LARVAE OF *DIPLOPRION BIFASCIATUM,* *BELONOPERCA CHABANAUDI* AND *GRAMMISTES SEXLINEATUS* (SERRANIDAE: EPINEPHELINAE) WITH A COMPARISON OF KNOWN LARVAE OF OTHER EPINEPHELINES

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ABSTRACT

Morphology is described for larvae of two species of the epinepheline serranid tribe Diploprionini and one of the tribe Grammistini, and known larvae of other epinephelines are compared. Early stage eggs and development of larvae of *Diploprion bifasciatum* are described from 144 laboratory-reared specimens, and postflexion larvae of *Belonoperca chabanaudi* are described from wild-caught specimens. Fourmanoir's (1976) description of postlarval *Grammistes sexlineatus* is modified and expanded. The second and third dorsal-fin spines of larval *D. bifasciatum* are remarkably elongate, reaching lengths many times that of the body. These spines are thin and flexible, and each is encased in a sheath of tissue that exhibits patterns of pigment that change ontogenetically. Larvae of *Belonoperca* have several elongate dorsalfin spines that may attain lengths comparable to those of the second and third dorsal spines of *D. bifasciatum*; however, only net-collected specimens in which the spines are broken are available. With these descriptions of larval diploprionins, larvae of representatives of all epinepheline tribes are known. Larval epinephelines differ in patterns of pigmentation, head spination, sequence of fin formation and morphology of elongate dorsal spines. The considerable morphological diversity among epinepheline larvae may aid in elucidating the phylogeny of the subfamily.

As presently defined (Johnson, 1983) the serranid subfamily Epinephelinae comprises five tribes: Niphonini, Epinephelini, Diploprionini, Liopropomini and Grammistini. (Herein, the term epinephelin refers to the tribe Epinephelini, whereas epinepheline refers to the subfamily). Larvae of the monotypic *Niphon* have been described (Johnson, 1988), and larvae of many epinephelin genera are known (see Kendall, 1984, for a review; Leis, 1986). Hubbs and Chu (1934) described and illustrated two juvenile specimens (31 and 49 mm SL) of *Diploprion bifasciatum,* but larvae of all genera of the Diploprionini (*Aulacocephalus, Belonoperca* and *Diploprion*) are undescribed. Larvae of *Liopropoma* (includes *Pikea*) are well known (Fourmanoir, 1971; Kendall, 1979; 1984; Kotthaus, 1970); those of the other liopropomins, *Jeboehlkia* and *Rainfordia,* are undescribed. Within the Grammistini, larval *Grammistes* (Fourmanoir, 1976), *Rypticus* (Aboussouan, 1972; Kendall, 1979) and *Pseudogramma* (Kendall, 1979; Leis and Rennis, 1983) have been described and illustrated, and Fourmanoir (1976) illustrated the head and anterior portion of the body of larval *Aporops.* Larvae of the remaining grammistin genera, *Pogonoperca, Grammistops* and *Suttonia,* are unknown.

The initial impetus for this paper was the rearing of eggs and larvae of *Diploprion bifasciatum* by one of us (PLC), and the description of that reared series is a primary purpose of this paper. In addition we compare the reared larvae with several wild-caught specimens, comment on habitat and spawning behavior of *D. bifasciatum,* describe postflexion larvae of *Belonoperca chabanaudi* and *Grammistes sexlineatus,* compare the morphologies of known larvae of all genera of the subfamily Epinephelinae and briefly discuss the possible functional significance of elongate dorsal spines in larval epinephelines. This study should help others identify larvae of epinepheline serranids and will form the framework for a phylogenetic analysis of epinepheline genera using characters of both larvae and adults.

METHODS AND MATERIALS

Larvae were measured under a stereomicroscope with a calibrated ocular micrometer. Measurements are as defined by Leis and Rennis (1983). Characterizations of body shape (e.g., elongate, deep) follow the broad categories defined by Leis and Trnski (1989). Notochord length (NL) was measured in preflexion and flexion specimens, standard length (SL) in postflexion specimens. Drawings were made with the aid of a camera lucida. Examination of head spines, internal pigment and certain osteological features was facilitated by clearing and staining selected specimens.

Adult *Diploprion bifasciatum* were collected in the vicinity of the Motupore Island Research Station of the University of Papua New Guinea, southeast of Port Moresby. Fishes were captured, by SCUBA divers using multiprong spears, within one half hour of the time spawning would naturally have occurred, placed in individual plastic bags and returned to the laboratory. Gametes were obtained using gentle pressure on the abdomen and mixed in a bowl of seawater. About one hour elapsed between collection and stripping, and the adults were dead or dying at the time of gamete removal. Fishes not already dead were anesthetized with a solution of quinaldine and alcohol in seawater and then rinsed in seawater prior to stripping.

Rearing was accomplished in 80-liter aquaria at temperatures of 26–29°C. Aquaria were illuminated 24 h per day with a single 20-watt fluorescent fixture and aerated with air stones. Larvae initially were fed wild zooplankton of the 53–125 μm fraction, but the size of zooplankton was increased with increasing size of larvae. Zooplankton fed to late-stage larvae was supplemented with newly-hatched brine shrimp.

Early stage eggs and larvae were sampled from the aquaria and preserved in 3% unbuffered formalin or 95% ethanol. In efforts to prevent damaging the elongate dorsal filaments, larvae were dipped from the aquarium in a glass bowl and chilled to a point near death so they would not struggle when put into preservative. Behavior of larvae and coloration were noted during the rearing period.

In the following list of material examined, institutional abbreviations follow those of Leviton et al. (1985). *Diploprion bifasciatum* (reared material): USNM 290877, 290878 (29 eggs); 290879, 17 specimens, 1.5–2.0 mm NL; 290880, 13, 2.6–2.8 mm NL; 290881, 4, 2.4–2.8 mm NL; 290882, 18, 2.8–3.1 mm NL (1 specimen, 2.9 mm NL, cleared and stained); 290883, 8, 2.9–3.1 mm NL; 290884, 13, 3.0–3.3 mm NL (2 specimens, 3.0 and 3.1 mm NL, cleared and stained); 290885, 4, 3.3–3.4 mm NL; 290886, 9, 3.0–3.6 mm NL (1 specimen, 3.6 mm NL, cleared and stained); 290887, 1, 3.3 mm NL; 290888, 2, 4.0 and 4.3 mm NL; 290889, 5, 3.6–3.9 mm NL (1 specimen, 3.9 mm NL, cleared and stained); 290890, 5, 3.3–3.8 mm NL; 290891, 2, 4.6 and 4.7 mm NL (4.7-mm NL specimen cleared and stained); 290892, 3, 3.8–6.6 mm NL (1 specimen, 6.3 mm NL, cleared and stained); 290893, 1, 3.6 mm NL (cleared and stained); 290894, 1, 8.8 mm SL; 290895, 4, 9.8–15.5 mm SL; 290896, 2, 7.3 and 11.0 mm SL (cleared and stained); 290919, 1, 16.2 mm SL; (wild-caught specimens): CSIRO AS06/82, stn. 1(1), 2, 5.7 and 7.1 mm NL; AS06/82, stn. 1(2), 1, 5.8 mm NL; AS05/83, stn. 6(3), 1, 10.4 mm SL; AS03/83, stn. 2(1), 1, 10.9 mm SL; USNM 285416, 1, 13.3 mm SL; 174258, 1, 31.4 mm SL. *Belonoperca chabanaudi*: ZMUC P43671, 1, 6.9 mm SL; P43672, 1, 7.2 mm SL; P43673, 1, 8.8 mm SL; USNM 309607, 1, 11.8 mm SL. *Grammistes sexlineatus*: AMS I. 24997-002, 1, 5.5 mm SL; 24997-004, 1, 6.2 mm SL; 24997-003, 1, 9.7 mm SL; 24996-001, 1, 11.4 mm SL; ZMUC P43674, 1, 6.5 mm SL; P43675, 2, 6.6 and 7.3 mm SL; P43676, 3, 7.1–8.2 mm SL (1 specimen, 7.9 mm SL, cleared and stained). *Liopropoma*: MCZ 81674, 2, 11.5 and 14.0 mm SL; 85974, 1, 17.9 mm SL; 85971, 1, 22.5 mm SL; 85972, 1, 25.0 mm SL; ZMUC uncat., DANA Sta. 3868, 1, 5.9 mm SL. *Rypticus*: ARC 427341, 1, 11.7 mm SL (cleared and stained); MCZ 67224, 1, 5.9 mm SL; 85830, 1, 10.5 mm SL; 85829, 1, 12.9 mm SL; 85828, 1, 16.7 mm SL. *Pseudogramma*: MCZ 79310, 20, 5.8–14.5 mm SL; 64172, 1, 7.0 mm SL; 79036, 1, 12.0 mm SL; 79311, 1, 14.0 mm SL; 79318, 1, 14.2 mm SL; 79299, 1, 15.0 mm SL; VIMS 08274, 1, 3.6 mm NL; 08275, 1, 5.7 mm NL; 08276, 1, 11.4 mm SL, cleared and stained.

Diploprion bifasciatum
Figures 1–3, Plate 1A

Diploprion bifasciatum Cuvier inhabits coral and rocky reefs in shallow inshore waters of the Indo-West Pacific. It ranges from India and Ceylon in the Indian Ocean eastward to the Solomon and New Hebrides Islands, southward to New Caledonia and Australia and northward to southern Japan (Springer, 1982). A second species of *Diploprion*, *D. drachi* Esteve, is restricted to the Red Sea.

