

Osteological Development in the Red Sea Bream, *Pagrus major*

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Abstract The developmental process of all osteological elements except the scale in the red sea bream, *Pagrus major*, was described from prelarvae to late juveniles. The larvae at first-feeding stage exhibited only some elements of head skeleton and pectoral fin-supports, which were mostly cartilaginous structures except the maxillary and cleithrum. The completion of osteological structures was characterized by the formation of accessory cartilages 7 and 8 of the caudal skeleton and the ossification of middle radials of dorsal and anal fin-supports. Reared and wild specimens reaching this stage seemed to be different in size. An attempt to summarize the osteological development was made on the basis of the counts of considerable changes, e.g., the initial appearance of cartilage, the full complement of cartilages, the beginning of ossification and the full complement of ossified structures for respective elements. A histogram of those counts against total length consisted of several peaks suggesting the ontogenetic intervals in this species.

Recently, information on the cartilaginous-osteological development of teleostean fishes has been increasing (see, Kohno and Taki, 1983; Potthoff *et al.*, 1984), to provide the basic knowledge for larval taxonomy and systematics (Dunn, 1983), developmental functional morphology (Kohno *et al.*, 1983; Kohno *et al.*, 1984) and production of larvae for fish farming (Matsuoka, 1982).

Matsuoka (1982) reported the developmental process of the vertebral column and caudal skeleton in reared and wild specimens of the red sea bream, *Pagrus major* (Temminck et Schlegel). Kohno *et al.* (1983) also examined the osteological and morphological development of some characters related to swimming and feeding functions in a relatively limited size range of the same species. The present study was undertaken to pursue the development of all osteological elements, except the scale, from their initial appearance to completion in this species.

Materials and methods

A series of 376 laboratory-produced specimens from prelarvae to juveniles up to 40.0 mm in total length, reared in Fukui Prefectural Fisheries Farming Center, was used for most of the descriptions. Supplemental observations were made on 25 specimens (range 31.0–72.0 mm TL) reared in the Aquaculture Research Laboratory, Nagasaki Prefectural Institute of Fisheries, 14

wild specimens (range 35.0–83.4 mm TL) caught in the coastal area of Onomichi, Hiroshima Prefecture and a wild specimen (151.0 mm TL) caught in Wakasa Bay.

Specimens fixed in 10% formalin solution were cleared and stained, using the method of Taylor (1967) for bone, and the method of Dingerkus and Uhler (1977) for both bone and cartilage.

Total length was measured after clearing and staining.

Some specimens fixed in Bouin's solution were embedded in paraffin, sectioned at 5–8 μ m, stained with hematoxylin, eosin and alcian blue and used for histological observation.

Bone terminology generally followed Houde and Potthoff (1976), Leiby (1979, 1981) and Rosen and Parenti (1981).

Results

Neurocranium. In a 2.90 mm TL specimen, shortly prior to onset of feeding, the ethmoid plate, trabecula and parachordal cartilages were present and joined together. The lateroventral parts of the auditory capsules were condried and connected with the parachordals (Fig. 1A).

In a 4.35 mm TL specimen, the supraorbital bars and occipital processes were condried (Fig. 1B).

In a 5.90 mm TL specimen, complete cartilaginous auditory capsules were formed. The epiphysial tectum and ectethmoid bars were condried. The frontals and parasphenoid

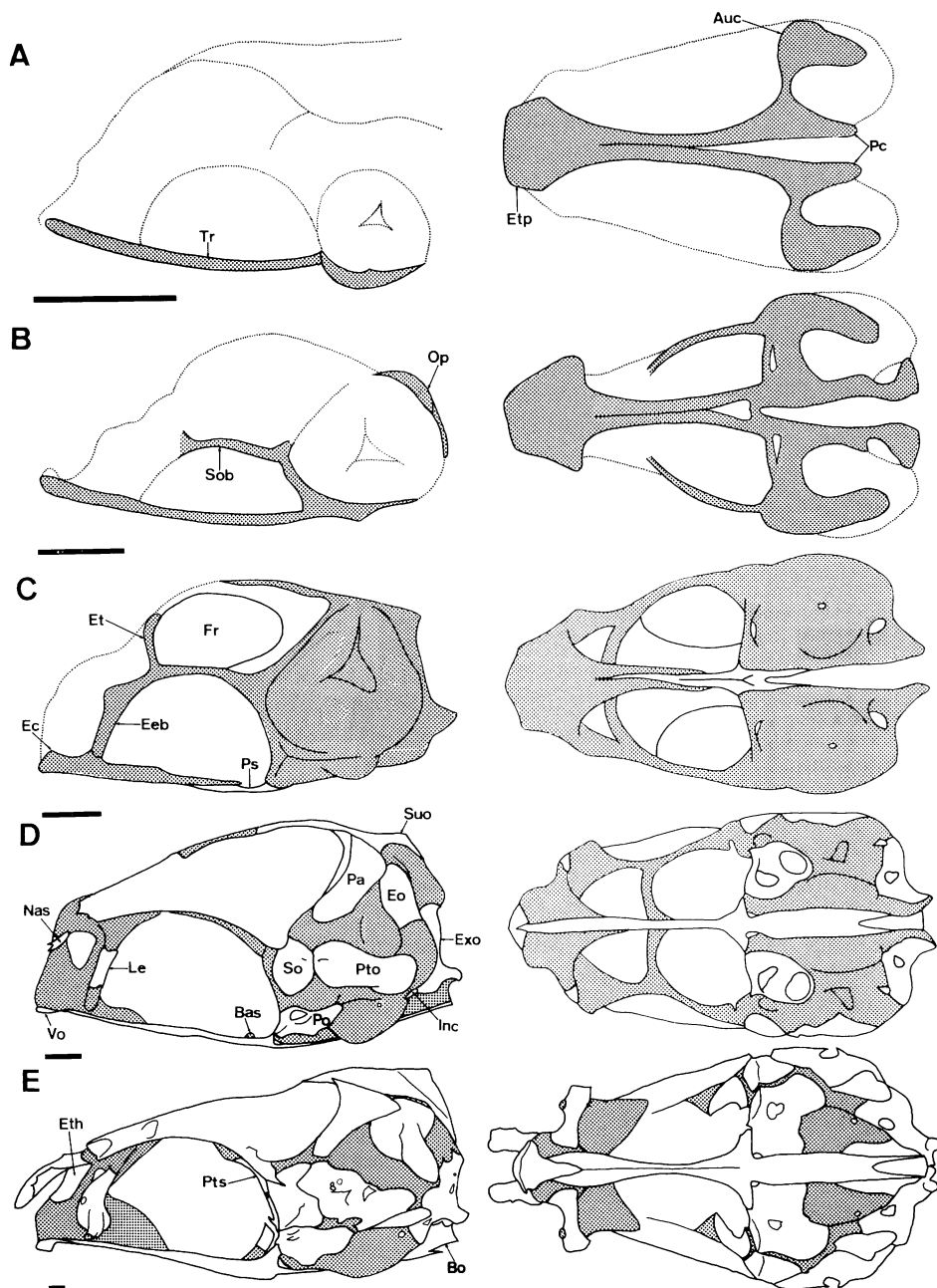


Fig. 1. Development of neurocranium in *Pagrus major*. A, 2.90 mm in total length. B, 4.35 mm. C, 5.90 mm. D, 8.50 mm. E, 20.1 mm. Left, lateral view. Right, ventral view. Stippled area, cartilage. Open area, ossified portion. Auc, auditory capsule; Bas, basisphenoid; Bo, basioccipital; Ec, ethmoid cartilage; Eeb, ectethmoid bar; Eo, epiotic; Et, epiphyseal tectum; Eth, ethmoid; Etp, ethmoid plate; Exo, exoccipital; Fr, frontal; Inc, intercalar; Le, lateral ethmoid; Nas, nasal; Op, occipital process; Pa, parietal; Pc, parachordal; Po, prootic; Ps, parasphenoid; Pto, pterotic; Pts, pterospheneid; So, sphenotic; Sob, supraorbital bar; Suo, supraoccipital; Tr, trabecula; Vo, vomer. Scale bars indicate 0.2 mm.

