

Osteological Development of Fins and Their Supports of Larval Grey Triggerfish, *Balistes capriscus*

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Abstract The osteological development of the fins and their supports are described from cleared and stained specimens of *Balistes capriscus*, ranging from 3.2 to 23.5 mm SL. The first basal pterygiophore which sustains the anterior two dorsal spines is originally composed of two elements and their fusion occurs very early in the larval stage. The paired structure of the rudimentary fin ray elements of the pelvic complex is confirmed. The centrum-hypural plate of the caudal fin originates from fusion of the urostyle and four hypurals.

Based on osteological study, very important papers on phylogeny of superfamily Balistoidea were recently published (Matsuura, 1979; Tyler, 1980), however both authors worked on adult fish, and did not study developmental osteology. As pointed out by Ahlstrom and Moser (1976) and Dunn (1983), the development of osteological structures of teleost larvae is of demonstrable value in phylogenetic studies and can help elucidate systematic relationships. Furthermore, osteological structures of adult fish sometimes show a high degree of fusion, especially in advanced teleost groups, such as Scombroidei and Balistoidei, making it difficult to correctly identify bony elements (Tyler and Matsuura, 1981).

Osteological development of balistid larvae has not been described in the literature. Matsuura and Katsuragawa (1981) described the morphological development of larval *Balistes capriscus* Gmelin, 1788. The purpose of this study is to document in detail the osteological development of fins and supporting bones of this species, which we consider important for phylogenetic studies of balistoids, and to facilitate identification of osteological structures.

Materials and methods

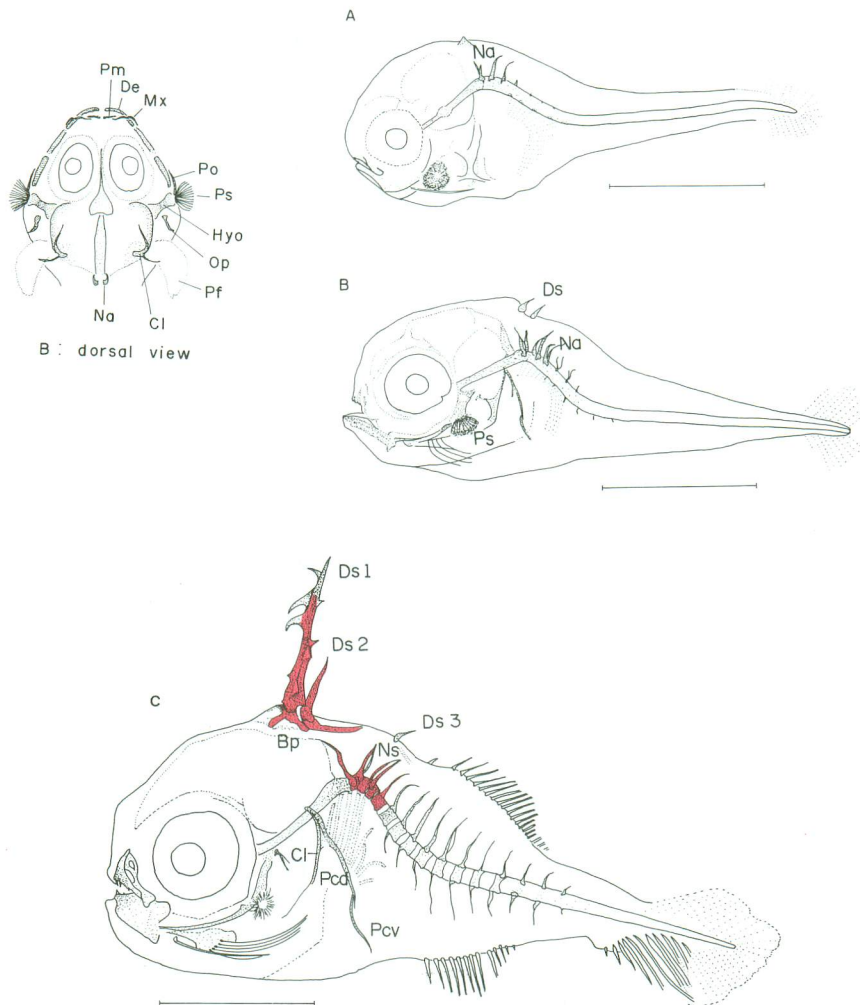
The specimens in this study were the same ones used by Matsuura and Katsuragawa (1981). The larvae were collected with the Bongo nets in the region between Cabo Frio (23°S) and Cabo de Sta. Marta Grande (29°S).

