

LARVAE OF THE MOORISH IDOL, *ZANCLUS CORNUTUS*, INCLUDING A COMPARISON WITH OTHER LARVAL ACANTHUROIDS

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ABSTRACT

The larvae of *Zanclus cornutus* are described and illustrated based on one postflexion and several preflexion specimens. In addition to general morphology and pigmentation, bony ornamentation of the head bones and other osteological features are described in detail. Head bones and the associated ornamentation are illustrated for larval *Zanclus*, *Siganus*, *Luvarus* and *Naso*. These and other aspects of the morphology of larval acanthuroids are compared and discussed within the context of a phylogenetic hypothesis proposed in other current work. Larval characters corroborate the monophyly of the Acanthuroidei and the phyletic sequence, Siganidae, Luvaridae, Zanclidae, Acanthuridae. The Acanthuridae is represented by three distinct larval forms.

The moorish idol, *Zanclus cornutus* (Linnaeus), Family Zanclidae, occurs in tropical waters of the Indo-Pacific and eastern Pacific. Like the closely related Acanthuridae, adult *Zanclus* are reef-associated fishes, but the young are specialized for a relatively prolonged pelagic existence. The specialized pelagic pre-juvenile is termed the "acronurus" stage, and, at least in acanthurids, may reach a length of 60 mm or more before settling (Leis and Rennis, 1983). Strasburg (1962) briefly described 13.4 and 16.0-mm SL specimens of the monotypic *Zanclus* and illustrated the larger specimens. Eggs, preflexion larvae and small postflexion larvae of *Zanclus* have not been described (Leis and Richards, 1984). The primary purposes of this paper are to describe a 9.5-mm SL postflexion larva of *Zanclus* and to compare its morphology to that of postflexion larvae of other acanthuroids in a phylogenetic context. Preflexion larvae of *Zanclus* are also briefly described based on three specimens (2.8-3.2-mm NL).

MATERIALS AND METHODS

The postflexion specimen (MCZ 62046) was identified from a 10-m RMT (rectangular mid-water trawl) sample taken in the Solomons Sea (6°14'S, 151°50'E; 18 May 1981; depth of water 7,403 m) by R. Harbison of the Woods Hole Oceanographic Institution. The preflexion larvae were collected in the Great Barrier Reef-Coral Sea area and tentatively identified by J. Leis of the Australian Museum, Sydney, and are deposited in that collection.

All illustrations were prepared using a stereomicroscope with camera lucida attachment. Preliminary illustration of the 9.5-mm larva was prepared from the whole specimen, which was then cleared and stained for cartilage and bone to allow more accurate description and illustration of head spines, scales and internal pigmentation (Fig. 1). A similar procedure was followed for one of the preflexion specimens (Fig. 2B). Illustrations of the head bones and pterygiophores of other larval acanthuroids were prepared from cleared and stained specimens. Measurements were made using a calibrated ocular micrometer. Notochord length (NL) is from the tip of the upper jaw to the tip of the notochord in preflexion larvae. Standard length (SL) is from the tip of the upper jaw to the posterior margin of the hypural plate in postflexion larvae. All lengths are SL unless otherwise indicated. In the descriptions of pigment, melanophores are external unless otherwise indicated. Osteological abbreviations are: Aa, anguloarticular; Bo, basioccipital; Br, branchiostegal; Cl, cleithrum; Co, coracoid; D, dentary; DR, distal radial; DS, dorsal-fin spine; Eo, epioccipital; Es, extrascapular; Ex, exoccipital; F, frontal; I, infraorbital; IL, interoperculo-mandibular ligament; In, intercalar; Io, interopercle; L, lacrimal; LE, lateral ethmoid; MK, midventral keel; Mx, maxilla; N, nasal; NS, neural spine; O, opercle; P, parasphenoid; Pa, parietal; Pcl, postcleithrum; Pd, predorsal; PG, pelvic girdle; Pmx, premaxilla; Po, preopercle; PR, proximal-

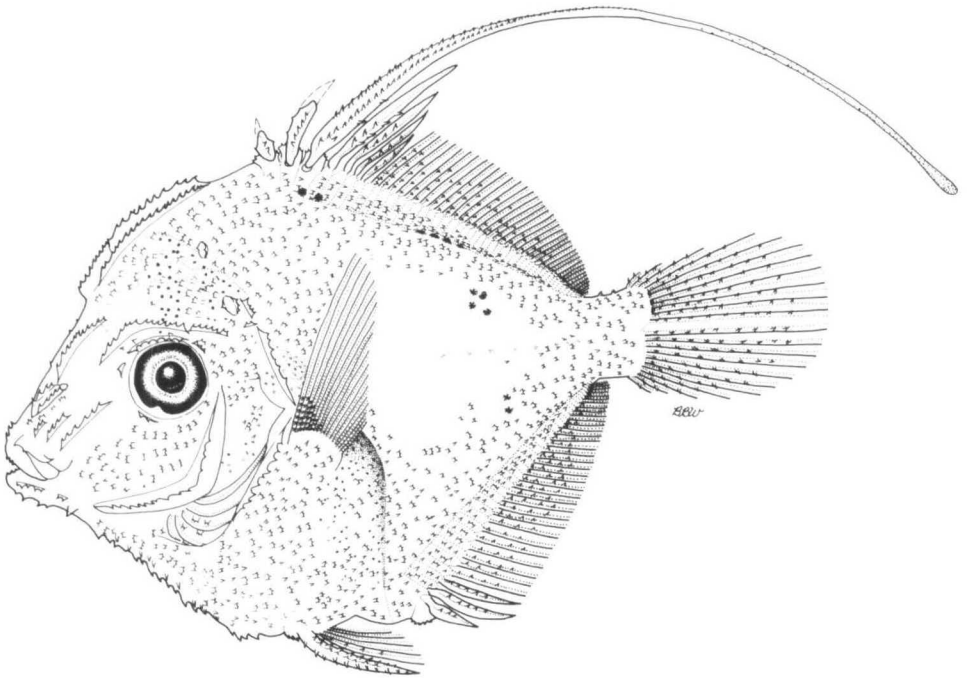


Figure 1. *Zanclus cornutus*, postflexion larva, 9.5 mm SL, MCZ 62046.

middle radial; Pr, prootic; Ps, pterosphenoid; Pt, pterotic; Ptt, posttemporal; Ra, retroarticular; S, supraoccipital; Sc, scapula; Scl, supracleithrum; So, subopercle; and Sp, sphenotic.

Material examined is listed below. All specimens are cleared and stained except where indicated by a "w" following the stated lengths. Institutional abbreviations are those recommended by Leviton et al. (1985). GRH numbers refer to uncatalogued MCZ specimens.

Zanclus cornutus—AMS I.23557-001 (2.8-mm NL, w); AMS I.24515-002 (3.0-mm NL, w); AMS I.23724-003 (3.2-mm NL); MCZ 62046 (9.5 mm).

Siganus sp.—MCZ 63119 (2, 7.7–9.7 mm); USNM 109355 (2, 16.0–24.3 mm).

