0	13	13
41.70	86	3	83	65	3	62	18	12	6	6	6	4	3	2	1	13	13	1	0	12	13
44.85	78	2	76	60	4	56	19	13	6	6	6	4	4	2	2	13	13	1	0	12	13
46.00	79	3	76	63	3	60	19	13	6	6	6	4	4	2	2	12	12	0	0	12	12
48.60	78	2	76	61	3	58	19	13	6	6	6	4	3	2	3	13	12	5	0	7	12
50.30	75	3	72	59	5	54	19	13	6	6	6	4	4	2	2	13	13	7	0	5	13
53.10	79	7	72	60	7	53	19	13	6	6	6	5	4	1	2	14	13	4	1	10	12
57.50	75	3	72	59	4	55	19	13	6	6	6	4	4	2	2	12	12	6	0	6	12
92.65	81	39	42	62	40	22	19	13	6	6	6	5	5	1	1	12	13	7	7	5	6
96.00	77	35	32	60	39	21	19	13	6	6	6	5	4	1	2	13	12	4+	4+	9	8
97.75	76	28	48	59	26	33	18	13	5	6	6	5	5	1	1	12	13	8	7	4	6
104.35	74	32	42	60	35	25	18	12	6	6	6	5	4	1	2	13	13	8	6	5	7

Fin ray number spans all fin columns.

T, total; BR, branched; UBR, unbranched; L, left side; R, right side; +, ray damaged for accurate count.

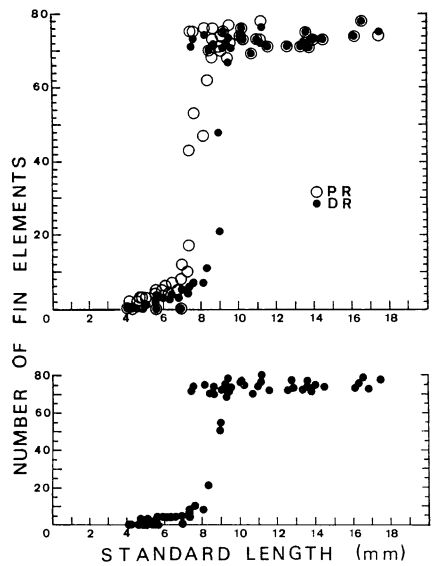

Fig. 3. Development of pterygiophore (above) and ray number (bottom) of dorsal fin in *Paralichthys olivaceus*. DR, distal radial; proximal. PR, radial.

by 9.55 mm SL.

Dorsal and anal fin skeletons. Each soft ray is articulated to a small distal radial as a simple hinge whilst the distal radial is located between 2 elongated proximal radials (Fig. 2). There is not a ball and socket articulation between pterygiophores as found in most teleost fishes (Lindsey, 1955), because the proximal radial lacks a defined posterodorsal process. The anteriormost dorsal proximal radial is enlarged and supports 3 rays: those posterior rays articulate through corresponding distal radials whereas the 1st ray articulates directly to the anterior process of 1st proximal radial. The first anal proximal radial is modified into a large rod and supports 4 rays: the anteriormost ray articulates directly to it, the 2nd ray through a supernumerary distal radial, whereas the 2 posteriormost rays articulate by 2 common distal radials. A reduced element which appears later druing ontogeny is described under the name of supernumerary distal radial. The first anal proximal radial, so-called the 'abdominal rod', closes the abdominal cavity posteriorly together with the 1st haemal spine.

The anal fin consists of 58–64 pterygiophores plus a supernumerary distal radial associated to 59–65 rays, whereas the dorsal fin exhibits 73–85 pterygiophores associated to 74–86 rays (Table 1). Posterior rays are apically separated looking like branched rays. Their number is variable (Table 1). This species lacks spine-like rays as well as median radials.