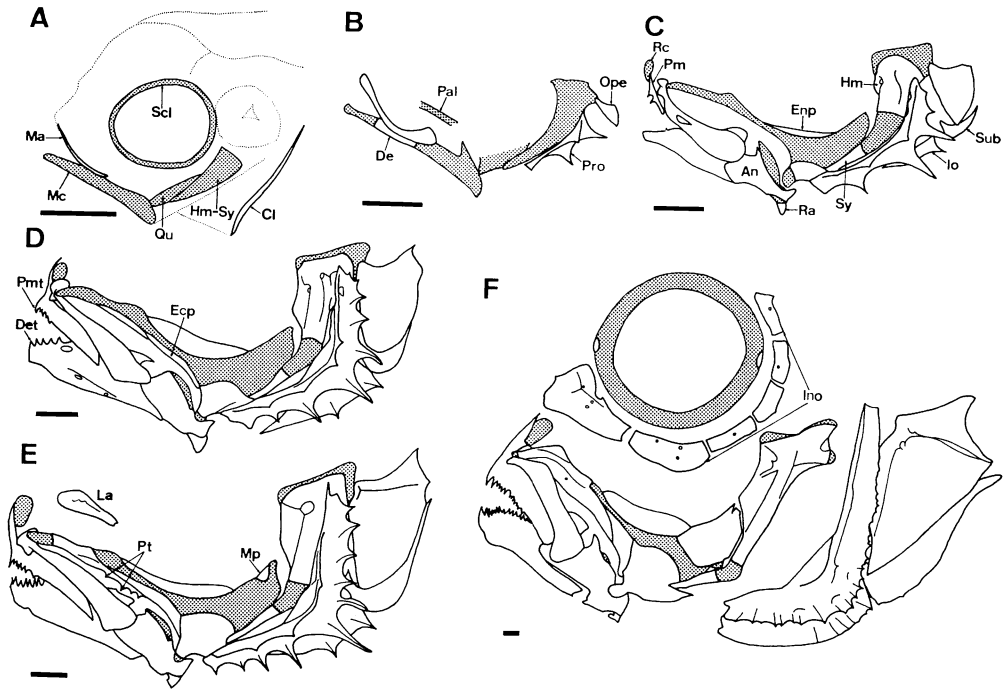


Fig. 2. Development of sclerotic and infraorbital bones, suspensorium, opercular bones and upper and lower jaws in *Pagrus major*. A, 2.90 mm in total length. B, 4.35 mm. C, 5.90 mm. D, 6.85 mm. E, 8.50 mm. F, 20.1 mm. Lateral view. Sclerotic is removed in B–E. Stippled area, cartilage. Open area, ossified portion. An, angular; Cl, cleithrum; De, dentary; Det, dentary teeth; Ecp, ectopterygoid; Enp, endopterygoid; Hm, hyomandibular; Hm-Sy, hyomandibular-symplectic cartilage; Ino, infraorbital; Io, interopercle; La, lachrymal; Ma, maxillary; Mc, Meckel's cartilage; Mp, metapterygoid; Ope, opercle; Pal, palatine; Pm, premaxillary; Pmt, preopercle; Pt, palatine teeth; Qu, quadrate; Ra, retroarticular; Rc, rostral cartilage; Scl, sclerotic; Sub, subopercle; Sy, symplectic. Scale bars indicate 0.2 mm.

were formed by fibrous ossification. The ethmoid cartilage was a small dorsal flange on the ethmoid plate cartilage. There was no direct cartilaginous connection between the trabecula and auditory capsule cartilage. This interspace was replaced by the parasphenoid (Fig. 1C).

The parietals (fibrous ossification), epiotics, pterotics, sphenotics, prootics, supraoccipital, exoccipital and basioccipital were almost simultaneously ossified at about 6.5 mm TL. The basioccipital was initially formed by fibrous ossification, surrounding the anterior tip of notochord, but later the ossification extended to the adjacent cartilaginous region.

In a 8.50 mm TL specimen, the frontals fully extended and made up the dorsal wall of neuro-

cranium. The nasals, vomer and intercalars were formed by fibrous ossification. The parasphenoid extended along almost the entire length of the base of the neurocranium. A small cartilaginous basisphenoid existed on the parasphenoid. The ethmoid cartilage was fully developed and the lateral ethmoids were ossified (Fig. 1D).

The pterosphenioids were preformed as cartilage and later ossified at about 9 mm TL. The ethmoid and basisphenoid were ossified at about 9 and 10 mm TL, respectively. All elements of the neurocranium appeared at about 10 mm TL, though the cartilaginous area still considerably existed in the neurocranium of a 20.1 mm TL specimen (Fig. 1E).

The intercalars became obscure in a 151.0 mm TL specimen, because of fusion with the

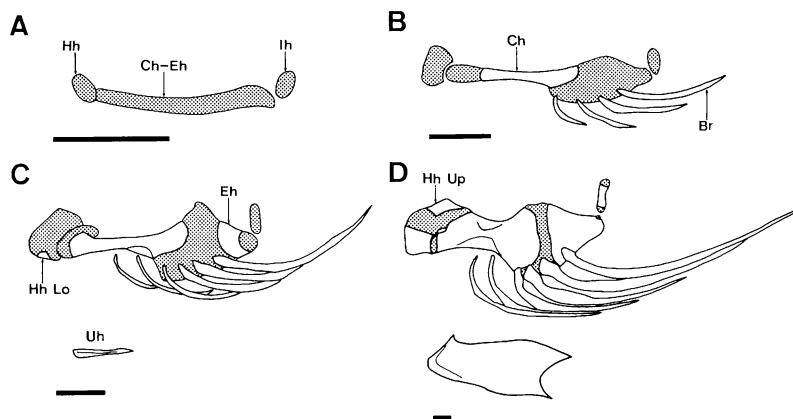


Fig. 3. Development of hyoid arch in *Pagrus major*. A, 2.90 mm in total length. B, 5.90 mm. C, 6.85 mm. D, 20.1 mm. Lateral view. Basihyal is shown in Fig. 4. Stippled area, cartilage. Open area, ossified portion. Br, branchiostegal ray; Ch, ceratohyal; Ch-Eh, ceratohyal-epihyal cartilage; Eh, epihyal; Hh, hypohyal; Hh Lo, hypohyal lower; Hh Up, hypohyal upper; Ih, interhyal; Uh, urohyal. Scale bars indicate 0.2 mm.

pteroics (Tomiya, 1931).

Sclerotic and infraorbital bones. In a 2.90 mm TL specimen, the lateral edge of eye capsule was surrounded by a thin sclerotic cartilage or eye band (Fig. 2A).

In a 8.50 mm TL specimen, the lachrymal was formed by fibrous ossification (Fig. 2E). Five infraorbitals were also formed by fibrous ossification between about 9 and 13 mm TL.

The anterior ossified area in the sclerotic cartilage appeared at about 15.5 mm TL and the posterior one appeared at about 20 mm TL (Fig. 2F).

Jaws. In a 2.90 mm TL specimen, the Meckel's cartilage was fully developed, framing the lower jaw, and the flangellumlike maxillary was formed on the upper jaw edge by weak fibrous ossification (Fig. 2A).

The dentary began to be formed outside the anterior region of Meckel's cartilage by fibrous ossification by about 4 mm TL (Fig. 2B). The angular and retroarticular were ossified on the posterior region of Meckel's cartilage by about 5 mm TL.

In a 5.90 mm TL specimen, all elements of upper and lower jaws except the splenial appeared. The premaxillary (fibrous ossification) and rostral cartilage were present. Small premaxillary and dentary teeth also appeared (Fig. 2C), more visible in a 6.85 mm TL specimen

(Fig. 2D).

The splenial was ossified on the laterodorsal face of posterior region of Meckel's cartilage at about 8.5 mm TL.

Suspensorium. In a 2.90 mm TL specimen, the hyomandibular-symplectic and quadrate cartilages were present (Fig. 2A).

In a 4.35 mm TL specimen, the mid region of palatine began to be condried (Fig. 2B).

By about 5 mm TL, the quadrate, symplectic and hyomandibular were ossified, and the cartilage contiguous to the quadrate extended to the metapterygoid region.

In a 5.90 mm TL specimen, the endopterygoid was formed by fibrous ossification (Fig. 2C).

In a 6.85 mm TL specimen, the ectopterygoid was formed by fibrous ossification and the palatine cartilage possessed the ossified ventral keel (Fig. 2D).

In a 8.50 mm TL specimen, the palatine cartilage was ossified in the mid region and a few small teeth were temporarily formed on the posterior ventral edge of palatine. The metapterygoid was ossified (Fig. 2E).