Luvarus imperialis—MCZ 55287 (5.8 mm, w); MRRI 05790139 IKMT (7.2 mm); MCZ 55291 (10.5 mm); MCZ 60721 (19.2 mm).

Naso sp.—MCZ 63120 (6, 5.0–8.1 mm); MCZ 63121 (5, 9.3–15.4 mm); USNM 259787 (33.0 mm).

Prionurus scalprum—USNM 70753 (6, 24.5–42.8 mm).

Acanthurus sp.—USNM uncat. (2, 2.8–3.4-mm NL); GRH 1041 (2, 5.1–7.5 mm); MRRI 05821006 IKMT (7.1 mm); USNM 240072 (2, 8.7–10.2 mm).

Ctenochaetus sp.—GRH 1007 (9.0–11.8 mm); USNM 262157 (27.5 mm); USNM 163616 (32.2 mm).

Paracanthurus hepatus—GRH 1051 (9.7 mm, w); USNM 133993 (29.6 mm).

Zebrasoma sp.—USNM 279326 (5.4 mm); GRH 1046 (5.7 mm); USNM 279439 (7.9 mm, w); GRH 1054 (9.6 mm); USNM 279437 (18.6 mm); USNM 109355 (27.0 mm).

DESCRIPTION

Postflexion Larva, Figure 1.—The fins are fully developed with a complete complement of spinous and soft rays: Dorsal VII, 41; Anal III, 34; Pectoral 17; Pelvic I, 5; Caudal 8+8 principal, 3+3 procurent. There are 9+13 myomeres. The body is deep and laterally compressed; maximum depth at the pectoral fin is 75% SL. The head tapers to a small terminal mouth, giving the body a distinctive "kite" shape. The gut is coiled, and the long hindgut extends ventrally at midbody; snout to anus length is 50% SL.

The mid-brain is dome-shaped and is housed in a dome-like cranial cavity; the

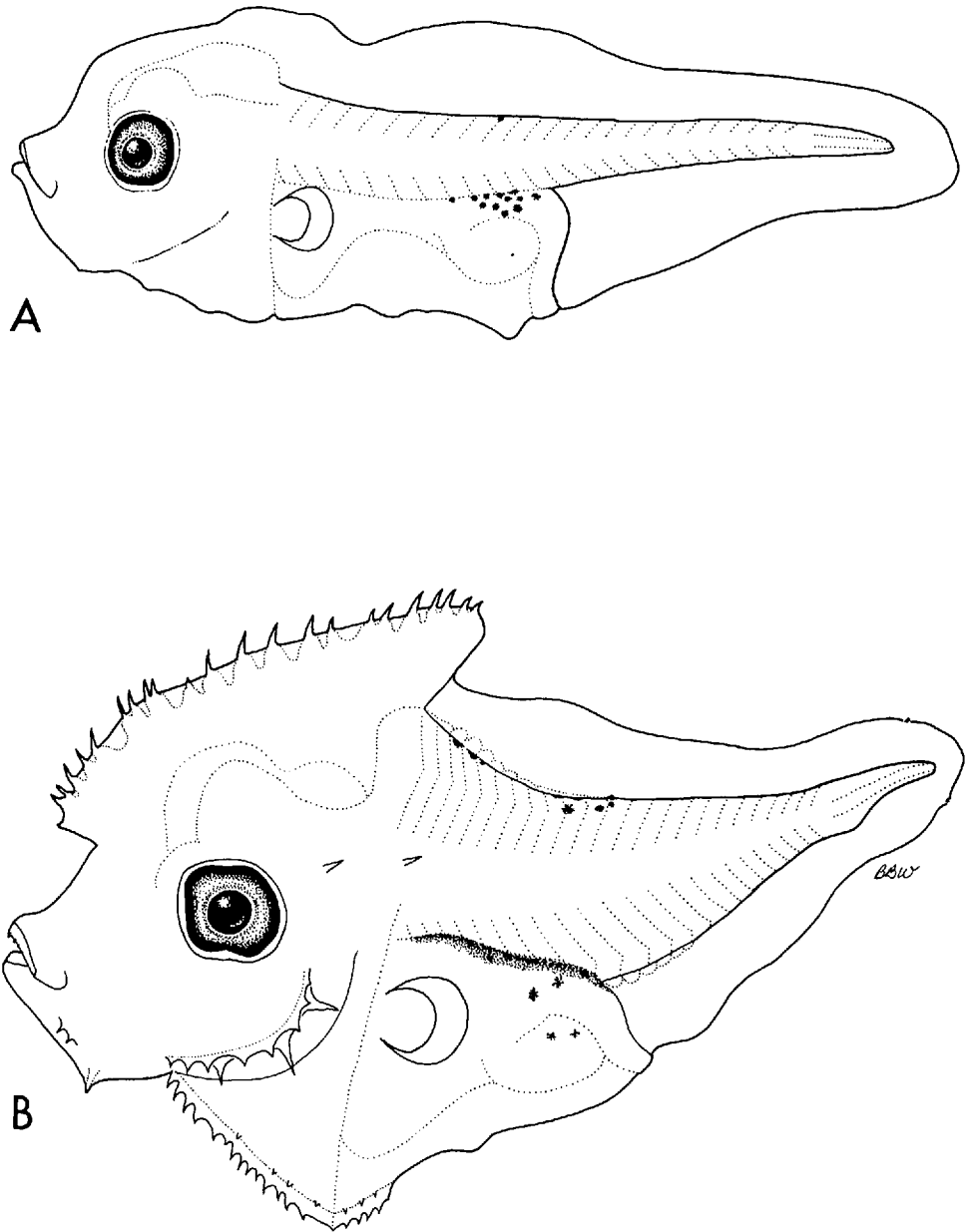


Figure 2. *Zanclus cornutus*, preflexion larvae. A. 2.8 mm NL, AMS I.23557-001. B. 3.2 mm NL, AMS I.23724-003.

cavity is larger and slightly more pointed than the mid-brain, leaving a considerable vacant space dorsally. A similar, but much smaller cranial cavity houses the forebrain.

