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Larvae and Juveniles of the Deepsea "Whalefishes" *Barbourisia* and *Rondeletia* (Stephanoberyciformes: Barbourisiidae, Rondeletiidae), with Comments on Family Relationships

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ABSTRACT. Larvae of the deepsea "whalefishes" *Barbourisia rufa* (11: 3.7–14.1 mm nl/sl) and *Rondeletia* spp. (9: 3.5–9.7 mm sl) occur at least in the upper 200 m of the open ocean, with some specimens taken in the upper 20 m. Larvae of both families are highly precocious, with identifiable features in each by 3.7 mm. Larval *Barbourisia* have an elongate fourth pelvic ray with dark pigment basally, notochord flexion occurs between 6.5 and 7.5 mm sl, and by 7.5 mm sl the body is covered with small, non-imbricate scales with a central spine typical of the adult. In *Rondeletia* notochord flexion occurs at about 3.5 mm sl and the elongate pelvic rays 2–4 are the most strongly pigmented part of the larvae. Cycloid scales (here reported in the family for the first time) are developing by 7 mm; these scales later migrate to form a layer directly over the muscles underneath the dermis. By 7 mm sl there is a unique organ, here termed Tominaga's organ, separate from and below the nasal rosette, developing anterior to the eye. Larvae of the two species of *Rondeletia* can be distinguished by the presence or absence of developing spongy bone in the pectoral girdle and sphenotic by at least 9 mm and by the counts of the vertebrae, pelvic-fin rays, and dorsal hypural bones in smaller larvae. The presence of Tominaga's organ in the gibberichthyid *Gibberichthys* suggests that "the whalefishes", Barbourisiidae, Rondeletiidae, and Cetomimidae, as a group are paraphyletic, and that *Rondeletia* and *Gibberichthys* are sister taxa.

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The deepsea "whalefish" families Rondeletiidae and Barbourisiidae have been considered close relatives since the description of the latter family by Parr (1945). Recent authors have considered them part of a separate order Cetomimiformes (Ebeling & Weed, 1973), part of a "stephanoberycoid assemblage" (Rosen, 1973) or part of a suborder of the Beryciformes (Rosen & Patterson, 1969; Keene & Tighe, 1984; Moore, 1993). We follow Johnson & Patterson (1993) and Nelson (1994) in recognizing two orders: Stephanoberyciformes (Melamphaidae, Stephano-

berycidae, Hispidoberycidae, Gibberichthyidae, Rondeletiidae, Barbourisiidae, Cetomimidae, Megalomycteridae, Mirapinnidae) and Beryciformes (Holocentridae, Berycidae, Diretmidae, Anoplogastridae, Trachichthyidae, Anomalopidae, Monocentridae), respectively sequential sister groups to the Percomorpha. Recently Colgan *et al.* (2000) questioned the monophyly of the Stephanoberyciformes based on partial 12S and 16S rDNA sequences. Further consideration of family relationships within the Stephanoberyciformes is in the Discussion.

In their description of a 6.2 mm larval specimen of the anomalopid *Kryptophanaron*, Baldwin & Johnson (1995) reported that larvae of 10 of the 16 recognized stephanoberyciform and beryciform families had been described. They also noted that larval specimens of two additional families, Rondeletiidae and Barbourisiidae, had been identified from collections. The purpose of this paper is to describe those specimens and to comment on family relationships based on the larval characters.

Boehlert & Mundy (1992) described an 11.3 mm larva from near Hawaii that they tentatively placed in the Stephanoberycidae as either *Malacosarcus* or an undescribed form. Body shape, meristics, and the lack of scales at that size preclude identification as either *Barbourisia* or *Rondeletia*.

The family Barbourisiidae is monotypic. *Barbourisia rufa* was described by Parr (1945) from the Gulf of Mexico. The species has since been collected from the Atlantic, Pacific and Indian Oceans from >60°N to 45°S; at least 100 specimens have been collected (Kotlyar, 1995; Paxton, unpubl.). Captures have been with both benthic nets between 350 and 1500 m and pelagic nets to at least 800–2000 m. *Barbourisia rufa* attains 390 mm SL and the sexes are separate (Paxton, unpubl.). Struhsaker (1965) figured the distinctive scales, and osteological features of the gill arches and caudal skeleton were described by Rosen (1973). Ebeling & Weed (1973) also summarized selected features of *Barbourisia*. In his phylogenetic analysis of the "trachichthyiform" fishes Moore (1993) coded 25 osteological characters for *Barbourisia*. Johnson & Patterson (1993) discussed cranial sensory features and other selected aspects of the osteology, including the intermusculars (also discussed and tabulated by Patterson & Johnson, 1995). Kotlyar (1995) described and figured the osteology, based primarily on a cleared and stained specimen 212 mm sl. Colgan *et al.* (2000) detailed partial sequences of 12S and 16S rDNA for the species.

The Rondeletiidae includes *Rondeletia bicolor* Goode & Bean (1895) and *R. loricata* Abe & Hotta (1963). Parr (1929) described the osteology of *R. bicolor*, and Paxton (1974) described that of *R. loricata* and summarized distributional data for both species. Selected osteological features have been described by Ebeling & Weed (1973), Rosen (1973), Moore (1993), Johnson & Patterson (1993), and Patterson & Johnson (1995). Bast & Klinkhardt (1990) described specimens of *R. loricata* from the northeast and southwest Atlantic. Kotlyar (1996) detailed the osteology of *R. loricata* with many illustrations, and analysed the distributions of both species. Colgan *et al.* (2000) detailed partial sequences of 12S and 16S rDNA of *R. loricata*. The species are meso- and perhaps bathypelagic, with captures from 250–2000 m in open nets. *Rondeletia loricata* occurs between 58°N and 48°S in all three oceans. *Rondeletia bicolor* is most common in the Caribbean and western North Atlantic between 0° and 37°N, with only one record from the South Atlantic and two records from the South Pacific (Paxton, 1974; unpublished). Maximum size of the genus is 113 mm sl.

Materials and methods

Institutional abbreviations follow Leviton *et al.* (1985). TH is the Tokai Regional Fishery Research Laboratory, Tokyo, the specimens of which have recently been transferred to NSMT. Standard length = sl; notochord length = nl. The abbreviations of measurements follow Paxton (1989: 139); P2 = pelvic fin. All measurements are in sl and mm unless otherwise indicated. Most of the larvae were found in the Dana Collections at ZMUC (Table 1); the fishing depths are estimated to be one third the amount of wire out (Bertelsen, 1951: 198). Most of the juveniles are from MCZ.

All measurements of larvae were made with an ocular micrometer in a dissecting microscope. Measurements of juveniles and adults were made with dial calipers. Meristics of adults are mostly from xrays. Selected specimens were stained with alcian blue for cartilage and/or alizarin for bone.

Identifications

Identification of larval *Barbourisia rufa* was based on the presence of non-imbricate scales with a central spine (Struhsaker, 1965: fig. 1) and abdominal pelvic fins, both characteristic of adults, and was confirmed with comparative meristics of the other families in the orders (Keene & Tighe, 1984). Adult *Acanthochaenus, Hispidoberyx*, and *Stephanoberyx* have similar but fewer and much larger spiny scales; their vertebral count of 30–34 (Keene & Tighe, 1984; Yang *et al.*, 1988) differs from the 40–44 vertebrae of *Barbourisia*.

Identification of larval *Rondeletia* (3.5–9.7 mm) was based on fin-ray and vertebral counts and abdominal pelvic fins. Smaller larvae were distinguished by pelvic-fin and vertebral counts: 6 and 26–27, respectively, in *R. bicolor*, 5 and 24–26, rarely 27 in *R. loricata* (Paxton, 1974). The largest larvae and small juveniles (over 8.5 mm) were identified to species by the presence (*R. loricata*) or absence (*R. bicolor*) of spongy, honeycomb-like ossifications of the main bones of the pectoral girdle, with posterior extensions on the posttemporal dorsally and cleithrum ventrally. This was facilitated by comparison of the larvae with a series of juvenile specimens (12.6 to 21.7 mm) that are recognizable by adult features such as vertical rows of lateral-line neuromasts, abdominal pelvic fins and brown colour.

No distinct metamorphosis from larval to juvenile stage is present in either family, rather a gradual transition occurs. We have arbitrarily chosen the completion of the adult condition of the lateral-line system on the body to distinguish larvae from juveniles. In *Barbourisia* the largest larva at 14.1 mm has enlarged scales in an open lateral-line trough, while the smallest juvenile at 30.0 mm has the enlarged scales within a closed lateral-line canal. In *Rondeletia*, lateral-line head pores and vertical rows of papillate superficial neuromasts are visible in a 12.6 mm *R. loricata* and a 14.4 mm *R. bicolor*, but not in a 9.7 mm *R. loricata* considered the largest larva. The 13.5 mm *R. bicolor* lacks visible features of the lateral-line system, but is completely faded and in poor condition. Based on

Table 1. *Barbourisia rufa* material examined. Abbreviations: cl, closing net; * = cleared and stained; # = drawn.

specimen	catalogue	size (mm)	location	depth (m)	day/night	date
1	AMS I29035-003	3.7	14°40'S 145°15'W	0–10	D	31 Jan 1989
2 #	AMS I29176-002	4.8	14°56'S 147°52'W	0–5	D	14 Feb 1989
3	USNM 363086	4.9	21°32'N 157°45'W	0–0.7	N	14 Dec 1985
4	AMS I24586-007	5.0	21°16'N 157°32'W	0–1	?	13 Jun 1972
5 *	ZMUC P2340802	6.2	1°15'N 136°07'E	0–33	N	14 Jul 1929
6 #	AMS I29174-002	6.6	14°56'S 147°52'W	0–5	D	14 Feb 1989
7 #	MCZ 75627	7.5	2°06'N 33°38'W	0–70	?	16 Mar 1977
8 *	USNM 363087	10.0	33°59'N 76°22'W	0–63	?	15 Sep 1994
9	USNM 305035	13.1	19°25'N 156°18'W	0–50	N	27 Sep 1988
10 *	ZMUC P2340803	13.4	10°51'S 168°40'W	0–33	N	29 Oct 1928
11 *#	ZMUC P2340804	14.1	15°56'S 172°30'W	0–66	N	7 Nov 1928
12	AMS I18823-001	30.0	21°25'N 158°25'W	825–1150 cl		17 Mar 1971
13	SIO 88-172	34.6	6°55'N 177°48'W			14 Mar 1987
14	TH 865522	45.6	29°59'N 134°11'E	0–1040		18 Jul 1986
15	AMS I26869-001	89	off Zanzibar	0–200		1965
16	AMS I27260-001	92	21°23'N 158°18'W			17 Jun 1973
17 *	AMS I18824-001	100	25°25'N 158°25'W	250–300 cl	N	23 Apr 1971
18	AMS I22812-001	114	18°08'S 116°43'E	0–800		5 Apr 1982
19 *	AMS I27261-001	133	0°08'N 154°02'W	?		2 Mar 1969

similarities of body shape and fin development with the larger juveniles, it is assumed to be the smallest known juvenile. Head pores and papillate neuromasts are visible in some, but not all, of the juveniles of both species less than 20 mm sl depending on their skin condition.

Results

Barbourisia rufa Parr, 1945

Fig. 1

Eleven larvae 3.7–14.1 mm were examined, six preflexion specimens 3.7–6.6 mm and five postflexion specimens 7.5–14.1 mm (Table 1). The three ZMUC specimens are faded and transparent, having been stored for decades in formalin, and have now been stained with alizarin. The 13.1 mm USNM specimen retains pigment, but unfortunately had the pelvic fins removed, apparently by an overzealous plankton sorter attempting to "clean" the specimen. In the three largest specimens >13 mm sl, the skin is inflated, loose and balloon-like around the body, and appears to have little connection to the underlying muscle. The four smallest larvae (5.0 mm nl and smaller) are very slender, distinguished by long, abdominal pelvic fins. The body is deeper anteriorly and slender posteriorly in the two largest preflexion specimens >6 mm nl, moderately deep in the smallest postflexion specimen 7.5 mm sl, and deep and globose in the four largest postflexion specimens. The jaws are relatively short and obliquely directed in all five postflexion specimens (Fig. 1).

