

# *Belonoperca pylei*, a new species of seabass (Teleostei: Serranidae: Epinephelinae: Diploprionini) from the Cook Islands with comments on relationships among diploprionins

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**Abstract** *Belonoperca pylei* is described from five specimens collected at depths of 68–122 m from Rarotonga, Cook Islands. It differs from all other known diploprionin serranids in having IX, 10 dorsal-fin rays, III, 7 anal-fin rays, and a color pattern composed primarily of yellow and orange pigments. Cladistic analysis of epinepheline morphology supports monophyly of the diploprionin genera *Belonoperca* and *Diploprion* and suggests that *Belonoperca* is the sister group of *Diploprion* plus the monotypic *Aulacocephalus*.

**Key words.** — Serranidae; *Belonoperca*; Cook Islands; phylogeny; larval morphology.

Diploprionin serranids comprise a small group of Indo-Pacific shorefishes known for their ability to secrete a neurotoxin from special cells in the epidermis (Randall et al., 1971, 1980). Diploprionins are members of the subfamily Epinephelinae, a large and diverse group of seabasses recognized as monophyletic by Johnson (1983) based on absence of an autogenous distal radial on the first dorsal-fin pterygiophore and elongation of the spine serially associated with this pterygiophore in larvae. Baldwin and Johnson (1993) provided cladistic evidence that the subfamily Epinephelinae comprises five monophyletic tribes (Niphonini, Epinephelini, Diploprionini, Liopropomini, and Grammistini) and presented a partially resolved generic phylogeny of the subfamily. Relationships within the Diploprionini (as well as the speciose Epinephelini) are unresolved.

Recently, five specimens of an undescribed epinepheline serranid were collected from Rarotonga, Cook Islands, by Richard L. Pyle (Bernice P. Bishop Museum) and Charles J. Boyle (Cook Islands Aquarium Fish, Rarotonga) who are employing new diving technology to explore deep-reef areas inaccessible with conventional SCUBA (Pyle, 1996). The new species has several features considered diagnostic for the Diploprionini by Baldwin and Johnson (1993), including rugosity on the neurocranium and circumor-

bitals, small ridges of tissue on the bases of the dorsal and anal fins, and ctenoid scales in which a bar from the first circulus projects posteriorly along the midline (see also McCully, 1961; Johnson, 1983). Comparisons of the new species with other diploprionins (*Aulacocephalus temmincki*, *Belonoperca chabanaudi*, *Diploprion bifasciatum*, and *Diploprion drachi*) suggest that it represents the second known species of *Belonoperca*. Fowler and Bean (1930) described *B. chabanaudi* from two specimens, one from the Celebes (now Sulawesi) and the other from Borneo. *Belonoperca* was redescribed by Randall et al. (1980) when the identification in *B. chabanaudi* of epidermal cells containing the skin toxin “grammistin” led to its placement in the family Grammistidae. As shown by Johnson (1983) and Baldwin and Johnson (1993), “grammistids” are epinepheline serranids, and *Belonoperca* is a member of the epinepheline tribe Diploprionini. Presence of grammistin confined to epidermal cells is a diagnostic feature of diploprionins; other “soapfishes” (*Grammistes*, *Grammistops*, *Pogonoperca*, and *Rypticus*) have epidermal toxin cells and large dermal toxin glands and are basal members of the epinepheline tribe Grammistini (Randall et al., 1971; Baldwin and Johnson, 1993).

The objectives of this paper are to describe the new species of *Belonoperca*, distinguish it from *Belono-*

*perca chabanaudi*, and comment on relationships within the Diploprionini. Additionally, we describe the morphology of a larval *Belonoperca* from the Philippine Sea that may be an additional specimen of *B. pylei*.

## Materials and Methods

Institutional abbreviations are as listed in Leviton et al. (1985) except "KPM," which refers to the Kanagawa Prefectural Museum of Natural History, Japan. Counts and measurements follow Anderson and Heemstra (1980). All measurements were made with vernier calipers to the nearest tenth of a millimeter. Vertebral and other skeletal counts were made from radiographs or cleared and stained specimens. Drawings were made with the aid of a camera lucida. Scale bars in all figures represent 1 mm.

Characters used in investigating phylogenetic relationships within the Diploprionini were polarized with the Liopropomini and Grammistini as the first outgroup and the Epinephelini as the second, following the proposed phylogeny of epinepheline tribes of Baldwin and Johnson (1993): (in phyletic sequence) Niphonini, Epinephelini, Diploprionini, Liopropomini, Grammistini. Members of the subfamily Epinephelinae are referred to in the text as "epinephelines," those of the tribe Epinephelini as "epinephelins."

Comparative serranid material examined in the investigation of relationships included the following ("cs" indicates a cleared and stained specimen, "r" indicates a radiograph): *Anyperodon leucogrammicus*, USNM 218817, 1 specimen, cs. *Aporops bilinearis*, USNM 338449, 1, cs. *Aulacocephalus temmincki*, AMS I.23362-001, 1; KPM NI-001051, 1; MCZ 5959, 1, (dorsal gill arches cs); 5987, 1, r; USNM 64640, 1, cs, r; 71332, 1, r; 57754, 1, r. *Belonoperca chabanaudi*, USNM 89982, 1, holotype, r; 93363, 1, paratype, r; 217873, 1, cs; 345767, 2; 230435, 1; 259803, 1. *Centropristis striata*, USNM 317539, 1, cs. *Cephalopholis fulva*, USNM 269803, 1, cs. *Diploprion bifasciatum*, USNM 218889, 1, cs; 228044, 1; 183096, 3. *Diploprion drachi*, USNM 345948, 1, cs; 205489, 1, r. *Grammistops ocellatus*, USNM 218873, 1, cs. *Liopropoma susumi*, USNM 218726, 1, cs; 334292, 3. *Niphon spinosus*, USNM 296642, 1, cs. *Pikea mexicana*, no data, 1, cs. *Plectropomus maculatus*, USNM 218818, 1, cs; 174285, 1. *Pseudogramma gregoryi*, USNM 327571, 1, cs. *Rainfordia opercularis*, USNM 203247, 1, cs. *Trachypoma macracanthas*, NMNZ P. 5559, 1, cs.