The palatine teeth disappeared by about 15.5 mm TL (Fig. 2F).

Opercular bones. All elements of the opercular apparatus were formed by fibrous ossification. The preopercle and opercle appeared at about 3.5 mm TL (Fig. 2B). The interopercle and

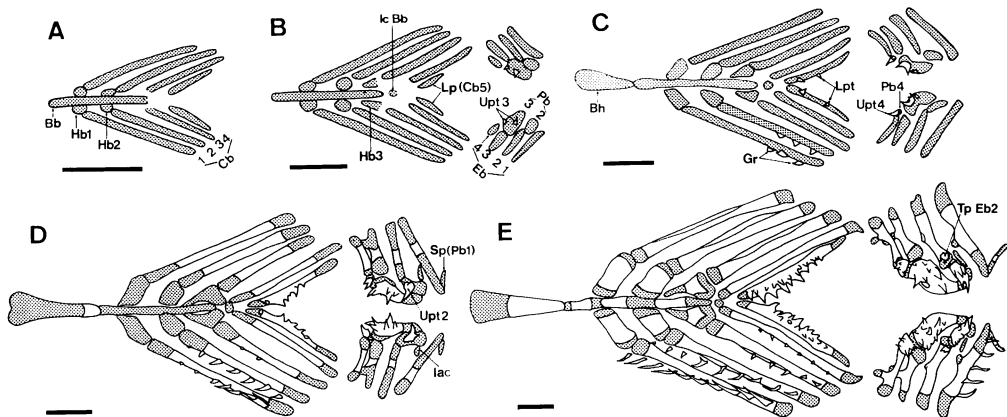


Fig. 4. Development of upper and lower branchial arches in *Pagrus major*. A, 2.90 mm in total length. B, 4.35 mm. C, 5.90 mm. D, 6.85 mm. E, 10.0 mm. Upper branchial arches, ventral view. Lower branchial arches, dorsal view. Gill rakers of right body side are removed in C-E. Stippled area, cartilage. Open area, ossified portion. Bb, basibranchial; Bh, basihyal; Cb, ceratobranchial; Eb, epibranchial; Gr, gill raker; Hb, hypobranchial; Iac, interarcual cartilage; Ic Bb, isolated cartilage of basibranchial; Lp, lower pharyngeal; Lpt, lower pharyngeal teeth; Pb, pharyngobranchial; Sp, suspensory pharyngeal; Tp Eb 2, tooth plate of epibranchial 2; Upt, upper pharyngeal teeth. Scale bars indicate 0.2 mm.

subopercle appeared at about 5 mm TL (Fig. 2C).

The preopercular and interopercular spines were noticeable in the earlier stages (Fig. 2B-E), but later became vestigial (Fig. 2F).

Hyoid arch. In a 2.90 mm TL specimen, the hypohyal, ceratohyal-epihyal and interhyal cartilages were present (Fig. 3A).

In a 5.90 mm TL specimen, the ceratohyal was ossified in the anterior region of ceratohyal-epihyal cartilage and four branchiostegal rays were formed by fibrous ossification (Fig. 3B). The basihyal was condried (Fig. 4C).

The branchiostegal rays began to be formed from posterior to anterior at about 4.5 mm TL and the full complement of six rays was accomplished by about 6.5 mm TL.

In a 6.85 mm TL specimen, the lower hypohyal was ossified in the lower region of hypohyal cartilage and the epihyal was also ossified in the posterior region of ceratohyal-epihyal cartilage. The urohyal was formed as a thin rod by fibrous ossification (Fig. 3C). The posterior tip of basihyal was ossified (Fig. 4D).

The upper hypohyal was ossified at about 8 mm TL in the upper region of hypohyal cartilage.

The urohyal gradually extended vertically

with growth (Fig. 3D).

Branchial arches. In a 2.90 mm TL specimen, the basibranchial, two pairs (first and second) of hypobranchials and four pairs (first to fourth) of ceratobranchials were present as cartilage, but there was no trace of upper branchial arches (Fig. 4A).

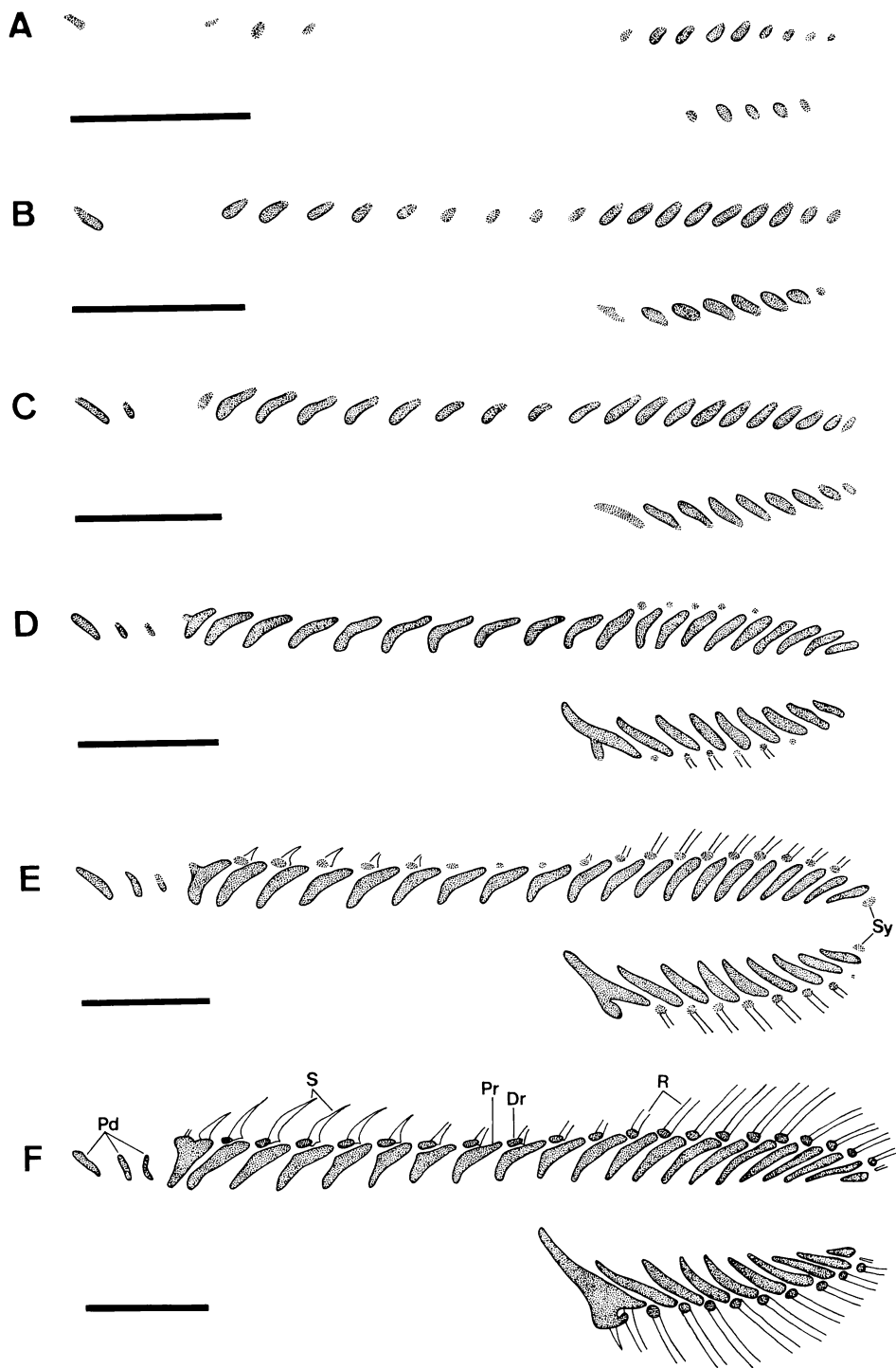
The isolated cartilage of basibranchial, third pair of hypobranchials, a pair of lower pharyngeals (fifth pair of ceratobranchials), three pairs (first to third) of epibranchials and two pairs (second and third) of pharyngobranchials were condried between about 3.5 and 4 mm TL. A few upper pharyngeal teeth were also formed on the third pair of pharyngobranchials.

In a 4.35 mm TL specimen, the fourth pair of epibranchials was condried (Fig. 4B).