In the larvae, eye diameter, pectoral- and pelvic-fin lengths and body depth (only in postflexion specimens) are relatively greater than those of the juveniles and adults, while the snout length is less. Nostrils are visible only as small slits anterior to the eye in the largest larvae, although a small nasal pit becomes apparent at 6.6 mm nl. The distinctive elongate pelvic fin reaches the equivalent of beyond the hypurals by 6.6 mm nl and at least the 4th ray retains this relative length at least until the 14.1 mm larvae, while the pelvic-fin insertion changes from closer to the pectoral-fin origin to closer to the anal-fin origin through the same size range (Fig. 1b,d). The growth of some elements (pectoral and pelvic fins) becomes isometric by small juvenile size (30 mm), but the small juvenile specimens are not in good enough condition to determine if the 4th fin ray is longer than the other rays. The eye diameter becomes isometric only at more than 150 mm sl. Variation in other measurements (e.g., pectoral-fin origin to anus and body depth) is due to the flabby nature of the specimens resulting in imprecise measurements. A comparison of the larval shape of *Barbourisia rufa* (Fig. 1d) with that of the adult (Rofen, 1959: fig. 3) shows the striking transformation in head shape, snout length, and jaw angle. By 30 mm the shapes of these elements are similar to those of the adult.

Pigmentation. Many of the larval specimens are faded. The eye is solid black, except for the white lens. There are two layers of melanophores over part of the head and anterior half of the body by 13 mm when the skin separates from the body; a layer of larger, lighter and more widely spaced melanophores just under the skin and a deeper layer overlying the viscera and part of the brain.

Small, evenly-distributed melanophores are present dorsally and dorsolaterally on the entire head in the smallest specimen. The density and size of melanophores vary as the larvae develop. However in larger preflexion larvae, melanophores tend to be stellate and more densely arranged over the brain. In the largest specimen superficial melanophores are present circumorbitally, on the cheek and the upper half of the opercles. More closely spaced melanophores are on the top of the head in the supra-occipital-posterior frontal area. A deeper layer of darker, more widely spaced melanophores covers the visible lobes of the brain above and behind the orbit. A few melanophores are present on the lower jaws throughout larval development. The small melanophores on the dorsal surface of the head extend posteriorly to the nape and are distributed over the entire musculature of the trunk and tail.

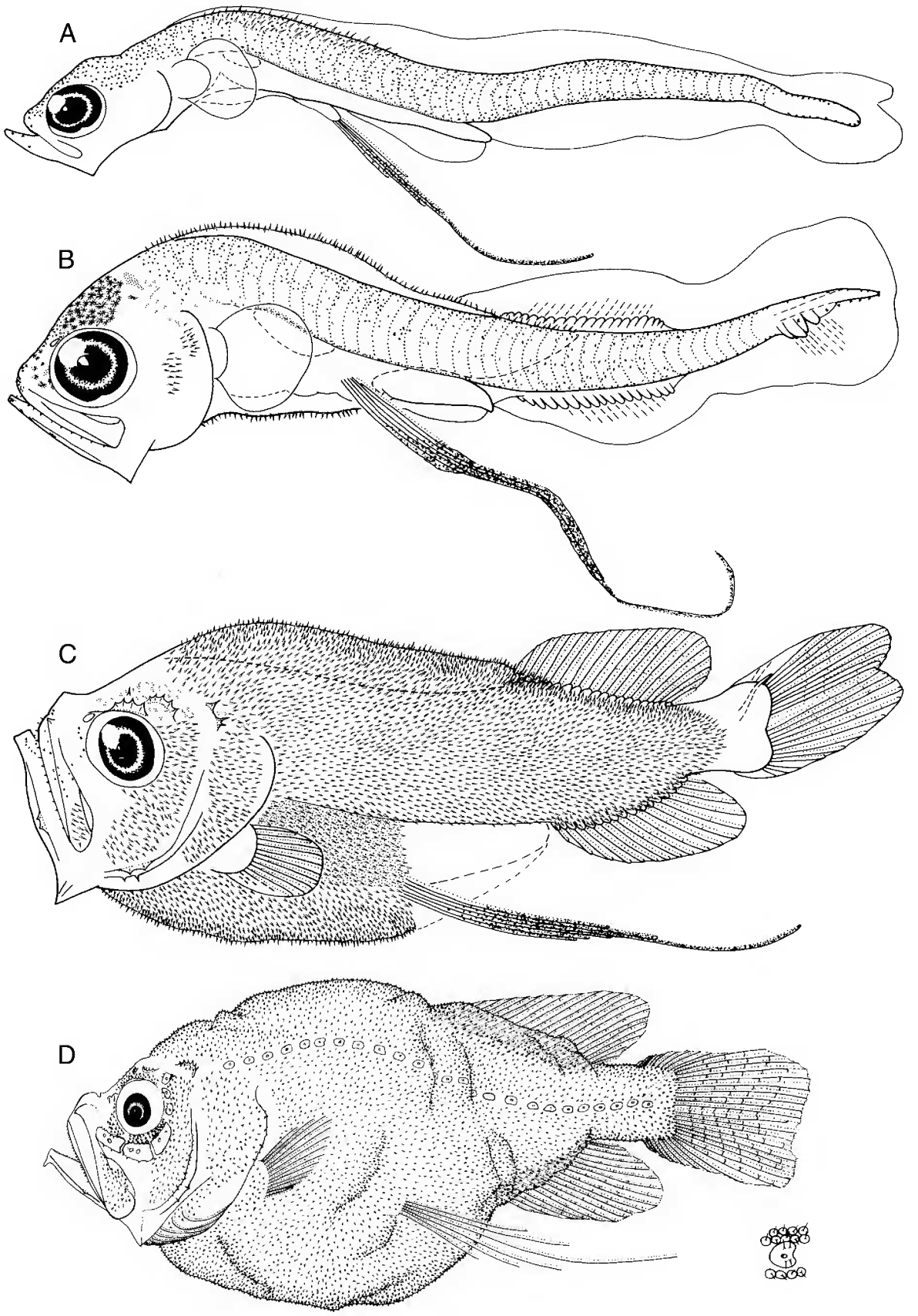


Figure 1. *Barbourisia rufa* larvae. a, AMS I29176-002, 4.8 mm nl; b, AMS I29174-002, 6.6 mm nl, spinules shown in profile only, with distribution indicated by dashed line across posterior of gut and anterior of tail; c, MCZ 75627, 7.5 mm sl, note missing posterior of gut; d, ZMUC P2340804, 14.1 mm sl, with enlargement of left lateral-line scale no. 20 and adjacent body scales illustrated below caudal fin.

The melanophores on the notochord tip are restricted to the dorsal and ventral margins. In postflexion larvae, small melanophores are distributed fairly evenly throughout the loose, balloon-like skin that covers the body, except over the abdominal cavity, where they extend ventrally only about to the level of the pectoral fin. Beneath the loose skin, the wall of the abdominal cavity is evenly covered with somewhat larger, more closely-spaced melanophores. This internal layer of peritoneal pigment extends almost to the ventral margin of the body in the region behind the pelvic girdle. Small melanophores are also found beneath the loose skin on the epaxial musculature, where they are more sparsely distributed and tend to concentrate along, and thus delineate, the myosepta and horizontal septum. The dorsal, anal, caudal and pectoral fins are unpigmented, except for two melanophores on each side of the base of the dorsal-most principal caudal ray only in the largest (14.1 mm) specimen. Pelvic fins are unpigmented proximally. Small melanophores cover both the membranes and elements, and extend to the tips of the pelvic fins.

The three 30–46 mm juvenile specimens are faded white in preservative and presumably were the original red-orange colour of adults. The carotenoid pigment is alcohol soluble and is bleached in preservation (Herring, 1976). In the largest two specimens (the smallest is completely faded) melanophores overlying the brain and muscle mass show through the skin. Those on the body are in two layers, one in a transparent sheet of tissue under the skin with light streaks of pigment, and another of lighter, more widely scattered streaks closely associated with the muscle bands. The peritoneum is solidly pigmented black. The basal half of the fourth pelvic-fin ray has large dark melanophores. By 89–114 mm, the two layers of pigment over the musculature are light but distinct, and a single large pigment spot remains near the base of the fourth pelvic-fin ray under the skin; scattered light melanophores are on the basal portions of all pelvic-fin rays in the least faded specimen. The posterior half of the medial side of the gill cover has a layer of moderately dense melanophores. In fresh specimens over 300 mm sl, the sheet of tissue between the skin and muscles is pigmented with brown blotches and a single large black spot is visible after dissection at the base of the fourth pelvic-fin ray. The inside of the gill cover is solid black.

Scales. Scales are present in the smallest specimen. They are small, round and non-imbricate with a single, central spine and appear identical in form to the adult scale illustrated by Struhsaker (1965). They are restricted to the dorsal surface of the trunk with at most 3–4 longitudinal rows of scales. This dorsal shield spreads in all directions; by late preflexion the scales extend over the trunk and tail from the nape to just beyond the anus, over the anterior and middle of the gut, but not onto the posterior-most portion of the gut. Two small patches are also present on the opercle. Scales develop progressively more posterior on the tail in postflexion larvae, and become more extensively distributed on the head. In the smallest postflexion specimen scales cover the tail except for the caudal peduncle. A few rows of scales extend over the base of the anterior-most dorsal-fin rays. The preopercle and opercle are almost entirely covered, and scales are also present postorbitally and on the maxilla. In the largest larva the scales cover the entire trunk and tail, and extend forward to cover much of the head, with the exception of the lower jaw, snout, premaxilla and anterior portion of the maxilla, some aspects of the frontals, the anterior three infraorbitals, and posterior surface of the preopercle. The gular region is scaleless anterior to the cleithral symphysis, but there is an elongate median patch 6–7 scales wide in the 13.4 mm specimen behind the lower jaw symphysis. An envelope of scale-bearing skin extends about ⅓ of the way out the dorsal-and anal-fin rays of the three largest specimens. In the 30 mm juvenile and larger specimens scales extend to the tip of the snout and to the tips of all the fin rays.

In the preflexion specimens specialized lateral-line scales are not apparent. We cannot ascertain whether the lateral-line trough is scaleless at this stage or whether it is covered with small spined scales. We do not expect that the specialized lateral-line scales will transform from body scales. The two smallest postflexion specimens are somewhat damaged, and the rippled skin makes scale distribution difficult to observe. In the three 13.1–14.1 mm postflexion specimens enlarged scales extend along the lateral line from the head to the base of the caudal fin, with one good count of 33 scales. These scales are 2–4 times the size of the body scales, have a central foramen and four spines, two dorsal and two ventral (Fig. 1d). The small body scales are absent between adjacent lateral-line scales. In 30 and 34 mm juvenile specimens the lateral line has invaginated to form a canal that is overgrown with skin. The overlying skin is pierced by small pores, but is only partially covered with small body scales in a series of narrow strips between the pores. Enlarged lateral-line scales, each with a central foramen, lie in the bottom of the lateral-line canal. No enlarged spines remain, but each scale has dorsal and ventral extensions that run laterally along the walls of the lateral-line canal. Each extension consists of two narrow elements that may represent the four spines present on each scale in the larvae. There is a neuromast on each lateral-line scale, innervated by a branch of the lateral-line nerve that emerges through the foramen of each scale. In a 133 mm specimen the dorsal and ventral extensions of the lateral-line scales extend further laterally and support approximately half of the roof of the canal. Each pair of extensions is strengthened by a series of small cross struts (Paxton, 1989: fig. 5a).