Habitat. —Observations of behavior and collections of adult *D. bifasciatum* were made off the south coast of New Guinea near Port Moresby, Papua New Guinea by one of us (PLC). *Diploprion bifasciatum* usually was found in inshore reef areas
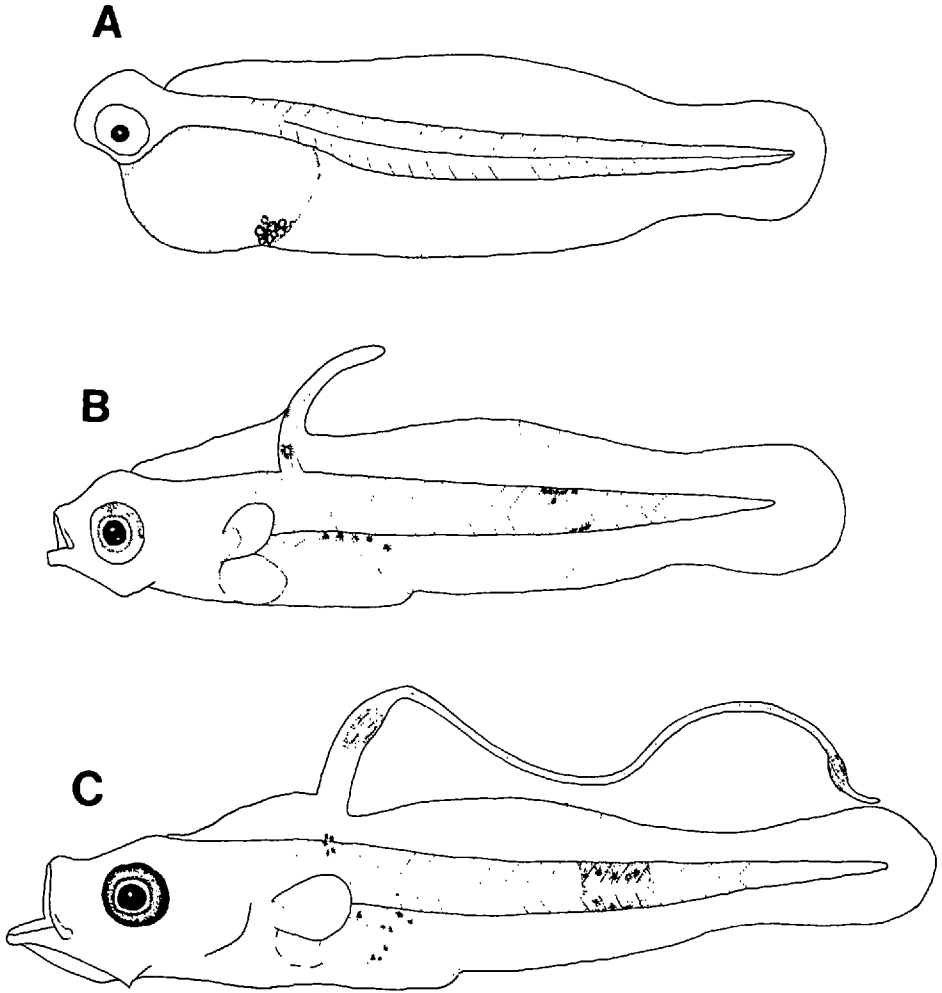
Figure 1.   Preflexion larvae of *Diploprion bifasciatum*: A) USNM 290880-6, 2.8 mm NL, 24 h post hatch; B) USNM 290882-12, 2.8 mm NL, 48 h post hatch; C) USNM 290884-8, 3.1 mm NL, 78 h post hatch.

where water visibility was typically 5–15 m. Generally, juveniles were found farther inshore than adults, but individuals less than about 60 mm SL were never seen. Observations and collections of spawning adults were made at two locations in the Bootless Bay area, southeast of Port Moresby. At Lion Island, *D. bifasciatum* usually occurred along a steep reef slope between a shallow, narrow reef fringing the east side of the island and a mud bottom starting about 18–20 m. The slope was approximately 30–45° and covered with coral and gorgonians. *Diploprion bifasciatum* also was collected south of Loloata Island where a shallow reef extends south of the island for about 1 km. The reef drops abruptly from a depth of 1 m via a series of shelves to a mud bottom at 20–27 m. In some areas, a vertical face exists at the lower limit of the reef, and adult *D. bifasciatum* usually were found in such areas. The two collection sites were similar, with vertical relief reaching to a sediment bottom, and in both localities fishes were collected near the reef-
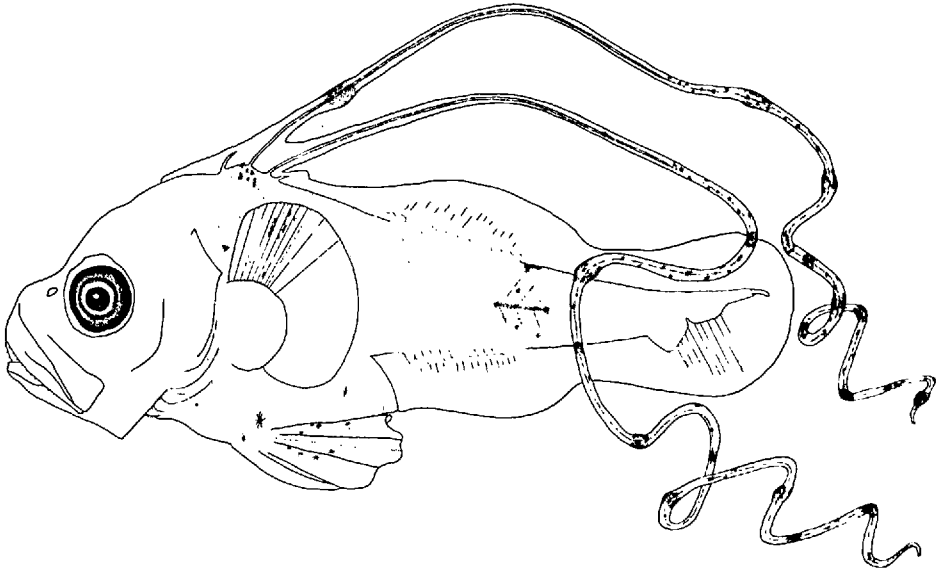
Figure 2. Larva of *Diploprion bifasciatum* undergoing notochord flexion: USNM 290892-2, 6.6 mm NL, 12 days post hatch.

mud interface. *Diploprion bifasciatum* inhabited greater depths at Loloata Island, where the reef-mud interface was deeper.

Spawning.—A group of a few *D. bifasciatum* was observed repeatedly in both areas described above. At Lion Island, one male swam continuously in a single direction at the juncture between the reef and mud during late afternoon, covering about 200 m horizontally in 10 min and passing in and out of small caves and ledges that make up much of the lower edge of the reef. At the end of one transit of this area, the male would reverse direction and cover the same bottom in the opposite direction. Females followed a similar pattern but swam at only about half the speed and often in a direction opposite that of the male. When a male and female encountered one another while engaged in this swimming activity, courtship and spawning often followed. Spawning behavior observed in this study did not differ significantly from that described by Thresher (1984) for *D. bifasciatum* off One Tree Island, Great Barrier Reef. Thresher (1984) observed males that appeared to be controlling spawning territories and "courting" passing females. Spawning occurred after a male and female swam closely together upwards in the water column to a height between 7 and 14 m. After releasing gametes, the fish immediately returned to the bottom, the female left the area and the male continued to patrol his area. On days that spawning was observed in this study, the female was visibly swollen with eggs in late afternoon. On several occasions, females in an unswollen condition were observed to engage in courtship behavior without spawning; in such cases, courtship lasted only a few seconds and was followed by an ascent similar to, but much shorter than, that observed during actual spawning. In one case, a pair went through two short ascents in quick succession without gamete release.

Data are insufficient to comment on the occurrence of seasonal, diel or lunar periodicity in spawning, but the presence of visibly swollen females in late afternoon appears to be a reliable indicator that spawning will occur that evening.
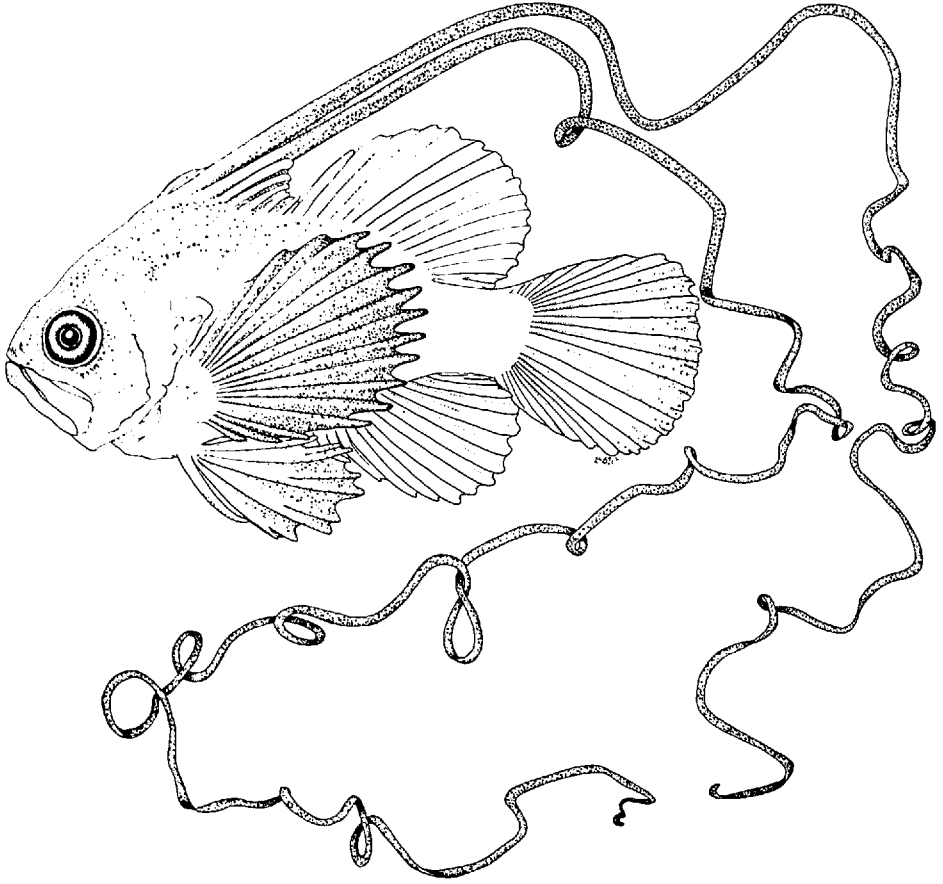
Figure 3. Postflexion larva of *Diploprion bifasciatum*: USNM 290919, 16.2 mm SL, 24 days post hatch.

Colin (1989) commented on the use of the visible condition of the female as an indicator of daily spawning potential in butterflyfishes (*Chaetodon*).

Eggs. —Eggs are pelagic, spherical and have a smooth unpigmented chorion. Two hours after fertilization, eggs appear to be in the blastula stage and are 1.0–1.1 mm in diameter. Multiple oil globules (approximately 20–40, 0.06–0.2 mm in diameter) are scattered throughout a homogenous yolk that underlies the cap of blastomeres. A perivitelline space usually is well developed.