By 12 days a. h. the dorsal fin skeleton begins to form. The smallest specimen (4.60 mm SL) shows 2 cartilaginous proximal radials, whereas other specimens have 2 or 3 in addition to a sole modified ray (Fig. 2A). Distal radial cartilages appear by 14 days a. h. (over 4.75 mm SL), the anteriormost being formed a little after the 2nd distal radial (Fig. 2B, C). By 14–17 days a. h. the anterior process of 1st proximal radial is present in most specimens (Fig. 2D). At this stage the dorsal fin support is located on the cranium behind the eyes. Subsequent development consists of formation of new pterygiophores posteriad. During the postlarval stage 5 (rarely 6) elongated rays are observed anteriorly, although all of them are still unossified. The pterygiophore number is described in relation to fish length (Fig. 3). The proximal radial number increases suddenly by 20–21 days a. h., whereas that of the distal radials by 24–25 days a. h. Afterward these numbers increase steadly by almost a full complement during the metamorphic period. Dorsal ray development proceeds posteriad except for the anteriormost; this 1st ray appears later and never becomes elongated. It articulates directly to the anterior process of 1st proximal radial. The dorsal ray number is depicted by Fig. 3 in relation to fish length. Ossification begins at the anterior pterygiophores and seems to proceed posteriad. By 40 days a. h. (over 16 mm SL) ossification is well established among proximal radials (Fig. 2H) but posteriorly. Distal radials partly ossify very late, over 100 mm SL and never completely (Fig. 2I). Dorsal rays, in contrast, ossify by 30 days a. h. A 9.55 mm SL specimen exhibits 6 anterior rays lightly ossified whereas by 11.13 mm SL 61 rays were stained. Thus ossification seems to proceeds posteriad. Ossification of dorsal rays coincides with a shortening of the anterior 5 elongated rays. Ray branching seems to be a very delayed process since it is observed among juveniles over 40 mm SL. Ray branching starts from posterior rays anteriad, individuals being over 90 mm SL when branch-