Head spines. No head spines are developed in the preflexion specimens, and the infraorbitals are unossified. In the smallest postflexion specimen the orbital rims of all six infraorbitals (including the dermosphenotic) bear small spines that may be on body scales. In the largest postflexion specimen the ventral rim of each infraorbital also has a single row of small spines. The interopercle bears 4–5 spines along its ventral margin that may also be scale spines. The preopercle has 2 small spines on the lateral surface and 2 small spines on the posterior margin in the smallest postflexion larva. None of the other opercular or pectoral-series bones bear spines. The supraorbital ridge is serrate in the smallest postflexion larva. From 13.1 mm the supraorbital edge of the frontal bears several longitudinal ridges each with one or two spines resulting in a triangular-shaped cluster of spines, medial to which are two transverse serrate ridges of bone forming walls for a portion of the supraorbital commissure of the lateralis system. A narrow upright bony strut lies medial to the anterior-most ridge.

There is a single extrascapular anterior to the posttemporal in all postflexion larvae, with the slightly raised anterior margin bearing several spines. The nasal bone has a single minute spine on the lateral rim in the postflexion larvae, and there are several small spines on the ventrolateral surface of the supramaxilla that are scale spines. There is a low ridge with 1–2 small spines laterally on the dentary in postflexion larvae only.

Fin formation. In the second largest preflexion specimen 6.2 mm nl, the median fins appear to be developing in both anterior and posterior directions. There are about 18 dorsal- and 14 anal-fin bases and approximately 14 and 11 incipient rays, respectively (Table 2). The caudal fin has about five dorsal and eight ventral rays. The dorsal-most pectoral-fin rays have begun to differentiate in the largest preflexion specimen. The pelvic-fin origin is initially slightly closer to the head than the anus. It has four well-developed rays in the smallest specimen, five rays by 4.8 mm and six rays by 6.2 mm. The fourth ray is produced and up to 50% longer than the other longest rays, but is often broken. The pelvic fins are initially close to each other and the ventral body margin. In postflexion larvae the pelvic fins are widely separated from one another and located higher on the body than in the preflexion larvae. By 30 mm and larger, the pelvic fin is much shorter, ending far forward of the anal-fin origin, and closer to the ventral margin of the body. All four postflexion specimens have full fin-ray complements in all fins (although the pelvic fins are missing in the largest specimen). Only the three cleared and stained postflexion larvae have visible supraneurals, with six or seven present.

Dentition. A single row of small triangular teeth is apparent on the premaxilla and dentary of the 6.2 mm larva. By 6.6 mm, the premaxilla and dentary have two rows of widely spaced, small, triangular teeth. Teeth increase in number as larvae develop. By 13 mm the teeth have become conical-triangular and are closely set in two rows, and by 34 mm the teeth have the adult form of a broad band of small conical teeth with about six tooth rows across the band. At 100 and 133 mm the teeth have a slightly enlarged tip, are depressible orally and the largest teeth are in the inner row. With increasing specimen size, the number of teeth across the jaw increases.

Internal anatomy. In smaller preflexion specimens the gut is narrow and folded anteriorly and straightens before exiting near the anal-fin origin. In larger preflexion larvae the gut is thick and folded. In the two larger ZMUC specimens the stomach is obscured by the liver; the intestine is considerably folded with a short straight section directed posteroventrally to the anus. A small swimbladder is evident in the smallest specimen, and is visible in larger specimens until the skin thickens. In the postflexion specimens it is present under the kidneys and extends as a space over the intestine. The swimbladder is regressed in adult *Barbourisia* (Bertelsen & Marshall, 1984: 382).

Caudal skeleton. In the 6.2 mm preflexion larva the parhypural and at least 4 hypurals are evident on the ventral side of the notochord posteriorly. The last several centra are not yet fully formed. In the two largest cleared postflexion specimens there are three epurals, two uroneurals, two urostylar centra (the compound PU1-U1 and a separate U2), one parhypural and six hypurals. The first epural originates over the posterior edge of the neural crest of PU2. The parhypural and hypurals 1 and 2 articulate with an oblong block of cartilage lying along the ventral surface of PU1-U1. Hypurals 3 and 4 articulate with U2. In the 100 and 133 mm specimens hypural 3 articulates with both the base of U2 and the cartilage anterior to that centrum. The bases of hypurals 3 and 4 are in close contact with U2, but not fused to it. The cartilage between hypurals 2 and 3 remains unossified in the larvae and the 100 mm specimen

Table 2. *Barbourisia rufa* counts. Abbreviations: A, anal-fin rays; Cprin, principal caudal-fin rays; Cproc, procurrent caudal-fin rays; D, dorsal-fin rays; LL, lateral line; Myom, myomeres; P, pectoral-fin rays; P2, pelvic-fin rays; Supran, supraneural elements; Vert, vertebrae; † fin bases only; ‡ fins removed; horizontal broken line indicates limit of preflexion and postflexion specimens; solid line indicates limit of larvae and juveniles; others as in Table 1.

specimen	size	D	A	P	P2	Cprin	Cproc	Supran	Myom/Vert	LL scales
1	3.7	—	—	—	4	—	—		41	
2	4.8	—	—	—	5	—	—		42	
3	4.9	—	—	—	5	—	—		42	
4	5.0	—	—	—	5	—	—		42	
5 *	6.2	c. 18	c. 14	—	6	c. 5+8	—		42–43	
6	6.6	20 †	16 †	—	6	5+5	—		41	
7	7.5	21	17	12+	6	10+9	2+3			
8 *	10.0	20	17	12+	6	10+9	9+8	7	42	
9	13.1	22	18	13	‡	10+9	9+8			
10 *	13.4	22	17	14	6	10+?	9+?	6	42	
11 *	14.1	21	17	13	6	10+9	10+9	6	42	33
12–14	30.1–47.3	21	16	12–13	6				41–43	25/26
15–23	88.0–169	19–22	16–18	12–14	6				41–42	28–34
24–36	250–305	20–21	16–17	12–14	6				41–43	28–34
37–48	318–386	20–23	16–18	12–14	6				40–43	25–34

and is about one-third ossified in the 133 mm specimen. In these larger specimens the first epural originates over the anterior end of PU2.

Rosen (1973: 492) described the caudal skeleton of *Barbourisia* as sharing with *Rondeletia* and the cetomimids a "complex joint of the upper hypurals with a cartilaginous plug on the hinder end of the compound centrum", but his figure 120 of *Barbourisia* shows no cartilage in this region and shows hypural 4 fused with the second ural centrum. We have examined Rosen's specimen and find both his description and his illustration to be in error. There is no exposed cartilage plug joint and although hypural 4 articulates tightly with PU2, it is not fused to it. We place little significance on the presence or absence of Rosen's so-called cartilage plug, as it is a general pattern in teleost fishes for the parhypural and hypurals 1 and 2 to develop together along a single block of cartilage ventral to PU1-U1 (Potthoff & Tellock, 1993; GDJ, pers. observ.). The degree of exposure of their cartilage in adults is merely a function of the extent of ossification of the bases of the proximal portions of the three elements. Thus, the "cartilage plug" is large and well exposed in larval *Barbourisia* and juveniles, but by 133 mm is almost fully covered by the ossified bases of the parhypural and hypurals 1 and 2.

Distribution. The 11 larvae (6 preflexion, 5 postflexion) are distributed as follows: Pacific—Hawaii 2, 1; Tuamotus 3, 0; Samoa 0, 2; Indonesia 1, 0; Atlantic—USA 0, 1; Brazil 0, 1 (Table 1, Fig. 2). The species is now known from all oceans, with adult specimens from 65°N to 40°S in the Atlantic, 50°N to 50°S in the Pacific, and 5–20°S in the Indian Ocean (Kotlyar, 1995; Paxton, unpublished). All larvae were caught with open nets, fishing from the surface to a maximum depth of 70 m (Table 1).

Five of the six preflexion larvae were caught in the upper 10 m, with two of these caught at one m or less. All five postflexion larvae were caught in nets fishing to at least 33 m.

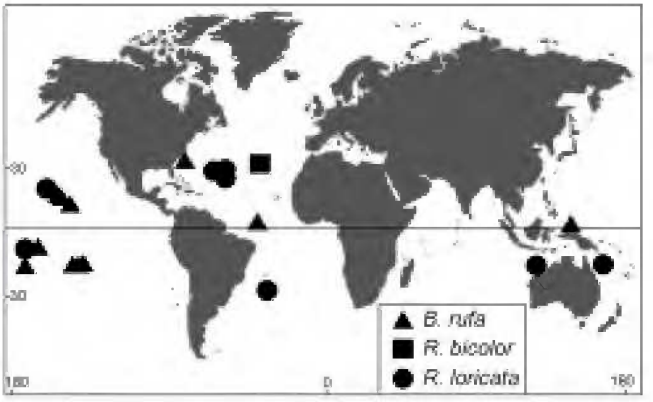


Figure 2. Geographic distribution of larval *Barbourisia rufa*, *Rondeletia bicolor*, and *R. loricata*, symbols may represent more than one specimen.

Rondeletia bicolor Goode & Bean, 1895

Figs. 3, 4, 8

Only one larva 7.2 mm sl is known; it is postflexion. However, the next smallest specimen, 13.5 mm sl, was originally assumed to be a larva; it lacks pigment and has been cleared and stained (Fig. 3). It is now considered to be the smallest known juvenile, based on its similarity of shape and fin formation to the next largest specimens, and the differences in larvae and juveniles of *R. loricata* of similar sizes (see Identification section above). Many of the features of this smallest juvenile are included in the larval description below. Four specimens 14.4–21.7 mm have the loose, uniformly dark brown skin of adults and the smallest has clearly developed head pores and vertical rows of papillate superficial neuromasts of the lateral-line system; they are here considered juveniles. Both of the smallest specimens have been cleared and stained and the amount of connective tissue is not apparent. In the second smallest juvenile, considerable fibrous connective tissue is present between the skin and muscle mass, as is typical of adults. The head and body of the two smallest specimens are moderately deep, with the body particularly short in the larva. The tail region is more slender in the smallest juvenile. The jaws are relatively short and directed obliquely in the larva and two smallest juveniles. In a 17 mm juvenile the jaws have lengthened to reach the level of the middle of the eye (the adult position) and are almost horizontal. The only figures of adult *R. bicolor* are that in the original description (Goode & Bean, 1895: plate 17, fig. 1), and a painting of Bermuda specimens (Harry, 1952: plate 1), neither of which adequately illustrate characters considered important now. The new illustration (Fig. 4) is based on a 60 mm sl specimen from the central Atlantic kindly provided by K. Hartel of MCZ.

Pigmentation. The two smallest specimens have faded with 80+ years storage in formalin and the only remaining pigment is that dark brown covering the stomach of the 13.5 mm specimen. The 14.4 mm specimen is covered with the loose, uniformly dark brown skin characteristic of preserved adults. At this size an even layer of subdermal melanophores is present under the gelatinous connective tissue over the main muscle mass. At 60 mm light irregular streaks are present on the surface of the muscles.

Scales. At 7.2 mm two parallel rows of small, circular, cycloid scales extend from the top of the opercle to the level of the PU1+U1 centrum of the caudal skeleton. The scales are arranged approximately one per myomere and number 24–25 per row. The scales of each row are separated by a space equal to one half to one scale diameter and the two rows are separated by an equal space. The scales overlie the skin and are very weakly ossified, picking up much less alizarin than the fin rays or other developed bones. Two other rows of scales are developing on either side of the dorsal midline, where seven smaller scales are present from the level of the preopercle to half way to the dorsal-fin origin. A few apparent scale primordia are present in the area between the pectoral- and pelvic-fin bases. No other scales are apparent on the body or head.