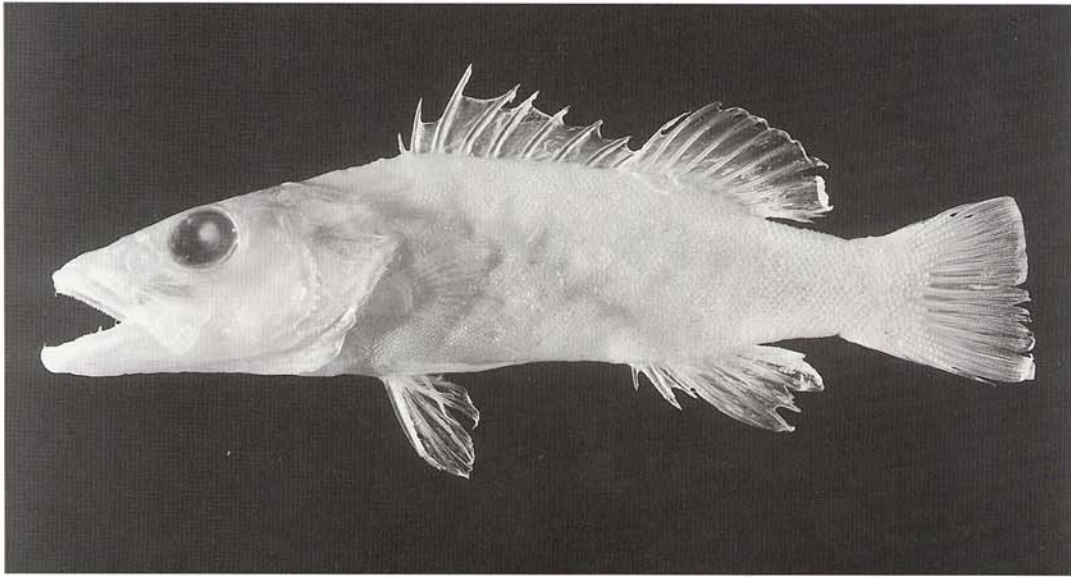
## *Belonoperca pylei*, sp. nov. (Figs. 1–3; Table 1)

**Holotype.** BPBM 37615, 68.0 mm SL, Cook Islands, Rarotonga, 85–122 m, quinaldine and hand net, R. L. Pyle and C. J. Boyle, 1989–1991.

**Paratypes.** USNM 345768, 55.6 mm SL, Cook Islands, Rarotonga, 85–122 m, quinaldine and hand net, R. L. Pyle and C. J. Boyle, 1989–1991; USNM 345848, 61.9 mm SL, cleared and stained specimen, Cook Islands, Rarotonga, 122 m, quinaldine and hand net, R. L. Pyle, February 1994; BMNH 1997.10.22.2, 52.9 mm SL, Cook Islands, Rarotonga, 85–122 m, quinaldine and hand net, R. L. Pyle and C. J. Boyle, 1989–1991; BPBM 37426, 51.9 mm SL, Cook Islands, Rarotonga, 68 m, quinaldine and hand net, R. L. Pyle, 26 December 1989.

**Diagnosis.** A species of *Belonoperca* distinguishable from all other diploprionins by the presence of IX,10 dorsal-fin rays, III,7 anal-fin rays, and a unique color pattern characterized most prominently by yellow and orange pigments. Also useful in distinguishing *B. pylei* is the following combination of characters: head pointed, snout long; lower jaw slightly projecting; upper and lower jaws with canine teeth; vertebrae 10+14; pseudobranchial filaments 14–18; procurent caudal-fin rays 9–10+8–9; trisegmental anal-fin pterygiophores 4–5; epineurals 9–10; body depth 21–26% SL; first dorsal spine length 3.1–4.0% SL; caudal-peduncle depth 9.8–12% SL.

**Description.** Counts and proportional measurements of holotype, followed parenthetically by extremes for the species if the value for any paratype is different from that of holotype. Dorsal-fin rays IX,10; anal-fin rays III,7; principal caudal-fin rays 9+8, upper and lower unbranched; upper procurent caudal-fin rays 9 (9–10), none segmented; lower procurent caudal-fin rays 8 (8–9), none segmented; pectoral-fin rays 14; pelvic-fin rays I, 5; tubed lateral-line scales 74 (71–76); diagonal scale rows ca. 95 (84–97), scale rows difficult to count because thick skin obscures them in certain areas, especially on nape, bases of dorsal and anal fins, cheek, and abdomen; scale rows from dorsal-fin origin to lateral line 9 (9–11); scales above lateral line to middle of spinous dorsal fin 6 (5–6); scale rows from anal-fin origin to lateral line 38 (37–43); circumpeduncular scales 49 (48–50); gill rakers, including rudiments, on first gill arch 7+14 (6–7+13–14), total 21 (20–21); pseudobranchial filaments 16 (14–18); branchiostegal rays 7; vertebrae 10+14; formula for configuration of supra-neural (predorsal) bones, anterior neural spines, and anterior dorsal pterygiophores 0/0/1/1+1/1/ (following symbolization of Ahlstrom et al., 1976); trisegmental dorsal-fin pterygiophores 6 (6–8); trisegmental



**Fig. 1.** *Belonoperca pylei*, new species, holotype, BPBM 37615, 68.0 mm SL, Rarotonga, Cook Islands. Photograph by Carl Hansen, USNM.



**Fig. 2.** *Belonoperca pylei*, paratype, USNM 345848, 61.9 mm SL. Aquarium photograph by R. L. Pyle, BPBM.

tal anal-fin pterygiophores 4 (4–5); epineural bones 9 (9–10); pleural ribs on vertebrae 3 through 10; epurals 2 (2–3).