General Development of Larvae. —Morphometric data and counts are given in Table 1. Recently hatched larvae (1.5–2.0 mm NL) have a large ovoid yolk (52.6–80.0% NL) with numerous small oil globules at the posterior end; the number of oil globules is approximately the same as noted for early-stage eggs. The body is dorso-ventrally flattened over the yolk, the eyes are unpigmented, the mouth is not formed, median-fin folds are slightly to well developed and the intestine is apparent only as it bends ventrally towards the anus, which is located slightly posterior to midbody (55.0–57.9% NL). Before the yolk is completely absorbed (in all specimens by 3.4 mm NL), the body becomes laterally compressed and changes in shape from moderately deep in preflexion larvae (body depth 12.9–

Table 1. Morphometric data and counts of larval *Diploprion bifasciatum*. Body length is in mm; other morphometric values are expressed as %body length. Parentheses enclose the number of specimens measured; where more than one specimen was examined, values are means followed by standard deviation. Values between dashed lines represent counts and measurements of specimens undergoing notochord flexion

Body length	Preanal length	Predorsal length	Snout length	Eye diameter	Body depth at P₁ base	Body depth at anus	Depth caudal peduncle	Head length
1.5–2.0 (12)	57.0; 2.2	—	—	—	—	15.2; 0.4	—	—
2.1–3.0	48.0; 2.2 (46)	30.5; 1.7 (29)	6.9; 0.2 (29)	6.9; 0.2 (29)	18.4; 4.3 (46)	14.6; 2.1 (46)	—	22.5; 2.4 (42)
3.1–4.0 (39)	48.2; 2.0	31.4; 1.8	6.8; 0.9	7.6; 1.4	18.2; 2.3	14.3; 1.9	—	25.2; 1.5
4.1–5.0 (3)	47.1; 1.6	31.6; 1.1	8.1; 1.4	8.1; 1.4	22.0; 1.3	16.9; 0.8	—	27.8; 0.1
6.3 (1)	50.0	28.6	9.5	9.5	31.7	25.4	—	—
6.6 (1)	48.5	27.3	9.1	9.1	33.3	27.3	—	28.8
7.3 (1)	63.0	38.4	11.0	11.0	39.7	24.7	11.0	37.0
8.8 (1)	56.8	31.8	11.4	11.4	42.0	36.4	14.7	38.6
9.8 (1)	56.1	34.7	13.3	11.2	42.9	32.7	13.3	34.7
10.7 (1)	57.0	31.8	10.3	11.2	44.9	37.4	15.0	35.5
11.0 (1)	58.2	38.2	10.9	10.9	46.4	38.2	14.0	40.9
13.3 (1)	50.4	30.1	9.0	9.8	45.1	39.8	13.8	39.8
15.5 (1)	51.6	32.3	10.3	10.3	45.2	37.4	15.8	41.3
16.2 (1)	52.5	28.4	8.6	10.5	47.5	42.6	15.8	39.5
(Wild-caught specimens)								
5.7 (1)	49.5	40.8	8.7	8.7	34.9	24.8	—	33.5
5.8 (1)	51.4	41.4	10.0	10.0	30.0	22.9	—	35.7
7.1 (1)	56.1	42.1	11.7	9.4	40.9	32.1	—	40.9
10.4 (1)	59.4	39.3	12.8	8.8	36.9	30.5	12.8	41.7
10.9 (1)	55.2	38.3	10.7	9.2	41.4	33.7	13.0	39.8
13.3 (1)	57.9	30.1	10.5	10.5	49.6	40.6	15.0	42.1
31.4 (1)	56.1	30.6	6.1	9.6	45.9	41.4	15.9	35.0

Table 1. Continued

Body length	Length of P₁ fin	Length of D spine II	Length of D spine III	Yolksac length	Dorsal fin	Anal fin	Pectoral fin*	Pelvic fin	Caudal fin	
									Principal	Procurrent
1.5–2.0 (17)	—	—	—	60.1; 7.7	—					
2.1–3.0	13.3; 1.7 (23)	35.8; 26.0 (29)	—	14.5; 9.1 (45)	0–I,–	—	—	—	—	—
3.1–4.0	15.4; 1.5 (27)	118.9; 69.4 (38)	7.6; 5.3 (7)	4.3; 2.0 (17)	I–II,–	—	—	—	—	—
4.1–5.0 (3)	13.2; 2.3	130.8; 7.3	35.4; 7.1	—	II,–	—	—	—	—	—
6.3 (1)	19.0	69.8	76.2	—	IV,–	—	8	I,5	3 + 3	—
6.6 (1)	21.2	166.1	224.4	—	IV,–	—	9	I,5	4 + 4	—
7.3 (1)	31.5	186.3	230.1	—	VIII,15	II,12	18	I,5	9 + 8	2 + 2
8.8 (1)	39.8	127.3+	102.3+	—	VIII,14	II,12	18	I,5	9 + 8	2 + 2
9.8 (1)	42.9	285.7	391.8	—	VIII,15	II,13	18	I,5	9 + 8	3 + 4
10.7 (1)	44.9	—	—	—	VIII,15	II,12	17	I,5	9 + 8	4 + 4
11.0 (1)	48.2	261.8	392.7	—	VIII,15	II,12	17	I,5	9 + 8	6 + 6
13.3 (1)	46.6	228.6	457.1	—	VIII,14	II,12	18	I,5	9 + 8	6 + 5
15.5 (1)	46.5	343.2	760.0	—	VIII,14	II,12	18	I,5	9 + 8	7 + 5
16.2 (1)	50.6	500.6	876.5	—	VIII,15	II,12	17	I,5	9 + 8	8 + 7
(Wild-caught specimens)										
5.7 (1)	7.3	34.9+	27.7+	—	II,–	—	—	I,3	—	—
5.8 (1)	7.1	30.0+	24.3+	—	II,–	—	—	I,4	—	—
7.1 (1)	11.7	40.9+	23.4+	—	V,16	II,12	15	I,5	6 + 6	—
10.4 (1)	32.1	54.6+	46.6+	—	VIII,16	II,12	17	I,5	9 + 8	4 + 4
10.9 (1)	30.6	72.0+	64.3+	—	VIII,16	II,12	17	I,5	9 + 8	5 + 5
13.3 (1)	43.6	78.2+	12.0+	—	VIII,15	II,12	17	I,5	9 + 8	7 + 7
31.4 (1)	34.1	63.7	22.9	—	VIII,15	II,12	17	I,5	9 + 8	9 + 8

* Postflexion specimens often appear to have one fewer pectoral-fin ray than the value listed in this column because the two dorsalmost rays are very close to one another and usually encased in a single sheath.

30.4% NL at pectoral-fin base) to deep in postflexion specimens (body depth 39.7–47.5% SL), the intestine coils and shortens slightly (43.3–52.2% NL), an inconspicuous swimbladder forms, the eyes become pigmented and the mouth opens. The eye is round, and its horizontal diameter remains approximately equal to or slightly larger than the length of the snout throughout development. The mouth increases in size ontogenetically, the maxilla reaching to or nearly to the anterior margin of the eye before flexion, to a point just posterior to the middle of the eye after flexion. A prominent rostral cartilage appears after flexion. Scales are lacking in all specimens examined.

Pigmentation. —The reared larvae of *D. bifasciatum* were preserved in 1986, and pigmentation of small specimens has faded considerably. Our description and illustrations were made before pigment had faded. Notes on color of living larvae are provided in a subsequent section (see "Observations of living larvae").

Larvae <2.8 mm NL lack melanophores. In the smallest larvae with pigment, pattern of pigmentation is as follows (Fig. 1B): the eye is partially pigmented; one to a few small melanophores usually are present near the base of the second dorsal-fin spine; posteriorly, there is a small patch of melanophores at the dorsal and ventral margins of the body approximately midway between the anus and posterior tip of notochord; a faint patch is present on the second dorsal-fin spine just dorsal to the finfold; and there is a horizontal series of melanophores on the dorsal surface of the gut just anterior to the point where the gut bends ventrally towards the anus.

The number of melanophores contributing to the patch of pigment on the anterior portion of the trunk (base of second dorsal spine) increases with development of the larva, and in postflexion specimens, this patch is internal as well as external and lies beneath the first through fifth dorsal-fin spines.

The dorsal and ventral patches of pigment on the posterior portion of the trunk (or "tail" of Leis and Rennis, 1983) expand ventrally and dorsally, respectively, such that a band of melanophores encircles the tail in late preflexion larvae. In specimens undergoing notochord flexion, this band of pigment no longer completely encircles the body but terminates above the ventral margin and is heaviest dorsally and midlaterally. After flexion, a few melanophores may reappear on the anal-fin base, and eventually (ca. 13.0 mm and larger), the tail is lightly covered with scattered melanophores.

Gut pigmentation also changes considerably during ontogeny. In preflexion larvae, pigment on the dorsal surface of the gut expands ventrally, forming a saddle of pigment over the gut. This saddle appears to break up during flexion: several small, distinct, external melanophores become apparent on the ventral surface of the gut, and several large melanophores appear on the gut laterally and dorso-laterally. After flexion, these external melanophores often are absent.

Melanophores appear on the peritoneum dorsal to the swimbladder in yolksac larvae and increase in number ontogenetically; flexion and postflexion larvae have a shield of pigment over the swimbladder.

The sheath surrounding the elongate second dorsal-fin spine develops one to four pigmented swellings in yolksac larvae, and the number of these swellings increases with growth. Just prior to flexion, the sheath surrounding the third dorsal-fin spine may develop one or two pigmented swellings. Specimens undergoing notochord flexion have numerous pigmented swellings as well as small melanophores between these enlarged areas. After flexion, the sheaths surrounding the elongate spines are lightly pigmented proximally (ca. 5 mm) but become

completely covered distally with small melanophores. Additionally, scattered pigment usually is present on the membrane between anterior dorsal-fin spines.

Pigment on the pectoral and pelvic fins generally appears in specimens undergoing notochord flexion, but prior to flexion, a few melanophores may be present on the dorsal portion of the pectoral-fin bud. During flexion, pigment is lightly scattered on the dorsal rays of the pectoral fin and appears as elongate melanophores along the lengths of the third and fourth rays; elongate melanophores also are present along the lengths of and on the membrane between the pelvic-fin rays. After flexion, small melanophores are present on and between all rays of the pectoral fin and become very dense distally, rendering the tips almost black. Small melanophores also are present on and between the rays of the pelvic fin but do not become denser distally.

Preflexion larvae lack melanophores on the head. During flexion, one melanophore may be present on the frontal just dorsal to the eye, and several melanophores are present on the spinal cord anteriorly. In postflexion larvae, scattered melanophores appear on the frontals, snout, lacrimal, bones of the opercular series, jaws and branchiostegals. Several melanophores appear internally on the brain, and there is more pigment on the spinal cord. In an 11.0-mm SL specimen, internal melanophores are present along the entire length of the spinal cord, being very dense anteriorly, more diffuse posteriorly.

In the largest specimen examined (16.2 mm SL) the entire body is covered with scattered melanophores that are most dense anterodorsally.

Spination. —Head spines are not prominent in any reared specimens examined. They first appear in the form of two small preopercular spines in larvae undergoing notochord flexion. It is difficult to see head spines in whole specimens, and the following description is based on cleared and stained material. In a 7.3-mm SL specimen, the medial ridge of the preopercle bears three small smooth spines, and the lateral ridge bears three minute spines. Also, four small spines are present on the supraorbital ridge of the frontal bone. In an 11.0-mm SL specimen, there is an additional small spine on the medial preopercular ridge and two very small spines on the posttemporal. The three opercular spines characteristic of all serranids first become evident after flexion. Supraorbital spination is not evident in specimens >11.0 mm SL, and preopercular spines, if present, are covered with thick skin in specimens 15.5 mm SL and larger. All head spines except those on the opercle are absent in the largest specimen examined (16.2 mm SL). A few to many larval teeth are present on the premaxilla in late preflexion and flexion larvae. Larval teeth are small laterally projecting spines that are exserted on the premaxilla and appear to be resorbed during development of the larva. In postflexion specimens, numerous vertically projecting minute teeth are present in both jaws.