A series of larvae and juveniles from 3.2 mm to 23.5 mm body length were cleared and stained

with alcian blue and alizarin red for cartilage and bone by a combined method after Taylor (1967) and Dingerkus and Uhler (1977). Body length was measured before the clearing and staining process using a portable micrometer attached on a binocular dissecting microscope. Two types of body length measurements were made: notochord length (NL) was taken from the anterior tip of the upper jaw to the posterior tip of notochord before and during notochord flexion and standard length (SL) was taken from the anterior tip of the upper jaw to the posterior border of the hypurals after complete notochord flexion.

Illustrations were made with a camera lucida attached to binocular dissecting microscope. For specimens smaller than 4.7 mm NL the entire body was drawn and for larger specimens only the fins and supporting bones were drawn. Drawings were made of the left side of the body, with the exception of several neural spines of smaller specimens for which both left and right side spines were drawn. Alcian blue stained structures were shown with faint stippling and ossified structures stained with alizarin red were shown in red. Since alcian blue stains mucopolysaccharides, not only the cartilaginous bones but also membranous bones were stained in formalin fixed specimens. Therefore, all bone structures stained with alcian blue were shown with stippling in figures and the cartilaginous bones were indicated in text.

Osteological terms and abbreviations used in this study follow those used by Potthoff (1975) and Matsuura (1979):



Osteological development

First dorsal fin and supporting bones. The first dorsal fin of balistids consists of three elements: three dorsal spines, two basal pterygiophores and one supraneural (Matsuura, 1979). Development of the three elements occurs during very early in the larval stage. At 3.2 mm NL (Fig. 1A) the first dorsal spine appears above the first neural spine and at 3.3 mm NL (Fig. 1B) the second dorsal spine is also present. At 3.9 mm NL (Fig. 1C) two dorsal spines are present in the adult position, with the first dorsal spine locked on the medial edge of the basal pterygiophore and the anterior edge of the second dorsal spine base. At this size the basal pterygiophores are clearly separated, one

at the base of each dorsal spine. These two pairs of dorsal elements were faintly stained with alizarin red, indicating the beginning of ossification. The third dorsal spine and supraneural are also present at this size, but the third basal pterygiophore is not yet formed.

Figure 1D shows a larva of 4.5 mm NL and a dorsal view of the basal pterygiophores. The two basal pterygiophores are further developed and the posterior one is elongated posteriorly forming a groove on dorsal side. Two wing-like projections are present at the mid-lateral region of the anterior basal pterygiophore. Later, these fuse posteriorly with edges of the posterior basal pterygiophore. After complete fusion of two basal pterygiophores, there remain two pairs of fenestrae on the wing-like projec-