Body moderately elongate, depth 3.9 (3.9–4.7) in SL, and compressed, width 2.7 (2.1–2.7) in depth; head length 2.4 in SL; snout pointed and elongate, length 2.9 (2.9–3.4) in HL; orbit diameter 5.6 (4.0–

5.6) in HL; interorbital space flat, the least width 7.5 (6.7–8.3) in HL; caudal peduncle long, 2.4 (2.0–2.5) in HL; caudal peduncle depth 3.7 (3.6–4.2) in HL, 1.6 (1.4–2.0) in caudal-peduncle length.

Mouth large, lower jaw projecting slightly beyond upper jaw; maxilla reaching posteriorly to vertical through posterior 1/4 of eye, length 2.3 (2.0–2.3) in



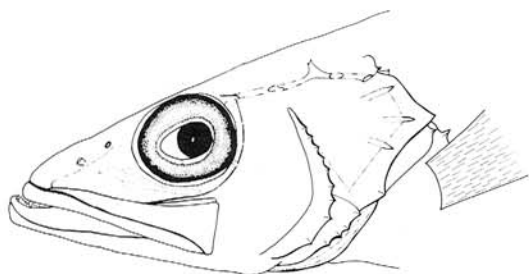


Fig. 3. *Belonoperca pylei*, paratype, USNM 345768, 55.6 mm SL. Left lateral view of head. The numerous tiny head scales not illustrated—see text for description.

HL; posterodorsal edge of maxilla not covered by elements of circumorbital series when mouth closed; supramaxilla well developed, length between 1/3 and 1/2 length of maxilla; depth of maxilla (including supramaxilla) 6.9 (6.2–6.9) in HL; premaxilla with band of small slightly to greatly recurved conical teeth comprising about 5 rows anteriorly, narrowing to 1–2 rows posteriorly; inner teeth and several along anterior part of outer row longer; 1 (0–2) enlarged canine tooth at most anterolateral point of upper jaw on left side, 2 (1–2) adjacent enlarged canine teeth on right, (note: medial tooth of enlarged pair on right side of holotype now broken); dentary with 4–5 rows of small, slightly to strongly recurved conical teeth

Table 1. Measurements (in mm) of type specimens of the nominal species of *Belonoperca*

Species	<i>B. pylei</i>					<i>B. chabanaudi</i>	
	Holotype BPBM 37615	Paratype USNM 345768	Paratype BMNH 1997.10.22.2	Paratype BPBM 37426	Paratype USNM 345848*	Holotype USNM 89982	Paratype USNM 93363
Standard length	68.0	55.6	52.9	51.9	61.9	117.3	118.2
Head length	28.4	22.9	21.6	21.7	25.7	45.2	44.1
Snout length	9.8	7.5	6.5	6.3	9.0	14.9	14.2
Orbit diameter	5.1	4.9	5.2	5.5	5.1	8.7	8.9
Postorbital length of head	13.4	11.1	9.9	10.0	11.4	21.4	21.1
Upper jaw length	12.5	11.0	10.7	10.2	12.3	21.4	20.3
Maxilla width	4.1	3.7	3.4	3.3	3.8	7.5	7.0
Interorbital width	3.8	3.4	3.1	2.9	3.1	9.2	9.2
Body depth	17.4	13.7	11.9	11.0	15.6	33.6	32.8
Body width	6.5	6.1	5.5	5.3	6.4	14.4	13.6
Predorsal length	29.2	24.5	23.3	24.1	23.5	50.1	49.7
Preanal length	47.3	38.6	36.8	37.0	43.2	83.1	80.3
Caudal peduncle length	11.9	10.8	10.6	9.7	10.4	27.1	26.6
Caudal peduncle depth	7.7	6.2	5.2	6.0	7.2	19.1	17.3
Pectoral fin length	8.9	7.8	7.1	7.9	9.5	18.0	16.6
Pelvic fin length	11.4	9.1	7.9	9.7	9.6	22.6	21.4
Anal fin base length	9.6	7.6	7.4	8.4	9.1	13.9	13.7
Upper caudal-fin lobe length	14.1	10.9	11.0	8.2	12.6	29.5	27.1
Lower caudal-fin lobe length	13.2	12.7	10.9	7.8	12.2	25.2	Damaged
First dorsal spine length	2.6	2.0	2.1	1.6	2.0	6.2	6.9
Longest dorsal spine length	8.6 (3rd)	6.3 (3rd)	7.9 (3rd)	5.7 (3rd)	6.8 (3rd)	13.2 (4th)	15.1 (4th)
Penultimate dor. spine length	5.0	3.8	3.8	3.2	5.1	1.5	1.7
Last dorsal spine length	3.6	3.1	2.9	2.9	4.8	4.9	6.0
First dorsal ray length	6.6	6.0	6.0	6.2	6.9	15.3	14.7
Longest dorsal ray length	8.8 (2nd)	6.5 (2nd)	6.7 (3rd)	6.7 (2nd)	8.3 (2nd)	16.9 (2nd)	17.2 (2nd)
First anal spine length	2.5	1.9	2.3	1.7	2.1	2.6	2.8
Second anal spine length	5.3	3.7	4.0	3.9	4.0	8.9	8.9
Third anal spine length	4.7	3.7	4.0	4.0	3.9	N/A	N/A
Longest anal ray length	8.5 (2nd)	7.5 (2nd)	7.3 (2nd)	7.8 (2nd)	8.7 (2nd)	15.3 (2nd)	17.9 (2nd)
Pelvic spine length	11.4	9.1	7.9	9.7	9.6	22.6	21.4

\* Measurements recorded prior to clearing and staining specimen.

anteriorly and 2 rows posteriorly, some anterior teeth noticeably longer than posterior teeth; 1 (1–2) slightly enlarged canine tooth at anterolateral corner of lower jaw on each side; 1 (1–3) enlarged canine tooth at about mid-length of dentary on left side, and 2 (0–3) closely-set enlarged canine teeth on right; vomer with chevron-shaped patch of conical teeth with about 3 rows, teeth in posteriormost row largest; palatine with long band of small teeth, 1 or 2 rows anteriorly, narrowing to 1 row posteriorly; tongue long, reaching in front of vomer, slender and toothless.