Meristics and Fin Formation. —Adult *Diploprion bifasciatum* have 10 + 14 vertebrae, not 11 + 14 as reported by Schultz (1966:188) and Leis and Rennis (1983: 73). Ossification of vertebrae begins during flexion. In a 7.3-mm SL specimen, the anterior 20 centra and the urostylar centrum are fully ossified, the 21st centrum is partially ossified (dorsal and ventral saddle-shaped ossifications just beginning to meet) and the 22nd and 23rd centra are unossified. Ossification of vertebrae is complete in an 11.0-mm SL specimen.

The exact sequence of completion of fins could not be determined solely from the reared material because specimens in the critical size range (between 6.3 and 7.3 mm) are not available. Combining information from reared and wild-caught

material, the sequence of completion appears to be pelvic-anal-soft dorsal and pectoral-spinous dorsal-caudal.

The second and third dorsal-fin spines appear before flexion and become extremely elongate during ontogeny. The second dorsal-fin spine appears within 48 h of hatching in larvae 2.8 mm NL or larger, the third in most larvae >3.5 NL. Each of these spines emerges and grows encased in a sheath of tissue that first develops well-spaced, small pigmented swellings along its length, but later loses the swellings and becomes more uniformly pigmented. The spines are flexible and thin, and taper in diameter distally (e.g., from ca. 0.15 to <0.02 mm in an 11.0-mm cleared and stained specimen). In some specimens, these ossified spines extend to the distal tip of the filamentous sheath, but in a 6.3-mm SL cleared and stained specimen, the spines form loops within the filament and fall short of its terminus. The elongate spines and surrounding sheaths appear as fragile, somewhat flattened filaments, and were broken in most specimens. Accurate measurement of these spines was further hindered by the tendency for the somewhat elastic filaments to wind around the body or one another. In the largest reared specimen (16.2 mm SL), the second and third dorsal spines are approximately 500 and 876% SL, respectively. However, those spines apparently were much longer before the larvae were preserved. In living larvae of 12–15 mm, the third dorsal spine was ca. 300 mm, or 20–25 times the length of the body! Furthermore, the filaments were not coiled in life as they are in preserved material. Preservation appears to shrink (possibly resulting in the looping of the spine mentioned above) and alter the elasticity of the filaments.

Other dorsal-fin spines begin developing during flexion, the first and fourth spines appearing before those more posterior. In a 7.3-mm SL specimen, the second, third and fourth dorsal-fin spines have paired lateral fossae near the bases, whereas the other spines do not. In an 11.0-mm SL specimen, all spines except the eighth have these paired fossae (Fig. 4). Posterior spines of the dorsal fin develop directly into spines. The eighth dorsal-fin element is identifiable as a spine by its lack of segmentation and by the shape and position of, and articulation with, its associated distal radial (Johnson and Keener, 1984). The cartilaginous pterygiophores of the soft dorsal and anal fins appear during flexion, and the rays are completely formed in a 7.1-mm NL wild-caught specimen. Dorsal and anal fins are complete in all postflexion specimens examined.

The pectoral fin appears as a large bud at approximately the same time as the second dorsal-fin spine develops, but rays are not evident until flexion. Eight or nine rays are present dorsally in reared specimens undergoing notochord flexion. The pectoral fin is complete in all postflexion specimens examined.

The pelvic-fin bud forms later than the pectoral, appearing first in a 4.0-mm NL specimen, but it is the first fin to complete development. A 6.3-mm NL flexion specimen has the full complement (I,5) of pelvic-fin rays.

The caudal fin is the last fin to complete development. The notochord is undergoing flexion in 6.3- to 7.1-mm specimens, and flexion is complete in a 7.3-mm specimen. Three to six principal caudal-fin rays are present in both the upper and lower lobes of the caudal fin in flexion specimens, but no procurrent rays are evident. In a 7.3-mm SL specimen, all principal caudal-fin rays (9 + 8) are present, and there are four procurrent rays. Adult *D. bifasciatum* have 17 procurrent caudal-fin rays (9 + 8). It is difficult to count procurrent rays in whole postflexion specimens because the rays are surrounded by thick tissue. A cleared and stained specimen of 11.0 mm SL has six procurrent rays dorsally and ventrally.

Comparison with Wild-caught Larvae.—Several wild-caught specimens were available for comparison with the reared material. Morphometric data and counts
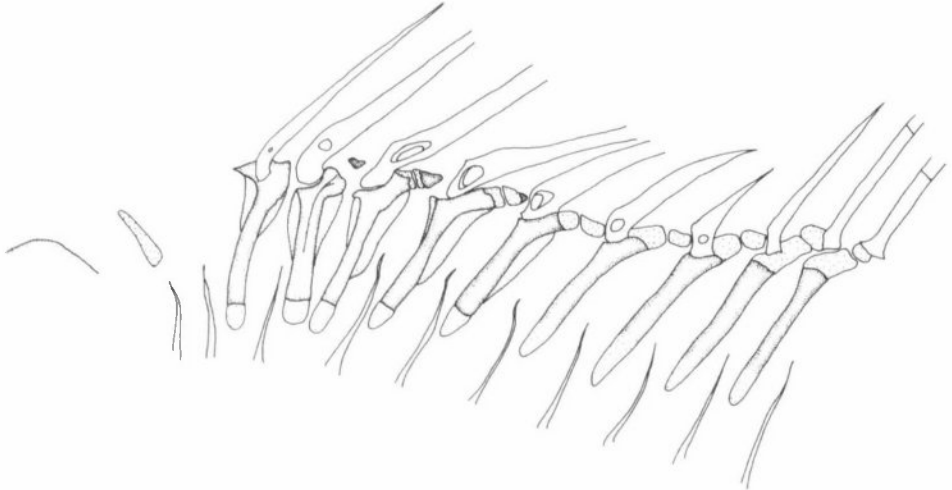
Figure 4.   Spinous dorsal fin of an 11.0 mm SL larva of *Diploprion bifasciatum*: USNM 290896-1.

of the wild-caught specimens are given at the bottom of Table 1. In general, reared and wild-caught specimens are similar morphometrically, but in preflexion and flexion specimens, wild-caught larvae have a larger head (reflected in head length and predorsal length) and smaller pectoral fin, or pectoral-fin bud. The most notable differences between measurements of all wild-caught and reared specimens are lengths of the second and third dorsal-fin spines. These spines and the associated filamentous sheaths are broken in all wild-caught specimens, undoubtedly an artifact of their collection with nets.

Counts of reared and wild-caught specimens are similar except that reared specimens have 14 or 15 dorsal-fin soft rays and 17 or 18 pectoral-fin rays, whereas most wild-caught specimens have 16 dorsal soft rays and 15 or 17 pectoral rays. All of these counts are within known extremes of numbers of fin rays for *D. bifasciatum* (Leis and Rennis, 1983).

With few exceptions, pigmentation of the wild-caught larvae agrees with that of reared specimens. In the wild-caught larvae, fewer melanophores contribute to the patches of pigment on the anterior and posterior portions of the trunk, gut, pectoral and pelvic fins (postflexion specimens completely lack pigment on posterior portion of the trunk), and the elongate second and third dorsal spines usually lack pigment (these spines broken and the surrounding sheaths damaged in all wild-caught specimens).

Head spination in the wild-caught larvae is more conspicuous than in the reared material (Fig. 5). Head spines of reared larvae are difficult to observe in whole specimens, but those of the wild-caught larvae are larger and can be seen clearly in whole specimens. Additionally, more supraorbital spines are present in the wild-caught larvae (five to eight vs. four in most reared specimens). The small differences in meristics and spination between the reared and wild-caught specimens could be due to the small sample size examined, the rearing process (Blaxter, 1984 and Hunter, 1984) or, possibly, variation between populations of *D. bifasciatum* in New Guinea (locality adults were collected for obtaining gametes) and the northwest continental shelf of Australia (locality most wild-caught larvae were obtained).
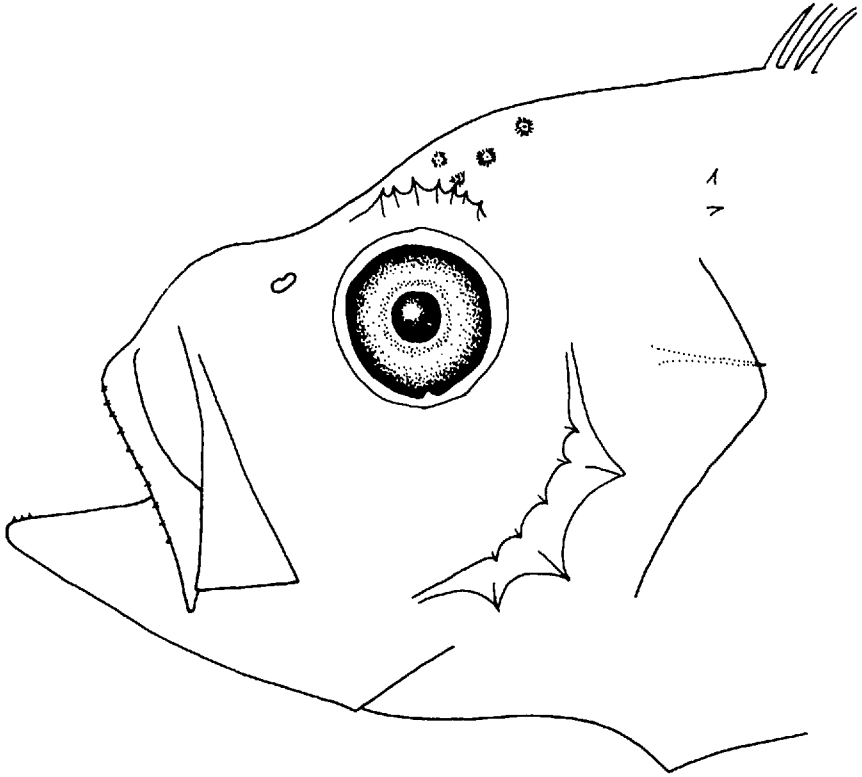
Figure 5.   Head spination in a wild-caught larva of *Diploprion bifasciatum* (CSIRO, AS05/83, 7.8 mm SL).

Growth. — Eggs hatched 19 h after fertilization at 26–29°C. Yolk was depleted in all specimens by 4.3 d. Both specimens undergoing notochord flexion were 12-d old, no specimens younger than 12 d had undergone flexion and two specimens had not begun flexion by 12–13 d. No specimens between 13 and 18 d are available; in the 18-d old specimen, most fins are complete. We estimated growth of the larvae by plotting body length vs. age (Fig. 6). Simple linear regression yields a slope of 0.40 mm d^{-1} with a variance of 0.88. The high variance appears to be primarily due to the unusually small (3.4–3.6 mm NL) specimens of 12 and 13 d and the very large size difference among 23-d old specimens (7.3–15.5 mm). Some of this variation may be attributable to shrinkage of larvae in preservative.