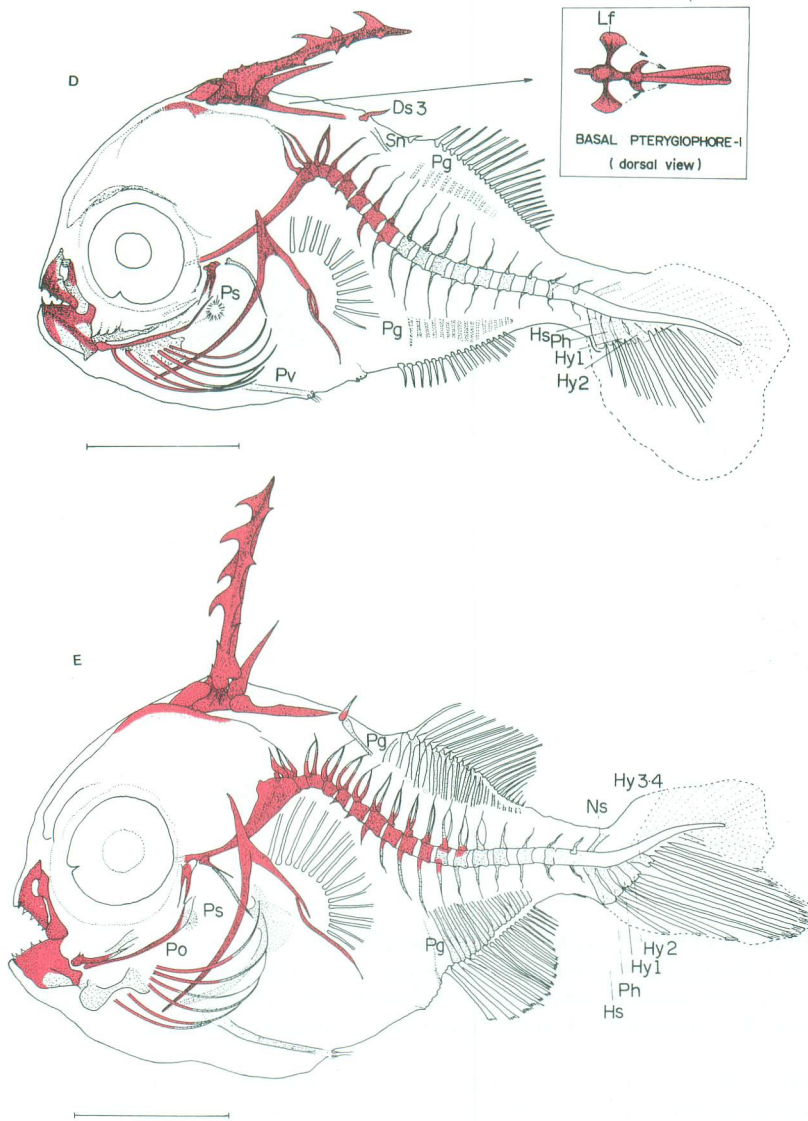


Fig. 1. Cleared and stained specimens of *Balistes capriscus* larvae, ranging from 3.2 to 4.7 mm NL. Alcian blue stained structures are shown in faintly stippled and ossifying one in red. A, 3.2 mm NL; B, 3.3 mm NL; C, 3.9 mm NL; D, 4.5 mm NL; E, 4.7 mm NL. Symbols: Bp, basal pterygiophore; Cl, cleithrum; De, dentary; Ds, dorsal spine; Hs, haemal spine; Hy, hypural; Hyo, hyomandibular; Mx, maxilla; Na, neural arch; Ns, neural spine; Op, opercle; Pcd, dorsal postcleithrum; Pcv, ventral postcleithrum; Pf, pectoral fin; Pg, pterygiophore; Ph, parhypural; Pm, premaxilla; Po, preopercle; Ps, tuft of setae (preopercle spines); Pv, pelvis; Sn, supraneural. Scale bars: 1.0 mm.

tions (=lateral flange) and the bifid latero-ventral projection at the basal portion of the second dorsal spine fit into the posterior fenestrae of the lateral flange.

Fusion of the first two basal pterygiophores occurs at about 4.7 mm NL (Fig. 1E). Since

their fusion becomes so complete that it is impossible to distinguish the limits of each basal pterygiophore in adult fish. For this reason, Matsuura (1979), Tyler (1980) and others considered them as the first basal pterygiophore. As shown in Fig. 1D, the first basal pterygiophore

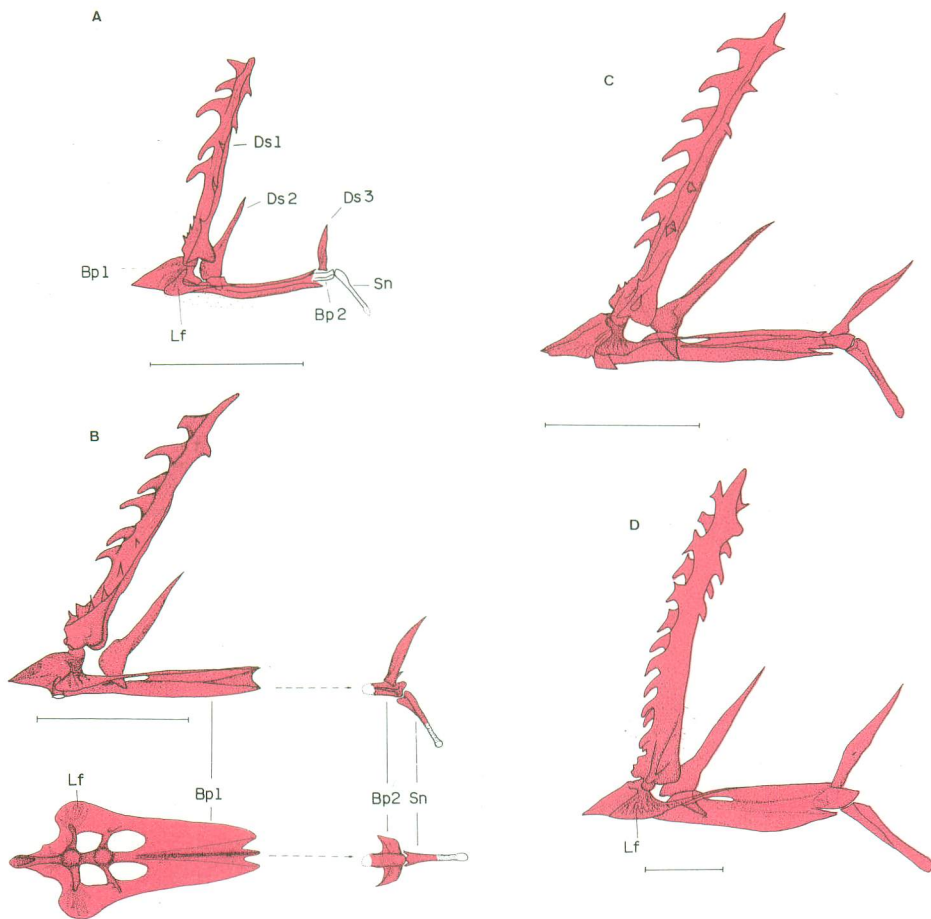


Fig. 2. Lateral view of the spinous dorsal fin and its supporting bones in *Balistes capriscus* larvae. Fig. 2B shows the lateral and dorsal views of the first and second basal pterygiophores presented separately. A, 4.5 mm NL; B, 5.8 mm SL; C, 6.7 mm SL; D, 12.8 mm SL. Symbols: Bp, basal pterygiophore; Ds, dorsal spine; Lf, lateral flange; Sn, supraneural. Scale bars: 1.0 mm.

phore of the above mentioned authors originates from two components and their second basal pterygiophore corresponds to the original third basal pterygiophore.