Distinctive scales cover much of the head and body. Each scale (Fig. 3B) consists of a roughly ovoid basal plate with a vertically oriented, fan-like, laminar projection extending outward at right angles to the plate; the distal margin of each laminar projection bears one to several (usually three) small spines. Scales are

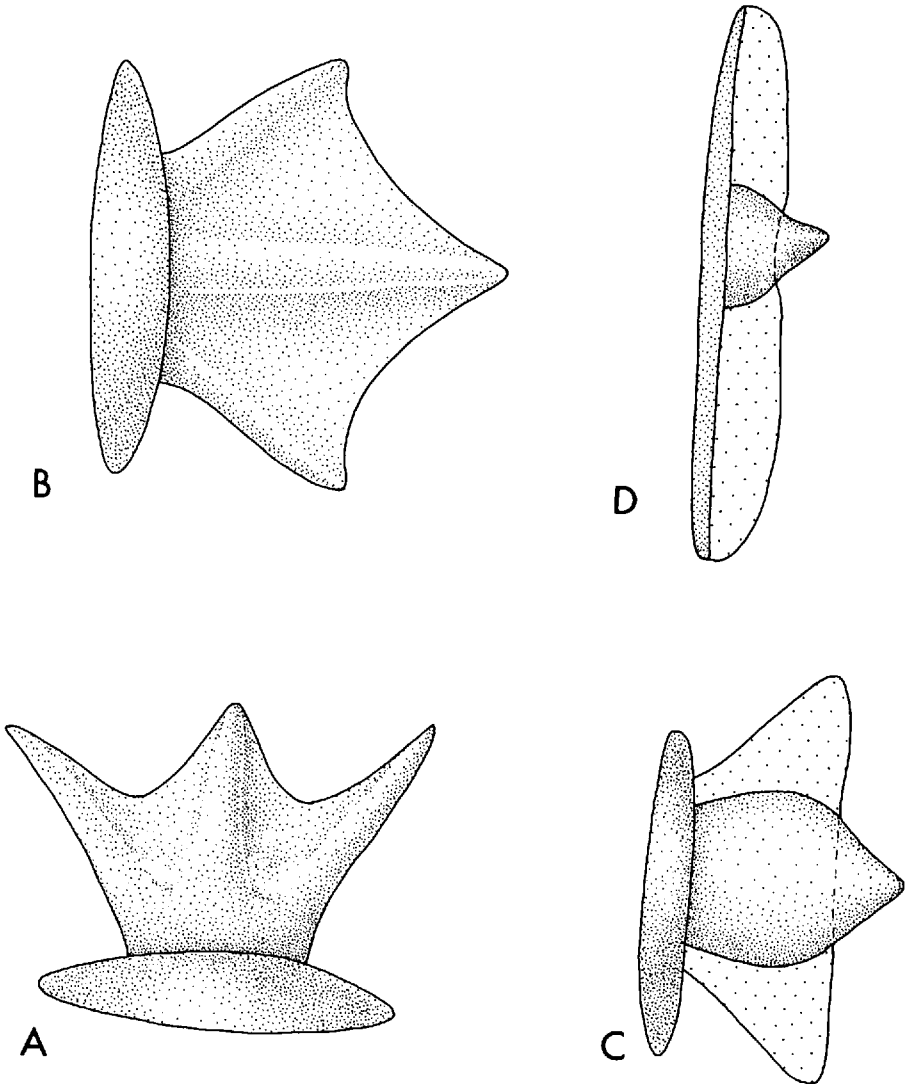


Figure 3. Larval scales, oriented as they are along the body; sparser stippling represents specialized connective tissue. A. *Luvarus imperialis*, 10.5 mm SL, MCZ 55291, ventral view. B. *Zanclus cornutus*, 9.5 mm SL, MCZ 62046, posterior view, right side. C. *Naso* sp., 11.0 mm SL, MCZ 63121, posterior view, right side. D. *Acanthurus* sp., 10.4 mm SL, USNM 240072, posterior view, right side.

present over most of the head and body except midlaterally posterior to the pectoral fin, where only a few isolated scales are beginning to develop.

In the head region, scattered melanophores are present internally over the brain, on the medial side of the opercle, just ventral to the gill filaments on the branchial septum, and over the dorsolateral and posterior surface of the gut. Two discrete melanophores are present on each side of the body below the fourth dorsal spine, one anterior and one posterior to the fourth pterygiophore. Ventral to the bases of dorsal soft rays 11–19, there are four dash-like melanophores on the left side, two on the right; an additional dash-like melanophore is present on the right side,

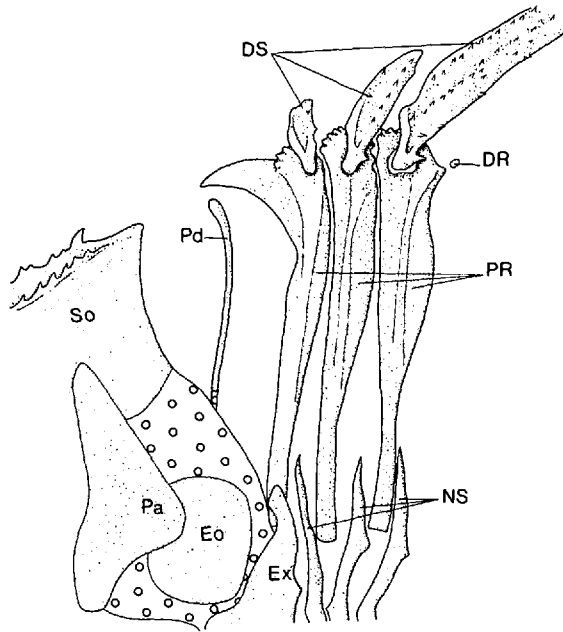
ventral to the base of soft ray 19. Three to four stellate melanophores are present on each side below the area between dorsal soft rays 16–20 (neural spine of vertebra 15), approximately midway between the dorsal-fin base and the lateral midline. Two stellate melanophores lie approximately midway between the lateral midline and the anal-fin base, directly above the bases of anal soft rays 13–16. Three melanophores are present along the bases of the fin rays of the upper lobe of the caudal fin, and light melanistic pigment occurs variously along the filamentous third dorsal spine. A median row of eight melanophores is present internally above the notochord between the neural spines of vertebrae 12–19.

The three anteriormost dorsal-fin spines are stout and triradiate in cross section, with conspicuous spinules extending along the bases of the lateral ridges of each spine (Figs. 1 and 4A). The first two spines are short, but the third is extremely elongate ($1.2 \times SL$) and filamentous distally (in the 16.0-mm SL specimen described by Strasburg, 1962, the third spine was $2.1 \times SL$). The third spine also bears spinules near the margin of the anterior ridge, along the proximal one-third of its length. The posterior four dorsal spines are also triradiate and bear a few spinules proximally along the margins of each lateral ridge; these spines are relatively slender and are not produced. The pelvic spine is stout and triradiate with spinules along each ridge; it is not elongate but is approximately equal in length to the adjacent well-developed pelvic soft rays. The three anal spines are also triradiate with spinules extending along the lateral ridges; the first two are particularly stout, and the first is about one-half the length of the other two which are subequal to the adjacent anal soft rays. Soft rays of the dorsal, anal and caudal fins are spinulose; spinules are also present on the lateralmost pelvic soft ray and dorsalmost 9–10 pectoral rays.