In the 13.5 mm juvenile the scales remain very weakly ossified and can only be seen with certain angles of reflected light. The scales of the two rows in the lateral-line region

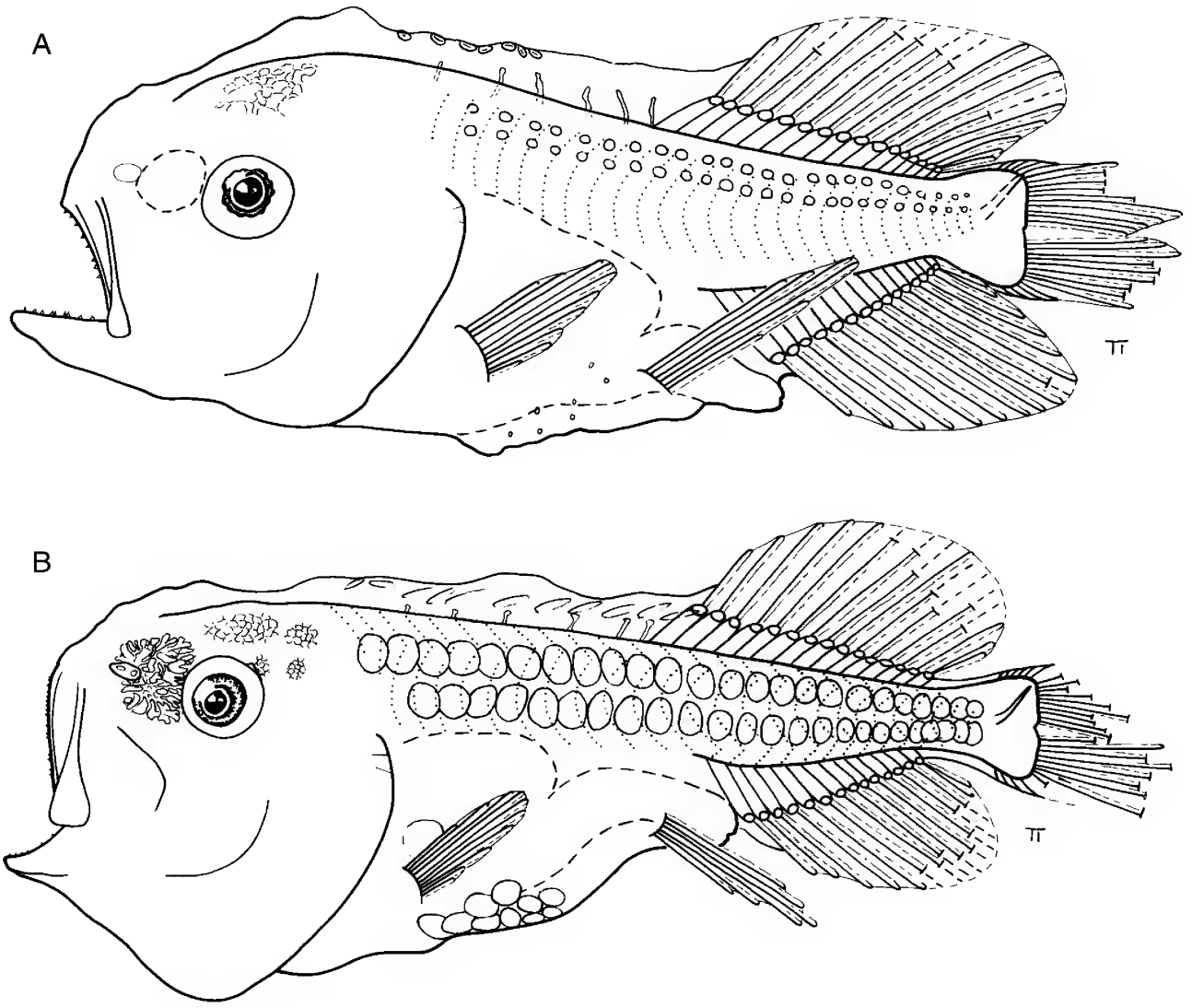


Figure 3. *Rondeletia bicolor*. a, ZMUC P2340805, 7.2 mm sl larva, note outline of Tominaga's organ anterior to eye (dashed line); b, ZMUC P2334327, 13.5 mm sl juvenile, Tominaga's organ is extensive anterior to the eye.

have increased in size so that some scales overlap slightly within each row. These scales are now embedded in the skin at a slight angle with the anterior edge of each scale deeper in the tissue. They are dorsoventrally ovoid and the space between the two rows is only about one-tenth of a scale diameter, with the two rows sometimes touching. The scales extend to the urostyle and number 24 in a row. A row of scales on either side of the dorsal midline extends from the level of the preopercle to the dorsal-fin origin and numbers 10–11 small circular scales. There is another group of circular scales in a triangular area between the pectoral- and pelvic-fin bases and the ventral midline. There is no indication of spines on any scale of either specimen. Further description of scales in larger specimens is presented after the larval descriptions.

Head spines. There are no strong head spines in the two smallest specimens. Two very weak spines are present on the opercle of the 7.2 mm larva. In the 13.5 mm juvenile a spine is beginning to develop on the dorsal end of a ridge on the anterior orbital margin of the sphenotic. In the larva the infraorbitals are just beginning to ossify and a small amount of spongy bone is present only in the posterior portion of the frontal. In the smallest juvenile, spongy bone is evident on the frontal, sphenotic, parietal, supraoccipital, epioccipital and pterotic. All elements of the pectoral girdle lack spongy bone in both of the smallest two specimens.

Fin formation. In the larva, all of the fins have the complete complement of rays (Table 4). None of the 6 rays of the pelvic fin is greatly produced, with the 3rd–5th rays longest. In both of the two smallest specimens the longest rays extend to the base of anal-fin ray 4–5. In the 14–17 mm juveniles the rays extend only to the anal-fin origin, whereas in the 60 mm adult the pelvic-fin rays do not reach the anal-fin origin. In both of the two smallest specimens the pelvic-fin origin is at about the level of the 10th vertebra, slightly anterior to the dorsal-fin origin and about ⅔ of the way between the head and anal-fin origin. The pelvic fins are in about the same position in the smaller juveniles (< 20 mm), but the pelvic fin of the 60 mm specimen is closer to halfway between the head and anal-fin origin. Both of the smallest specimens have 6 supraneurals anterior to the dorsal-fin origin.

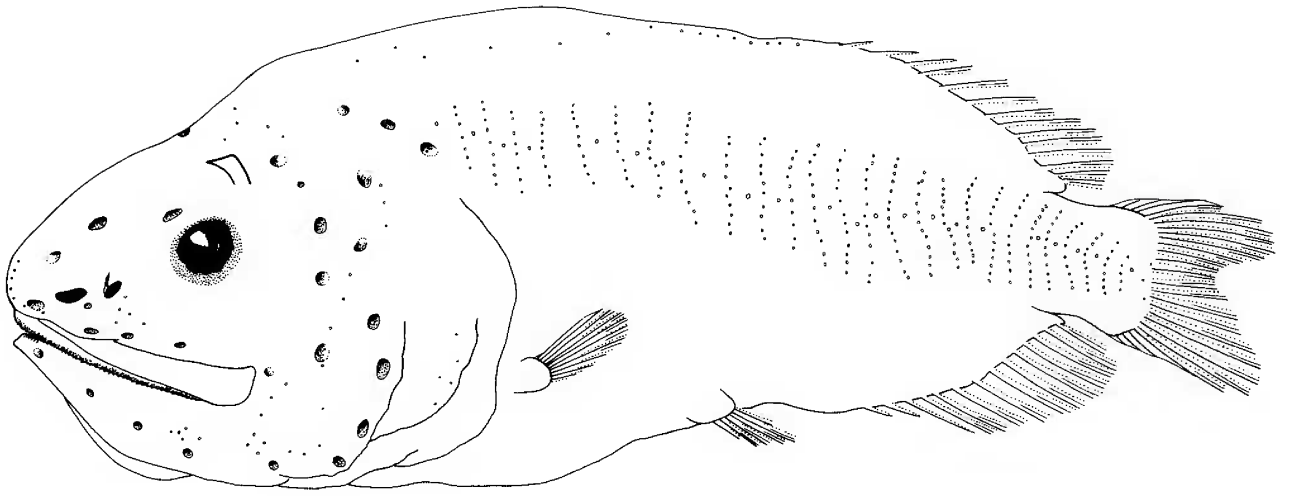


Figure 4. *Rondeletia bicolor*, AMS I18415-001, 60.0 mm sl adult.

Dentition. The 7.2 mm larva has a single row of small, triangular teeth in both jaws. The premaxillary teeth are widely spaced, those of the dentary closely set with some almost touching at their bases. The teeth of the 13.5 mm juvenile are very closely set in both jaws, but still primarily in one row. In the 17 mm juvenile the teeth are in 1–2 rows, while in a 60 mm adult there are 5–6 small conical teeth rows across the oral surface of each jaw.

Internal anatomy. In the 7.2 mm larva the stomach is moderately large, occupying about ⅔ of the abdominal cavity, and appears to have a smaller anterodorsal portion and a larger posterior portion. The intestine emerges from the anteroventral region of the posterior portion of the stomach. Coiling of the intestine is not clear; the intestine ends in a long straight section in the ventral abdominal cavity from the level of the stomach to the anus slightly closer to the anal-fin origin than the pelvic-fin base. A small mass of tissue at the top of the stomach may represent a developing, non-functional swimbladder. In the 13.5 mm juvenile the stomach occupies about ½ the abdominal cavity. The intestine emerges from the anteroventral arm of the stomach with apparently some folding on the right side of the stomach. The course of the intestine to the anus, about midway between the pelvic-fin base and anal-fin origin, is unclear. No pyloric caeca are apparent. The swimbladder is not apparent. Adults also lack a swimbladder (Parr, 1929).

A large mass of globular white tissue is present anterior to the orbit and posterior and medial to the nostrils and developing nasal rosette in both of the two smallest specimens. Tominaga (1970) briefly described similar tissue in an adult *R. loricata*, and we here term it Tominaga's organ. In the 7.2 mm larva the organ is slightly smaller than the orbit and extends anteriorly to the posterior margin of the developing nasal organ. In the 13.5 mm juvenile the organ is larger than the orbit and extends to the anterior margin of the nasal organ. The adult condition is described more fully following the description of the larvae of *R. loricata*.

Caudal skeleton. All specimens have a full complement of caudal elements and fin rays. There are three epurals (the first originating over the dorsal crest of preural centrum two), two uroneurals, one parhypural and six hypurals (two ventral and four dorsal). In the two smallest specimens ural centrum 2 is a separate, distinct ossification that abuts against and appears to be fusing with the base of hypural 4. The base of hypural 3 articulates along the notochord in the space between PU1-U1 and U2. In the 7.2 mm larva the distal tips of the parhypural and hypurals 1–5 are unossified and hypural 6 is a tiny ossification dorsal to hypural 5. Uroneural 2 is very small and epurals 2 and 3 are unossified. In the 13.5 mm juvenile all hypurals and epurals are completely ossified. Hypurals 1 and 4 are the largest and hypural 6 remains autogenous. In both specimens the parhypural and hypurals 1 and 2 articulate with a large oblong cartilage below the urostylar centrum. Hypurals 1 and 2 are fused distally in both specimens, and in the larger they have also fused proximally, similar to the condition in our third cleared and stained specimen, a 21.7 mm sl juvenile. Parr (1929: fig. 18) figured the caudal skeleton, presumably of an adult specimen, with little description. His figure shows the proximal but not the distal fusion of hypurals 1 and 2 and does not show hypural 6.

Distribution. All specimens examined for this study were collected in the western North Atlantic, where most specimens of this species have been collected (Table 3; Fig. 2; Paxton, 1974; Kotlyar, 1996). In an addendum, Paxton (1974: 188) noted a single adult specimen collected in the southeast Pacific at 25°48'S 108°46'W (near Easter Island off Peru) that Kotlyar (1996: 220) considered most likely based on an error in determination or labelling. The original information was received in 1970 about a 1969 SIO expedition to that area, and is unlikely to be a labelling error. The 83 mm specimen was re-examined recently by H.G. Moser and R. Rosenblatt and found to be correctly identified, with the diagnostic bony hook over the orbit present. In addition, a 44 mm specimen from 15°S 175°W in the central Pacific collected in 1927 (ZMUC P2334334) was identified by the first author and confirms the presence of *R. bicolor* in the South Pacific.

The larva and juveniles were all caught with open nets, with the larva caught in the upper 50 m and the juveniles in nets fishing from 200 to 1100 m depth.