Anterior nostril in short tube, centrally situated between proximal tip of maxilla and anterior edge of orbit; posterior nostril a small circular opening about midway between anterior nostril and anterior edge of orbit. Pupil egg-shaped, the narrower end directed anteriorly.

Opercle with 3 flat spines, middle spine longest and slightly closer to lower spine than upper; posterior margin of preopercle with 12 (9–12) serrae on left side, 9 (8–10) on right; subopercle with 2 (1–2) spines on left side, 1 (1–2) on right; interopercle with 5 (4–5) serrae on each side; small area of posterior margin of both cleithrum and postcleithrum exposed just above pectoral base, cleithrum with 2 (1–2) small spines on exposed area, postcleithrum with 1 posterodorsally directed spine.

Lateral line complete, running parallel to dorsal body contour to about sixth dorsal spine and then sloping down towards mid-lateral axis of body; lateral line ending at center of hypural margin and followed posteriorly by 3 (3–5) untubed scales on caudal-fin base; most scales on head and body small and ctenoid; pectoral fin and abdomen bearing some scales that lack cteni; head scaleless except for cheeks, operculum, and posttemporal region of neurocranium; scales on operculum larger than scales on cheek; scales on outer principal caudal rays at least reaching a point one third length of rays, terminating on proximal bases of central rays; pectoral, pelvic, dorsal, and anal fins naked.

Certain areas of body covered by layer of thick skin that is whitish in preservative and especially dense on nape, bases of dorsal and anal fins, cheek, and abdomen. A piece of skin dissected from near base of anal fin, histologically sectioned and stained with hematoxylin-eosin, containing darkly stained cells in epidermis similar to the Type 2 toxin cells described by Randall et al. (1971, 1980) in *Diploprion*, *Aulacocephalus*, and *B. chabanaudi*. No cells in sections of skin exhibiting positive reaction with Sudan Black B, a stain useful in identifying Type 1 epidermal toxin cells of *B. chabanaudi* (Randall et al.,

1980) and epidermal toxin cells and dermal toxin glands in true soapfishes (e.g., Randall et al., 1971; Baldwin and Johnson, 1993). Skin of fresh specimen of *B. pylei* tasting bitter when licked (J. E. Randall and R. L. Pyle, pers. comm., 7 January 1998), corroborating the presence of an epidermal toxin.

Origin of dorsal fin above eighth (seventh-eighth) lateral-line scale; first dorsal spine about half the length of second spine; third dorsal spine usually longest, 3.3 (2.7–3.8) in HL; dorsal fin strongly notched, last dorsal spine 7.9 (5.4–7.9) in HL, first dorsal soft ray 4.3 (3.5–4.3) in HL; soft dorsal and anal rays branched; origin of anal fin at vertical through base of second dorsal soft ray; first anal spine nearly half (nearly half to slightly more than half) the length of second anal spine; second anal spine slightly longer than third (slightly shorter to slightly longer), length of second spine 5.4 (5.4–6.4) in HL; caudal fin emarginate; pectoral fin rounded, the longest ray 3.2 (2.7–3.2) in HL, two uppermost and two lowermost rays unbranched; origin of pelvic fin below upper base of pectoral fin; pelvic fin reaching posteriorly to vertical through base of fifth or sixth dorsal spine, longest ray 2.5 (2.2–2.7) in HL.

Description of color based on transparencies of three specimens maintained in an aquarium after capture until death (R. L. Pyle, pers. comm.): a ca. 25-mm juvenile (subsequently eaten by a larger specimen of *B. pylei*), a 51.9 mm subadult (BPBM 37426) and a 61.9 mm adult (USNM 345848, Fig. 2)—categorization of specimens into life-history stages based on size and differences in color pattern, not maturity. In general, changes in coloration involving loss of yellow coloration on trunk of juvenile and appearance of pink-orange spots (few in number and large initially, more numerous and smaller in largest specimen); head remaining primarily yellow throughout development. Juvenile almost entirely yellow, slightly rosy posteriorly and on operculum; thin white stripe extending midlaterally from caudal peduncle to posterior edge of operculum; each dorsal spine yellow, membrane between spines unpigmented. Subadult with yellow head except cheek and most of opercle rosy (tips of opercular spines yellow); dorsally, yellow continuing from head posteriorly along base of spinous dorsal fin; ventrally, the brilliant yellow of head becoming paler beneath posterior part of eye, continuing as pale yellow/tan stripe (about 1/2 eye diameter in height) to about middle of anal fin; between yellow above and tan below, lateral aspect of trunk with three roughly horizontal rows of orange spots, ranging in size from about size of pupil to only slightly smaller than orbit; spots separated from one

another by network of white pigment; soft dorsal and anal fins pale yellow; dorsal-fin spines yellow; pale orange streak along pelvic-fin spine, yellow at base of spine; central caudal rays white at base, outer principal rays orange; procurrent rays orange to pale orange. Adult similar to subadult except tips of upper and lower jaws slightly rosy; trunk with about 4–5, and caudal peduncle with about 3, roughly horizontal rows of spots each about the size of the pupil, dorsal and ventralmost spots yellow-orange, midlateral ones more rosy, background rosy white; first and second dorsal spines yellowish, other dorsal spines rosy; anal-fin spines and pelvic-fin spine with streak of pale pink-orange.

*Color of holotype in alcohol.* — Pale yellow with numerous tiny melanophores on tips of upper and lower jaws, snout, frontals, nape to near origin of dorsal fin, dorsal part of cheek, and opercle; pigment heaviest on opercle, where melanophores concentrated around bases and along proximal lengths of the three spines. Trunk and fins without melanophores. All paratypes with tiny melanophores on head similar to those of holotype, but without heavy concentration on opercle. The smallest specimen, BPBM 37426, also with dots on anterior and ventral edges of lacrimal, with scattered dots on dorsal part of trunk (heaviest anteriorly, from origin of dorsal fin to beneath pectoral-fin base), and with several spots on

membrane of fourth dorsal spine (near midpoint of the length of the spine, in a vertical row along its posterior border).