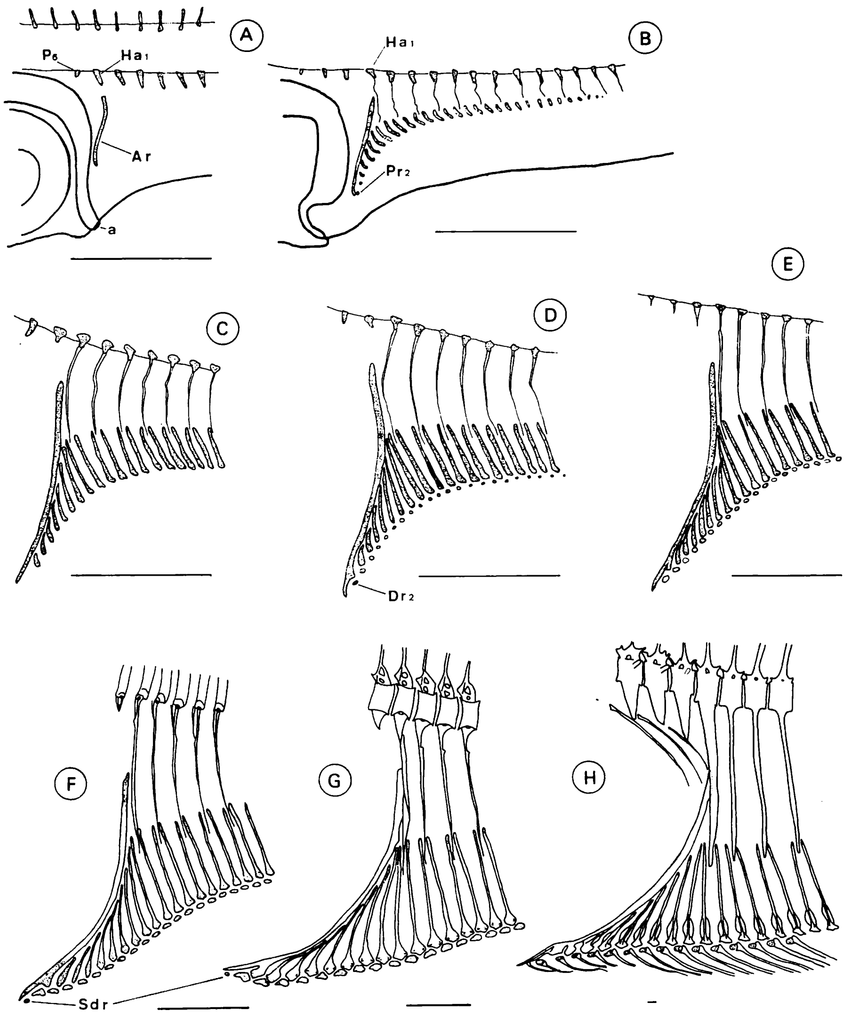

Fig. 4. Development of anterior part of anal fin support in *Paralichthys olivaceus*. A, 6.98 mm SL; B, 7.35 mm SL; C, 8.31 mm SL; D, 9.00 mm SL; E, 9.37 mm SL; F, 11.13 mm SL; G, 17.43 mm SL; H, 107.15 mm SL. a, anus; Ar, abdominal rod; Dr, distal radial; Ha, haemal arch; Pa, parapophysis; Pr, proximal radial; Sdr, supernumerary distal radial. Stippled areas show cartilage. Open areas show developing ossification. Scales indicate 1 mm.

ing becomes noticeable (Table 1).

Anal fin support begins to develop by 17 days a. h., being an abdominal rod, the sole cartilaginous structure at this stage (Fig. 4A). The smallest specimen bearing it is 5.95 mm SL, though the abdominal rod is consistently present over 6.32 mm SL. It is located below the 1st haemal arch and vertically oriented behind the abdominal cavity. The pterygiophore number seems to be proportional to fish length (Fig. 5). Unlike the abdominal rod, the following proximal radials are very small (Figs. 4B and following). By 20–21 days a. h. up to 27 distal radials are developing in specimens over 8.95 mm SL. The anteriormost distal radial corresponds to the 2nd one of the juveniles. The first distal radial or supernumerary distal radial forms by 30–31 days a. h. (7.48–12.08 mm SL), usually in specimens over 11 mm SL or already having an almost full complement of proximal radials (Fig. 4F). Like dorsal pterygiophores new elements are added posteriad. Anal fin rays appear suddenly around 8 mm SL. It was not possible to detect the order of formation, though

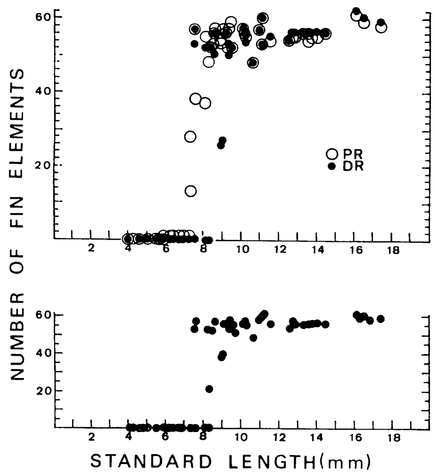

Fig. 5. Development of pterygiophore (above) and ray number (bottom) of anal fin in *Paralichthys olivaceus*. Symbols like Fig. 3.

the anteriormost ray is clearly the last one to be formed. Ossification is first noticeable on the abdominal rod by 30 days a. h. at over a size 9.50 mm SL (Fig. 4F). Among 40 day old specimens ossification is already settled in most proximal radials (Fig. 4G) but lacking in distal radials. Like the dorsal fin, anal distal radials ossify at over 100 mm SL. Central rays are the first to ossify, and then ossification spreads out anteriorly and posteriorly. That process begins about 30 day a. h. (9.55–12.08 mm SL) and almost finishes ten day later. Anal ray branching begins very late. In individuals at sizes over 90 mm SL branching becomes noticeable (Table 1). The abdominal rod is always the largest proximal radial. It meets the developing 1st haemal spine thus closing the abdominal cavity (Fig. 4B). As development proceeds it changes in shape from a vertical rod to a distinct arc. The following 5 or 6 proximal radials are close to the abdominal rod, but never fuse to it, at least on the surveyed fish.

Pectoral fin skeleton. The pectoral girdle consists of posttemporal, supracleithrum, cleithrum, coracoid, scapula, 2 postcleithra, 4 radials and an outer series of small cartilages associated to the pectoral rays. The ray count ranges from 12 to 14, mostly 13 (Table 1).

The posttemporal is somewhat modified by grooves and enclosed tubes associated to a sensory line branch. The cleithrum supports the scapula and coracoid near mid-height. Characteristically the coracoid exhibits a produced anterior process ventrally directed. Radials differ in size as well in shape, the outer radial being the longest. Postcleithra are so firmly attached to each other that it is difficult to distinguish them as 2 structures at the first glance.