The typical duration of the planktonic period is unknown. The largest wild-caught specimen (34.1 mm SL) was collected with a dipnet, and the presence of elongate dorsal spines in that specimen indicates that at least some individuals of *D. bifasciatum* may remain planktonic for extended periods. It is possible, however, that most settle much earlier. Based on growth rate data for the reared larvae, the 34.1-mm SL specimen is approximately 85 d old.

Observations of Living Larvae. — At 24 h post hatch (2.3–2.8 mm NL), larvae had numerous chromatophores. Orange chromatophores were present on the tip of the snout, anterior portion of each eye, anterior part of brain, anterior and posterior margins of the yolk sac, at several locations along the dorsal and ventral margins of the body and on the pectoral-fin bud. Three triangular-shaped patches of white
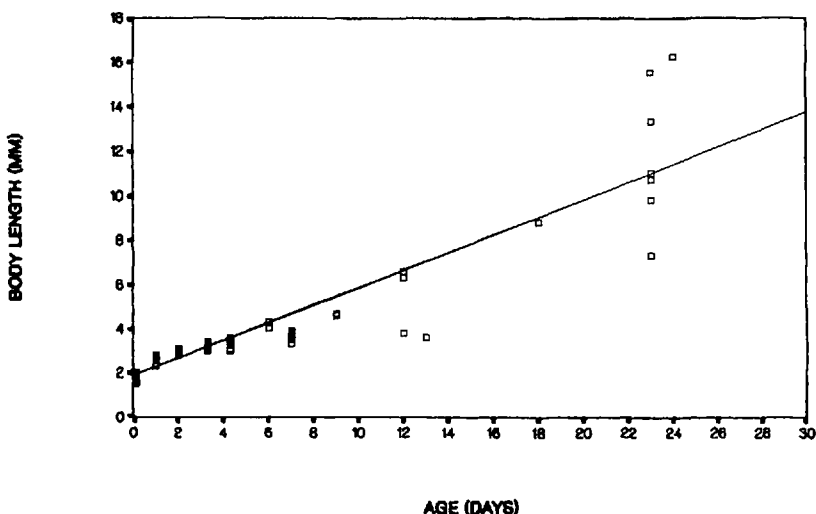
Figure 6. Regression of body length on age, showing growth in reared specimens of *Diploprion bifasciatum*.

chromatophores were present on the fin folds: one on the distal margin of the dorsal-fin fold approximately midway between the anus and tip of the notochord, one on the ventral-fin fold opposite the dorsal patch, and a third on the ventral-fin fold just posterior to the anus. At 48 h post hatch (2.8–3.1 mm NL), the second dorsal-fin spine emerged (even before the eyes were completely pigmented) covered with white chromatophores distally. The opposing dorsal and ventral triangular-shaped patches of white chromatophores were present (Fig. 1B), as were the patches of orange chromatophores described above. Additionally, melanophores were present on the eye, over the gut, on the proximal base of the second dorsal-fin spine and on the tail, approximately midway between the anus and distal tip of the notochord. At 65 h post hatch (ca. 3.0–3.3 mm NL), the eyes were fully pigmented and larvae began to feed. When zooplankton were added, larvae actively oriented themselves within the water column and immediately began feeding. Early-stage larvae would position themselves close to the food item and then strike from an S-posture. In later larval stages, the pectoral fins were used in feeding strikes. The filamentous second and third dorsal-fin spines were not used in feeding.

Larvae were not reared through metamorphosis. At 23- and 24-d post hatch, when rearing was terminated, the larvae were actively feeding and appeared to be growing well.

Belonoperca chabanaudi
Figure 7

Belonoperca chabanaudi Fowler and Bean inhabits Indo-Pacific waters from the east coast of Africa eastward to Samoa and the Gilbert Islands (Springer, 1982). Adults reach 145 mm and inhabit reefs, generally hiding in caves during the day (Randall, 1986).

The following description is based on four wild-caught specimens, ranging in size from 6.9 to 11.8 mm SL. Our identifications of larval *Belonoperca* are based on comparisons of meristic features of larvae and adults (Leis and Rennis, 1983:
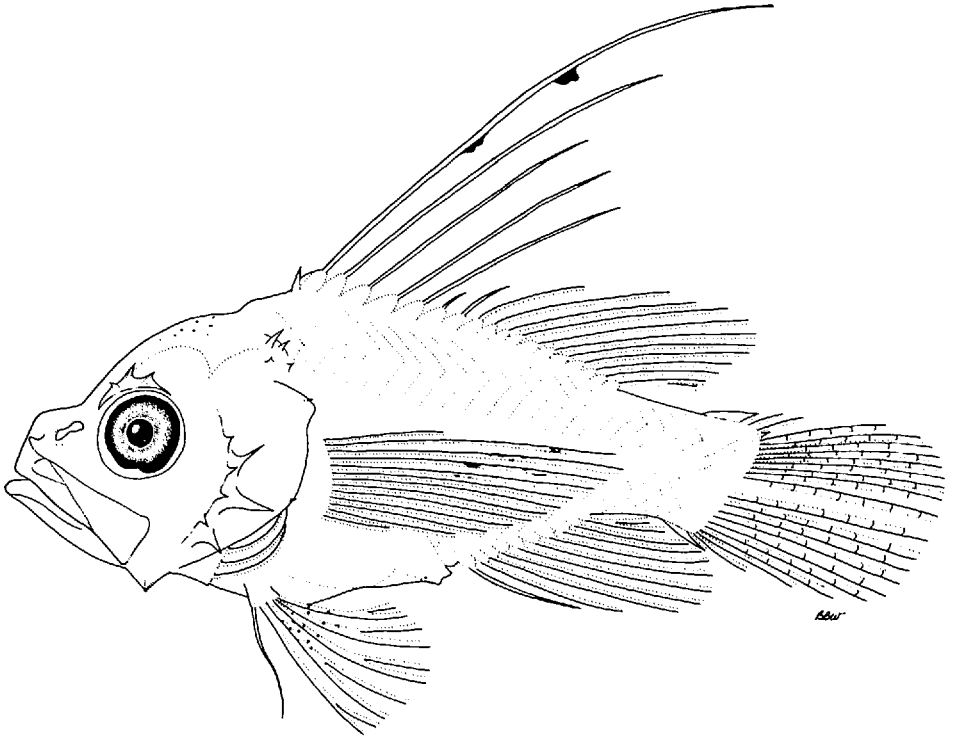
Figure 7.   Postflexion larva of *Belonoperca chabanaudi*: ZMUC P43671, 6.9 mm SL; dorsal fin drawn from USNM 309607, 11.8 mm SL.

73); particularly diagnostic is the combination of dorsal-, anal- and pectoral-fin rays. Morphometric data and counts are given in Table 2.

Postflexion larvae are moderately deep (body depth 36.4–41.7% SL at pectoral-fin base). The eye is round and smaller in diameter than the length of the snout. The mouth is large, the maxilla reaching to just beyond the middle of the eye. The pectoral fin is large, reaching 44.3% SL in an 8.8-mm SL specimen; it may attain an even greater length in larger specimens (fin rays broken in the 11.8-mm SL specimen). All specimens examined have the full complement of dorsal-, anal-, pectoral-, pelvic- and principal caudal-fin rays. Procurrent rays of the caudal fin are the last elements to complete development, but the full complement is present in the 11.8-mm SL specimen. The ninth element of the dorsal fin and second element of the anal fin, which in adults are spinous, are segmented in all specimens examined. These elements are represented by "i" in Table 2.

The second through sixth dorsal-fin spines are thin, flexible and elongate. It is impossible to determine if their lengths approach those of the second and third dorsal spines of *Diploprion* because these spines are broken in all specimens. All of the elongate spines of *Belonoperca* are associated with or surrounded by bits of tissue that probably are remnants of sheaths that cover the elongate elements. Fragments of tissue surrounding the second dorsal spine bear one or two small, pigmented, fleshy flags.

In the smallest specimen (6.9 mm SL), a group of very faint melanophores extends ventrally from the base of the eighth dorsal soft ray to just below midbody. The anterior portion of the trunk lacks pigment. Several melanophores are present

Table 2. Morphometric data and counts of larval *Belonoperca chabanaudi* (Body length is in mm SL; other measurements are expressed as %body length)

Body length	Preanal length	Predorsal length	Snout length	Eye diameter	Body depth at P, base	Body depth at anus	Depth caudal peduncle	Head length	Length of P, fin
6.9	60.5	37.2	13.0	10.1	39.1	37.7	15.9	39.1	40.6
7.2	58.3	40.3	13.9	9.7	41.7	36.1	15.5	41.2	38.9
8.8	60.2	39.8	15.9	9.1	36.4	34.1	14.8	39.8	44.3
11.8	66.1	38.1	11.9	11.0	40.7	39.0	15.3	43.2	22.9+

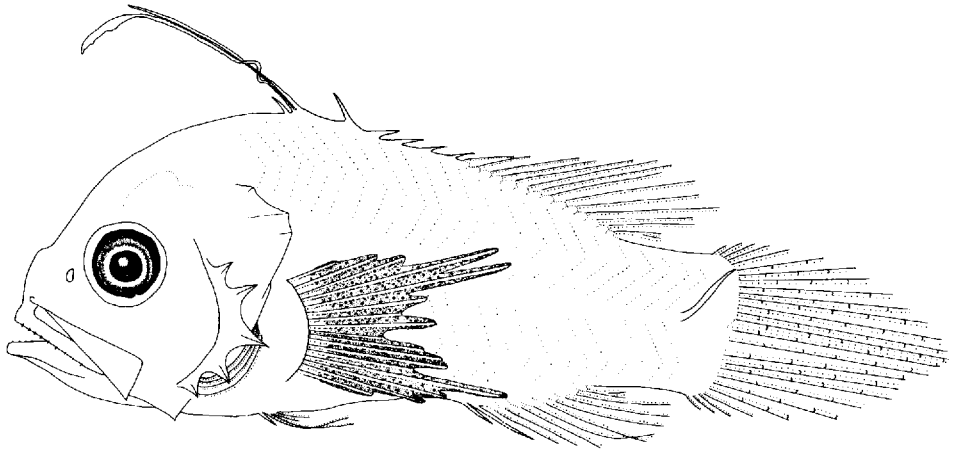| Body length	Length of D spine II	Length of D spine III	Length of D spine IV	Length of D spine V	Length of D spine VI	Dorsal fin	Anal fin	Pectoral fin	Pelvic fin	Caudal fin	
										Principal	Procurrent
6.9	46.4+	52.2+	29.0+	26.1+	14.5+	VIIIi,10	Ii,8	13	I,5	9 + 8	4 + 4
7.2	19.4+	23.6+	26.4+	29.2+	8.3+	VIIIi,10	Ii,8	13	I,5	9 + 8	3 + 3
8.8	72.7+	36.4+	30.7+	42.0+	22.7+	VIIIi,10	Ii,8	14	I,5	9 + 8	5 + 4
11.8	52.5+	17.8+	31.4+	44.9+	39.0+	VIIIi,10	Ii,8	14	I,5	9 + 8	8 + 7

Figure 8. Postflexion larva of *Grammistes sexlineatus*: ZMUC P43674, 6.5 mm SL; pectoral fin drawn from right side of specimen.

on the upper rays of the pectoral fin and on the proximal portion of the pelvic fin. Anal and caudal fins are without pigment. There are several small melanophores on each frontal bone. In larger specimens, the number of melanophores on the frontals increases, and no pigment is evident on the trunk and pelvic fin, but possibly it has faded.