A few lower pharyngeal teeth appeared at about 5 mm TL.

In a 5.90 mm TL specimen, the fourth pair of pharyngobranchials was condried, with a respective single tooth. The fourth pair of pharyngobranchials remained cartilaginous even in the largest specimen examined, 151.0 mm TL. The gill rakers were present on the first and second pairs of ceratobranchials (Fig. 4C).

Beyond about 6 mm TL, the four pairs of



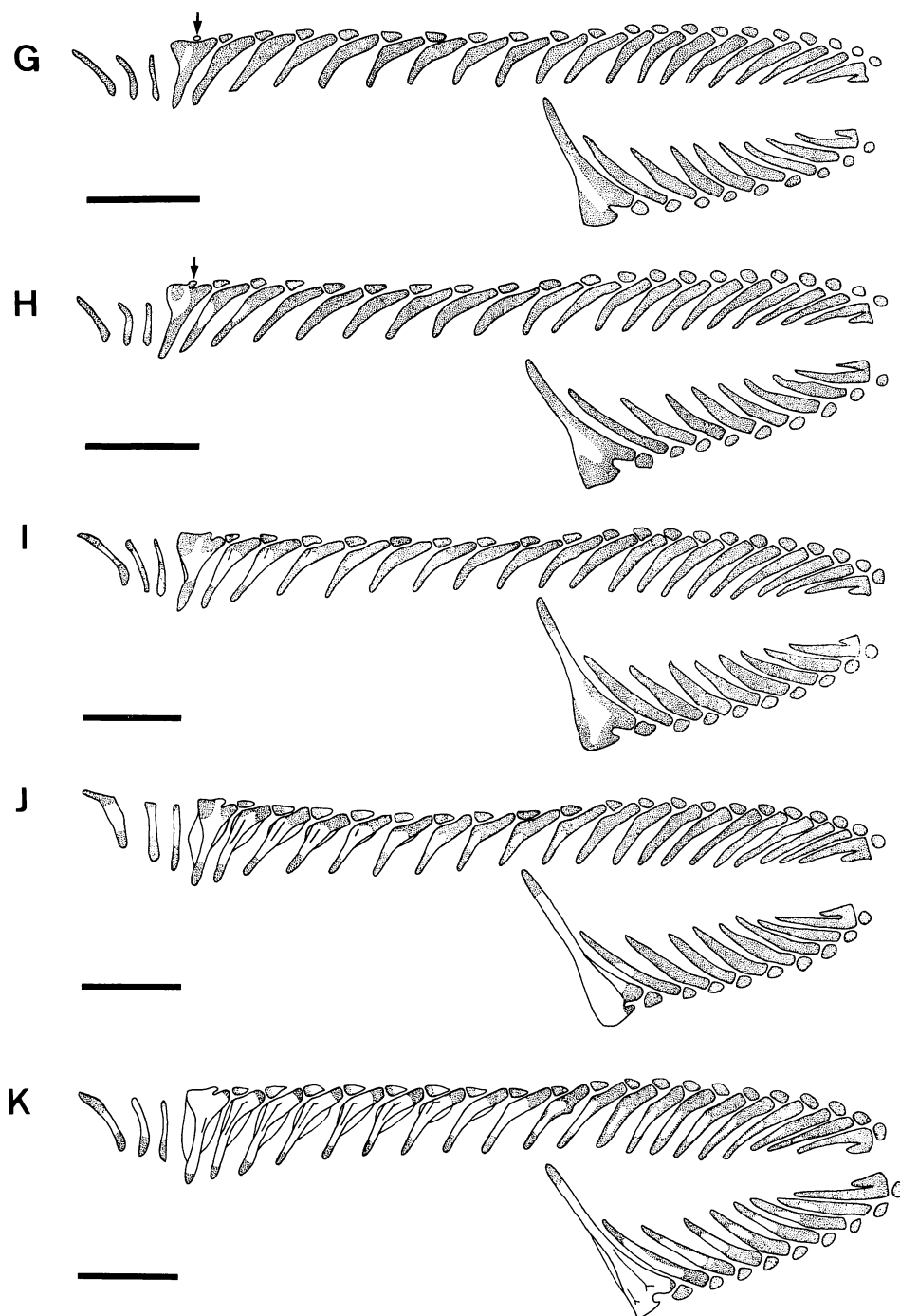


Fig. 5. Development of dorsal and anal fin-supports in *Pagrus major*. A, 5.80 mm in total length. B, 5.85 mm. C, 6.40 mm. D, 6.85 mm. E, 7.25 mm. F, 7.75 mm. G, 8.50 mm. H, 8.85 mm. I, 9.75 mm. J, 10.0 mm. K, 10.5 mm. Lateral view. Rays are removed in G–K. Arrows in G and H show transient first distal radial of dorsal fin-supports. Stippled area, cartilage. Open area, ossified portion. Dr, distal radial; Pd, predorsal; Pr, proximal radial; R, soft ray; S, spine; Sy, stay. Scale bars indicate 0.5 mm.

ceratobranchials and a pair of lower pharyngeals were ossified, and a pair of suspensory pharyngeals (first pair of pharyngobranchials) was condried.

In a 6.85 mm TL specimen, the four pairs of epibranchials and the second and third pairs of pharyngobranchials were ossified. A few teeth were present on the second pair of pharyngobranchials. A pair of rodlike cartilages, interarcual cartilage of Allis (1915), was present between the first epibranchial and second pharyngobranchial. The gill rakers began to be formed on the third pair of ceratobranchials (Fig. 4D).

The gill rakers on the fourth pair of ceratobranchials were present beyond 7 mm TL. Three ossified regions of basibranchial and the tooth plates on the second pair of epibranchials were formed at about 7.5 and 8 mm TL, respectively. Three pairs of hypobranchials were ossified between about 8 and 8.5 mm TL. A pair of suspensory pharyngeals was ossified at about 10 mm TL. All elements of the branchial arches appeared at this stage (Fig. 4E).

Dorsal and anal fin-supports. Three predorsals were condried from anterior to posterior between about 6 and 7 mm TL (Fig. 5A–D).

The cartilage formation of dorsal proximal radials proceeded anteriorly and posteriorly from two centers, around the third and fifteenth ones, respectively, between about 6 and 6.5 mm TL (Fig. 5A–C).

In the case of anal proximal radials, the cartilage formation proceeded anteriorly and posteriorly from the fourth or fifth one between about 6 and 6.5 mm TL (Fig. 5A–C).

The first proximal radials of dorsal and anal fin-supports possessed the anterior cartilaginous process (Fig. 5D, E), which was not separated from the main parts even at the initial appearance.

After the full complement of proximal radials, the cartilage formation of dorsal and anal distal radials proceeded in the similar sequence as the proximal radials by about 7.5 mm TL (Fig. 5D, E, F).

Shortly after the appearance of distal radials, the rudiments of dorsal and anal fin rays were formed and ossified, and the full complements were accomplished by about 8 mm TL (Fig. 5E, F).

The stay cartilage in dorsal and anal fin-

supports was formed at about 7 mm TL as the separated cartilage mass (Fig. 5E, F) but later fused with the immediate anterior middle-proximal radial (Fig. 5G).

Just above the first proximal radial of dorsal fin-supports, a small cartilage was temporarily formed (arrow in Fig. 5G) and articulated with the second spine. It seemed to be a vestigial distal radial but shortly later fused with the first proximal radial (arrow in Fig. 5H). Such a cartilage was not observed in the first proximal radial of anal fin-supports.

The ossification of dorsal and anal fin-supports started simultaneously at the first proximal radials at about 8.5 mm TL (Fig. 5G). The following ossification proceeded posteriorly in the dorsal proximal radials (Fig. 5H, I), and when it reached around the tenth one, the second proximal radial of anal fin-supports began to be ossified (Fig. 5J). The posteriormost proximal radials of dorsal and anal fin-supports were ossified at about 10.5 mm TL (Fig. 5K).

The ossification of distal radials proceeded from anterior to posterior between about 9 and 15.5 mm TL in the dorsal fin-supports, and between about 10 and 15.5 mm TL in the anal fin-supports, respectively (Fig. 5I, J, K).

The predorsals were ossified between 8.7 and 9.7 mm TL. The anteriormost one was the last to be ossified (Fig. 5H, I).