Among the fins the pectoral fin is the first to develop although it is also the latest to become completely formed. The pectoral bud appears at hatching (2.62–2.85 mm SL). It consists of a rudimentary and cartilaginous coraco-scapula which promptly becomes articulated to the pectoral blade cartilage. The coraco-scapula becomes roughly triradiated or L-shaped (Fig. 6A) because the formation of a striking posterior process is found on the coracoid portion by the 3rd day a. h. (2.65–3.25 mm SL). At this stage a very thin dermal finfold is located outside the pectoral blade cartilage; they will become rays and radials respectively. The cleithrum is barely discernible and looks like a filament without proper connection to the coraco-scapula cartilage (like Fig. 6B) by 14 days a. h. (4.75–5.48 mm SL). However, the cleithrum ossifies later, by 25 day a. h. as evidenced by alizarin uptaking (Fig. 6C). A conspicuous notch appears at the anterior margin of the coraco-scapula which later, by border closing, becomes the scapula foramen (Figs. 6C–E). The supracleithrum and the posttemporal are lightly ossified (Fig. 6F) by 30 day a. h. (9.55–12.08 mm SL). The upper postcleithrum develops before the lower one also by 30 days a. h. in some specimens, though larger specimens bear both slightly ossified ones (Fig. 6F). A small propterygium forms from the blade cartilage prior to complete detachment of radial cartilages by 40–42 day a. h. (11.57–17.43 mm SL). That small propterygium becomes articulated to the innermost ray and represents the 1st small cartilage of the outer series (Fig. 6G). The coraco-scapula presents two distinct centres of ossification which separate them into two structures. The posterior coracoid process enters into regression whilst the anterior one becomes the same as the process of adult fishes, mainly during 30–40 days a. h. The pectoral rays experience a short period where they are unossified and have the appearance of dense fibrilose rods onto the dermal