Table 3. *Rondeletia bicolor* material examined. Abbreviations and symbols as in Table 1.

specimen	catalogue	size	location	depth (m)	day/night	date
1 *#	ZMUC P2340805	7.2	31°59'N 59°52'W	0–50	N	24 Oct 1913
2 *#	ZMUC P2334327	13.5	17°41'N 60°58'W	0–200	N	27 Nov 1921
3	MCZ 50681	14.4	23°13'N 44°56'W	0–1100		15 Oct 1973
4	ZMUC P2334332	17.0	19°04'N 65°43'W	0–900	DN	09 Mar 1922
5	ZMUC P2334328	18.0	19°01'N 65°23'W	0–600	N	03 Jan 1922
6 *	ZMUC P2334331	21.7	24°05'N 74°36'W	0–650	D	15 Feb 1922
7 #	AMS I18415-001	60.0	9°15'N 49°16'W			22 Sep 1973

Table 4. *Rondeletia bicolor* counts. Abbreviations, symbols and lines as in Table 2; D hypurals = dorsal hypurals.

specimen	size	D	A	P	P2	Cprin	Cproc	Supran	Myom/Vert	scale rows	D hypurals
1 *	7.2	15	15	10	6	10+9	5+4	6	27	24/25	4
2 *	13.5	15	14	10–11	6	10+9	5+5	6	27	24	4
3	14.4	14	14	10	6	10+9	5+4				
4	17.0	15	15	10	6	10+9	5+5		27		
5	18.0	15	14	10	6	10+9	5+5			25	
6 *	21.7	15	14	10	6	10+9	5+5	7	27		4

Rondeletia loricata Abe & Hotta, 1963

Figs. 5, 6

Eight larvae 3.5–9.7 mm sl, one flexion and seven postflexion, were examined (Table 5). In specimens 8.8 mm and larger, there is a moderate to large amount of gelatinous, fibrous connective tissue between the skin and muscle mass and the skin is loose and slightly inflated, somewhat reminiscent of lophiiform larvae (Pietsch, 1984). Large amounts of thick connective tissue under the skin are typical of the adults of both species of *Rondeletia*. The head and body of the smallest specimen are moderate in depth, becoming deeper with increasing size (4.1–4.6 mm). The head and anterior body are deepest in the 8.8–9.7 mm larvae. The 12.7 mm juvenile *R. loricata* is deeper in both head and body than the 13.5 mm *R. bicolor*. The eye is large and the snout short in the smallest specimens, while by 8.8–9.7 mm the snout and eye sizes approach the ratio typical of the juvenile and adult. In the smallest larvae (3.5–4.6 mm) the jaws are short and moderately oblique, and almost or just reach the level of the anterior margin of the orbit. The jaws lengthen in the 8.8–9.7 mm larvae and become almost horizontal by 12.7 mm. Jaw length displays allometric growth in the juveniles (Paxton, 1974: fig. 2), with the posterior end of the upper jaw nearing the level of the middle of the orbit only in a 22 mm juvenile.

Pigmentation. The larva retaining the most pigment is a 4.6 mm specimen (Fig. 5a) collected in 1985. The remaining larval specimens were collected at least 25 years ago and the three smallest were collected more than 80 years ago and stored for most of that time in formalin. All are faded to a greater or lesser degree. The 4.6 mm larva has the body and head covered with widely spaced melanophores. All of the fin rays are unpigmented except those of the pelvic fin, which are densely covered with melanophores that are larger and darker than those on the head and body. Some myoseptal pigment is present in the region of preural centra 2–3, but the subdermal melanophores typically found on the surface of the muscles in the larger larvae are not evident. The stomach is dark, as in all the larvae.

In the 3.5 and 4.1 mm larvae faded melanophores are visible on the pelvic-fin rays, and to a lesser extent under the posterior bases of the dorsal and anal fins of the smaller specimen. The eye is dark while all the remaining tissues of the head and body are yellowish to light brown. In the 8.8 mm and 9.6 mm larvae all the pigment in the skin has faded and only the pelvic-fin rays have distinct melanophores. In the 9.7 mm larva (Fig. 5c), the skin of the head and body is covered with light, closely-spaced melanophores. In this specimen, small widely-spaced melanophores are present on the surface of the muscle mass underneath the skin and connective tissue, as in the 9.6 mm specimen (Fig. 5b). This subdermal pigment extends from the base of the skull back to the end of the caudal peduncle. In the 12.5–14 mm juveniles the skin is uniformly dark brown as in adults; the pelvic fins have lost much pigment distally and are only slightly darker than the body skin proximally. At this size the neuromasts of the lateral-line system on the body are visible. Pigment extends onto the bases of the rays of all the other fins. The subdermal pigmentation also increases and at 14.1 mm extends over the main muscle mass and is also visible on the skull bones. In the region of the posttemporal there are three layers of melanophores, one in the skin, one within the spongy bone and one on the surface of the muscles that have been overgrown by the posterior extension of the posttemporal. By 33 mm the subdermal pigmentation is reduced to light irregular streaks over the muscles that are visible also in adult specimens after the connective tissue has been removed.

Scales. Scales are visible in our specimens at 8.8 mm and above. In the 9.6 mm specimen two rows of round, thin

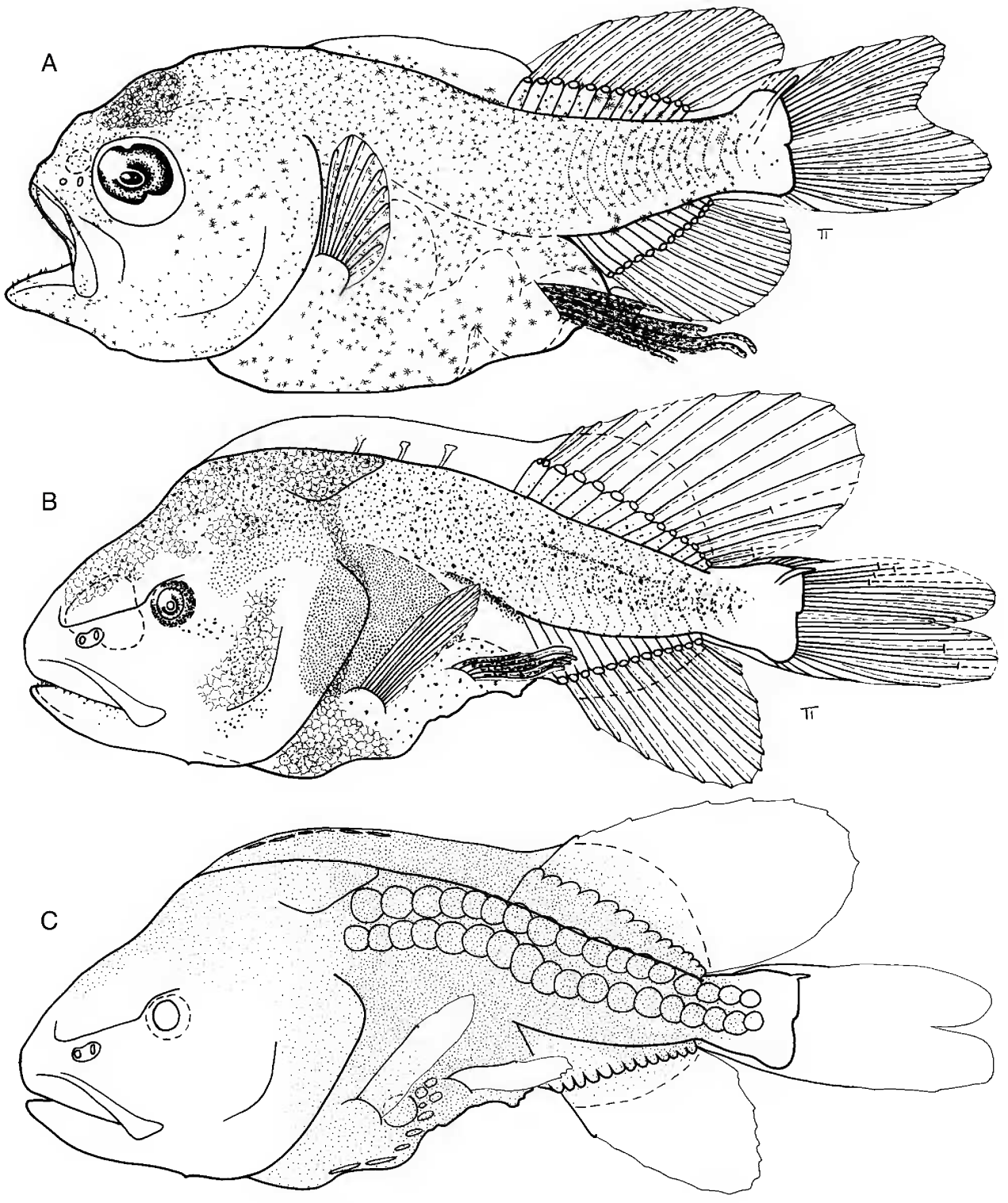
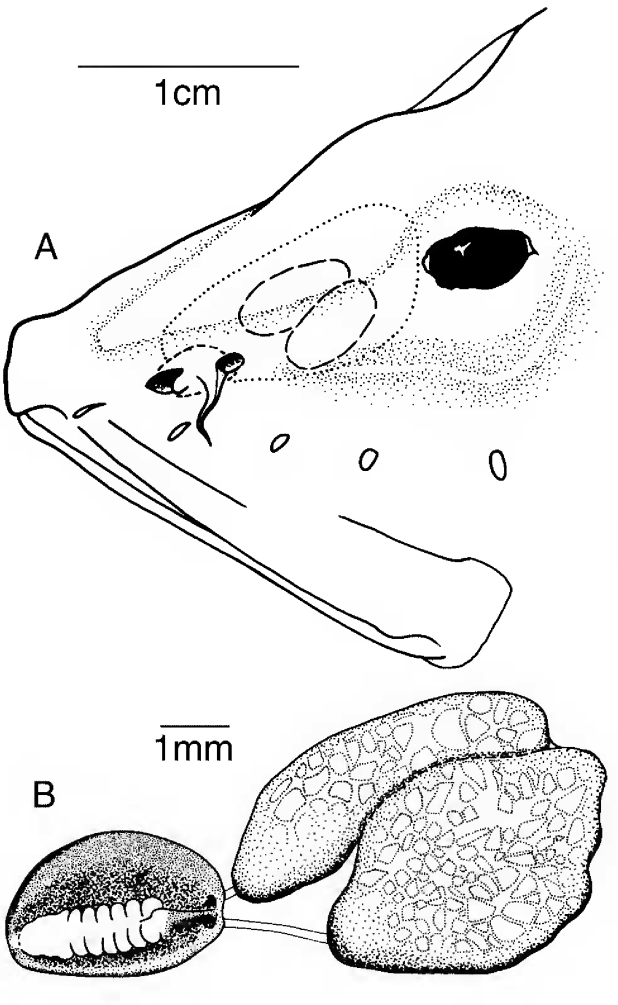


Figure 5. *Rondeletia loricata*. a, AMS I25228-001, 4.6 mm larva, note outline of Tominaga's organ anterior to eye (dashed line); b, LACM 36982-1, 9.6 mm larva showing internal pigment, outline of Tominaga's organ (anterior to eye), spongy bone of head and pectoral girdle, and supraneural bones; c, outline of b. showing predorsal scales, trunk and tail scales, and external pigment; pigment derived from 9.7 mm larva (MCZ 50683).

scales overlie the skin and extend from above the opercle to the caudal peduncle (Fig. 5c); each row includes 17–18 scales. Seven smaller scales are present in a row just off the dorsal midline over the posterior portion of the head. One large and nine smaller scales are present below and behind the pectoral-fin base.