**Distribution.** *Belonoperca pylei* has been taken by divers only from the type locality of Rarotonga, Cook Islands. An undescribed larval *Belonoperca* with counts matching those of *B. pylei* (see “Larval Morphology” below) was collected in the Philippine Sea.

**Etymology.** We take pleasure in naming this new species for Richard L. Pyle, whose diving explorations of deep-reef areas have led to the discovery of many new species of marine life, including the new serranid described herein.

**Comparisons.** Measurements of all type specimens of *Belonoperca pylei* and *B. chabanaudi* are provided in Table 1, and characters useful in separating the two species are summarized in Table 2. *Belonoperca pylei* and *B. chabanaudi* have 9 dorsal-fin spines (rarely 10 in *B. chabanaudi*—Randall et al., 1980) and 10 dorsal-fin soft rays, but they differ in the configuration of the dorsal fin (Fig. 4). The penultimate dorsal-fin spine is slightly longer than the last dorsal spine in *B. pylei* (6.2–8.2% SL vs. 5.3–7.8% SL, respectively), whereas the penultimate spine is

**Table 2.** Characters useful in separating *Belonoperca chabanaudi* and *B. pylei* (data for *B. chabanaudi* are from this study and Randall et al. [1980])

Species (SL in mm)	<i>B. chabanaudi</i> (49.2–118.2)	<i>B. pylei</i> (51.9–68.0)
Counts		
Dorsal-fin rays	VIII (rarely IX), I–10	IX, 10
Anal-fin rays	II, 8	III, 7
Pseudobranchial filaments	18–21	14–18
Procurrent caudal rays	8–9+7–8	9–10+8–9
Anal-fin trisegmental pterygiophores	6	4–5
Epineurals	8	9–10
Measurements (%SL)		
Body depth	28–29	21–26
Interorbital width	7.8–8.5	5.0–6.1
Caudal-peduncle depth	15–16	9.8–12
1st anal spine length	2.2–3.0	3.3–4.3
1st dorsal spine length	5.3–6.7	3.1–4.0
Penultimate dorsal spine length	1.2–1.4	6.2–8.2
Last dorsal spine length	4.2–7.5	5.3–7.8
1st dorsal ray length	12–15	9.7–12
Preserved coloration	Dark brown	Pale yellow
Canine teeth	Absent	Present
Posterior border of maxilla	Concave in large specimens	Not concave

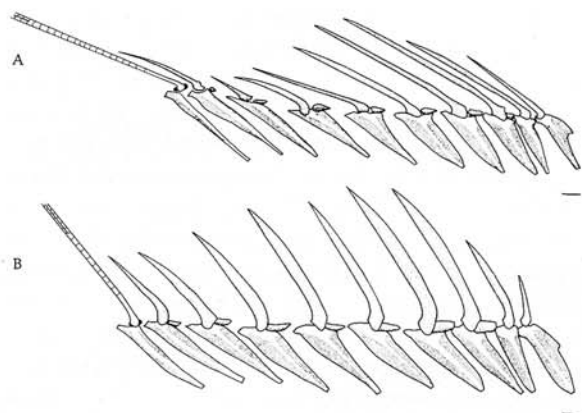


Fig. 4. Spinous dorsal fin, right lateral view. A) *Belonoperca chabanaudi*, USNM 217873, 67.5 mm SL; B) *B. pylei*, USNM 345848, 61.9 mm SL.

considerably shorter than the ultimate spine in *B. chabanaudi* (1.2–1.4% SL vs. 4.2–7.5% SL). This short penultimate spine in *B. chabanaudi* creates a deep indentation in the outline of the dorsal fin between the preceding spines and the rest of the fin, which comprises the last spine and the soft rays; the dorsal-fin count for *B. chabanaudi* is thus customarily expressed as VIII-I,10 (rarely IX-I,10—Randall et al., 1980). In *B. pylei*, the dorsal fin is continuous, and the last spine is clearly part of the spinous dorsal fin (IX,10). Other diploprionins have more dorsal-fin rays than either species of *Belonoperca* (IX,12 in

*Aulacocephalus*, usually VIII or IX,15 in *Diploprion*).

Another feature useful in separating *B. pylei* and *B. chabanaudi* is number of anal-fin spines. *Belonoperca pylei* has three anal-fin spines (III,7), whereas *B. chabanaudi* has two (II,8). Other diploprionins have more anal-fin elements than *Belonoperca* (III,9 in *Aulacocephalus*, II,12 in *Diploprion*). *Belonoperca pylei* and *B. chabanaudi* also differ slightly in several other meristic and morphometric features (Table 2), as well as in the presence of canine teeth in *B. pylei* (canine teeth lacking in *B. chabanaudi*).

Living and preserved color are strikingly different in the two species: *B. pylei* is pale yellow in preservative, yellow and reddish in life; *B. chabanaudi* is dark brown in preservative and dark blue or black in life, with a large yellow blotch behind the dorsal fin (Randall et al., 1980:4). Juveniles of *B. chabanaudi* have numerous dark spots (each spot the size of pupil or smaller) on the trunk, but larger specimens (e.g., 113 mm SL) are covered by very small dark dots (Randall et al., 1980: figs. B,C). Specimens of *B. pylei* greater than 68 mm SL are unknown, but if the species attains larger sizes, the spots on the trunk may become relatively smaller.