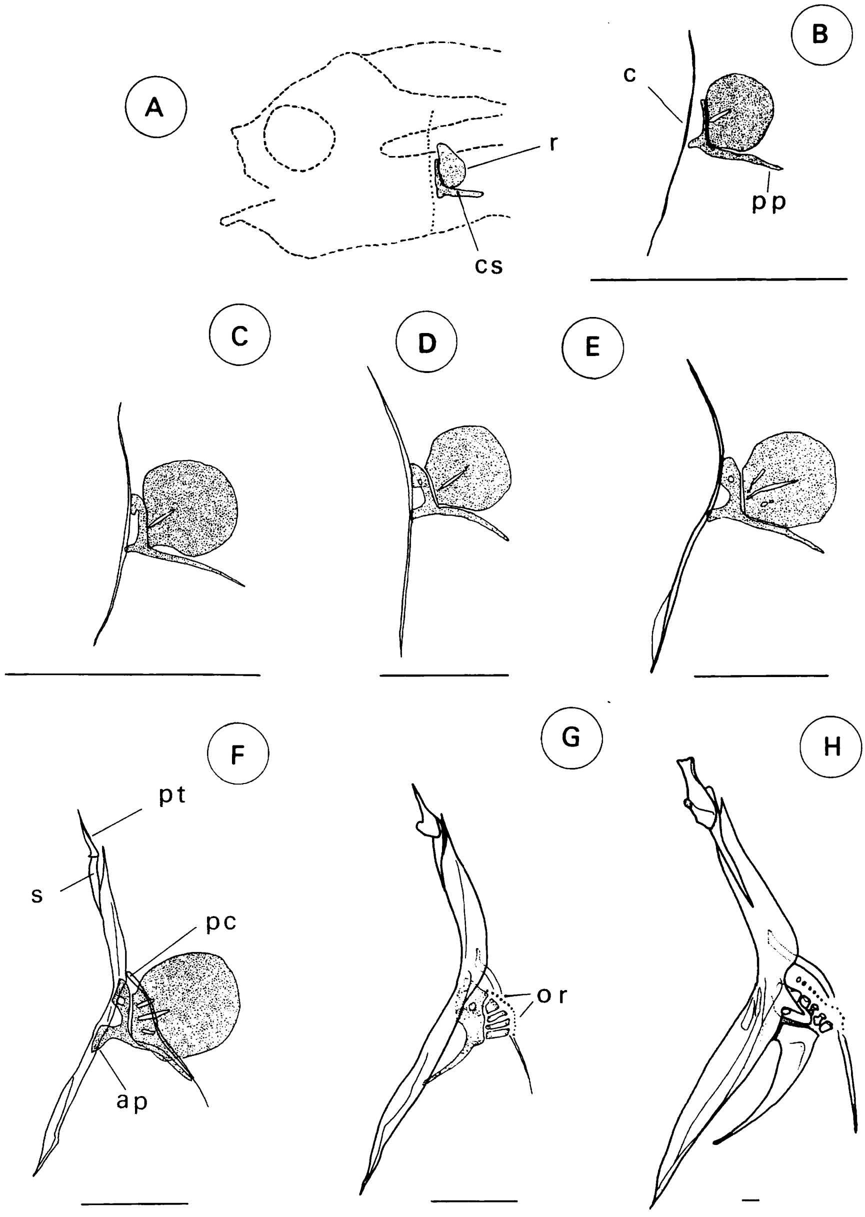

Fig. 6. Development of pectoral fin support in *P. olivaceus*. A, 3.25 mm SL; B, 5.58 mm SL; C, 6.12 mm SL; D, 8.31 mm SL; E, 9.37 mm SL; F, 11.10 mm SL; G, 16.51 mm SL; H, 38.90 mm SL. ap, anterior process; c, cleithrum; cs, coraco-scapula; or, outer cartilages; pc, postcleithra; pp, posterior process; pt, posttemporal; r, radial; s, supracleithrum. Stippled areas show cartilage. Open areas show developing ossification. Scales indicate 1 mm.

finfold. Development of pectoral ray number is shown in Fig. 7. The rays ossify at 40 days at sizes over 16 mm SL. Ray branching begins on the left side by 41.70 mm SL, when a sole branched ray is present (Table 1). Conversely, the rays on the right side begin branching by 53.10 mm SL. In the surveyed range branched ray number increases up to 8 rays on the left side whereas 7 is the maximum number on the right side. Except for this asymmetry no other