Head spines. Head spines are lacking in all our larval specimens. At 4.6 mm there is a considerable amount of spongy, sculptured bone in the supraorbital region of the frontal. The pectoral girdle is weakly ossified with neither spongy bone nor posterior expansions of the posttemporal or cleithrum present. However, the dorsal portion of the



cleithrum is wider than that of a 7.2 mm *R. bicolor*. In the 9.6 mm specimen spongy bone is well developed dorsally on the frontals and supraoccipital, with separate lateral patches on the parietal/pterotic and preopercle, and on most elements of the pectoral girdle—the posttemporal, supracleithrum and cleithrum. Posterior extensions of spongy bone are developing dorsally and ventrally on the posttemporal and cleithrum respectively.

Fin formation. At 3.5 mm the dorsal, anal and pelvic fins have the full complement of rays (Table 6). The third and fourth rays of the pelvic fin are the longest, extending beyond the anal-fin base; these two rays are about one-third longer than the second and fifth rays and almost twice as long as the first pelvic-fin ray. At 8.8–9.7 mm, pelvic-fin rays 2 and 5 are subequal to rays 3 and 4 and all extend to anal-fin rays 2–3. Pelvic-fin rays 3 and 4 are the same absolute length (1.5–1.6 mm) in both the 4.6 and 9.7 mm specimens; the negative allometry is also evident in small juveniles. In adults the pelvic-fin rays do not reach the anal-fin origin. The pelvic-fin base is much closer to the anal-fin origin than to the pectoral-fin base at 4.6 mm. By 9.7 mm the pelvic-fin base is closer to midway between the two fins than to the anal-fin origin, similar to the adult condition.

The pectoral fins are damaged in the smallest larva, but at least three rays are visible on the right fin. By 4.6 mm all but the last ray is ossified. In the four smallest larvae the pectoral fin is relatively high on the side of the body. By

Figure 6 (left). *Rondeletia loricata*, AMS I21141-001, 73.4 mm adult. a, position of Tominaga's organ; dotted line—outline of cavity of Tominaga's organ; long dashed line—outline of lobes of Tominaga's organ; short dashed line—cavity of nasal organ; scale = 1 cm. b, detail of Tominaga's organ, anterior to left, showing anterior ducts to cavity of nasal organ; scale = 1 mm.

Table 5. *Rondeletia loricata* material examined. Abbreviations and symbols as in Table 1.

specimen	catalogue	size	location	depth (m)	day/night	date
1	ZMUC P2334325	3.5	26°46'N 54°14'W	0–8	N	16 Jul 1920
2	ZMUC P2334326	4.5	28°20'N 63°50'W	0–8	N	21 Jul 1920
3 *	ZMUC P2334323	4.6	28°49'N 54°10'W	0–17	N	15 Jul 1920
4 #	AMS I25228-001	4.6	14°33'S 145°36'E	0–40	D	11 Feb 1985
5	NSMT PL108	5.0	17°00'S 118°00'E	0–75	N	21 Jan 1993
6	ZMUC P2334335	8.8	11°00'S 172°37'W	0–333	DN	02 Nov 1928
7 *#	LACM 36982-1	9.6	21°23'N 158°18'W			23 Jun 1971
8	MCZ 50683(1)	9.7	23°08'S 32°22'W	0–110		09 Mar 1967
9	MCZ 50684	12.6	25°52'N 36°48'W	0–140		30 Nov 1970
10 *	MCZ 50679(1)	12.7	23°02'S 32°15'W	0–175		09 Mar 1976
11	MCZ 50679(2)	13.0				
12	AMS I27620-001	13.0	21°23'N 158°18'W			11 May 1972
13	MCZ 50679(3)	13.2				
14	MCZ 50683(2)	13.2				
15	MCZ 50679(4)	13.3				
16	MCZ 50683(3)	14.1				
17	MCZ 50680	15.5	27°03'N 53°56'W	0–1000		08 Oct 1972
18 *	MCZ 50679(5)	18.3				
19 *	AMS I20522-001	23.8	22°N 158°W	0–1000	N	05 Nov 1976
20 *	AMS I20314-011	37.1	33°28'S 152°33'E	0–900	D	14 Dec 1977
21 *	AMS I20307-011	60.4	33°28'S 152°25'E	0–900	DN	13 Dec 1977
22 *	LACM 9254-33	94	32°13'N 120°41.5'W	0–400	N	18 Oct 1966

Table 6. *Rondeletia loricata* counts. Abbreviations, symbols and lines as in Tables 1 and 2. Specimen between dashed lines is undergoing notochord flexion. + = present but accurate counts not possible.

specimen	size	D	A	P	P2	Cprin	Cproc	Supran	Myom/Vert	scale rows	D hypurals
1	3.5	13	12	>3	5	c. 5+4	—		24	—	
2	4.5	13	12	?	5	10+9	—				
3 *	4.6	13	12	?	5	?	—	—	24	—	?
4	4.6	13	13	9(1)	5	10+9	—				
5	5.0	14	13	8+	5	?	—				
6	8.8	13	13	10	5	10+9	—			+	
7 *	9.6	14	13	10	5	10+9	5+4	3	24	17–18	3
8	9.7	13	12	10	5	10+9	3?+2?				
9	12.6	14	13	10	5	10+9	5?+4?				
10 *	12.7	13	13	10	5	10+9	4-5+4	3	24	?	3
18 *	18.3	13	14	11	5	9+9	4+4	3	24	?	3
19 *	23.8	13	13	10	5	?	?	4	25	?	3
20 *	37.1	14	13	9	5	10+9	5+4	4	25	?	?
21 *	60.4	14	13	10	5	10+9	5+4	?	25?	?	3
22 *	94	14	13		5	10+9	5+5	7	26	?	3

9.7 mm the pectoral-fin base is in a lower position as in the adults. The caudal fin is damaged in the smallest larva, where there are approximately 5+4 incipient principal rays. By 4.5 mm the notochord is fully flexed and the caudal fin has the full complement of principal caudal rays. Procurrent rays are apparent from 9.6 mm. Only the 9.6 mm larva has visible supraneurals, with three.

Dentition. At 4.6 mm a single row of tiny triangular teeth are present in both jaws. Those of the dentary are closely set, the spacing of those on the premaxilla unclear. In the smallest juveniles at 12.7 mm both jaws bear a single row of closely set, conical teeth.

Internal anatomy. None of the four smallest larvae (3.5–4.6 mm) is transparent enough to see details of the internal organs. The stomach is large, occupying half or more of the abdominal cavity. In the three largest larvae 8.8–9.7 mm the stomach is small to massive, occupying one-third to two-thirds of the abdominal cavity, presumably depending on the amount of stomach contents. None of these larvae is clear enough to see other details. In a 12.7 mm cleared and stained juvenile the stomach fills about one half the abdominal cavity, and the intestine exits from the anteroventral margin of the stomach. The intestine has one loop in the dorsal portion of the coelom to the right of the stomach and another smaller loop further posterior, exiting through a short straight section anterodorsal to the anus. Other organs, such as swimbladder and pyloric caeca, are either undeveloped or have been digested in the clearing process.

Tominaga's organ is visible in the 4.1–4.6 mm larvae. It may be present in the 3.5 mm larva, but the poor condition of the specimen makes it difficult to discern. The organ is initially small and is located above the nasal organ. As the snout elongates, Tominaga's organ extends posteriorly to fill most of the gap between the nasal organ and the eye. The anterior margin of Tominaga's organ is dorsomedial to the anterior of the nasal organ in all postflexion larvae.

Caudal skeleton. The smallest cleared and stained larva, 4.6 mm sl, is damaged in the caudal area. In the 9.6 mm larva the bone is well stained with alizarin. Cartilage stained well and bone poorly in the 12.7 mm juvenile. Both the cleared and stained larva and 12.7 mm juvenile have the same caudal elements: three epurals, at least one uroneural, two ural centra (PU1-U1 and U2), five hypurals (two ventral and three dorsal) and one parhypural. The parhypural and hypurals 1 and 2 articulate with a large oblong cartilage ventral to PU1-U1; the haemal spines of preural vertebrae 2–4 also articulate with a cartilage ventral to their respective centra. Hypural 3 articulates with the notochord at the space between PU1-U1 and U2, while hypural 4 articulates with U2.

Distribution. Four of the eight larvae were collected in the central and western North Atlantic, one in the North Pacific near Hawaii, two in the South Pacific near Samoa and in the Coral Sea, and one in the eastern Indian Ocean off NW Australia (Table 5; Fig. 2). The species is recorded from all oceans between 47°N and S (Paxton, 1974; Kotlyar, 1996).

The eight larvae were all taken with open nets, fishing to a maximum of 333 m. The two smallest larvae were taken in the upper 8 m, while the next two smallest larvae were taken in nets fishing to 17 and 40 m. The shallowest capture depth is 110 m for the 10 juveniles less than 20 mm sl, and eight of these were caught with open nets fishing only to 110–175 m (Table 3). The vast majority of adult specimens over 50 mm sl have been caught with nets fishing below 400 m (Bast & Klinkhardt, 1990; Paxton, unpublished). Thus there is a clear indication of ontogenetic descent, beginning when the larvae reach 4–5 mm sl.

Scales

Scales of adult *Barbourisia rufa* were described and figured by Struhsaker (1965). Scales have not been reported previously in the family Rondeletiidae. Developing individual scales were first seen in cleared and stained larvae, as described above. In the cleared and stained 21.7 mm juvenile *R. bicolor* in poor condition, no scales are

visible. However, in the cleared and stained 18.3 mm *R. loricata* very thin scales are visible in two separate rows, with scales within a row overlapping by 10–30% of scale length. In this specimen, and confirmed by dissection in smaller, unstained juveniles, the scales are underneath the skin in the presumed connective tissue over the underlying body muscles. Strands of presumed connective tissue attach the anterior end of the scales to the underlying muscle and the posterior end of the scales to the overlying skin. A very thin layer of overlapping scales is visible in some specimens (those with the best preservation?) 35–85 mm sl, embedded in presumed connective tissue between the skin and muscle on the side of the body. These scales are so thin, and take up stain so poorly, that they have never been identified, or at least described previously, in larger cleared and stained specimens.

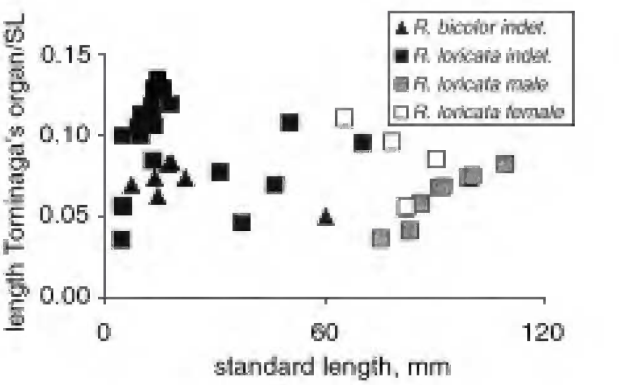


Figure 7. Length of Tominaga's organ as %sl/sl; "indet."—sex indeterminate (larvae and juveniles) or not determined (adults).

Tominaga's organ

Tominaga (1970) briefly described an unnamed structure lying under the frontal between the nasal rosette and orbit of *R. loricata*. The organ was described as having two subequal lobes with no apparent external openings or ducts. Based on histology, each lobe was comprised of multiple globules with hollow centres and the large cells surrounding the cavities stained well with the acidic dyes acid violet, phloxin and light blue. Tominaga did not propose a function for this organ.

Rondeletia loricata. Dissection of 20 specimens 31–109 mm sl (not listed in the material examined) representing both sexes confirmed the above description. The organ, here termed Tominaga's organ, develops in a cavity in front of the eye that extends dorsally below the lateral shelf of the frontal, anteriorly medial to the posterior half of the nasal cavity and posteriorly to, or medial to the anterior portion of, the orbit (Fig. 6a, Pl. 1a). The lining of the cavity has sparse grey-brown pigment, as does the covering of the two lobes of Tominaga's organ. The lobes are light yellow or orange-pink in colour and about equal in length, but the lateral lobe is somewhat larger in width and therefore volume. The lobes are posteromedial to the nasal organ and do not reach the level of the posterior margin of the floor of the nasal cavity in which the nasal rosette lies (Pl. 1b). The lateral ethmoid is greatly reduced in relation to other stephanoberycoids, (see Kotlyar, 1996: fig. 1b) with Tominaga's organ filling much of the space normally occupied by that bone.