Hereafter, in order to avoid confusion in nomenclature, we refer to the fused basal pterygiophore which sustains the anterior two dorsal spines, as the first basal pterygiophore, and the third basal pterygiophore, which sustains the third dorsal spine and is articulated to the anterior basal pterygiophore, as the second basal pterygiophore. At this size the dorsal spines and the first basal pterygiophore are ossified, while the supraneural is still cartilaginous.

The second basal pterygiophore was first noticed at 4.9 mm NL (Fig. 2A). The wing-

like lateral projections of the first basal pterygiophore are well developed and the posterior edge of the first basal pterygiophore reaches to the anterior edge of the second one.

Figure 2B shows lateral and dorsal views of the dorsal spines of a larva of 5.8 mm NL. To demonstrate the form of each component, the third dorsal spine and supporting bones were separated from the anterior one and drawn separately. At this size the wing-like lateral projections (=lateral flange) of the first basal pterygiophore are completely fused. The second basal pterygiophore also has wing-like lateral projections which fit into the posterior edge of the first basal pterygiophore. By changing the angle of the second dorsal spine, we can demon-

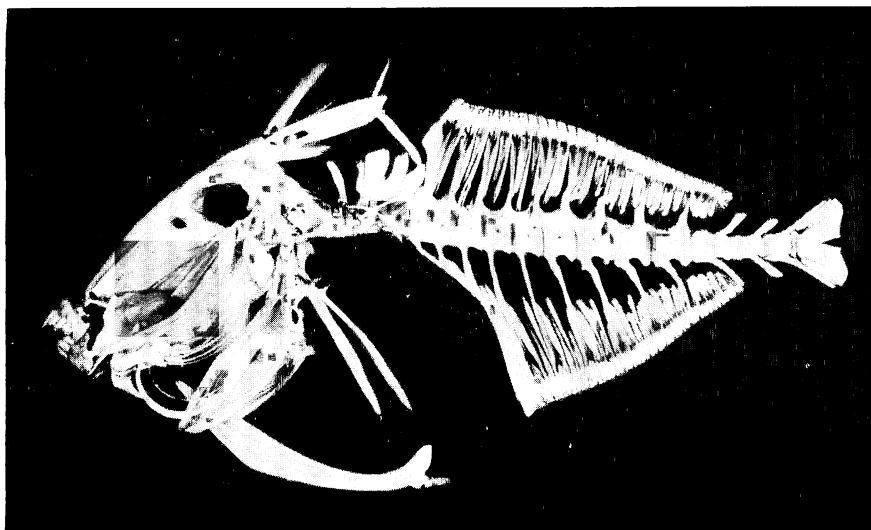


Fig. 3. Skeletal structure of *Balistes capriscus* adult, 245 mm SL; (photo: R. Carneiro).

strate the locking mechanism of the first dorsal spine.

At 6.7 mm SL (Fig. 2C) the posterior edge of the first basal pterygiophore is articulated with the anterior edge of the second one and the form and position of the first dorsal fin components are almost the same in the adult (Fig. 3). The posterior end of the supraneural ends above the tip of the 5th neural spine just anterior to the base of the first pterygiophore of the second dorsal fin which is located at the interneural space of the 5th and 6th neural spines. The first and second dorsal fin components are all ossified with exception of the distal halves of the second dorsal fin rays.

There is no remarkable change in shape of the dorsal fin components at the size of 12.8 mm SL (Fig. 2D). The dorsal groove of the first basal pterygiophore is deeper than before and it can receive the second dorsal spine. The posterior end of the supraneural almost reaches of the tip of the 5th neural spine and ventral tip of the first pterygiophore of the second dorsal fin is now deeply inserted in the space between the 5th and 6th neural spines.

Pectoral girdle and suspensorium. The larval pectoral fins are present in the smallest specimen at 3.2 mm NL and the thin cleithrum and dorsal and ventral postcleithra are visible at this size (Fig. 1A, B). At 3.9 mm NL (Fig. 1C) the postcleithra are more developed and the upper

one articulates with the upper part of the cleithrum. At this size the two postcleithra are not fused. Ossification of the cleithrum and postcleithra starts at about 4.7 mm NL and the cartilaginous coraco-scapular blade appears. The dorsal part of the cleithrum has a posterior process at this size. At 5.8 mm NL (Fig. 4A) all components of the pectoral girdle and suspensorium with exception of the posterior radial are well ossified and the scapular foramen is present. At 12.8 mm SL (Fig. 4B) the lower part of the cleithrum is enlarged and articulates with the coracoid. No interosseous space was observed between the cleithrum and coracoid in adult fish (Fig. 3).