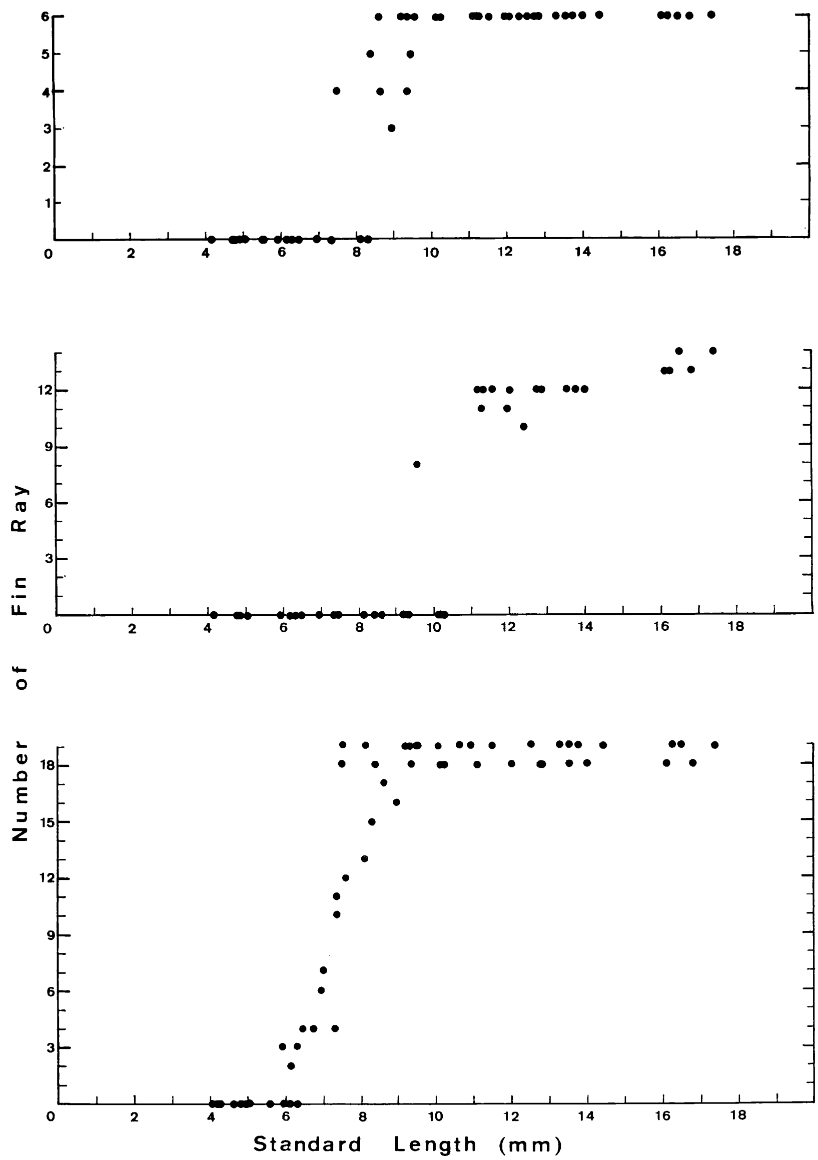

Fig. 7. Development of ray number of pelvic (above), pectoral (middle) and caudal fin (bottom) in *Paralichthys olivaceus.*

significant difference is observed during the flounder development, though there is a minor displacement of posttemporal attachment to neurocranium.

Pelvic fin skeleton. The pelvic girdle consists of basipterygium associated to 6 rays. The basipterygium is a compounding of an anterior process like an elongated shaft, obliquely directed into and hidden by the lower portion of the cleithrum, which ends ventrally in an expanded area sagitally flattened.

A lateral bud of connective tissue could be observed in the belly prior to positive identification of the basipterygium through alcian blue treatment. The cartilaginous basipterygium is evident by 20–21 days a. h. in most specimens over 7.30 mm SL. It is located behind the pectoral girdle. The anterior process looks reduced and remains in a horizontal plane (Fig. 8A). Afterward this process grows into an intercleithra space shaped like the typical basipterygium of this fish (Fig. 8B–E). Three small radial-like cartilaginous masses are recorded by 40 days a. h. (over 16 mm SL), which probably become associated to ray bases, though later they are not recorded among juveniles. The ray occurs among larger 20 day old specimens, though they appear at minor lengths (i.e., 7.49 mm SL) within older specimens. Development and ossification of pelvic rays follow an inner-outer sequence. The ray number development is shown in Fig. 7. Ossification begins by 30 days a. h. (over 11 mm SL) in both, the basipterygium and rays (Fig. 8D). Even at 40 days a. h. the lower part of the basipterygium still remains cartilaginous (Fig. 8E). Branching of pelvic rays apparently start later after metamorphosis. By 38.90 mm SL inner 4 rays of both sides are already branched, and subsequently branching reaches up to 5 in number (Table 1) the smaller ray remaining unbranched. No significant differences are reported between the blind and ocular side in this fin.

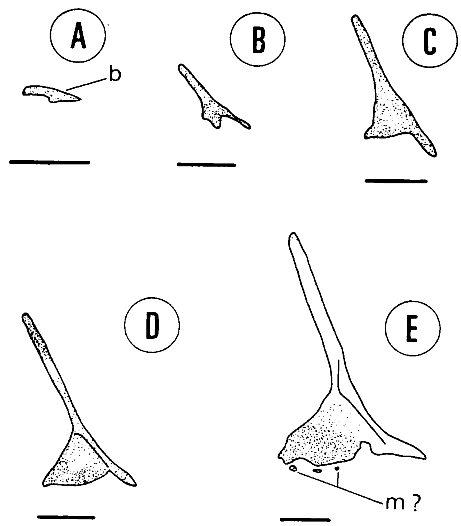

Fig. 8. Development of pelvic fin support in *Paralichthys olivaceus*. A, 7.35 mm SL; B, 8.31 mm SL; C, 9.37 mm SL; D, 11.13 mm SL; E, 16.51 mm SL. b, basipterygium; m, metapterygium. Stippled areas show cartilage. Open areas show developing ossification. Scales indicate 0.25 mm.