**Larval morphology.** We have tentatively identified a 7.7-mm SL larval specimen (USNM 348384, Fig. 5) from the Philippine Sea as *B. pylei*. It is apparently a diploprionin because it has 24 vertebrae, two

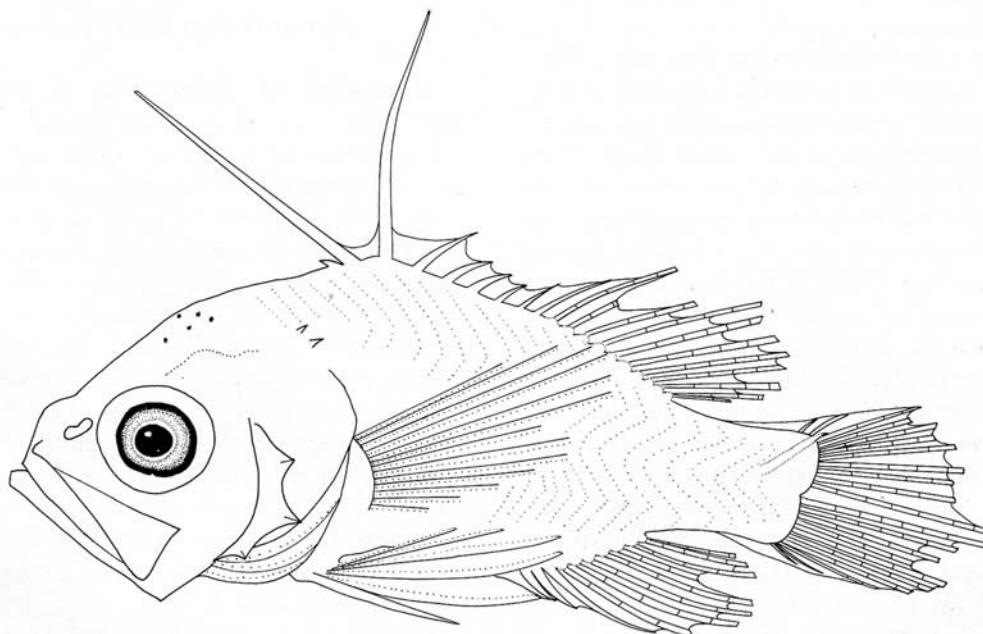


Fig. 5. Larval specimen of *Belonoperca pylei*? from the Philippine Sea, USNM 348384, 7.7 mm SL.



elongate but non-serrate dorsal-fin spines, three spines on the medial preopercular ridge (but no elongate spine at angle), and a long pectoral fin (36% SL) (see Baldwin et al., 1991: table 4). The presence of 19 total dorsal- and 10 total anal-fin rays in the larva indicates it is a specimen of *Belonoperca*. As noted under "Comparisons" above, *B. chabanaudi* and *B. pylei* can be distinguished on the basis of number of anal-fin spines (two vs. three, respectively) and the configuration of the dorsal fin (IX,10 in *B. pylei*, usually VIII-I,10 in *B. chabanaudi*, the penultimate spine of the latter considerably shorter than the ultimate spine). Baldwin et al. (1991) described larval *B. chabanaudi* from four specimens, 6.9–11.8 mm SL, and noted that the ninth element of the dorsal fin and second element of the anal fin, which in adults are spinous, are segmented in all larval specimens. Those elements must therefore transform into spines later in ontogeny. In the *Belonoperca* larva from the Philippine Sea, the second anal-fin element is clearly spinous, whereas the ninth dorsal- and third anal-fin elements resemble soft rays in being considerably less robust than preceding spinous elements. However, those elements are not segmented and lack the conspicuous round distal radial that is prominent at the base of other soft rays, suggesting that they will ultimately become spines. If, as in *B. chabanaudi*, the last anal spine transforms from a soft ray, the adult complement of anal spines in the new *Belonoperca* larva will be three, a feature unique to *B. pylei* among known species of *Belonoperca*. Pending further investigation of the distribution of this species, we describe this larval specimen as "*B. pylei*?"

The larva with moderately deep body (body depth 36% SL at pectoral-fin base); eye round and slightly smaller in diameter than length of snout (eye diameter 10% SL, snout length 11% SL); mouth large, maxilla reaching posteriorly to point about midway between center and posterior margin of eye; gut short but coiled, anus located at point just posterior to mid-body (preanal length 69% SL); dorsal fin originating over upper edge of opercle (predorsal length 39% SL); pectoral fin large, longest ray 36% SL and reaching base of 14th dorsal-fin element.

Most fins apparently fully formed. Dorsal fin with VIIIi,10 rays (ninth element a soft ray that presumably will later transform into a spine); second and third dorsal spines elongate (34% SL and 32% SL, respectively), but both broken and thus maximum lengths of spines unknown. Anal-fin rays Iii,7 rays; pectoral-fin rays 13; pelvic-fin rays I,5; principal caudal-fin rays 9+8; procurrent caudal-fin rays 4+4.

Several very small melanophores present on

frontal, but the larva otherwise unpigmented. Three well-developed spines of approximately equal size present on posterior margin of preopercle, one tiny spine present on subopercle, and one small spine present on both the supracleithrum and posttemporal.

Relative to other known diploprionin larvae, larval *B. pylei*? is distinctive in lacking supraorbital spination and spines on the lateral preopercular ridge and in having melanophores only on the head. In larval *Diploprion bifasciatum* and *B. chabanaudi*, there are 2–4 supraorbital spines, 3–4 lateral preopercular spines, and melanophores at least on the spinous dorsal-, pectoral-, and pelvic fins. It does not seem likely that the absence of certain head spines in larval *B. pylei*? is related to size because 6.9- and 7.2-mm SL specimens of larval *B. chabanaudi* and a 7.8-mm SL specimen of larval *D. bifasciatum* have well-developed supraorbital and lateral preopercular spines (Baldwin et al., 1991). Like *D. bifasciatum*, larval *B. pylei*? has elongate second and third dorsal spines, whereas the second through sixth dorsal spines are elongate in *B. chabanaudi* (Baldwin et al., 1991). Because larvae of the closest relatives of diploprionins have two elongate dorsal spines (e.g., *Liopropoma*) or one (epinephelins, grammistins), it seems likely that presence of two, vs. five, elongate dorsal spines is plesiomorphic for the tribe. Identification of larval *Aulacocephalus temmincki* and *D. drachi* are needed to allow better understanding of character-state evolution in larval diploprionins.