The stay cartilages of dorsal and anal fin-supports were ossified at about 25 mm TL (Fig. 6A).

The numbers of middle radials were considerably variable in both reared and wild specimens, ranging from two to four in dorsal and from one to four in anal fin-supports. About one half of specimens possessed three dorsal middle radials and two anal ones.

The middle radials were ossified from anterior to posterior on the cartilaginous regions contiguous to the ossified proximal radials (Fig. 6B, C, D). The ossification of anal middle radials slightly preceded that of dorsal ones. In the reared specimens smaller than 42 mm TL, no ossification of middle radials was observed. The smallest specimen with all ossified middle radials was 56.0 mm TL and the middle radials in the largest reared one examined, 72.0 mm TL, were still uncompleted. On the other hand, wild specimens beyond 45 mm TL exhibited

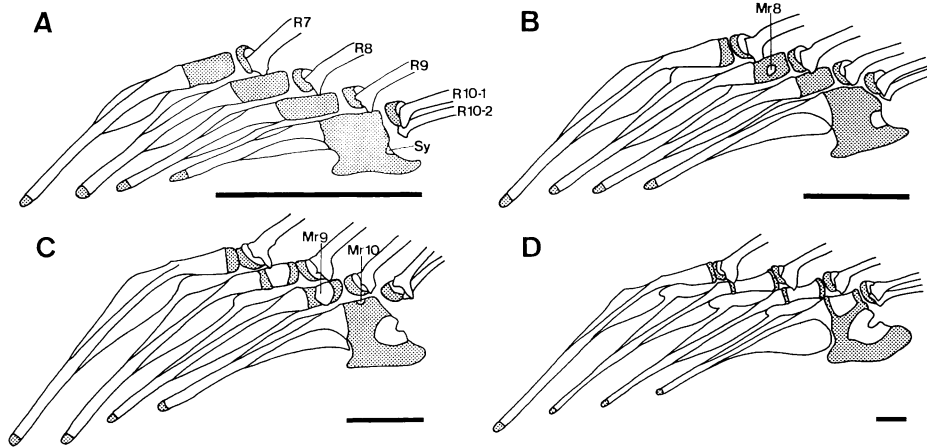


Fig. 6. Development of posterior part of dorsal fin-supports in *Pagrus major*. A, 25.6 mm in total length. B, 45.4 mm. C, 61.0 mm. D, 151.0 mm. Lateral view. Stippled area, cartilage. Open area, ossified portion. Mr, middle radial; R, soft ray; Sy, stay. Scale bars indicate 1 mm.

all ossified middle radials.

Pectoral fin-supports. In a 2.80 mm TL specimen, the needlelike cleithrum was formed by fibrous ossification, and the fin plate (Swinerton, 1905) and coracoid-scapula cartilages were present and continuous together. The former cartilage was relatively immature and one cell thick, but the latter was two or three cells thick. In the coracoid-scapula cartilage, the posterior process of coracoid was dominant (Fig. 7A).

The fin plate cartilage was creviced in the anterior middle region at about 3.5 mm TL (Fig. 7B).

The fin plate cartilage was separated from the coracoid-scapula cartilage at about 5 mm TL. The supracleithrum, posttemporal and lower postcleithrum were successively formed by fibrous ossification between about 5 and 5.5 mm TL. The anterior process of the coracoid gradually elongated. The scapular cartilage elongated dorsally and enclosed the scapular foramen (Fig. 7C, D).

The second crevice in the fin plate cartilage appeared dorsally and the third one ventrally on both sides of the first one between about 5.5 and 6 mm TL (Fig. 7D, E).

Between about 6 and 6.5 mm TL, the rudiments of fin rays began to be formed and ossified from dorsal to ventral, and the upper postcleithrum was formed by fibrous ossification.

A small cartilage, propterygium of Jessen (1972), was formed above the fin plate cartilage (Fig. 7F). Later the propterygium was fused with the inner basal half of marginal (uppermost) ray and ossified (Fig. 8A-E).

The lower and upper supratemporals were formed by fibrous ossification at about 8.5 and 9 mm TL, respectively (Fig. 7G, H).

The scapula and coracoid were ossified simultaneously at about 8 mm TL. The ossification center of the scapula was behind the scapular foramen, and that of the coracoid was in the basal part of the anterior process (Fig. 7G). The fin plate cartilage was completely divided by three crevices into four actinosts by about 9 mm TL. The ossification of the actinosts occurred from dorsal to ventral between about 8.5 and 9.5 mm TL (Fig. 7G, H).

The full complement of pectoral fin rays was accomplished by about 9.5 mm TL. The distal radials were condried from dorsal to ventral, following the appearance of fin rays (Fig. 7G), and their full complement was accomplished by about 11 mm TL. The distal radials were not ossified even in the largest specimen examined, 151.0 mm TL.

The cartilaginous posterior process of the coracoid was gradually shortened and almost disappeared between about 8.5 and 13 mm TL (Fig. 7G, H, I).

Pelvic fin-supports. The membranous fin

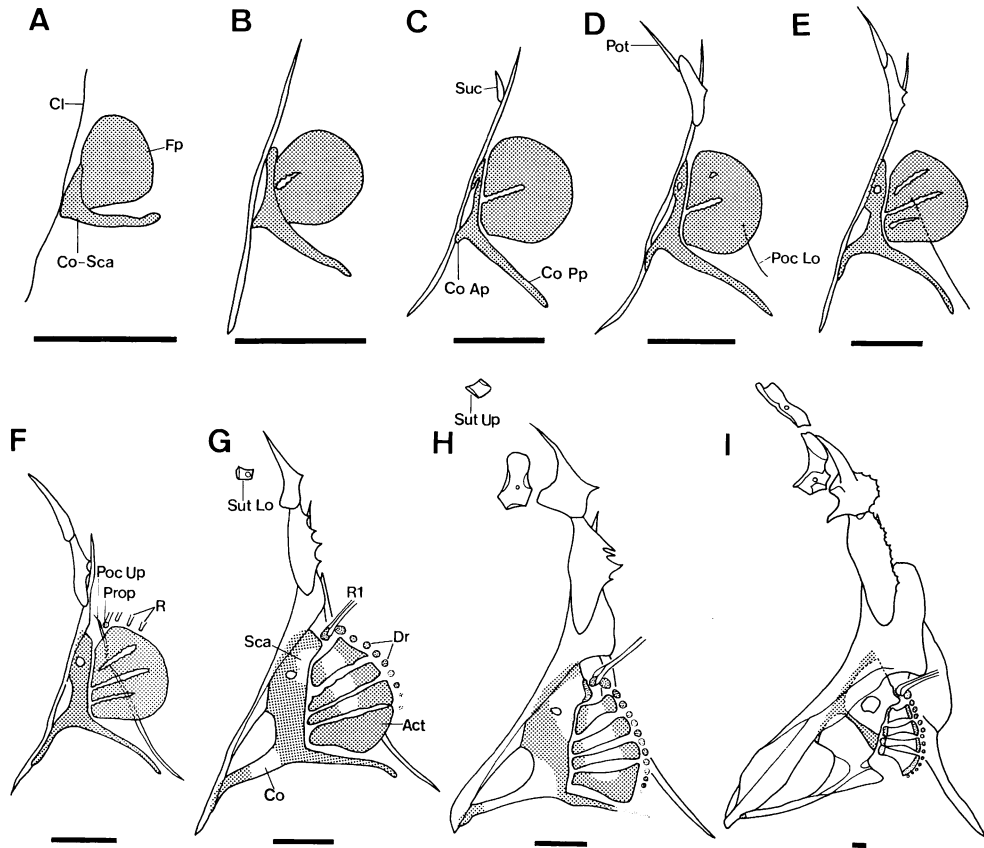


Fig. 7. Development of pectoral fin-supports in *Pagrus major*. A, 2.80 mm in total length. B, 3.70 mm. C, 5.25 mm. D, 5.50 mm. E, 5.85 mm. F, 6.40 mm. G, 8.80 mm. H, 10.0 mm. I, 35.0 mm. Lateral view. Rays except marginal one are removed in G–I. Stippled area, cartilage. Open area, ossified portion. Act, actinost; Cl, cleithrum; Co, coracoid; Co Ap, coracoid anterior process; Co Pp, coracoid posterior process; Co-Sca, coracoid-scapula cartilage; Dr, distal radial; Fp, fin plate cartilage; Poc Lo, postcleithrum lower; Poc Up, postcleithrum upper; Pot, posttemporal; Prop, propterygium; R, soft ray; Sca, scapula; Suc, supracleithrum; Sut Lo, supratemporal lower; Sut Up, supratemporal upper. Scale bars indicate 0.3 mm.

fold of the pelvic fin appeared at about 6 mm TL and the basipterygium was condried at about 6.5 mm TL (Fig. 9A). The basipterygium gradually elongated and began to be ossified at the posterior region at about 8.5 mm TL (Fig. 9B), and the anterior tip reached the cleithrum at about 10 mm TL (Fig. 9C).