Pelvic complex. The pelvic complex of *B. capriscus*, as in other balistids, consists of three major components: pelvis, encasing scales and rudimentary fin ray elements. Other components, such as a cartilage plug and the dorsal and ventral tendons of the pelvis, which were observed on adult specimens and used for phylogenetic analysis by Matsuura (1979), were not studied in this paper.

The pelvis and the rudimentary fin ray elements firstly appear at about 4.3–4.5 mm NL (Fig. 1D). At the same time notochord flexion starts and many components of the caudal complex also start to appear. The pelvis is rod-like and is stained faintly with alcian blue. At the posterior end of the pelvis, two pairs of tiny

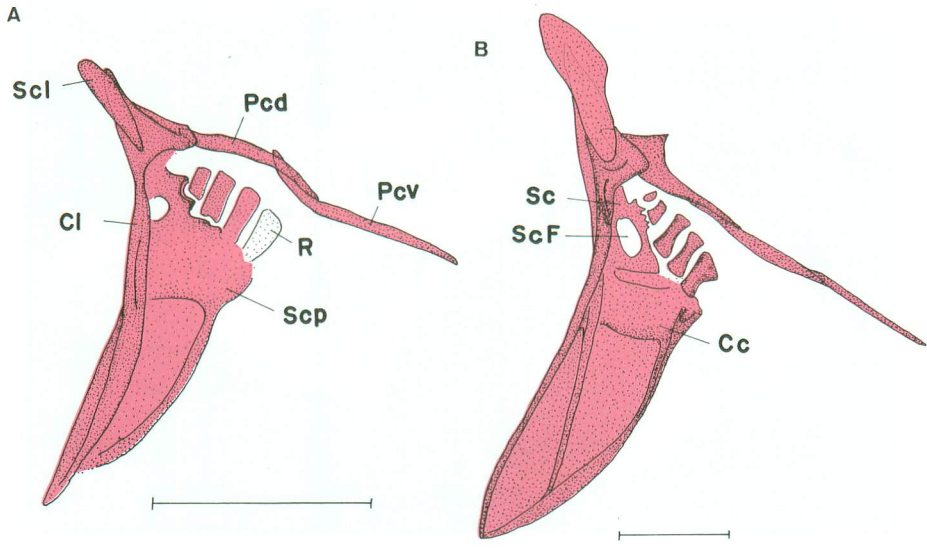


Fig. 4. Lateral external view of left side of pectoral girdle of *Balistes capriscus* larvae. A, 5.8 mm SL; B, 12.8 mm SL. Symbols: Cc, coracoid; Cl, cleithrum; Pcd, dorsal postcleithrum; Pcv, ventral postcleithrum; R, radials; Scp, scapula; ScF, scapular foramen; Scl, supracleithrum. Scale bars: 1.0 mm.

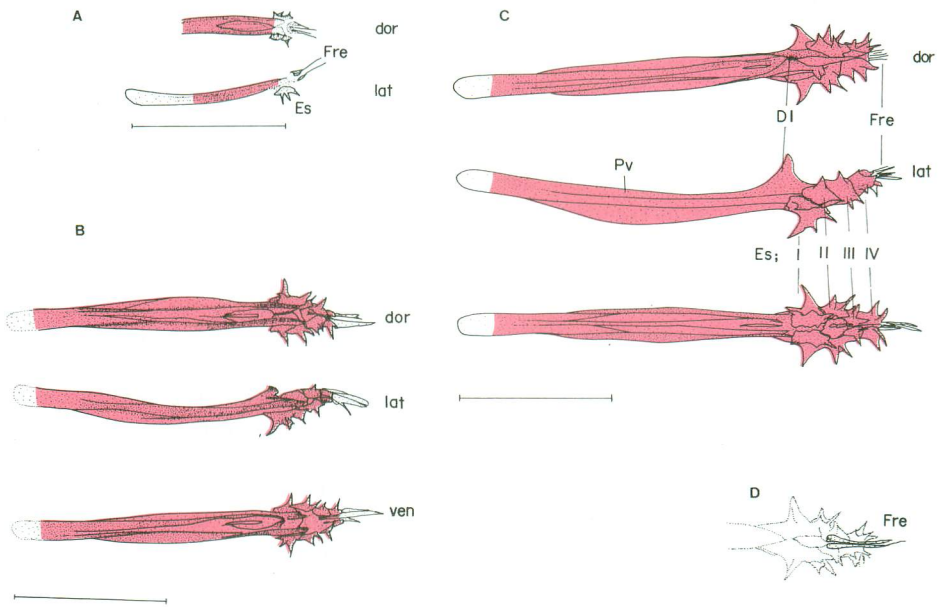


Fig. 5. Pelvic complex of *Balistes capriscus* larvae. A, 4.9 mm NL; B, 5.8 mm SL; C, 6.7 mm SL. Symbols: DI, dorsal lobe; Es, encasing scales; Fre, rudimentary fin ray elements; Pv, pelvis. Scale bars: 1.0 mm.