### Diploprionin Relationships

**Monophyly of *Belonoperca*.** Randall et al. (1980) provided a diagnosis of *Belonoperca* that we consulted to verify the generic placement of the new species. Of the features listed, *B. pylei* differs only in body depth (depth 3.5–3.7 in SL in *B. chabanaudi*, 3.9–4.7 in *B. pylei*) and in having a straight (vs. concave) posterior maxillary border (although some small specimens of *B. chabanaudi*, including our 67.5-mm SL cleared and stained specimen, have a straight posterior border, and the posterior maxillary border is slightly concave dorsally in the 68.0-mm SL holotype of *B. pylei*). Although Randall et al. (1980) stated that head squamation of *Belonoperca* is restricted to the operculum and nape, both species have small scales on the cheek. Also, Randall et al. (1980) gave 9+15 as the vertebral count for *Belonoperca*, but both species have 10+14.

Relative to *Aulacocephalus* and *Diploprion*, *B. pylei* and *B. chabanaudi* are strikingly similar in gen-

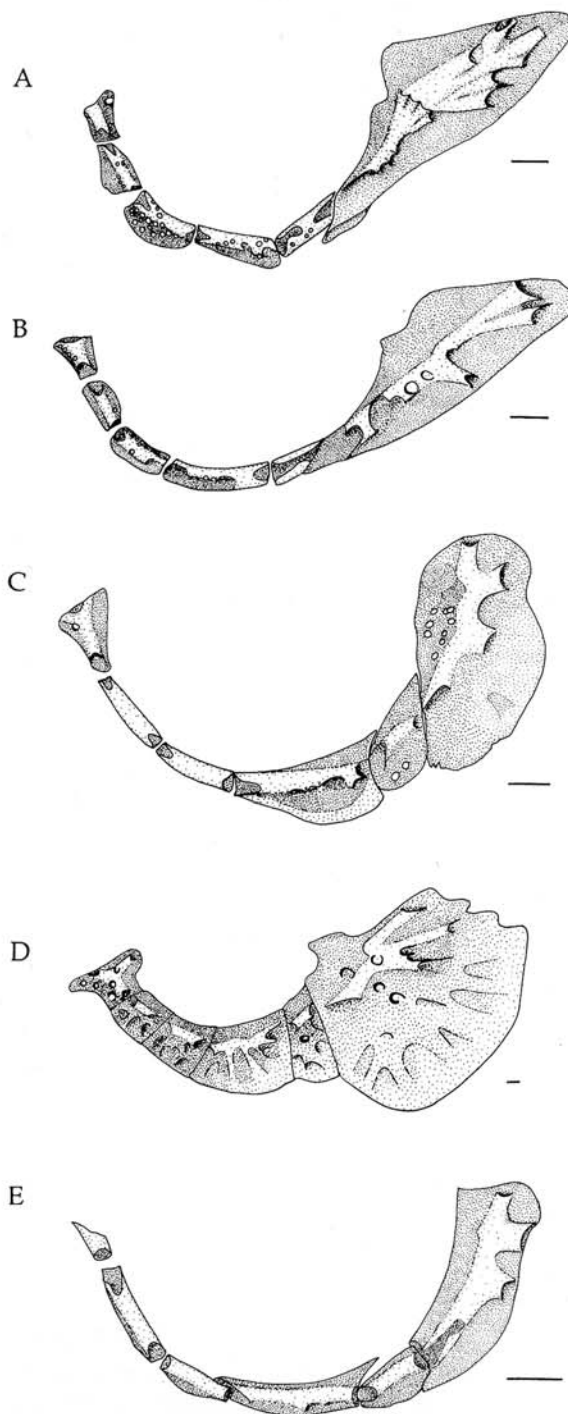


eral physiognomy. Although the new species differs from *B. chabanaudi* in several meristic and morphometric features, in having canine teeth in the upper and lower jaws, and in having a dramatically different color pattern (Table 2), we do not separate the two species generically because they share two derived features not present in other diploprionins or the outgroups:

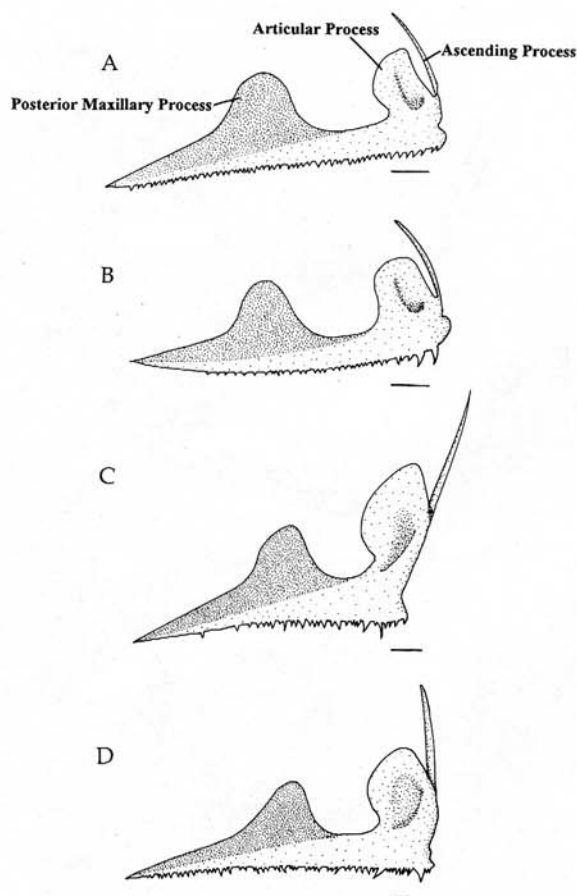
1. *Lacrimal with prominent anterodorsal projection extending onto snout* (Fig. 6).—In the outgroups and other diploprionins, the lacrimal is vertically elongate (Fig. 6C, E—more round in *Aulacocephalus*, Fig. 6D), and the main ramus of the cephalic sensory canal carried within the bone is oriented slightly diagonally to nearly vertically. If the lacrimal extends much onto the snout in those taxa (see discussion of *Aulacocephalus*+*Diploprion* below), only an anteroventral flange of the bone does so, not the canal-carrying portion (Fig. 6C, D), and the upper edge of the lacrimal does not closely approach the nostrils. In *Belonoperca*, the lacrimal is diagonally elongate; it has a prominent anterodorsal projection that carries the diagonally oriented main branch of the sensory canal well onto the snout (Fig. 6A, B), and the upper margin of the lacrimal forms a nearly horizontal border that closely approaches the nostrils (Fig. 3).