The rudiments of fin rays began to be formed and ossified from outer to inner at about 7 mm TL and their full complement was accomplished by about 8.5 mm TL.

A small cartilage, metapterygium of Sewertzoff (1934), was formed behind the basipterygium by about 9 mm TL (Fig. 9B). The meta-

pterygium was fused with the ventral basal half of the innermost fin ray and ossified later (Fig. 9D).

More detailed sequences of cartilaginous-osteological development in the reared specimens, including the vertebral column and caudal skeleton, are shown in Figs. 10 and 11.

Discussion

Some additional comments should be referred to concerning the osteological structures of *Pagrus major*. A few palatine teeth, not observed in the adults of spariform fishes (Nemipteridae, Sparidae and Lethrinidae) (Akazaki, 1962), tem-

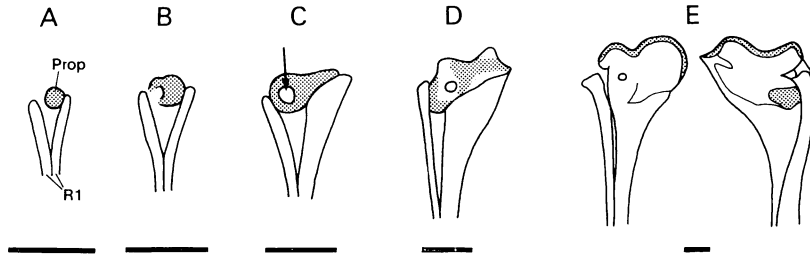


Fig. 8. Development of propterygium of pectoral fin-supports in *Pagrus major*. A, 6.25 mm in total length. B, 6.85 mm. C, 9.75 mm. D, 18.7 mm. E, 35.0 mm. Dorsal view (A-D). Dorsal (left) and ventral (right) views (E). Arrow in C shows canal through propterygium. Stippled area, cartilage. Open area, ossified portion. Prop, propterygium; R, soft ray. Scale bars indicate 0.1 mm.

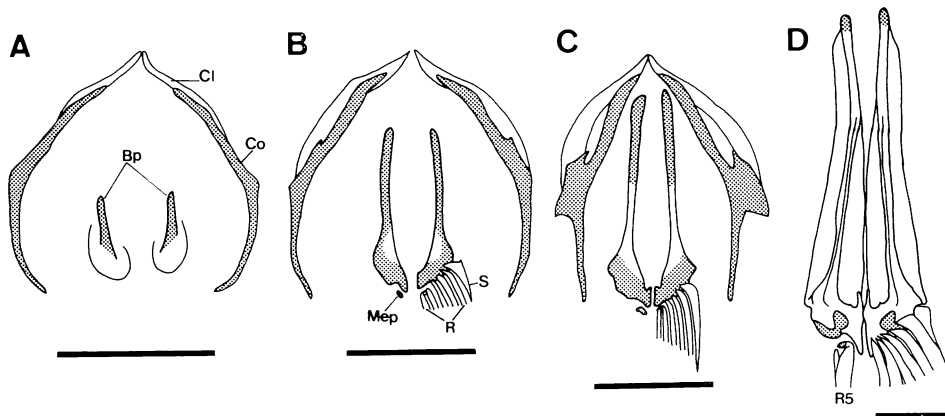


Fig. 9. Development of pelvic fin-supports in *Pagrus major*. A, 6.85 mm in total length. B, 8.85 mm. C, 9.75 mm. D, 20.0 mm. Ventral view. Pectoral fin-supports are also shown in A-C. Rays of right body side are removed in B and C and innermost ray fused with metapterygium is shown in D. Stippled area, cartilage. Open area, ossified portion. Bp, basipterygium; Cl, cleithrum; Co, coracoid; Mep, metapterygium; R, soft ray; S, spine. Scale bars indicate 0.5 mm.

porarily existed in the larvae and early juveniles of *P. major*. Shinohara (1966) reported that the palatine teeth tend to disappear with age in *Glabrilutjanus nematophorus* in the Lutjanidae, closely related to the spariform fishes. Therefore, the palatine teeth of *P. major* seem to be vestigial reduced structures in ontogeny as the intercalar, which disappears with growth by fusion with the pterotic (Tomiya, 1931).

In regard to the development of the first dorsal proximal radial in *P. major*, Kohno *et al.* (1983) and Kohno and Taki (1983) indicated its derivation from two cartilaginous pieces. Similar observations were made in *Morone americana* (Fritzsche and Johnson, 1980) and *Anisotremus*

virginicus (Potthoff *et al.*, 1984). In my observations, however, the usual development did not show the fusion of two elements or the formation of foramen within the first proximal radial described by Kohno *et al.* (1983: fig. 2C and D). Several larvae having a relatively large process or separated cartilage from the first proximal radial were observed, but they seem to become abnormal juveniles with the malformed first proximal radial or the additional proximal radial just anterior to the first one, frequently found in the reared specimens (Matsuoka, unpublished data). In spite of the lack of fusion during usual ontogeny, there is no doubt that the first dorsal proximal