All specimens except the largest (11.8 mm SL) have spines on the supraorbital ridge of the frontal, preopercle, subopercle, posttemporal and supracleithrum. Supraorbital spination consists of two strong spines and sometimes a third weaker spine anteriorly. The medial ridge of the preopercle bears three spines, three or four smaller spines are present on the lateral ridge and one very small spine is present on the subopercle. The supracleithrum and dorsal limb of the posttemporal each bear one small spine, and the ventral limb of the posttemporal has one or two spines. Several minute larval teeth are present on the premaxilla.

Grammistes sexlineatus
Figure 8

Grammistes sexlineatus (Thunberg) is known from the Red Sea and Indo-West Pacific from the African coast (as far south as East London) eastward to the Tuamotus and as far north as southern Japan (Randall et al., 1971; Randall, 1986). This shallow reef species attains a length of 27 cm (Randall, 1986).

Our description is based on 10 larvae (5.5–11.4 mm SL) identified by fin-ray counts and morphology of fin spines. *Grammistes* and *Pogonoperca* have similar numbers of fin rays (Leis and Rennis, 1983:73). Adults are separable on the basis of gross morphology, and presence of seven dorsal spines and two or three anal spines in *Grammistes* (vs. eight and always three, respectively, in *Pogonoperca*). We were unable to positively identify the 10 larval specimens as *Grammistes* solely on the basis of meristic features; although they appear to have seven dorsal- and two anal-fin spines, it is possible that an additional spine (or spines) could form indirectly from soft rays as in *Niphon* and epinephelins (Johnson, 1988). However, in adults of *Pogonoperca*, the eighth dorsal-fin spine is the shortest, whereas in *Grammistes*, the shortest dorsal spine is the seventh. In our larval specimens, the eighth dorsal element is longer than the seventh, and thus could

Table 3. Morphometric data and counts of larval *Grammistes sexlineatus* (Body length is in mm SL; other measurements are expressed as %body length)

Body length	Preanal length	Predorsal length	Snout length	Eye diameter	Body depth at P_1 base	Body depth at anus	Depth caudal peduncle	Head length
5.5	57.3	42.3	13.6	8.8	36.2	31.7	18.8	37.7
6.2	60.2	40.2	12.7	9.4	37.5	33.5	18.1	40.2
6.5	55.4	38.5	10.8	9.2	41.5	33.8	18.5	38.5
6.6	57.0	33.9	9.1	9.1	34.8	30.3	16.7	36.4
7.1	59.2	39.4	12.7	8.5	35.2	32.4	18.3	42.3
7.3	damaged	43.8	11.0	8.2	31.5	damaged	damaged	41.1
7.9	60.8	39.2	13.9	7.6	35.4	31.6	15.2	43.0
8.2	57.3	34.1	12.2	8.5	36.6	32.9	17.1	40.2
9.7	56.8	37.9	10.3	8.6	41.3	37.9	15.5	39.6
11.4	57.1	36.6	11.0	8.8	39.6	36.6	16.1	41.0

Body length	Length of P_1 fin	Length of D spine II	Dorsal fin	Anal fin	Pectoral fin	Pelvic fin	Caudal fin	
							Principal	Procurrent
5.5	31.7	28.7+	VII,13	II,9	17	I,4	9 + 8	3 + 3
6.2	33.5	66.9+	VII,13	II,9	17	I,4	9 + 8	4 + 3
6.5	32.3	60.0+	VII,14	II,9	17	I,5	9 + 8	5 + 4
6.6	34.8	24.2+	VII,13	II,9	17	I,4	9 + 8	4 + 4
7.1	29.6	28.2+	VII,13	II,9	17	I,5	9 + 8	5 + 4
7.1	30.1	27.4+	VII,13	II,9	17	I,5	9 + 8	4 + 4
7.9	31.6	27.8+	VII,13	II,9	17	I,5	9 + 8	5 + 4
8.2	30.5	19.5+	VII,14	II,9	17	I,5	9 + 8	5 + 4
9.7	25.8+	15.5+	VII,14	II,9	16	I,5	9 + 8	5 + 4
11.4	39.6	10.3+	VII,14	II,8	17	I,5	9 + 8	5 + 4

not represent the as yet untransformed eighth spine of *Pogonoperca*. Additionally, *Pogonoperca* has three anal-fin spines, the most posterior of which is the shortest, whereas in specimens of *Grammistes* with two anal spines, the third element (the first soft ray) is considerably longer than the spines. In our larvae, two spines are present, and the third segmented element is much longer than the spines; accordingly, the third anal-fin element could not represent the untransformed third anal spine of *Pogonoperca*. Possibly corroborating the identification of these larval specimens (from three separate collections) as *Grammistes* is the fact that this species is much more common in collections than *Pogonoperca*.

Fourmanoir (1976) illustrated an 11.0-mm SL specimen of *Grammistes* and described late larvae as being identifiable by the morphology and number of fin rays. He noted that *Grammistes* has five preopercular spines and that the first spine of the dorsal fin is elongate. In all specimens that we examined it is the second, not the first, dorsal-fin spine that is elongate, and Fourmanoir (1976) probably overlooked the tiny first spine which is borne in supernumerary association with the reduced first dorsal pterygiophore. To our knowledge, supernumerary spines of the first dorsal pterygiophore are not elongate in any epinephelines.

Morphometric data and counts are given in Table 3. All specimens are moderately deep (body depth 31.5–41.5% SL at pectoral base). The eye is round and its diameter usually is smaller than the length of the snout. The mouth is large, the maxilla reaching a vertical through middle of orbit. The pectoral fin is moderately large, reaching 39.6% SL in an 11.4-mm SL specimen. All specimens examined have the full complement of dorsal-, anal-, pectoral- and principal caudal-fin rays. A 6.5-mm SL specimen has the full complement of pelvic- and

Table 4. Comparison of known larvae of all epinephelines. S—stout, Se—serrate, EE—extremely elongate, F—filamentous, PREoP—preopercle, iop—interopercle, sb—subopercle, pt—posttemporal, scl—supracleithrum, ant.—anterior, ND—no data. Data are from material examined in this study, Fourmanoir (1976), Johnson (1984, 1988), Kendall (1979), Kendall and Fahay (1979), Leis (1986) and Leis and Rennis (1983)

Genus	Elongate dorsal spine(s)	Morphology elongate spine(s)	Body depth (%SL)	Length pectoral fin (%SL)	Head pigment	Dorsal tail pigment	Ventral tail pigment	Gut pigment	Fin pigment
Niphonini									
Niphon	3rd	S	30–35*	17	+	–	+	+	P_2, C
Epinephelini									
Cephalopholis	2nd	S, Se, EE	36	15	+	–	+	+	D_1, P_2
Epinephelus	2nd	S, Se, EE	35	17	+	–	+	+	D_1, P_2
Gonioplectrus	2nd, 3rd	S, Se	51	34	+	(Midlateral)		+	D_1, P_2
Mycteroperca	2nd	S, Se, EE	33–37	15–20	+	–	+	+	D_1, P_2
Paranthias	2nd	S, Se, EE	34	13	+	–	+	+	D_1, P_2
Plectropomus	2nd	S, Se, EE	32–35	14–17	+	–	+	+	D_1, P_2, C
Diploprionini									
Belonoperca	2nd–6th	EE, F	39–42	40–44	+	+	–	–	D_1, P_2, P_1
Diploprion	2nd, 3rd	EE, F	40–47	32–51	+	+	+	+	D_1, P_2, P_1
Liopropomini									
Liopropoma	2nd, 3rd	EE, F	23–32	14–26	+	–	–†	+	D_1
Grammistini									
Aporops	2nd	EE, F	ND	ND	ND	ND	ND	ND	ND
Grammistes	2nd	EE, F	32–42	30–33	–	–	–	–	D_1, P_2, P_1
Pseudogramma	2nd	EE, F	20–29	15–35	–	–	–	+	D_1, P_1
Rypticus	1st	EE, F	24–31	37–45	–	–	–‡	+	D_1, P_1

Table 4. Continued

Genus	Supraorbital spines	Large spine at angle of preop	Medial preop spines	Lateral preop spines	Other head spines	Precocious (≤4 mm NL) Fin development	Sequence§ of fin completion
Niphonini							
Niphon	1	+	4	3	iop, pt, scl	ant. D_1, P_2	P_2-(D_1-D_2-A)-P_1
Epinephelini							
Cephalopholis	1 to many	+	2–13	1	iop, sb, pt, scl	ant. D_1, P_2	ND
Epinephelus	1 to many	+	5	1	iop, sb, pt, scl	ant. D_1, P_2	ND
Gonioplectrus	many‖	+	7	ND	pt, scl	ND	ND
Mycteroperca	1 to many	+	5–10	1	iop, sb, pt, scl	ant. D_1, P_2	(P_2-D_1-A)-D_2-P_1
Paranthias	many‖	+	5	1	iop, sb, pt, scl	ND	ND
Plectropomus	1–4	+	5–7	1–2	iop, sb, pt, scl	ant. D_1, P_2	(P_2-D_1-A)-D_2-P_1
Diploprionini							
Belonoperca	2–3	−	3	3–4	sb, pt, scl	ND	ND
Diploprion	4	−	3–4	3	pt	ant. D_1	P_2-A-(D_2-P_1)-D_1
Liopropomini							
Liopropoma	−	−	5–6	3–5	iop, sb	ant. D_1	(D_2-A-P_1)-D_1-P_2
Grammistini							
Aporops	−	−	5	none	none	ND	ND
Grammistes	−	−	4–5	none	none	ND	P_2 last
Pseudogramma	−	−	5	none	iop, sb	ant. D_1, P_1	P_1-(D_1-D_2)-A-P_2
Rypticus	−	−	3	none	none	ant. D_1, P_1	P_1 first, P_2 last

* Measured at base of pelvic fin; all other measurements in this category made at pectoral-fin base.
† One specimen, 11.5 mm SL, with spot on ventral caudal peduncle.
‡ One specimen, 5.9 mm SL, with several spots along ventral caudal peduncle.
§ Parentheses indicate sequence is variable or unknown.
‖ It is unknown if the supraorbital ridge in these taxa, like that of *Cephalopholis, Epinephelus, Plectropomus* and *Mycteroperca* initially forms as a single spine.

procurrent caudal-fin rays, but neither of these fins is complete in a 6.6-mm SL larva nor in smaller specimens.