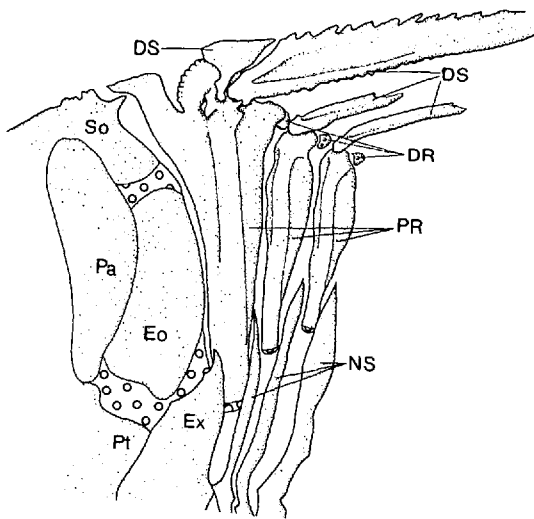
Bones of the head and pectoral girdle are extensively ornamented (Fig. 5A). A well-developed, serrate crest extends along the dorsal midline of the supraoccipital with a smaller serrate ridge along each side. Anterior to this median, tripartite, supraoccipital crest, there is a shorter, longitudinal, serrate ridge on each frontal. Each frontal also bears a long, arch-like, serrate ridge above the slightly serrate supraorbital ridge. Posteriorly, this arched frontal ridge almost joins a longitudinally serrate ridge on the pterotic. A single minute spine occurs on the lateral margin of each lateral ethmoid.

Of the infraorbital series, only the lacrimal, second infraorbital and dermosphenotic are ossified. There are one to three minute spines on each margin of the trough-shaped dermosphenotic, and three minute spines on the dorsal margin of the second infraorbital. The tear-shaped lacrimal bears three obliquely oriented, approximately parallel, serrate ridges on its lateral surface and three large spines along its anteroventral margin, the posteriormost of these being retrorse and larger than the other two. (See Randall, 1955, and Strasburg, 1962, for discussions of this retrorse spine in reference to the synonymy of *Z. canescens* with *Z. cornutus*.) Just dorsal to the lacrimal, two short, parallel, serrate ridges are present; these constitute the free edges of the walls of the trough-shaped nasal bone. Posteriorly, the medial nasal ridge approaches continuity with the anteriormost frontal ridge.

The damaged upper and lower jaws are reconstructed in Figures 1 and 5A. The premaxillae are damaged extensively, but the remnant of a well-developed, vertically oriented, spine-bearing ridge on the ascending process of the left premaxilla is evident. The ascending process of the right premaxilla is missing. The lower jaw is twisted and displaced from its normal position but is essentially complete. The retroarticular bears a slightly anterior curving, ventrally directed spine at its posteroventral corner; the interoperculo-mandibular ligament inserts at the base of this spine. On its lateral surface the anguloarticular bears a short, horizontally



A



B

Figure 4. Anterior dorsal pterygiophores and associated spines. A. *Zanclus cornutus*, 9.5 mm SL, MCZ 62046. B. *Acanthurus* sp., 10.4 mm SL, USNM 240072.

oriented, serrate ridge, which represents the dorsal wall of the mandibular sensory canal. Laterally and ventrally directed, serrate, horizontal ridges on the dentary also delineate the mandibular sensory canal.

The posterior margin of the preopercle is smooth, but the lateral ridge bears several minute spines along both the upper and lower limbs. The posterior margin of the opercle bears two widely spaced, blunt spines. The free margins of the subopercle and interopercle are smooth. The trough-like medial (dorsal) extrascapular bears a single minute spine on each ridge; the lateral (ventral) extrascapular lies just anterior to the posttemporal and bears several minute spines. The posttemporal bears a short, vertically oriented, serrate ridge, aligned, but not continuous with, a similar, though much longer ridge on the lateral surface of the supracleithrum. A short, horizontally oriented, serrate ridge is also present on the posttemporal, just ventral to the vertical ridge, and represents the ventral wall of the posttemporal sensory canal. The cleithrum bears serrations along its exposed, obliquely oriented, lateral margin. A ventrally serrate bony keel extends along the ventral midline from near the angle of the lower jaw to the cleithral symphysis; the lateral surfaces of this keel bear irregularly spaced spinules. A similar, but much shorter keel lies between the cleithral symphysis and the anterior end of the subpelvic keels of the pelvic girdle.

There are 9+13 vertebrae. The first and all succeeding neural arches are fused to their respective centra. There are 1+4 branchiostegal rays. The caudal skeleton comprises the following autogenous elements, all beginning to ossify: one parhypural; five hypurals; one uroneural; and one epural (only the posteriormost of the adult complement of three is evident). The neural spine of the second preural centrum is reduced, and the haemal spines of the second and third preural centra are autogenous.

The first dorsal pterygiophore bears a single supernumerary spine and inserts anterior to the first neural spine; its ventral tip is embraced by the exoccipitals so that it extends into the foramen magnum (Fig. 4A). There is a single predorsal bone; its ventral tip contacts the posterior midline of the neurocranium in an unossified area between the supraoccipital and the still separated epioccipitals (as in *Luvarus* and the acanthurids, the epioccipitals eventually meet synchondrally along the posterior midline). Each of the first three dorsal pterygiophores bears a ribbed median flange dorsally, around which its respective supernumerary spine can be rotated and locked at various positions. Each of the first two spines embraces its respective flange laterally, but the greatly elongate third spine is interlocked with its flange through a large central foramen. The first two pterygiophores lack distal radials.

The first anal pterygiophore is columnar and greatly enlarged with respect to the others. Dorsally, where it approaches the vertebral column, it is slightly expanded, bears a large cartilaginous tip, and is embraced anteriorly and posteriorly by the parapophyses of the ninth and the haemal spine of the tenth vertebrae, respectively. Ventrally, there is a large, ribbed, median flange like that on the anteriormost dorsal pterygiophore, around which the first anal spine can be rotated and locked.

The dorsal and ventral postcleithra are separate (Fig. 5A); the dorsal element is much shorter and somewhat broader than the ventral element, which is needle-like, slightly curved and does not reach the ventral margin of the body.

The pelvic girdle (Fig. 5A) is approximately T-shaped and is oriented so that its primary ramus is oblique (about 60° from the horizontal). The cartilaginous tip of the primary ramus articulates between the cleithra at a point about halfway from the scapula to the cleithral symphysis. At the posteroventral end of the

primary ramus, the subpelvic keel and postpelvic process extend anteriorly and posteriorly, respectively, to form the approximately horizontally oriented head of the inverted "T." Like the anteriormost dorsal and anal spines, the pelvic spine rotates around a ribbed median flange located near the middle of the head of the "T."

Preflexion Larvae, Figure 2.—There is no evidence of fin spines, soft rays or their corresponding internal supports with the exception of a few barely discernible dorsal- and anal-fin anlage in the 3.2 mm specimen. The mid-brain is large and dome-shaped as in the postflexion specimen, but the cranial cavity, vertically elongate in the latter, remains longer than it is high.

The 2.8-mm specimen (Fig. 2A) is relatively slender with a rounded head and long gut. The gut is straight to about mid-body where it makes a single coil and descends abruptly to the ventral body margin. Snout to anus length averages about 65% NL in all of the preflexion larvae. Body depth increases from 25% in the 2.8-mm specimen to 60% in the 3.2-mm specimen.

The 2.8-mm larva lacks bony ornamentation.