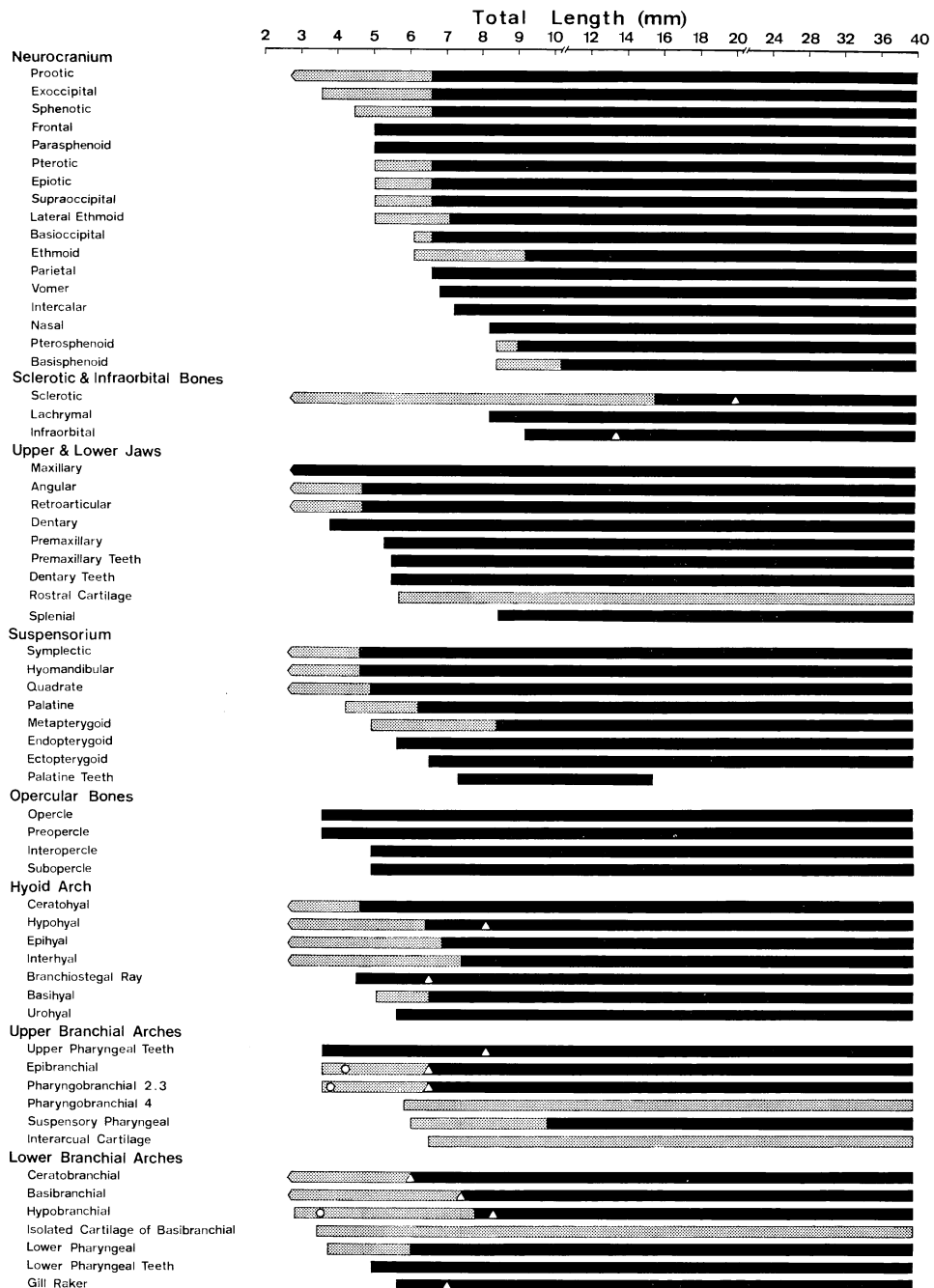


Fig. 10. Developmental sequence of head skeleton in reared *Pagrus major*. Stippled bar, cartilaginous state. Solid bar, ossified state. O, full complement of cartilages. Δ, full complement of ossified structures.

radial has been originally derived from at least two elements through evolution, when thinking that this proximal radial temporarily possesses

two distal radials as shown by the present study.

Kohno and Taki (1983) suggested that the

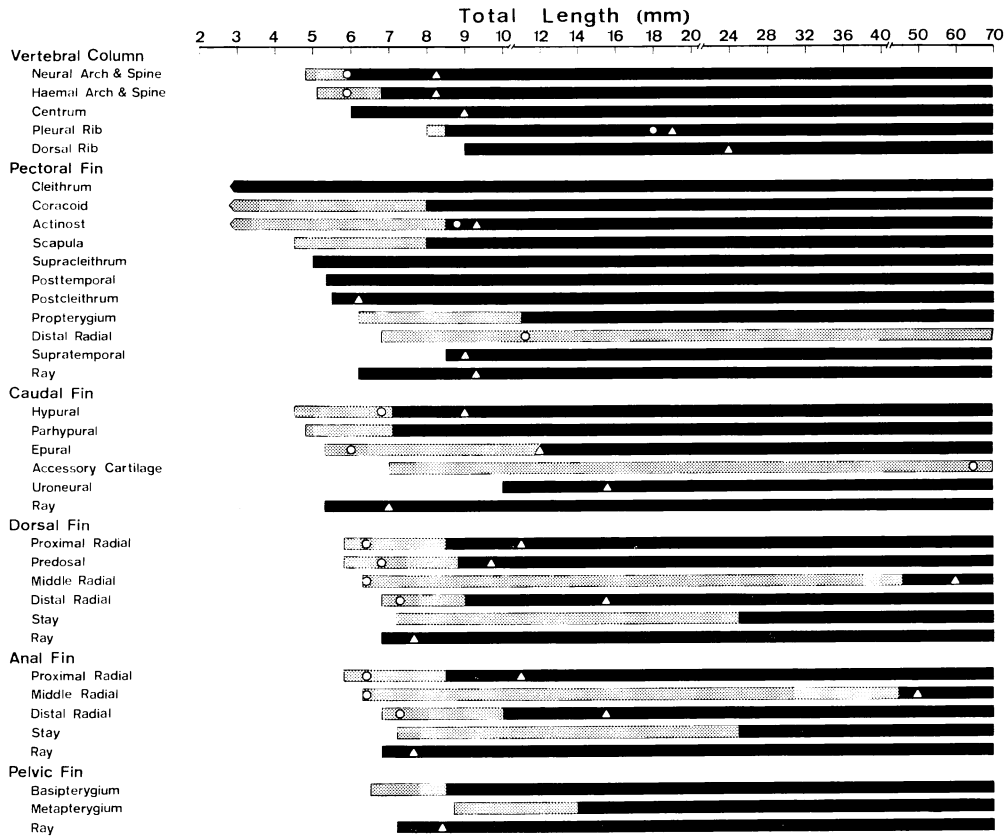


Fig. 11. Developmental sequence of vertebral column and fin-supports and rays in reared *Pagrus major*. Stippled bar, cartilaginous state. Solid bar, ossified state. Symbols are the same in Fig. 10.

“pectoral condyle” of *P. major* may be homologous with the distal radials. However, their “pectoral condyle” is not the structure represented by the same term by Starks (1930) but should correspond to the propterygium of Jessen (1972). The propterygium in the actinopterygians is generally characteristic of the fusion with the basal half of marginal (uppermost) ray and the penetration of nerve and vessel. Although the propterygium of *P. major* lacks the process of separation from the fin plate cartilage, different from that of *Clupea* (illustrated in Goodrich (1922)), *Engraulis* and *Oncorhynchus* (Kohno and Taki, 1983), it is not homologous with the distal radials.

Figures 12 and 13 summarize the counts of noticeable changes in the osteological development, for example, the initial appearance of cartilage, the full complement of cartilages, the beginning of ossification and the full comple-

ment of ossified structures for respective elements, based on Figs. 10 and 11. The counts were made in each 0.5 mm size range (less than 10 mm TL), each 1 mm (10 to 20 mm TL) or each 5 mm (beyond 20 mm TL). This treatment may be useful for total understanding of osteological development as an aggregation of qualitative changes.

Figure 12 shows the cumulative percentage of the counts of already occurred changes against total length for four skeletal groups, the neurocranium, head skeleton except the neurocranium, vertebral column and fin-supports and rays. It may show the “developmental degree of osteological characters”. All lines pass through a sigmoid pattern. In the head skeleton except the neurocranium, the value at first-feeding stage (about 3 mm TL) is the highest of four skeletal groups, about 20%, and it reaches about 95% at 10 mm TL. In the neurocranium, the value

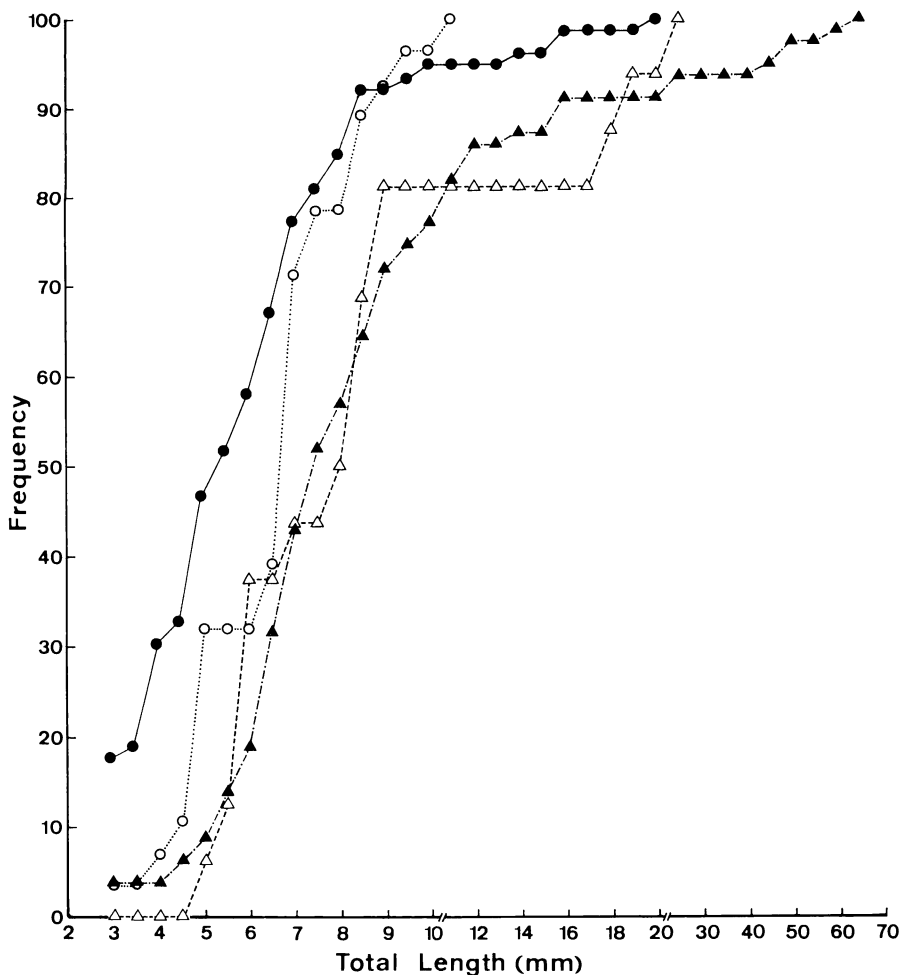


Fig. 12. Relationship between counts of osteological developmental changes (cumulative percentage) and total length for four skeletal groups in the reared *Pagrus major*. ○, neurocranium. ●, head skeleton except neurocranium. △, vertebral column. ▲, fin-supports and rays.