rudimentary fin rays are present; they become thinner distally. Up to 4.7 mm NL, no remarkable change in form can be noticed in the

pelvic girdle elements, but the pelvis is now heavily stained with alcian blue (Fig. 1E).

At 4.9 mm NL (Fig. 5A), a central part of the

pelvis is ossified. The dorsal view shows the paired rudimentary fin ray elements arranged horizontally and the lateral view shows the dorsal and ventral rudimentary fin ray elements of the left side. They seem to be separated at their bases, articulating on cartilaginous tissue of the pelvis. A pair of encasing scales appear at this stage, at ventro-lateral end of the pelvis.

At 5.8 mm NL (Fig. 5B) a small projection appears on the dorsal side of the posterior end of pelvis. This will later become a dorsal lobe. Four segments of encasing scales are present on the posterior end of the pelvis. From ventral view, it is clear that the segment II is composed of the three scales and other segments (I, III and IV) are composed of a pair of scales. The encasing scales partially cover the bases of the rudimentary fin ray elements.

At 6.7 mm SL (Fig. 5C) the form of the pelvis is similar to that of the adult, having a well developed ventral keel at the median part of the pelvis and the dorsal lobe. The number of encasing scales is the same as in the adult: 2, 3, 4 and 2, respectively for segments I, II, III and IV. At this size the encasing scales cover the bases of the rudimentary fin ray elements entirely and only the terminal filamentous part is visible. The entire group of rudimentary fin ray elements can be seen only by removing the encasing scales (Fig. 5D). The bases of the rudimentary fin ray elements are ossified. Fusion of the four rudimentary fin ray elements is complete in a specimen of 23.5 mm SL.

Caudal complex. The caudal complex of the Balistidae consists of one epural, an autogenous fifth hypural, an autogenous parhypural and a large plate composed of the centrum fused to most of the hypural elements (Tyler, 1980). In this study preural centrum 2 and its haemal and neural spines are included as a part of the caudal complex.

For the specimens examined in this study the development of the caudal structure starts later than that of the first dorsal fin and supporting bones. From 3.2–3.9 mm NL (Fig. 1A, B, C), the notochord is straight and its flexion was observed first on the specimen of about 4.5 mm NL (Fig. 1D), when the caudal fin elements also start to appear. At this stage five cartilaginous plates beneath notochord, correspond to the haemal spine, parhypural and three hypurals,

respectively from left to right. Above the notochord, only the neural spine of preural centrum 2 appears.

At 4.7 mm NL (Fig. 1E) the caudal structure is similar, but notochord flexion is more advanced and the last hypural has separated from anterior two hypurals at their distal ends. Of these three cartilaginous plates the anterior two correspond to the first and second hypurals and the posterior one seems to be a fusion of the third and fourth hypurals, since there is no evidence of a fourth hypural at size between 4.7 and 4.9 mm NL.

At 4.9 mm NL (Fig. 6A) all the structure of the caudal complex are not yet ossified. Notochord flexion is more advanced and all caudal fin rays are formed. The epural and the fifth hypural are recognizable. Since only two cartilaginous hypural plates articulate with the posterior end of the flexed notochord, we conclude that fusion of hypurals starts at a very early stage in balistids. At this size the lower and upper cartilaginous hypural plates are separated at their bases. The parhypural, now attached to the notochord, consists of only faintly-stained cartilaginous tissues.

At 5.8 mm NL (Fig. 6B) the major elements of the caudal complex are ossifying in an anterior to posterior direction. The urostyle and three preural centra are entirely ossified, but the neural and haemal spines of the second preural centrum, the parhypural and the fifth hypural are not entirely ossified. The ossified hypural plates articulate with the urostyle and are fused basally. This complex of two hypural plates and urostyle forms the centrum-hypural plate, posteriorly. The cartilaginous epural which had direct contact with the notochord in the 4.9 mm NL larva is now separated from the urostyle and the parhypural also becomes isolated from the urostyle.

All elements of the caudal complex are ossified at 6.7 mm SL (Fig. 6C) except the distal parts of the neural and haemal spines of preural centrum 2 and the epural. At this size neural and haemal processes are present at the anterior base of the urostyle. The base of the haemal spine of preural centrum 2 is separated from the centrum, a condition which continues up to 12.8 mm SL. In a larva of 23.5 mm SL this spine is connected to the centrum.