The two larger preflexion specimens have an extremely large, mostly cartilaginous, supraoccipital crest (50% NL); along the margin of the crest there are 23–26 long, slender, slightly curved spines projecting dorsally from the truncate peaks of irregular, roughly cone-shaped protrusions that give the crest margin a jagged appearance. A single spine protrudes from the as yet unossified pterotic region. The lateral ridge of the preopercle bears eight small spines. There are three large, approximately equally spaced spines on the posterior margin of the preopercle, one at the angle and one each on the upper and lower limbs; these three spines apparently become reduced with development and are totally lacking in the postflexion specimen. A tiny spine is present on the posterior margin of the supra-cleithrum. A serrate bony keel extends along the ventral midline from near the anterior tip of the preopercle to the cleithral symphysis; three to four minute spinules occur laterally along this keel. A similar, but much shorter keel lies just posterior to the cleithral symphysis. There is a sharp, slightly anteriorly curving spine on the posteroventral corner of the retroarticular. Two small spines are present on the ventral margin of the dentary.

In the 2.8-mm larva, pigmentation is restricted to a small cluster of 12 melanophores on the dorsolateral surface of the hindgut and a single melanophore on the dorsal midline at the tenth myomere, directly above the hindgut pigment. Pigmentation increases in the 3.0 and 3.2-mm specimens. A light sprinkling of melanophores covers the dorsolateral surface of the entire gut, with four or five large, stellate melanophores visible over the lateral surface of the hindgut. Two or three small melanophores occur on either side of the dorsal midline at the third and fourth myomeres. Posteriorly, one to three melanophores are present on the dorsal midline between the ninth and twelfth myomeres, and there are three small melanophores on each side just ventral to these.

Identification.—Characteristics of the larvae of the Acanthuroidei are discussed below in the section on comparison and relationships. Within the Acanthuroidei, the dorsal- and anal-fin ray counts, elongate, filamentous third dorsal spine, and retrorse lacrimal spine of the 9.5-mm SL specimen are unique to *Zanclus*. Evidence for assignment of the larger (3.0–3.2-mm NL) preflexion specimens to *Zanclus* is twofold. They share with the postflexion specimen a long, serrate, midventral keel anterior to the cleithral symphysis and a shorter one posterior to it (other larval acanthuroids either have a series of several short keels [Acanthuridae] or lack midventral keels altogether). Furthermore, these two specimens

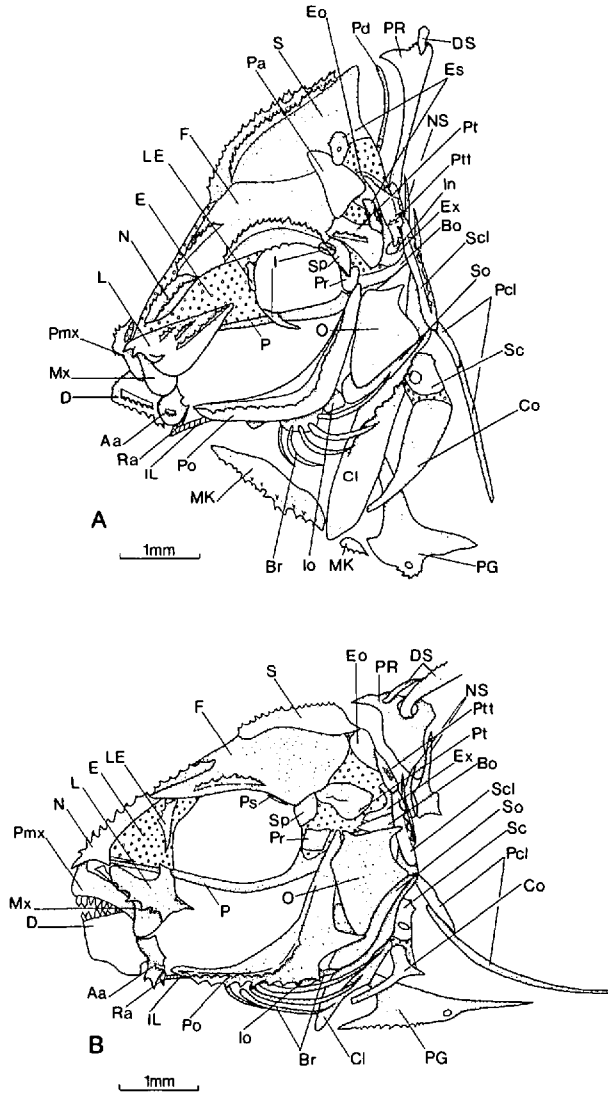


Figure 5. Head bones, suspensorium and pelvic spine excluded; larger stippling represents cartilage. A. *Zanclus cornutus*, 9.5 mm SL, MCZ 62046. B. *Siganus* sp., 9.7 mm SL, MCZ 63119.

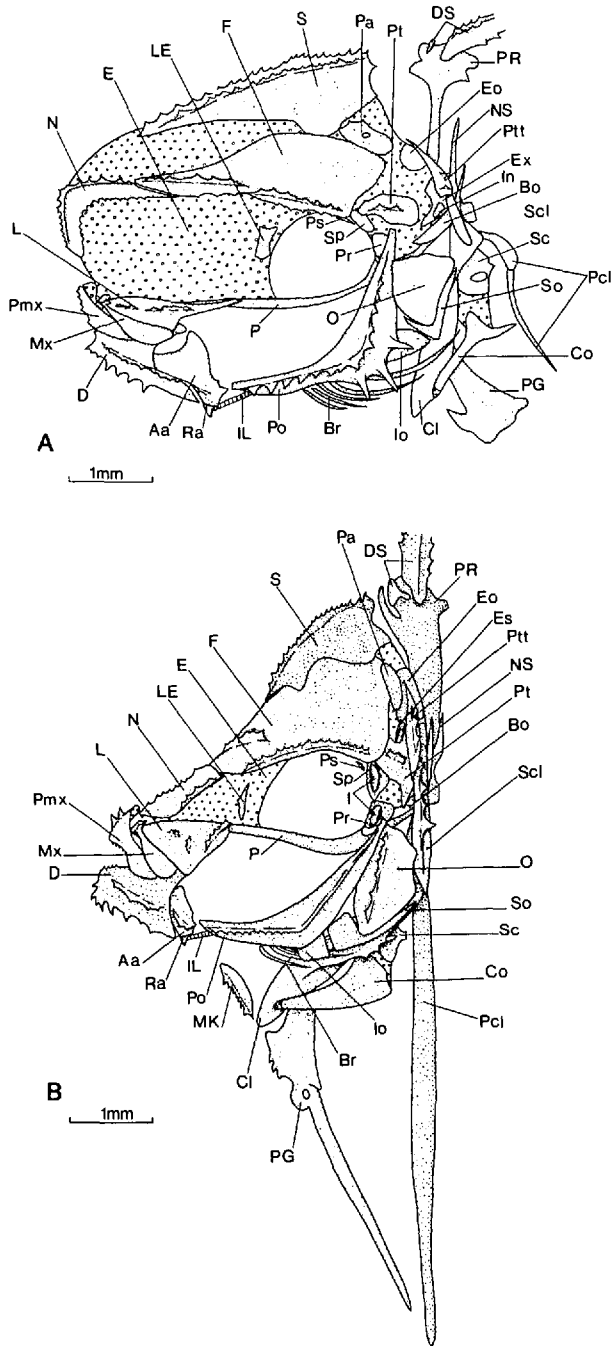


Figure 6. Head bones, suspensorium and pelvic spine excluded; larger stippling represents cartilage. A. *Luvarus imperialis*, 10.5 mm SL, MCZ 55291. B. *Naso* sp., 9.7 mm SL, MCZ 63121.