at first-feeding stage is considerably low as well as the vertebral column and fin-supports and rays, but it rapidly increases and reaches almost 100% at 10 mm TL. The head skeleton except the neurocranium, including the jaws, branchial arches, suspensorium, opercular bones and so on, directly operates for feeding and respiration, and the neurocranium protects the brain. The relatively early formation of these two skeletal groups, with the former preceding the latter, seems to be concerned with their most fundamental importance for larval survival. On the other hand, the vertebral column and fin-supports and rays are formed at relatively later

stages. The cumulative percentages of changes of both are zero or low at the first-feeding stage and not more than about 80% at 10 mm TL. The value of fin-supports and rays gradually increases up to 60–70 mm TL, and the delay of completion of the vertebral column is mainly due to the late appearance of its appendages, the pleural and dorsal ribs. These two skeletal groups increase the swimming activity and maneuverability of fishes with growth by increasing the rowing resistance to water, in addition to the development of myotomal musculature as a propulsive power source (Matsuoka and Iwai, 1984; Matsuoka, 1984).

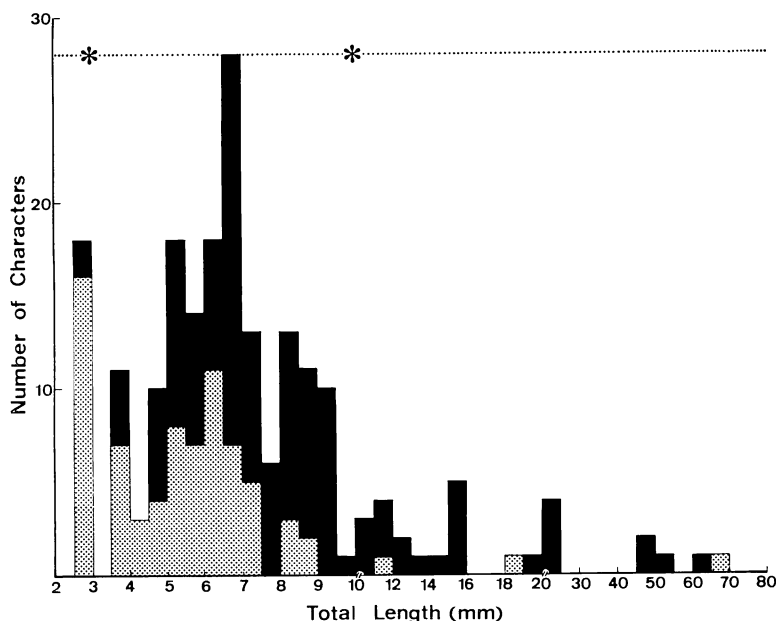


Fig. 13. Occurrence distribution of osteological developmental changes against total length in reared *Pagrus major*. Stippled, condensation. Solid, ossification. *, boundary between periods.

Figure 13 shows a histogram of developmental changes of all osteological elements except the scale against total length. This histogram seems to be divided into three major intervals delimited by about 3 and 10 mm TL (less than 3 mm, from 3 to 10 mm and beyond 10 mm TL) and some transitional characteristics also appear around these boundaries. For example, Kitajima (1978) reported that the yolk absorption as a transitional characteristic from prelarva to postlarva occurs at about 3.2 mm TL, and the pyloric caecum begins to be formed in 30-day old specimen (10.5 mm) (Tanaka, 1971) and the full complement of spines and segmented soft rays of dorsal and anal fins occurs at about 10.5 mm TL in reared specimens (Matsuoka, unpublished data), which seem to be transitional characteristics from postlarva to juvenile. Balon (1975, 1981) emphasized the saltatory processes in fish ontogeny and defined the intervals which consist of periods, phases and steps. Following his proposal, the foregoing two boundaries correspond to those between periods.

Balon (1975) proposed the two phases, proto-ptyerygiolarval and ptyerygiolarval, in the postlarval (or larval) period, as a convenient means of morphophysiological identification of develop-

mental levels. Unfortunately, his definition about the transition between those two phases is ambiguous and frequently difficult to discern (Snyder, 1976). If the commencement of differentiation of pterygiophores and rays within dorsal and anal fins (not caudal fin) is considered as the transitional characteristic between those two phases, the ptyerygiolarval phase of *P. major* begins around 6–7 mm TL. This stage corresponds to that of the highest peak in the osteological development shown in Fig. 13 and also of the most significant qualitative changes of myotomal musculature in the postlarval (or larval) period (Matsuoka and Iwai, 1984). Accordingly, the phases may be the natural intervals with some functional changes rather than the artificial ones. Balon (1975) identified no phases in the juvenile period which lasts until the beginning of first maturation, except in salmonids. On the other hand, two or three divisions within this interval were made by many authors (reviewed by Watanabe and Hattori (1971)), although their morphological definitions were indistinct. The present study suggests that the completion of cartilaginous-osteological structures is characterized by the formation of accessory cartilages 7 and 8 of

the caudal skeleton (Matsuoka, 1982) and the ossification of middle radials of dorsal and anal fin-supports. It may form a boundary between ontogenetic intervals, i.e. phases, within the juvenile period and the fishes beyond this boundary reach adult-like structures and functions except for organs concerned with maturation. Fukuhara (1976) suggested the boundary between juvenile and young fish based on the fin development in *P. major*. My observations show that the full complement of ray branching, especially in the pectoral fin, occurs at almost the same size as the completion of cartilaginous-osteological structures, at least in wild specimens (Matsuoka, unpublished data).

The saltatory development during the transition from one period into another, especially from prelarva (or eleutheroembryo), to postlarva (or larva), is generally accepted (e.g. Tanaka (1975)), but the existence of steps, the shortest interval in fish ontogeny bordered by developmental thresholds (Balon, 1975, 1981), is not sufficiently proven. The several peaks (e.g. in 3.5–4.0 mm, 5.0–5.5 mm, 6.5–7.0 mm, 8.0–8.5 mm TL, etc.) recognized in the postlarval (or larval) and juvenile periods in Fig. 13 may suggest thresholds between steps of osteological development. In this respect, further evidence should be accumulated, including the structural and functional changes in many other organs.

Generally, fish reach a certain developmental stage at various sizes. For example, the reared *P. major* showed a relatively wide range and overlapping of sizes at the respective stages of fin development (Fukuhara, 1976). The mode of size in specimens reaching a certain stage may be somewhat different between the rearing experiments. Also between reared and wild specimens there seem to be considerable size differences at the osteological developmental stages. The completion of osteological structures is accomplished at no longer than 45 mm TL in wild specimens, but at larger sizes, 56–72 mm TL or a little longer, in reared specimens as shown by the present study. Conversely, around the boundary from postlarva to juvenile, the osteological development in reared specimens proceeds at 1–2 mm smaller size than wild specimens (Matsuoka, unpublished data). Further studies in other organs are necessary to clarify why reared and wild specimens show

size differences at the same developmental stages in ontogeny.

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マダイの骨格形成

松岡正信

先に報告した脊柱と尾骨に続き、マダイの骨格系全般にわたってその発達過程を記載した。摂餌開始期には頭部骨格と胸鰭支持骨の一部だけが形成されていた。尾部付属軟骨 7, 8 の形成と背鰭、臀鰭の間担鰭骨の骨化を最後に骨格系は完成した。骨格系が完成する魚体長は天然魚と人工採苗魚でやや異なっていた。各骨について、軟骨の出現、軟骨の定数化、骨化の開始および骨構造の定数化といった変化を計数し、全長に対してヒストグラムを作成したところ、いくつかのピークが示された。これらは個体発生における骨格系の発達の段階性を示唆するものと思われる。

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