The olfactory nerve runs between the two lobes of Tominaga's organ to enter into the floor of the nasal cavity and central raphe. Two internal pores at the posterior end of the raphe of the nasal rosette open into this region, and a thin-walled duct runs from each pore to the anteromedial portion of each lobe of Tominaga's organ (Fig. 6b). Each duct appears to branch within the lobe, but these branches could not be followed.

The globular structure of the organ is visible with a dissecting microscope and clearly shown histologically. The cavities of the globules or chambers are lined by a single layer of cells, some of which are simple, squamous epithelium, while adjacent globules may be lined with simple cuboidal epithelium. One globule has some flocculent material that appears granular. The histological structure suggests a secretory function (J. Burns, pers. comm. June 2000). In one section elongation of the cavities and a duct lined with epithelial cells is visible. However, this could not be traced to the main duct to the nasal cavity, and no pattern or system of ducts could be found.

Measurements of the maximum length of individual Tominaga's organs of 33 *R. loricata* (Fig. 7) indicate the organ reaches its maximum relative size of 11–14% sl in juvenile specimens 13–20 mm sl. However, the organ continues to grow throughout life, as the longest measured (9.0 mm) is in a 109 mm specimen. There is no correlation of organ size or appearance with sex. At about 60 mm sl, increasing amounts of connective tissue are found in the cavity housing Tominaga's organ. By 90 mm and larger the cavity is almost filled with connective tissue, which also appears to invade the organ.

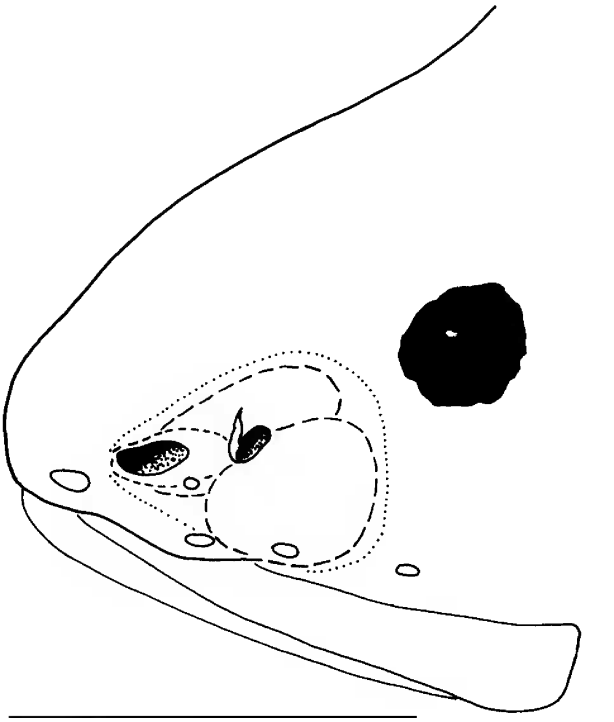


Figure 8. *Rondeletia bicolor*, AMS I18415-001, 60.0 mm sl adult, showing position of Tominaga's organ, line conventions as in Fig. 6, scale = 1 cm.

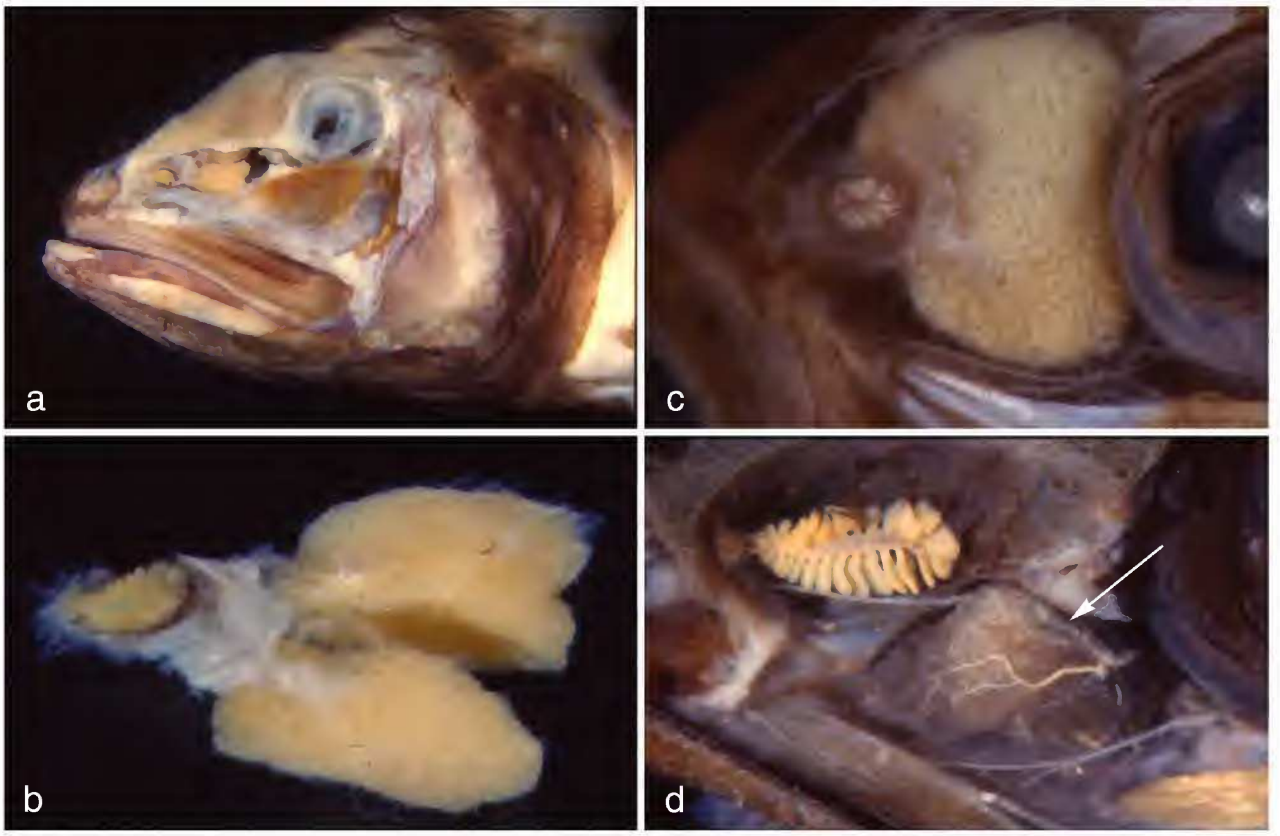


Plate 1. Tominaga's organ. a, *Rondeletia loricata*, USNM 206836, 83 mm sl; b, *R. loricata*, same specimen; c, *R. bicolor*, USNM 240130, 35 mm sl; d, *Gibberichthys pumilis*, USNM 207512, 75 mm sl, arrow indicates right dorsal margin of Tominaga's organ.

Rondeletia bicolor. Tominaga's organ is similar to that described for *R. loricata*, except for the following differences. The lobes of Tominaga's organ of *R. bicolor* are semi-equal in volume, with the medial lobe notably longer than the roughly spherical lateral lobe (Fig. 8). The lobes are medial to the nasal organ, with the lateral lobe extending anteriorly beyond the posterior margin of the nasal organ to a point about one quarter along the nasal rosette. The longer medial lobe extends anteriorly almost to the anterior end of the nasal rosette. Consequently the ducts from the pores at the end of the raphe enter nearer the midpoint of each lobe, rather than at the anterior margin as in *R. loricata*. The posterior floor of the nasal organ is tightly bound by tough connective tissue to the dorsal surface of the lobes in *R. bicolor*. Measurements of the few available specimens of *R. bicolor* do not indicate significant differences with *R. loricata* in the length of the organs in relation to standard length (Fig. 7). However, relative to snout length, both Tominaga's organ and the nasal rosette are larger in *R. bicolor* than in *R. loricata* (Figs. 6, 8; Pl. 1c).

Gibberichthys. A search for Tominaga's organ in other stephanoberyciform taxa (Table 7) revealed a similar

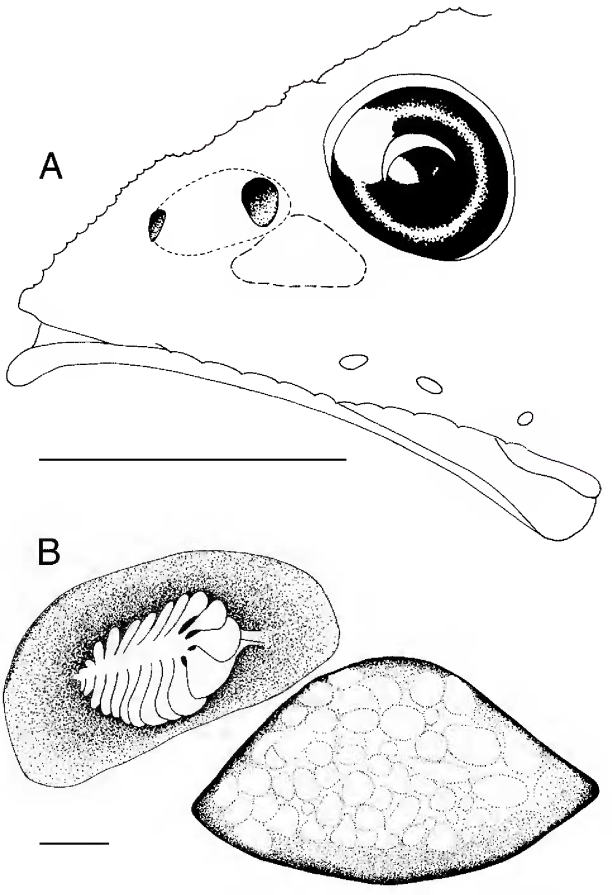


Figure 9 (right). *Gibberichthys pumilis*, CAS 14565, c. 67 mm. a, position of Tominaga's organ, line conventions as in Fig. 6, Tominaga's organ fills cavity, scale = 1 cm; b, detail of Tominaga's organ, anterior to left, nasal organ anterodorsal to Tominaga's organ, scale = 1 mm.

structure only in the gibberichthyids *Gibberichthys pumilis* and *G. latifrons*. The following description is based on two dissected specimens of *G. pumilis*; superficial dissection of *G. latifrons* revealed no basic differences. Tominaga's organ is medial to the lacrymal and ventromedial to a shelf of the lateral ethmoid, upon which the nasal rosette sits (Fig. 9). There are no pores at the posterior end of the nasal rosette, and no ducts or opening in Tominaga's organ are evident. The roughly pyramidal-shaped organ (Pl. 1d) has globular internal structure, but is not divided into distinct lobes. The slightly rounded dorsal surface of the organ is tightly bound to the ventral surface of the lateral ethmoid by connective tissue. Histology reveals globules lined with low epithelium and filled with flocculent tissue and purple granules that indicate secretory function. No globules lined with cuboidal epithelium, as seen in *Rondeletia loricata*, were apparent (J. Burns, pers. comm. June 2000).

Discussion

The larvae of *Barbourisia* and *Rondeletia* are easily recognized primarily because they exhibit adult characteristics at an early stage in development. Neither have highly specialized larval morphology, except for the large, precocious pelvic fins. By 10 mm larval *Barbourisia* have a few clusters of minute spines on some head bones and an inflated, balloon-like envelope of skin. They differ further from the adults in having relatively elongate pelvic fins, a smaller, more oblique mouth, larger eye, and shorter snout. Although the body is covered with the distinctive scales of the adult by about 6 mm nl, the lateral line is represented only by enlarged scales with no canal formation even at 13 mm. The changes that take place with attainment of the juvenile stage include loss of the spines on the head bones, reduction of the pelvic-fin rays, and formation and closure of the lateral-line canal. The smallest examined juvenile is 30.0 mm sl.