differ from all known preflexion acanthurid larvae in having moderately large (vs. tiny) preopercular spines, an enormous, jagged supraoccipital crest with relatively long, marginal spines, and a longer gut. *Zanclus* larvae are apparently less precocious than other acanthurids; these preflexion specimens lack the following structures that are well developed in known acanthurid larvae of equivalent size: anterior dorsal and anal spines and pterygiophores; pelvic girdle and spines; and well-ossified, single postcleithrum (on each side). In the smallest preflexion specimen, the supraoccipital crest is not yet characteristically jagged or spinous, and there are no preopercular spines or midventral keels; however the gut is extremely long relative to that of acanthurid larvae at this size, and there is a single pigment spot that corresponds to some of the diagnostic pigment of the larger specimens. We are thus confident in assigning this smallest specimen to *Zanclus*.

COMPARISON AND RELATIONSHIPS

In a treatise on the osteology and relationships of *Luvarus*, Tyler et al. (MS)¹ present a phylogenetic analysis of the Acanthuroidei, based on both adult and larval characters. They identify the Scatophagidae and Ephippidae as the first and second outgroups, respectively, and polarize adult and larval character states accordingly following the methodology of Maddison et al. (1984). It is not our purpose here to repeat the full character and phylogenetic analysis presented in Tyler et al. (MS)¹ but rather to emphasize and compare morphological features of larval acanthuroids. We believe it is most appropriate and meaningful to do this within the context of the phyletic sequence proposed by Tyler et al.¹: Siganidae, Luvaridae, Zanclidae, Acanthuridae. Larval characters supporting each successive monophyletic group are discussed below. We follow the character polarities hypothesized by Tyler et al. (MS);¹ see that paper for a detailed outgroup statement for each character.

We have identified and examined postflexion larvae of all acanthuroid genera except *Prionurus*. For *Prionurus* we have identified only transforming prejuveniles, the smallest of which (24.5 mm SL) fortunately retains larval scales and remnants of most aspects of larval ornamentation and skeletal configuration. Selected characters of larval acanthuroids are compared in Table 1.

Leis and Richards (1984) included in the Acanthuroidei the Siganidae, Luvaridae (following Tyler et al., MS),¹ Zanclidae and Acanthuridae and stated that the larvae of these families share the following, probably derived (assuming a percoid ancestry) features: long pelagic period; early forming, elongate, dorsal and pelvic spines; serrate fin spines; moderately to very deep, compressed body; serrate ridges on the head; silvery gut; 22–23 vertebrae; and 16–17 principal caudal rays (the latter two are not strictly larval characters). We concur with their delineation of the Acanthuroidei and note that acanthuroid larvae also share an unusual pelvic girdle in which the primary ramus extends obliquely upward from the horizontal to slightly oblique subpelvic keels and postpelvic processes; the postpelvic processes are relatively long, and, in siganids and acanthurids, the ventral margins of the subpelvic keels are exposed and serrate (Figs. 5 and 6). The configuration of the pelvic girdle in adults reflects some of these features but is less distinctive. Another notable feature of acanthuroid larvae is a slightly curved, ventrally directed spine at the posteroventral corner of the retroarticular; this spine constitutes the first area of ossification on the retroarticular, and the interoperculo-mandibular ligament inserts at its base. Some of the serrate ridges on the head referred to

¹ Tyler, J. C., G. D. Johnson, I. Nakamura and B. B. Collette. *Luvarus imperialis*: an oceanic acanthuroid. Manuscript.

by Leis and Richards (1984) are diagnostic for larvae of the Acanthuroidei; these are located specifically on the supraoccipital, frontals, nasals, anguloarticular and lateral ethmoids (spines on the latter lacking in *Luvarus* and most acanthurids). Head bones and associated ornamentation are illustrated for larval *Zanclus*, *Siganus*, *Luvarus* and *Naso* in Figures 5 and 6.

We agree with Leis and Richards (1984) and Tyler et al. (MS)¹ that siganids are the sister group of other acanthuroids. However, we interpret differently some of the larval characters cited by Leis and Richards (1984). Those authors stated that larvae of *Luvarus*, *Zanclus*, and the Acanthuridae share the following derived characters: kite-shaped body (agree); elongate snout (this results from the elongate ethmoid cartilage and is not limited to the larvae); extremely elongate dorsal and pelvic spines (in *Zanclus* the latter is not extremely long and the elongate dorsal spine is not the serial homologue of the elongate spine in *Luvarus* and the acanthurids); no elongate preopercular spines (relatively large preopercular spines are present in *Luvarus* and preflexion *Zanclus*, but not in acanthurids); early-forming, specialized scales (agree, but see description below); and reduced numbers of dorsal-fin spines (not a larval character). These larvae share several other specializations that are unique among perciforms, including a spine-bearing vertical ridge on the anterior surface of the ascending process of each premaxilla, serrate ridges on the lateral surface of the lacrimal, and a vertically elongate, dome-like cranial cavity that houses the dome-shaped midbrain. (There are also serrate ridges on the lateral surface and ventral margin of the dentary, but these are found in a few other larval perciforms, e.g., pomacanthids.) The early forming, specialized scales (lacking secondarily in *Paracanthurus* and *Zebrasoma*) are unique in having a single, broad-based, fan-shaped (*Luvarus* and *Zanclus*) or pentagonal to triangular (acanthurids) lamina that projects upright from the basal plate of each scale (Fig. 3). In percoids with larval scales, the upright projections are more rounded and spindle-like, and there are usually several on each scale. Our observations do not agree with those of Leis (1984), who stated that the larval scales of acanthurids pass through an "intermediate spinule stage" before changing into vertically arranged "triangular scales." The scales of acanthurids are not triangular (although they may have triangular projections) and do not pass through an unspecialized spinule stage.

Another synapomorphy of larval *Luvarus*, *Zanclus* and acanthurids is a locking mechanism for the anteriormost dorsal spines. The first dorsal pterygiophore (first three in *Zanclus*, see discussion below) bears a ribbed, median flange, around which the first supernumerary spine can be rotated and locked. The first supernumerary spine is connected by a stout ligament to the elongate second supernumerary spine (again, see discussion of this character in *Zanclus* below), providing a means for locking this much longer second spine in an upright position. A locking mechanism is retained in adult *Zanclus* and acanthurids, but is lost, along with the first supernumerary spine, in juvenile *Luvarus*.