Discussion

At the onset of exogenous feeding, swimming abilities become fundamental for searching and capturing prey especially if we consider the high proportion of zooplankton in the diet of *P. olivaceus* (Kuwahara and Suzuki, 1982; Minami, 1982). However, locomotive structures differ scarcely from that already present in the newly hatched larvae, that is, median finfold, pectoral fin bud and notochord. Prelarvae lack rigid mechanical support by which they apply stronger action to the medium without suffering deformation. The notochord offers limitations in this respect in spite of the advantage of its flexibility. Other main restrictions lie in the maneuverability and control of the body position. During the postlarval stage, these limitations are partly overcome by development of cartilaginous structures like pterygiophores, hypurals, neural and haemal arches, and dermal structures like fin rays, vertebral centra and ribs. After metamorphosis all locomotive structures are fully formed.

The caudal complex of *P. olivaceus* resembles that of American *Paralichthys* spp. described by Woolcott et al. (1968), though they made an erroneous interpretation of caudal structures and overlooked the 2nd epural (pictured in their fig. 2).

Fusion of hypural pieces occurs early during caudal development, so it is difficult to judge how many cartliage buds are really involucrated, especially on dorsal plate H 3+4. The actual dorsal plate currently represents 2 elements, but in fact I observed 3 to 4 primordial buds in *P. olivaceus*, and Barrington (1937) described 4 buds in *Pleuronectes platessa*. Other authors failed to note the compound nature of most hypural plates because, either staining methods did not show cartilage details, or just because hypural plates are really fused ab initio. The significance of this developmental trait remains open to question. From this study it is clear that neither uroneurals, urodermals nor ural centra are developed at all in *P. olivaceus*. Some authors consider the uroneural/urodermal as fused to some other caudal structure (e.g., Amaoka, 1969; Kim, 1973; Okiyama, 1974), or interpret other elements with it (e.g., Monod, 1968; Amaoka, 1969; Okiyama, 1974) in spite of the fact that the structure has never been observed during ontogeny (Thompson and Cleve, 1936; Barrington, 1937; Woolcot et al., 1968; Futch et al., 1972; Hensley, 1977; Futch, 1977;

Sumida et al., 1979; Tucker, 1982; present study) within Pleuronectiformes. Ural centra are only presumed by Hensley (1977) and Futch (1977) as being fused to the preural centrum 1 (urostyle of most authors).

Hypural 5 remains distinct throughout development in *P. olivaceus* as well in representatives of the Pleuronectidae (Barrington, 1937; Thompson and Cleve, 1936; Sumida et al., 1979), and the Soleidae (Futch et al., 1972). Conversely, the posteriormost epural, or the unique epural according to the case, merges to the upper hypural (H 5) in some bothid fishes (Hensley, 1977; Futch, 1977), and the same is reported by Tucker (1982) within the Paralichthyidae. An unfused condition may be regarded as primitive whilst a compound one as derived.

Among the Pleuronectiformes formation and ossification of caudal fin support proceed from the ventral side upward, whereas ossification of caudal rays begins near the central rays spreading out dorsally and ventrally. Only Tucker (1982) describes ossification starting ventrally but soon also beginning from the dorsal end of the fin support.

Some caudal characters considered of systematic value, such as presence or absence of uroneurals, lack proper support and consistence as evidenced here and in other developmental works, whereas others should be considered, like the epural number or fusion of epural to hypural 5. Moreover, based on developmental evidence some features can be recognized as primitive or derived, and so bear potential utility for reassessment of systematic characters within the Pleuronectiformes. Caudal terminology should be based on developmental origin as much as possible, especially in this group where fusion of tail structures is common.

The pattern of formation of dorsal and anal fin pterygiophores, that is, from anterior end posteriad, seems to be general within the Pleuronectiformes (Gutherz, 1970; Futch et al., 1972; Hensley, 1977; present author). Distal radial were observed to develop separated from and after serial proximal radial, so corroborating the view of Kohno and Taki (1983). The pattern of ossification differs though there are still few observations in this respect. Dorsal rays ossify from the anterior end posteriad in *Cyclopsetta mbriata* (Gutherz, 1970) and *P. olivaceus* (present author), whereas in *Citharichthys* spp. and *Etropus* spp. the ossification starts centrally spreading out anteriorly and posteriorly (Richardson and Joseph, 1973; Tucker, 1982), As for anal rays all authors agree that the ossification begins from the central rays (Richardson and Joseph, 1973; Tucker, 1982; present author). Pterygiophores of both dorsal and anal fins are reported to begin the ossification from the anteriormost as shown in this study, and the same was stated by Hensley (1977) in *Engyophrys senta*.