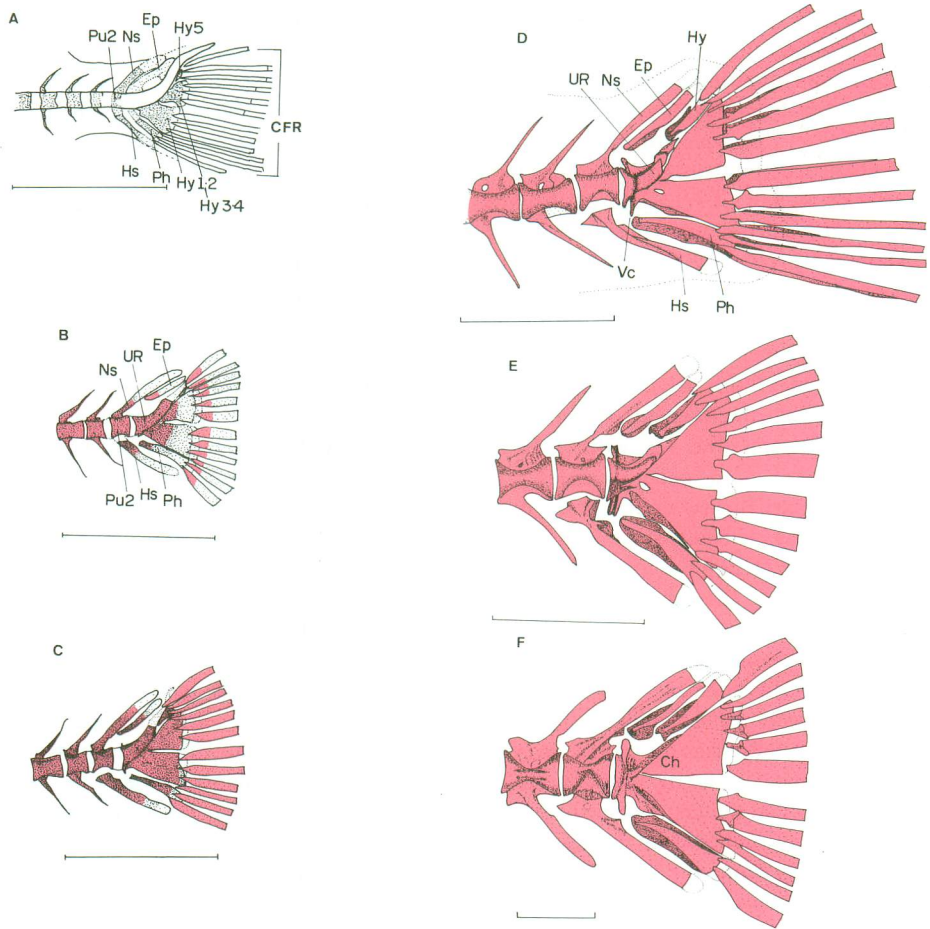


Fig. 6. Caudal complex of *Balistes caprisicus* larvae. A, 4.9 mm NL; B, 5.8 mm SL; C, 6.7 mm SL; D, 10.8 mm SL; E, 12.8 mm SL; F, 23.5 mm SL. Symbols: CFR, caudal fin rays; Ch, centrum-hypural plate; Ep, epural; Hs, haemal spine; Hy, hypural; Ns, neural spine; Pu 2, preural centrum 2; Ph, parhypural; UR, urostyle; Vc, vertical crest. Ossifying parts are shown in red. Scale bars: 1.0 mm.

Elements of the caudal complex of larger specimens were stained only with alizarin red (Fig. 6D, E, F). During these stages there is a constant growth in size and some modification in shape of all components. The larvae of 10.8 mm SL and 12.8 mm SL (Fig. 6D, E) have a urostyle consisting of two segments, indicating probably the original three centra before fusion. At 23.5 mm SL this segmentation disappears and caudal complex shows almost the same form as that of adult fish. The centrum-hypural plate has a well developed vertical crest and the central posterior cleft of the hypural plate is still very deep. No trace of uroneurals were observed during ontogeny.

Discussion

Some authors have classified the balistids and monacanthids into the single family Balistidae (Böhlke and Chaplin, 1968; Winterbottom, 1974; Nelson, 1976). However, based on extensive osteological studies, Matsuura (1979) and Tyler (1980) have recently established that each group is anatomically distinct, indicating there are two families, Balistidae and Monacanthidae. Balistids were considered as the ancestral group of the monacanthids and the more important osteological differences between them were reduction in size and forward displacement of the spiny dorsal fin and its basal

pterygiophores and the features associated with the more delicate teeth and jaws and their supporting structures (Tyler, 1980).