Leis and Richards (1984) were unable to clarify relationships among *Luvarus*, *Zanclus* and the Acanthuridae because no specialized larval characters shared by any two of these taxa were identified. Our data indicate that *Luvarus* is the sister group of *Zanclus* plus the Acanthuridae, as hypothesized by Tyler et al. (MS).¹ Larvae of the latter two taxa share several specializations lacking in larvae of *Luvarus* and the Siganidae. There are serrations on the obliquely oriented, lateral ridge of the cleithrum and one long (*Zanclus* and *Naso*) to several short (other acanthurids) serrate bony keels along the ventral midline anterior to the cleithral symphysis, and, except in *Naso*, posterior to the cleithral symphysis as well. There is a spine-locking mechanism on the first anal pterygiophore and pelvic girdle like

Table 1. Continued

Character	Acanthuridae						
	Siganidae	Luvianidae	Zanclidae	Naso	Prionurus	Acanthurus and Ctenochaetus	Zebrafish and Paracanthurus
Scales	-	+	+	+	+	+	-
Orientation	-	horiz.	vert.	vert.	vert.	vert.	-
Arrangement	-	irreg.	irreg.	rows	rows	rows	-
Projections	-	fan-shaped	fan-shaped	triangular	triangular	triangular	-
Specialized tissue	-	-	-	+	+	+	-
Basal plate	-	ovoid	ovoid	ovoid	elongate	elongate	-
Adult scale type	cycloid	spinulose	spinulose	spinulose	spinulose	ctenoid	spinulose

^a Extremely elongate and filamentous distally.

^b Elongate; precocious in those where preflexion larvae are known.

^c Dorsal and ventral elements fuse in juvenile.

^d Strut-like, dorsal and ventral elements not separate.

^e Moderately large in preflexion larvae, unlike known preflexion acanthurids.

^f Some serrations on medial ridge in larger (8-9 mm) specimens.

that on the dorsal pterygiophores. The scales (where present) and associated laminar projections (Fig. 3) are vertically oriented (vs. horizontally oriented in *Luvarus*).

Conflicting with the hypothesis that *Luvarus* is the sister group of *Zanclus* plus the Acanthuridae are three derived features, unique among acanthuroids, shared by larval *Luvarus* and *Zanclus*: tripartite supraoccipital crest, fan-shaped laminar projections on the scales; and absence of serrations on the subpelvic keels. Based on the well-corroborated hypothesis of Tyler et al. (MS)¹ (including the larval specializations listed above) these shared features are most parsimoniously interpreted as homoplasies, either having originated independently in the two genera or having characterized the common ancestor of *Luvarus*, *Zanclus* and the acanthurids and been reversed in the common ancestor of the latter.

Larval *Zanclus* are unique among acanthuroids in several respects. No other acanthuroid larvae have the large retrorse lacrimal spine or similarly located pigment spots dorsally on the main body surface and at the base of the dorsal fin. Particularly distinctive is the extremely long and filamentous third dorsal spine. This spine is serially associated with the second pterygiophore and interlocked with the third through a large transverse foramen (Fig. 4A). Surprisingly, this spine does not seem to be serially homologous with the pungent, serrate second dorsal spine of larval siganids, *Luvarus* and acanthurids, which is also elongate (although relatively much shorter than the long spine in *Zanclus*), and in acanthurids (Fig. 4B), is also interlocked with its supernumerary pterygiophore (the first) through a similar foramen. *Zanclus* is unique among larval acanthuroids in having a single supernumerary spine on the first dorsal pterygiophore, which, as in *Luvarus* and the Acanthuridae, inserts in the first interneural space and has its ventral tip embraced anteriorly by exoccipital flanges and posteriorly (by 20 mm or less) by the first neural spine. If the single supernumerary spine on the first dorsal pterygiophore in *Zanclus* has resulted from loss of the original first supernumerary spine (as happens ontogenetically in *Luvarus*), the extant, short first spine is the serial homologue of the elongate second spine of acanthurids.

Another possible explanation for the single supernumerary spine on the first dorsal pterygiophore in *Zanclus* is that the original first pterygiophore has become divided so that a single spine is now borne on each half of the original element. This seems unlikely because the second pterygiophore in *Zanclus* inserts posterior to the first neural spine, whereas the first inserts anterior to it and, just as in *Luvarus* and the acanthurids, is embraced ventrally by the exoccipitals and first neural spine. In any case, if the original first pterygiophore has become divided in *Zanclus*, then the short second spine (not the elongate third) would be the serial homologue of the elongate second spine in acanthurids.

We can offer no defensible hypothesis of morphological transformation that would place the third elongate and interlocked spine of *Zanclus* as the serial homologue of the second elongate and interlocked spine of acanthurids. One reviewer proposed the following, suggesting that it would require only two steps: if the ancestral condition was like that of *Zanclus*, an acanthurid-like configuration could have resulted from loss of the predorsal, the first pterygiophore and spine and the first vertebra in conjunction with fusion of the next two pterygiophores; this sequence of events would make the elongate spine in each group serially homologous. We reject this hypothesis for several reasons. First, outgroup comparison indicates that the *Zanclus* condition (unique among perciforms), not the acanthurid condition, is derived. Furthermore, although loss and fusion of pertinent structures might be viewed as a few relatively simple steps (though certainly more than two), the resulting interdigitation pattern for anterior pterygiophores

and neural spines would not be that seen in acanthurids, so that additional rearranging would be required; in addition, the new compound first pterygiophore of acanthurids would have to redevelop the specialized association with the neurocranium and first neural spine. Finally, the vertebral number is the same (9+23) in *Zanclus* and acanthurids, refuting the hypothesis of vertebral loss.

Larvae of the Acanthuridae share several distinctive specializations lacking in other acanthuroids. There is a vertical, serrate ridge on the lateral surface of the opercle (smooth in *Paracanthurus* and *Zebrasoma*). Preflexion larvae are not all identifiable to genus, but among all those examined to date, development of head and fin spines is extremely precocious. Leis and Rennis (1983) report that specimens as small as 1.8 mm NL have a serrate supraoccipital crest, and some other head spines. The anteriormost dorsal- and anal-fin pterygiophores and spines and the pelvic girdle and spines appear as early as 2.3 mm NL (Leis and Rennis, 1983) and are well developed by 3.0 mm NL. Although the pelvic spine is precocious, the pelvic soft rays appear late (barely visible and extremely short at 5–7 mm) and remain short and poorly developed to sizes as large as 15 mm. The second anal spine (visible by about 3 mm NL) becomes long and serrate, and the first anal pterygiophore is an enormous columnar strut, the expanded dorsal tip of which is capped by a large cartilage that is tightly embraced by needle-like parapophyses on the posterior three to four precaudal vertebrae. The postcleithrum is also precocious and ossifies (at about 3 mm) as a single, long strut that extends to the ventral margin of the body and braces the first anal pterygiophore at its anteroventral corner. In siganids and *Luvarus*, there are two postcleithra (on each side) in larvae and adults. *Zanclus* adults share the single postcleithrum of acanthurids (Tyler et al., MS),¹ but in *Zanclus* larvae there are two postcleithra of normal size and shape which apparently fuse at some late stage in juvenile development.