As noted above, the second dorsal-fin spine is elongate. It is thin, flexible and covered with fragments of tissue that usually bear a small amount of pigment. As in *Belonoperca,* the elongate element is broken, and we are unable to determine the actual length of the spine.

In all specimens the pectoral fin has many small melanophores on all rays, but the density of melanophores increases with increasing size of the larva. In the largest specimens (9.7 and 11.4-mm SL), melanophores are lightly scattered on the pelvic-fin rays, and in a 7.3-mm SL specimen, there appears to be some pigment ventrally at the base of the anal fin (damaged on this specimen). Except for the melanophores on the sheath of the second dorsal spine, no other pigmentation is evident.

Postflexion larvae of *Grammistes* have four or five spines on the medial preopercular ridge (five in all specimens >5.5 mm SL), three small opercular spines and several small larval teeth on the premaxilla in specimens <9.7 mm SL; there are no spines on the lateral ridge of the preopercle or on any other bones of the head.

Discussion

Morphological Comparisons of Epinepheline Larvae.—With the descriptions of larval diploprionins, larvae of at least some genera of each epinepheline tribe are known. Below, we briefly summarize and compare the morphologies of known larvae of all epinepheline tribes. The comparative information presented here is intended primarily to make it easier for others to identify larval epinephelines; additionally, this information is being incorporated in a phylogenetic analysis of the subfamily based on characters of adults and larvae. A summary of morphological variation in salient features among epinepheline larvae is given in Table 4.

Niphonini. Larval *Niphon* (Fig. 9A) is separable from larvae of all other epinephelines on the basis of a stout but smooth elongate third dorsal spine. Additionally, *Niphon* has a moderately produced pelvic-fin spine, a single supraorbital spine, prominent but smooth preopercular spines, including an enlarged spine at the angle, and small spines on the posttemporal and supracleithrum. Pigment is limited to a patch of melanophores at the posterior base of the anal fin, several melanophores on the frontals in postflexion specimens, two vertical bars of pigment on the proximal base of the caudal fin and a dense cap of melanophores covering the swimbladder and posterior portion of the gut.

Epinephelini. Epinephelin larvae (e.g., *Paranthias furcifer,* Fig. 9B) can be distinguished from known larvae of other serranids by the extremely elongate, strongly serrate second dorsal- and pelvic-fin spines that give these larvae a kite-shaped appearance. *Gonioplectrus* has a much deeper body than other epinephelins (Table 4) and also has elongate, stout, serrate third dorsal- and second anal-fin spines (Kendall and Fahay, 1979). Head spination of epinephelins comprises one to several supraorbital spines or a low serrate supraorbital ridge, well developed preopercular spines (spine at angle enlarged and serrate), sometimes small spines on the interopercle and subopercle and small serrate spines on the posttemporal and supracleithrum. Tail pigment generally is limited to melanophores at the ventral midline or midbody laterally. The pelvic and caudal fins may have one to several melanophores, the sheath surrounding the elongate second dorsal-fin spine in preflexion larvae usually has melanophores distally, postflexion larvae have several melanophores on the frontals and there is a dense dorsal cap of melanophores on the posterior portion of the gut and swimbladder.
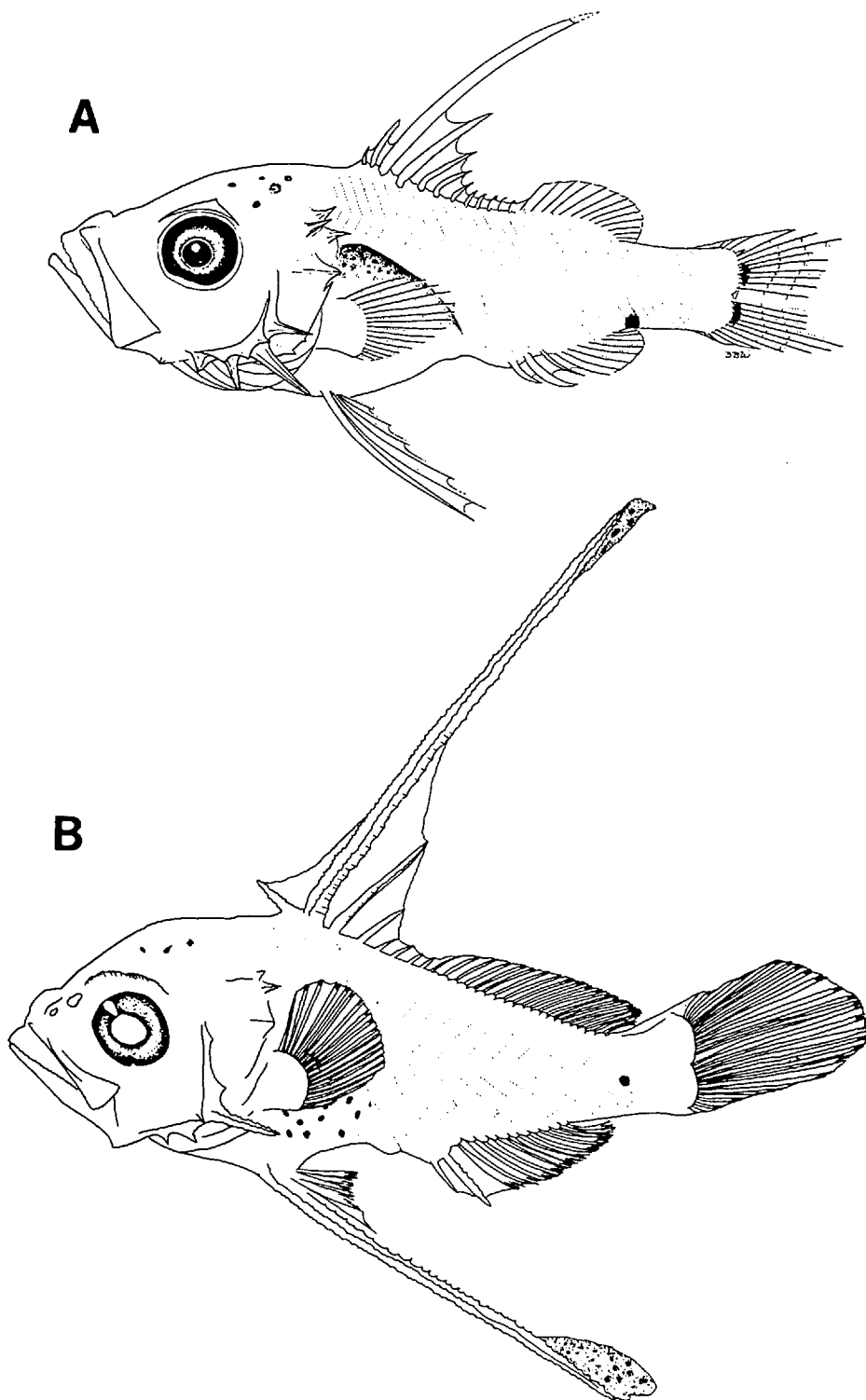
Figure 9.   A) Larva of *Niphon spinosus*, 7.0 mm SL (from Johnson, 1988); B) Larva of *Paranthias-furcifer*, 8.6 mm (from Kendall, 1979).

DIPLOPRIONINI. *Diploprion* differs from *Niphon* and most epinephelins in having a deeper body after flexion, but most notably in the absence of stout, pungent anterior dorsal-fin spines. As noted in the preceding description of larval *Diploprion*, the second and third dorsal-fin spines are thin, flexible, encased in pigmented sheaths and extend to lengths many times that of the body. Head spination is limited to small spines on the supraorbital, preopercle and posttemporal, and pigment is distinctive.

Belonoperca resembles *Diploprion* in lacking stout fin spines and having a large pectoral fin, but differs in having more prominent head spines. *Belonoperca* can be distinguished from known larvae of other serranids by the presence of five elongate dorsal-fin spines (second through sixth) that are thin, flexible and encased in fleshy sheaths. As noted, maximum lengths of the elongate spines in *Belonoperca* are unknown.

The posteriormost dorsal spine develops initially as a soft ray in *Belonoperca*. Johnson (1988) and Leis (1986) noted that only those epinephelines with more than eight dorsal spines exhibit indirect development of posterior spines. Thus, *Niphon* (13 dorsal spines), some epinephelins (5–12) and *Belonoperca* (9) have 1 or more posterior dorsal spines that initially develop as soft rays, whereas known larvae of all other epinephelines (8 or fewer) do not. Larvae of *Aulacocephalus* (nine) are undescribed, but we predict that the posteriormost dorsal spine develops indirectly.

LIOPROPOMINI. *Liopropoma* (Plate 1B) is more slender than epinephelins and diploprionins, but shares with *Diploprion* the presence of thin, flexible, extremely elongate second and third dorsal-fin spines encased in fleshy sheaths. The sheath of the second dorsal spine has several swellings distally, but the morphology (e.g., leaf-shaped, oblong) and number of these swellings varies considerably and may be species- or species-group specific; however, fin-ray counts vary little within the genus, and specific identification of the larvae will be difficult.The pectoral fin is not large or pigmented. The pelvic fin is small and is the last fin to complete development; this condition differs from that of *Niphon*, epinephelins and *Diploprion*, in which the pelvic fin is the first, or one of the first, fins to complete development. Head spination is poorly developed in *Liopropoma*; several small spines are present on the lateral and medial ridges of the preopercle, and there is one minute spine on both the subopercle and interopercle. Pigment on the trunk and tail generally is absent, but several melanophores are present on the frontal bones.

GRAMMISTINI. *Grammistes* shares with *Diploprion*, *Belonoperca* and *Liopropoma* the absence of stout spines in the fins, and the second, but not the third dorsal spine is elongate and encased in a filamentous sheath. As noted above, the elongate spine is broken in all specimens, so we were unable to establish its maximum length. The pectoral fin is large and pigmented, and, as in *Liopropoma*, the pelvic fin develops last. Five prominent spines are present on the medial ridge of the preopercle, but no other head spines are evident. Pigment is present on the pectoral fin, pelvic fin in some postflexion larvae and sheath surrounding the elongate dorsal spine, but appears to be absent on the trunk, tail and head.