Larval *Rondeletia* are extremely precocious (flexing at 3.5 mm) and even less specialized than those of *Barbourisia*, differing from the adult in having heavily pigmented and relatively longer pelvic fins, a smaller mouth and superficial scales, those on the lateral body arranged in two distinct rows. By 14 mm the juveniles look like miniature adults.

The two species of *Rondeletia* can be distinguished in the early larval stages by meristics and in late larvae and juveniles by posterior extensions of spongy bone in the posttemporal and cleithrum.

There have been conflicting descriptions of the caudal skeleton in the past based on adult osteology, with differences in the described number of dorsal hypurals not corresponding to species. Parr (1929: fig. 18) figured three dorsal hypurals with a question for *R. bicolor* and Kotlyar (1996: fig. 3d) showed two dorsal hypurals for *R. loricata*, while Ebeling & Weed (1973: fig. 5) illustrated four in *R. bicolor*, and Rosen (1973: fig. 121) and Paxton (1974) described three in *R. loricata*. Development of the bones of the caudal skeleton have clarified the different number of dorsal hypurals in the two species, four in *R. bicolor* and three in *R. loricata*. Thus, Parr (1929) apparently did not see the small, dorsal-most sixth hypural in his specimen of *R. bicolor*, and Kotlyar (1996) interpreted the fusing hypurals 3 and 4 of *R. loricata* as a single hypural 3.

The number of ossified supraneural elements above the vertebrae anterior to the dorsal fin also varies. Paxton (1974) described seven in a 94 mm *R. loricata*, while Kotlyar (1996) indicated three or four in his 93 mm specimen. Five larvae and juveniles here have three or four supraneurals, while the count of seven in the 94 mm specimen is verified. The larva and two juveniles of *R. bicolor* have six or seven supraneurals.

There are distinct differences in the relation of Tominaga's organ and the nasal rosette in adults of the two species of *Rondeletia*. Tominaga's organ is entirely posterior to the nasal organ in *R. loricata*, with the ducts entering the anterior end of Tominaga's organ. In *R. bicolor*, the anterior half of Tominaga's organ is medial to the nasal organ and the connecting ducts enter about midway along Tominaga's organ. The presence of two separate lobes, as well as ducts to the nasal cavity, in *Rondeletia* suggests that Tominaga's organ is more specialized in *Rondeletia* than in *Gibberichthys*.

Gross structure and histology suggest a secretory function for Tominaga's organ, but the nature of the presumed secretion is unknown. There is no difference in size correlated with sex where a number of specimens are available to measure in *R. loricata*, and the opening of the ducts into the nasal cavity seems incongruous for pheromone function. Perhaps the flap on the posterior nostril of *Rondeletia* is involved in dispersal of the secretion. In *Gibberichthys* any secretion would be internal, as no external opening is discernible. There is nothing in the structure to indicate luminescence. While magnetoreceptor cells have been described in the same general anatomical region, inside the nasal lamellae of the nasal organ of rainbow trout (Diebel *et al.*, 2000), homology with Tominaga's organ seems unlikely. Fresh tissue would be needed to detect intracellular magnetite. Other possibilites, such as a toxic repellent, are mere conjecture. Future study of fresh or better preserved specimens is needed.

The relationships of the Barbourisiidae and Rondeletiidae to other "beryciform" fishes remain problematic. However, they have frequently been associated with the Cetomimidae, sometimes as a suborder or superfamily, more recently with the Mirapinnidae and Megalomycteridae (Harry, 1952; Greenwood *et al.*, 1966; Ebeling & Weed, 1973; Rosen & Patterson, 1969; Paxton, 1989; Nelson, 1994). Parr (1929) placed the Rondeletiidae in the Xenoberyces (= Stephanoberyciformes), while Rofen (in Ebeling & Weed, 1973: 399) and de Sylva & Eschmeyer (1977) commented on the similarity of *Rondeletia* and *Gibberichthys*. Most recently all three whalefish families have been placed with other families Mirapinnidae, Megalomycteridae, Stephanoberycidae, Hispidoberycidae, Gibberichthyidae and Melamphaidae in an order or suborder (Rosen, 1973; Moore, 1993; Johnson & Patterson, 1993).

The most recent hypothesis of relationships among these families is that of Moore (1993, fig. 5). Based on one character (Y-shaped pattern of frontal ridges), he placed the Gibberichthyidae as the sister group of Stephanoberycidae + Hispidoberycidae in one lineage, which he considered to be the sister group of a second lineage comprising, in phyletic sequence, Rondeletiidae, Barbourisiidae, Megalomycteridae and Cetomimidae. Placement of Rondeletiidae within the latter lineage was again based on one character (loss of fin spines).

Table 7. Other specimens examined. [a] taken near the surface of 2743 m deep waters, [b] bottom trawl, [c] Moore & Merrett manuscript.

taxon	catalogue	no. (size, mm)	location	depth (m)	day/night	date
Anoplogastridae						
Anoplogaster cornuta	AMS I27174-003	1(29)	22°46'S 177°00'E	0–230		03 Sep 1987
Cetomimidae						
Cetostoma regani	SIO 70-95	1(116)	31°37'N 120°19'W	0–c.1100		22 Mar 1970
Ditropichthys storeri	AMS I21143-001	1(84)	21°25'N 158°25'W	0–3440		01 Jun 1976
Ditropichthys storeri	AMS I28177-001	1(142)	29°49'S 47°24'E		N	27 Dec 1988
Procetichthys kreffti	ISH 1188/71 holotype	1(236)	37°08'S 5°23'E	0–2200	N	21 Mar 1971
Gibberichthyidae						
Gibberichthys latifrons	AMS I15999-001	1(103)	11°17'S 142°47'W			7–8 Feb 1969
Gibberichthys pumilis	UMML 16213	1(7.8)	32°46'N 64°33'W	0–0.3[a]	N	03 Aug 1964
Kasidoron edom	CAS 14565 paratype	2(48.9–c.67)	29°16'N 86°55'W	660[b]		12 Feb 1970
Hispidoberycidae						
Hispidoberyx ambagiosus	MNHN unregistered	1(175)	S of New Caledonia	1350		10 Nov 1996
Megalomycteridae						
Ataxolepis apus	MCZ 60720	1(41)	17°06'N 73°37'W			18 Jun 1982
Melamphaidae						
Scopelogadus mizolepis	AMS I25858-008	1(89)	54°44'N 18°23'W	0–800	D	06 Jul 1986
Stephanoberycidae						
Acanthochaenus luetkeni	AMS I28176-001	1(94)	30°27.5'S 46°56.5'E	2680	D	26 Dec 1988
n.gen. n.sp.[c]	AMS I40443-001	1(134)	20°53'N 31°14'W	4522		04 Oct 1993
Trachichthyidae						
Hoplostethus latus	AMS I31163-007	1(100)	24°52'S 112°07'E	468		28 Jan 1991

The recently published DNA sequence data analysis (Colgan *et al.*, 2000), which did not include *Gibberichthys*, placed *Barbourisia* and *Rondeletia* as sister groups. We think that the unique presence of Tominaga's organ in *Rondeletia* and *Gibberichthys*, together with additional morphological characters discussed below, belies that hypothesis, and provides convincing evidence for a sister group relationship between the latter two taxa.

Moore (1993) did not discuss Rosen's (1973: 492) assertion that "on the evidence of the lateral-line canal, jaw musculature and pharyngobranchials *Rondeletia* is most closely related to *Gibberichthys*." Our observations confirm the striking similarities between the two taxa in jaw musculature (Rosen, 1973: fig. 37) and dorsal gill-arch elements (Rosen, 1973: figs. 122–124), and the distinctive presence in both taxa of vertical rows of free neuromasts as lateral-line organs. Furthermore, if one allows for loss of head and fin spines in *Rondeletia*, its general body form and relative proportions (e.g., very large head, at least 40% sl) more closely resemble those of *Gibberichthys* than any other stephanoberyciform. In addition, we note that the internal, non-imbricate, cycloid scales of *Rondeletia* are similar to those of *Gibberichthys*, as described by Parr (1934: 35) "... the squamation, which is on trunk and tail and consists of thin, but not excessively thin, cycloid scales, is entirely subcutaneous, i.e., the scale pockets are completely closed and covered by a thin, generally transparent, continuous sheet of epidermis without openings of any kind."

Our investigation of the above character evidence, not considered by Moore (1993), led us to reject his hypothesis and to agree with Rosen's (1973) suggestions that Rondeletiidae and Gibberichthyidae are sister taxa. Subsequent discovery that the complex, presumably secretory Tominaga's organ is shared uniquely among fishes by these two taxa, provides remarkably cogent corroboration of this hypothesis, even in the absence of a formal phylogenetic analysis of the Stephanoberyciformes, a project that we plan to undertake in the future. We do note that the apparent sister-group relationship of the Rondeletiidae and Gibberichthyidae indicates that "the whalefishes", Barbourisiidae, Rondeletiidae, and Cetomimidae, as a group are at best paraphyletic.

It is not our intention to rigorously examine relationships of these families (that will be the subject of a future study), but merely to compare features of their larvae. Aside from common features that characterize the adults, such as posterior placement of the pelvic, dorsal and anal fins, we find no evidence in the morphology of the larvae of *Barbourisia* and *Rondeletia* to suggest a close relationship between these two families. The large precocious pelvic fins found in larvae of both families are also present in larvae of the stephanoberyciform families Gibberichthyidae, Melamphaidae, and Stephanoberycidae.

The Gibberichthyidae have a distinctive "kasidoron" larva characterized most notably by an elaborate arborescent appendage that is an extension of the third pelvic-fin ray and a papillose epithelium (Robins & de Sylva, 1965). The figures of larval and juvenile *Gibberichthys* (Robins & de Sylva, 1965: fig. 1; Thorp, 1969: figs. 2, 3; de Sylva & Eschmeyer, 1977: figs. 1–3) indicate there is little space on the snout anterior to the eye for the presence of Tominaga's organ that exceeds 10% of sl in similar sized *Rondeletia*. Our examination of a 7 mm *Gibberichthys* confirms the short snout length at this size, but we have not dissected this paratype specimen. de Sylva & Eschmeyer (1977) also mentioned scale rows under the papillate lateral line of *Kasidoron* (= *Gibberichthys*), but did not indicate which of their four specimens (7.8, 12.1, 15.7, 21.2 mm) have them. Neither vertical rows of papillate superficial neuromasts nor scales are present in their 7.8 mm paratype. The similarity of the papillate epidermis of *Gibberichthys* to *Mirapinna* was noted by Robins and de Sylva (1965).

The elongate pelvic-fin ray of *Barbourisia* is simple and it is not the third as in *Gibberichthys*, but the fourth.

Although de Sylva & Eschmeyer (1977) discussed a distinctive, multibranched postlarval pelvic fin in the melamphaid genus *Poromitra*, they did not illustrate it and we have not seen a detailed description of this feature nor have we observed it in an actual specimen. None of the described melamphaid larvae (Keene & Tighe, 1984: figs. 205–207) share distinctive characters with *Barbourisia* or *Rondeletia*, and in all the pelvic fins are much farther forward. Larval *Acanthochaenus* (the only described stephanoberycid larva) are unremarkable with the exception of the bright violet coloration of fresh specimens (Kotlyar & Evseyenko, 1989). They share with both *Barbourisia* and *Rondeletia* enlarged posterior pelvic fins that, like those of *Rondeletia*, are heavily pigmented and lack elongate rays. Scales form relatively early, between 8.7–11.2 mm, and are spinous like those of the adult. The body is more heavily pigmented than the larvae of either *Barbourisia* or *Rondeletia*. Larval Cetomimidae remain unknown.

We conclude that the larval morphology of the stephanoberyciform fishes, as presently known, provides little evidence to elucidate the phylogenetic relationships of this relatively diverse and highly specialized group. Unfortunately, the larvae described to date are either relatively unspecialized or exhibit autapomorphic specializations. It is likely that larval and small juvenile specimens will be useful in clarifying structural homology of problematic characters such as the plate-like dorsal-fin "spines" of *Gibberichthys* and the additional "supraneural" elements of that genus, *Barbourisia* and *Rondeletia*.

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