The scales (Fig. 3C, D) of acanthurid larvae (lacking in *Paracanthurus* and *Zebrasoma*) are not only vertically oriented, as they are in *Zanclus*, but are arranged in ordered vertical rows. In contrast to the fan-shaped projections of *Luvarus* and *Zanclus* scales, the laminar projections on acanthurid scales are pentagonal or triangular with the apex of the triangle directed distally. The most remarkable aspect of the scales of larval acanthurids is the presence of a discrete ridge of firm, non-bony tissue along each basal plate. Superficially, this specialized connective tissue has a resilient texture like that of cartilage and stains definitively with alcian blue; however the characteristic "cellular matrix" of cartilage is not evident, even in histological sections.

The family Acanthuridae comprises six genera. We have not formulated a precise hypothesis of relationships among them, but we have observed three distinct postlarval forms that we believe encompass the six acanthurid genera, one representing *Naso*, one representing *Acanthurus*, *Ctenochaetus* and tentatively *Prionurus*, and one representing *Paracanthurus* and *Zebrasoma*.

Naso larvae (Leis and Richards, 1984, fig. 296, middle) are extremely deep bodied, and the pre- and postanal margins of the body are sharply inclined so that they meet in an acute angle at the anus. They have a narrow concave snout and a single, long, midventral keel like that in *Zanclus*. The larval scale plates are ovoid, all bear pentagonal to triangular projections and (as in *Luvarus*, *Zanclus*, and most percoids with larval scales) all develop directly into the adult scales, which in *Luvarus*, *Zanclus* and *Naso*, are spinulose.

Larvae of *Acanthurus* (Leis and Richards, 1984, fig. 296, upper) and *Ctenochaetus* are less deep bodied than larval *Naso*; the ventral margin of the body is more rounded and the pre- and postanal margins meet in an obtuse angle. They

have a convex or straight snout, lack spines on the lateral ethmoid ridge and have a series of short, midventral keels. In these larvae the scale plates are extremely vertically elongate (Fig. 3D), and most of those on the head lack the upright triangular projections found on the body scales. Furthermore, none of the larval scales transform into adult scales but are fully resorbed, the adult scales then forming anew. *Acanthurus* and *Ctenochaetus* are the only acanthurid genera that have true ctenoid (Johnson, 1984) adult scales (Tyler, 1970).

Based on examination of transforming prejuveniles, we believe *Prionurus* larvae are basically like those of *Acanthurus* and *Ctenochaetus*, and we were able to detect substantial differences only in details of scale morphology and transformation. In the smaller transforming *Prionurus* specimens, both larval and adult scales are present. The larval scales are vertically elongate like those of *Acanthurus* and *Ctenochaetus*, and the specialized connective tissue is still evident on a few of them. Unlike the latter two genera, however, upright triangular projections are borne on all scales, including those on the head. *Prionurus* also differs from these genera in mode of development of adult scales, which are spinulose rather than true ctenoid. Although most adult scales form anew in *Prionurus*, others form through direct transformation of the existing elongate larval scales which develop clusters of spinules on their lateral surfaces and gradually assume the round to ovoid configuration of the adult scales, apparently through fractionation or differential growth of the elongate plates.

Larvae of *Paracanthurus* and *Zebrasoma* differ trenchantly from those of *Acanthurus*, *Ctenochaetus* and *Prionurus* but share with them a series of short midventral keels, and a smooth ridge on the lateral ethmoid. The snout is somewhat narrower than that in larvae of the latter three genera, but the ventral body outline is similarly rounded. The pelvic spines are significantly longer than in other acanthurid larvae (>50% SL vs. <40% SL in 5–6 mm specimens). An enlarged retrorse spinelet at the base of the lateral ridges of each pelvic and second dorsal and anal spines is a unique specialization of larval *Paracanthurus* and *Zebrasoma*, provides for their easy recognition and, along with additional specializations described below, supports their relationship as sister taxa.

Larval *Paracanthurus* and *Zebrasoma* lack a number of features that are diagnostic of other acanthuroid larvae. The usual serrate ridges on the anterior region of the frontals and lateral surfaces of the dentaries never develop. The nasals and lacrimals ossify substantially later than in other acanthuroids (~8 mm vs. 4–5 mm) and lack the strongly serrate ridges usually associated with these bones in early postflexion acanthuroid larvae (some serrations appear on the medial ridge of the nasal in larger specimens [8–9 mm]). Larval *Paracanthurus* and *Zebrasoma* are also unique among acanthuroids (above siganids) in that they lack larval scales; the spinulose adult scales all form anew. An exception may be the single "scale" that transforms into the moveable spine that lies in a shallow groove on each side of the caudal peduncle in adults. *Acanthurus* and *Ctenochaetus* adults have a similar spine lying in a deeper groove on the caudal peduncle, while adult *Naso* and *Prionurus* have one to several immobile plates there (Tyler, 1970). The spine in *Acanthurus* and *Ctenochaetus* and the plates in *Naso* and *Prionurus* each develop through direct transformation of a preexisting larval scale, and in the former two the spine is well formed before resorption of the larval scales or development of the new adult scales begins. (Our observations do not agree with the statement of Leis and Richards, 1984, that the caudal peduncular armature in *Acanthurus* "forms directly without the unspecialized scale stage.") In *Paracanthurus* and *Zebrasoma* the spine-forming "scale" appears on the caudal peduncle well before adult scales begin to appear, and it seems likely that this

structure is the ontogenetic homologue of the larval scales in other acanthurids; however, as noted above, no other larval scales develop in these two genera.

Based on the well-corroborated hypothesis of Tyler et al. (MS),¹ the absence of scales and certain other features that characterize other larval acanthuroids is not primitive for larval *Paracanthurus* and *Zembrasoma* but is most parsimoniously interpreted as secondarily derived. These secondary absences may be the result of heterochronic shifts, because for each character postflexion *Paracanthurus* and *Zembrasoma* exhibit the state that characterizes the preflexion stage in other acanthurids. Thus, although we are not aware of clear examples of heterochronic expression in adult *Paracanthurus* and *Zembrasoma*, several characters appear to be pedomorphic within the larval stages of these genera. We suspect that heterochrony has played an important role in the evolution of the Acanthuroidei, and suggest that a thorough investigation of the dynamics of their development, beyond the scope and purposes of this paper, would be worthwhile.

ACKNOWLEDGMENTS

We thank the following individuals and their institutions for the loan of material: K. Hartel and K. Leim (MCZ); J. Leis (AMS); L. Knapp (SOSC); P. Keener (SCMRRI, incorrectly listed as SCMRI in Leviton et al., 1985). K. Hartel, on very short notice, packed and hand carried several lots of acanthuroid larvae to the senior author, among which the postflexion *Zanclus* was found. J. Leis generously provided several preflexion specimens that he suspected were larval *Zanclus*. J. Harshbarger (Registry of Tumors in Lower Animals, USNM) provided histological preparations of acanthurid scales. B. B. Collette (Systematics Laboratory, National Marine Fisheries Service) and V. G. Springer (USNM) read and commented on the manuscript. J. Leis and G. Moser (Southwest Fisheries Center, National Marine Fisheries Service, NOAA) provided critical reviews.

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DATE ACCEPTED: August 28, 1986.

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