Rypticus (Fig. 10A) has a produced dorsal spine that is very similar to that of *Grammistes* except that the first spine is the modified element in *Rypticus*. The first dorsal-fin pterygiophore in *Rypticus* lacks supernumerary spines; thus, the first dorsal spine is serially associated with the first pterygiophore and homologous to the second dorsal spine of *Grammistes*, which has the first spine in supernumerary association with the first pterygiophore. The pectoral fin completes development before all other fins and is quite large and pigmented. The pelvic fin
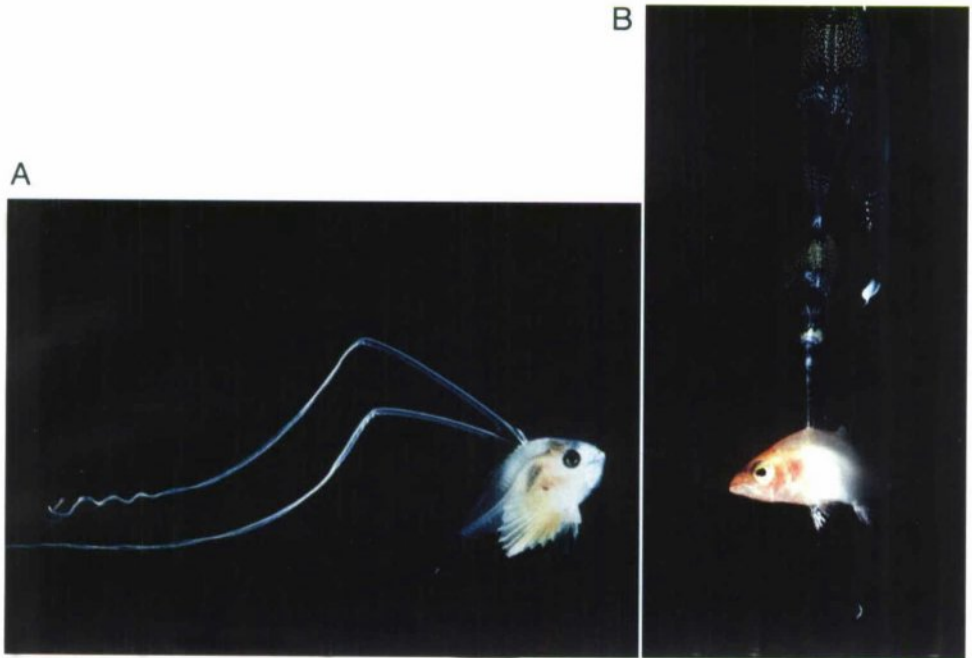
Plate 1.   A) In vivo photograph of larval *Diploprion bifasciatum*; B) In situ photograph of larval *Liopropoma* (photographs by G. R. Harbison).

is last to form. Head spination and pigmentation are similar to that of *Grammistes*, except that *Rypticus* has three (vs. five) spines on the medial preopercular ridge.

   Pseudogramma (Fig. 10B) has a pronounced second dorsal-fin spine. The elongate spine has been called the first by some authors, but the first (supernumerary) spine actually is exceedingly small and thus easily overlooked. As in *Grammistes* and *Rypticus* the pectoral fin is large and precocious, the pelvic fin is the last fin to complete development, the medial preopercular ridge bears five spines and external pigment is limited to the pectoral fin and sheath surrounding the elongate dorsal spine.

   Aporops (Fig. 10C) is very similar morphologically to *Pseudogramma*. Fourmanoir's (1976) illustration of the anterior portion of a larval *Aporops* shows the elongate body and tiny first dorsal-fin spine, thin, elongate second dorsal spine, moderately large pectoral fin, incompletely formed pelvic fin and five spines on the preopercle.

   Function of Elongate Fin Spines. — The functional significance of elongate dorsal-fin spines in larval epinephelines is unknown. It seems likely that the robust, pungent spines of the Niphonini and Epinephelini function to discourage potential predators, but the thin, flexible, filamentous spines of the other tribes may have different functions. In some ways, they resemble the elongate dorsal appendage (vexillum) of carapids. Govoni et al. (1984) analyzed in detail the vexillar structure and were unable to determine its explicit function. They suggested that it may
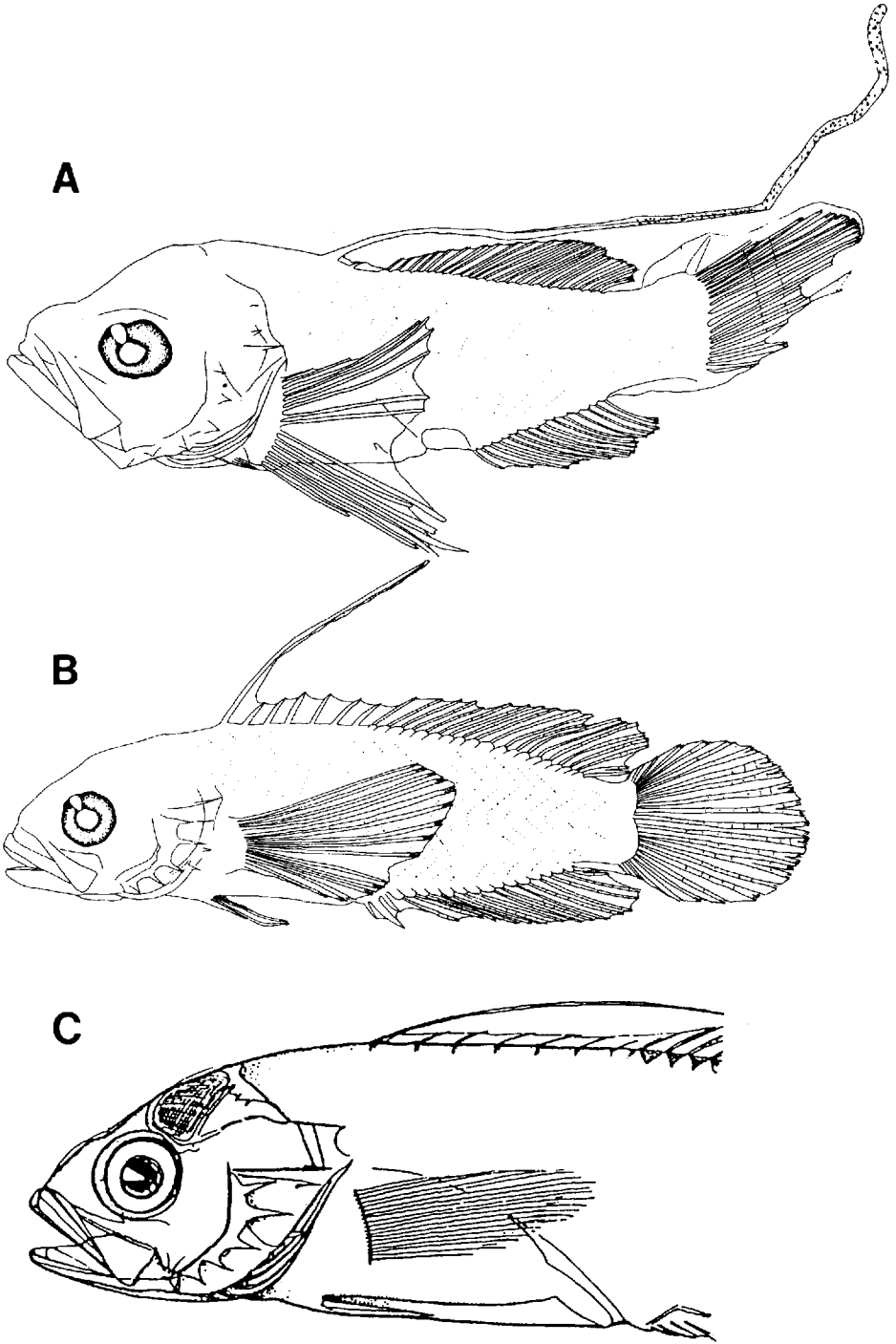
Figure 10.   A) Larva of *Rypticus* sp., 6.6 mm SL (from Kendall, 1979); B) Larva of *Pseudogramma gregoryi,* 10.2 mm SL (from Kendall, 1979); C) Anterior portion of larva of *Aporops* sp., 12 mm (from Fourmanoir, 1976).

have multiple functions, including predator deception (because the vexillum is pigmented and adorned with fleshy tabs), sensation (because it is innervated, although they found no free neuromasts, chemoreceptors or free nerve endings) and hydrodynamic effects (because of in situ observations of vexillar movement and the increased surface area it affords the larva). We have not examined the elongate filaments of epinephelines histologically, but it would be interesting to compare the microstructures of these appendages to the carapid vexillum. Below, we review some of the possible functions of the spectacularly elongate dorsal spines of larval epinephelines.

The elongate filaments certainly have a hydrodynamic effect when the larva is swimming because they increase the total surface area and, thus, the overall drag of the larva considerably, but whether this is a primary function or a necessary artifact is unknown. Hubbs and Chu (1934) noted that elongate rays in postlarval *Diploprion* and other fishes "no doubt" function in flotation; however, the use of the filaments as a flotation device in *Diploprion* seems unlikely because the presence of a swimbladder in early preflexion larvae suggests that neutral buoyancy is not a problem. A possible sensory function cannot be adequately evaluated without detailed examination of the filaments for nerves and sensory structures, but we note that the filaments of *Diploprion* and *Liopropoma* (Kotthaus, 1970) appear to be hollow except for the encased spine. The elongate filaments could play a role in energy storage by providing space for the assimilation of excess food; however, long, trailing filaments seem an unlikely place for energy storage because they probably are quite vunerable to predation. In fact, pigmented swellings or other variations in the shape of the filaments could attract predators, distracting them from the body of the larva (Govoni et al., 1984); swellings, when present, mostly occur on the distal portions of the filaments. The elongate filaments also might function in predator deception by increasing the apparent size of the larva (Moser, 1981), but the robust, elongate spines of *Niphon* and epinephelins would seem more effective in such deception. Presence in larvae of the skin toxin grammistin, a noxious chemical known to occur in adults of diploprionins and some grammistins, has not been documented. If grammistin is present in larvae, the filaments could play a role in predator deterrence by storing grammistin. However, the absence of grammistin in adult *Liopropoma*, which has elaborately ornamented dorsal filaments as a larva, sheds doubt on this possibility. Finally, it has been suggested that elongate rays of several disparate taxa (e.g., *Zu cristatus, Liopropoma, Arnoglossus, Cynoglossus*) may mimic siphonophore tentacles (Govoni et al., 1984). Potential predators might avoid prey resembling siphonophores. Alternatively, siphonophore mimicry may be an adaptation to attract food items. Tim Targett (pers. comm.) observed behavior of a living larva of *Liopropoma* in a bucket aboard a research vessel, and noted that zooplankton appeared to be attracted to the elongate filaments, which the larva kept suspended above its head. Harbison et al. (1977) found that species of five families of hyperiid amphipods associate with gelatinous zooplankton in relationships ranging from commensalism to obligate parasitism. Attracting prey by luring this fauna away from siphonophores, therefore, could be a primary function of elongate filaments in epinephelines. A thorough analysis of gut contents of larvae is beyond the scope of this study, but our examination of stomach contents of several larval *Liopropoma* revealed only remains of calanoid copepods.

In summary, the adaptive significance of the elongate, filamentous dorsal spines of epinephelines is unknown, but the advantages these filaments convey to the larvae must outweigh the disadvantages, particularly the high cost, in terms of energy expenditure, of dragging the filaments through the water. Further study of

the elongate filaments, including *in situ* observations and laboratory experiments, are necessary before a plausible functional explanation can be hypothesized.

ACKNOWLEDGMENTS

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