The tuft of setae on the cheek has been observed since very early stage (Fig. 1A). This structure was initially pointed out by Matsuura and Katsuragawa (1981), but their function is not known. A similar tuft of setae was observed in larval specimens of *Balistes vetula* in our collection and also observed in balistid larvae from the collection of the Southwest Fisheries Center, La Jolla, California (senior author's observation). In the first detailed morphological description of monacanthid larvae, Hildebrand and Cable (1930) did not mention any such structure on the cheek, but their illustration (fig. 2) shows a robust spine like structure on preopercle region. Our monacanthid larvae (probably *Stephanoleps* sp.) from plankton samples have a similar tuft of setae on the preopercle region at 3.2 mm NL. Thus, this structure seems to be a common characteristic of balistoid larvae, although its presence is temporary.

In alcian blue and alizarin red stained specimens, we have followed the tuft of setae up to 4.7 mm NL, when it disappeared (or was resorbed?). This disappearance coincides with the beginning of the process of ossification of the preopercle on which it is located.

It is well known that the number of pterygiophores is usually less than that of fin rays or spines, since the anteriormost or posteriormost pterygiophore may support one or more fin elements (Dunn, 1983). The same phenomenon was observed in the first dorsal fin of adult balistids. However, as shown previously, the first basal pterygiophores, which sustains the two anterior dorsal spines, originates from two elements which become fused at an early larval stage. Therefore, from an ontogenetic point of view, the number of dorsal spines of this species is the same as the number of basal pterygiophores. Fusion of the anterior two pterygiophores during the early larval stage was observed in recent studies *Morone americana* (Fritzsche and Johnson, 1980) and *Pagrus major* (Kohno et al., 1983).

Early in the development of the dorsal fin elements, the anterior two spines and the first basal pterygiophore form an efficient trigger

mechanism and preserved larvae normally were found with this mechanism in a locked state. Therefore, the defensive mechanism of the erected first dorsal spines in combination with the pelvic complex is important in early planktonic larvae as well as in juveniles and adults.

The pelvic complex of balistoids is a very characteristic structure and has provided useful characters for phylogenetic studies of the group (Tyler, 1962, 1968, 1980; Matsuura, 1979). Matsuura (1979) suggested that ontogenetic studies were needed to verify the origin of rudimentary fin ray elements in balistids. The first description of the origin of pelvic elements was made on larvae of *Monacanthus hispidus* (= *Stephanoleps hispidus*) by Hildebrand and Cable (1930); they observed two membranous ventral fins at a length of 1.7 mm NL. Later these were replaced by a single flexible membranous fin on the ventro-median line of body, which posteriorly became a strong and rigid pelvis. We could not confirm the presence of two membranous ventral fins on our smallest monacanthid larvae (about 2 mm NL); instead we found a single ventral spine with two filamentous fin ray elements on its terminal end. Probably, Hildebrand and Cable misinterpreted these structures as paired ventral fin elements.

In *Balistes capricus*, the caudal rays are supported by only two centra (the centrum-hypural plate and the preural centrum 2). Based on analysis of adult specimens, various authors (Monod, 1968; Tyler, 1968, 1980; Matsuura, 1979) considered that the centrum-hypural plate is composed of the urostyle fused to most of the hypural elements and the deep cleft on the posterior edge of the plate represents the division between the second and third hypurals. This was partly confirmed by our study, since the first and second cartilaginous hypurals were evident on larvae between 4.5 and 4.7 mm NL, but we could not recognize a division between the third and fourth hypurals. We can not conclude whether the third and fourth hypurals appear separately and fuse soon after, or whether they appear as a fused cartilaginous hypural plate. If the former is true, the fusion must be very rapid and we need many more specimens of this size range to verify this. The fifth hypural appeared initially at a position dorsal to the upper hypural plate and beneath the notochord

at 4.9 mm NL and it stayed at this position up to a larval size of about 7.0 mm SL. Then, with ossification of the hypurals, it moved to a position on the dorsal side of the urostyle.

Matsuura (1979) could not find any trace of the uroneurals in his adult balistid specimens. On the contrary, Tyler (1980) reported a pair of small nubbins of bone resting on the dorsal surface of the fifth hypural of *Balistapus undulatus*: he concluded that these are rudimentary uroneurals. In *Balistes capriscus* we found no evidence of uroneurals during caudal fin formation.

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Balistes capriscus (モンガラカワハギ科) の仔魚における鱭支持骨の形成

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モンガラカワハギ科の1種 *Balistes capriscus* の鱭支持骨の形成について、体長 3.2 mm から 23.5 mm の alcian blue と alizarin red で染色した標本にも

とづいて記載した。第1背鱭の前方2棘を支える担鱭骨は発生初期には2個の部分から成り、そのゆ合は体長 4.7 mm 頃におこる。腰骨先端の鱭条こん跡は、発生初期には2対の鱭条からなることが確認された。特化した尾骨は、urostyle と4個の hypural のゆ合からなる。