The presence of an enlarged 1st dorsal and anal proximal radial is widely recorded among teleost fishes. This observation suggests an early fusion of at least 2 pieces, e.g., Woolcot et al. (1968) and Frame et al. (1978) within the Pleuronectiformes. My findings in *P. olivaceus*, however, show the abdominal rod never derives from 2 pieces, as seems to occur commonly in the Perciformes (Kohno and Taki, 1983), but develops an expanded and complex distal head. The same seems true concerning the anteriormost dorsal proximal radial except for the Cynoglossidae, where a broad cartilage plate occupies the place of several anterior pterygiophores (Ochiai, 1966).

Elongated dorsal fin rays located anteriorly are frequently described during the early life period in most families but Pleuronectidae and Soleidae. When present, the anteriormost elongated ray usually corresponds to the 2nd ray since the 1st ray develops later and never becomes elongated. Their functional meaning is discussed by Moser (1981), whereas their systematic significance is pointed out by Okiyama (1967) and Amaoka (1979).

Sequence of formation of pectoral fin support seems to be common to Pleuronectiformes as well as most teleost fishes. All reports stated pectoral rays developing after eye migration except for *Chascanopsetta lugubris* (Amaoka, 1971), which can reach immense size prior to metamorphosis (i.e., 120 mm SL). The coracoid develops 2 processes during ontogeny in *P. olivaceus*. The posterior process appears in all teleosts but remains somewhat developed mainly among lower teleosts, whilst the anterior process develops well mainly among higher teleost fishes. The cleithrum spination is not developed in *P. olivaceus* as seems to be the rule among paralichthyid fishes (Amaoka, 1979).

Asymmetry in this group is mainly in position rather than in structure, concerning fins. However, Tucker (1982) reports differences in ossification timing between paired fins, and Futch (1977) describes minor ray counts on the right side. Other asymmetry, mainly of ray structure of the pectoral fin, is discussed with a wide material basis by Marsh (1977). As for *P. olivaceus*, a clear trend to fin ray simplification is evident on the blind side within the surveyed range. Marsh (1977), however, points out only segmented foreshortening but not fin ray simplification in the same species.

Sequentially the pelvic fin seems to be the latest to start formation in Pleuronectiformes (Okiyama, 1974; Hensley, 1977; Futch, 1977; Sumida et al., 1979; Tucker, 1982; Minami, 1982; present author), as well in most teleosts. However, completion of this fin occurs, characteristically, prior to pectoral completion in the group, whereas the opposite statement is usual among the Perciformes. Spination on the basipterygium is absent in *P. olivaceus* like in all reported paralichthyid fishes, in contrast to bothid species (Amaoka, 1979).

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(Department of Fisheries, Faculty of Agriculture, Kyoto University, Sakyo-ku, Kyoto 606, Japan)

ヒラメの鰭支持骨の発達

Eduardo F. Balart

ヒラメの対鰭および不対鰭支持骨の発達過程を記載し，それらの形成開始，形，骨化，計数形質について詳細に検討した．すべての鰭支持骨において，胸鰭 (2.62 mm SL)，背鰭 (4.60 mm SL)，尾鰭 (5.55 mm SL)，臀鰭 (5.95 mm SL)，腹鰭 (8.57 mm SL) の順序に従って，まず軟骨が形成された．眼球移動の後，ふ化後 40 日 (約 16 mm SL) までに鰭構造は完成し，部分的に骨化した．本研究は骨格系の発達過程の観察が魚の骨（たとえば尾骨）の同定や用語法を明らかにする可能性を示している．また，カレイ目に属する他魚種と比較したところ，本目魚種の鰭形成過程には基本的なパターンがあり，これは分類学的あるいは系統分類学的に有効である可能性を示唆している．

(606 京都市左京区北白川追分町 京都大学農学部 水産学教室)