The elongate lacrimal in *Belonoperca* contributes to the pronounced snout characteristic of the genus. Oddly, although the long pointed head of *Belonoperca* is unusual among epinephelins (and explains, in part, the etymology of the genus—the Greek “belos” meaning “arrow”—Fowler and Bean, 1930), no morphometric aspect of it is uniquely derived for the genus. The distinctive head shape in *Belonoperca* is a combination of a long snout and a shallow head. *Aulacocephalus* and *Diploprion* also have relatively long snouts, possibly another synapomorphy of the Diploprionini because most outgroups have a shorter snout; however, some groupers also have long snouts, and a better understanding of epinephelin relationships is needed to hypothesize the primitive condition for the tribe. The shallow head of *Belonoperca* is not derived within the Diploprionini because it characterizes most members of the Epinephelini, Liopropomini, and some Grammistini (the deep head of *Aulacocephalus* and *Diploprion* appears to be derived—see Character 13 below).

2. *Ascending process of the premaxilla curved posteriorly* (Fig. 7).—The ascending process of the premaxilla in the outgroups and other diploprionins is relatively straight (Fig. 7C, D). In *Belonoperca*, the ascending process curves posteriorly around the artic-



**Fig. 6.** Circumorbital bones, right side, lateral view. A) *Belonoperca chabanaudi*, USNM 217873, 67.5 mm SL; B) *B. pylei*, USNM 345848, 61.9 mm SL; C) *Diploprion bifasciatum*, USNM 218889, 70.0 mm SL; D) *Aulacocephalus temmincki*, lacrimal and second-fifth infraorbitals redrawn from Katayama (1959), sixth infraorbital and surface features drawn from USNM 64640, 124 mm SL; E) *Grammistes sexlineatus*, USNM 218886, 68.0 mm SL.



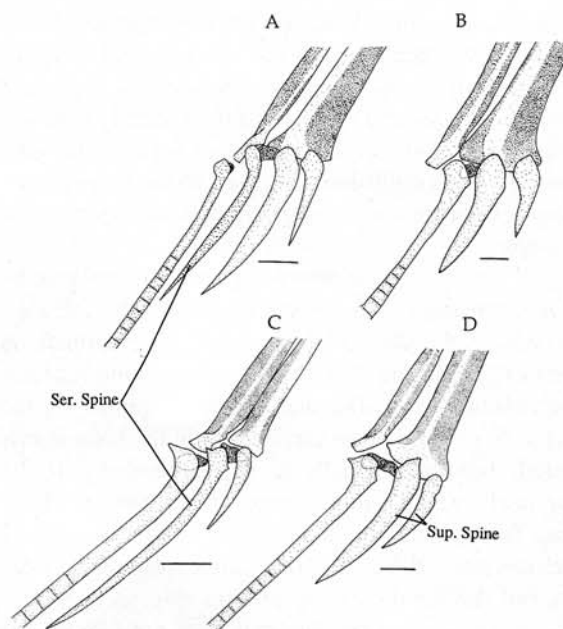
**Fig. 7.** Premaxilla, right side, lateral view. A) *Belonoperca chabanaudi*, USNM 217873, 67.5 mm SL; B) *B. pylei*, USNM 345848, 61.9 mm SL; C) *Diploprion bifasciatum*, USNM 218889, 70.0 mm SL; D) *Aulacocephalus temincki*, USNM 64640, 124 mm SL.

ular process of the premaxilla (Fig. 7A, B).

**Monophyly of *Diploprion*.** *Diploprion bifasciatum* (Kuhl & van Hasselt) Cuvier & Valenciennes, from the western Pacific Ocean to India, and *D. drachi* Roux-Estève & Fourmanoir, from the Red Sea, are the most deep-bodied diploprionins. Larvae of *D. bifasciatum* have been described (Baldwin et al., 1991), but early life history stages of *D. drachi* are unknown. The two species share numerous distinctive features, including the following derived ones:

3. *Vomerine teeth in two patches.*—The outgroups and other diploprionins have a single patch or continuous band of vomerine teeth. In *Diploprion*, vomerine teeth form two discrete patches separated from one another by a large gap.

4. *Two anal-fin spines, the first anal-fin pterygiophore serially associated with a soft ray* (Fig. 8).—



**Fig. 8.** Configuration of anal-fin spines and first anal-fin pterygiophore, right side. A) *Belonoperca pylei*, USNM 345848, 61.9 mm SL; B) *Diploprion drachi*, USNM 345949, 103 mm SL; C) *Belonoperca chabanaudi*, USNM 217873, 67.5 mm SL; D) *Diploprion bifasciatum*, USNM 218889, 70.0 mm SL. *Sup. Spine*—spine in supernumerary association with first anal-fin pterygiophore; *Ser. Spine*—spine serially associated with first pterygiophore.

Serranids typically have three anal-fin spines, two in supernumerary association with the first pterygiophore, the third associated serially and supported by a separate distal radial (as in *B. pylei*, Fig. 8A). *Belonoperca chabanaudi* and the two species of *Diploprion* have two anal-fin spines, but the conditions in the two genera are not homologous. In *B. chabanaudi* (Fig. 8C), the first pterygiophore is reduced in width relative to that of most other epinephelins (Fig. 8A, B, D; also see Baldwin and Johnson, 1993: fig. 16). It bears one supernumerary and one serially associated spine, indicating loss of one supernumerary spine (Fig. 8C). This condition is unique within the Epinephelinae and autapomorphic for *B. chabanaudi*. In both species of *Diploprion*, the first pterygiophore bears two supernumerary spines, but the element serially associated with it is a soft ray, indicating that the third spine is lost or fails to transform from a soft ray (Fig. 8B, D). *Grammistes sexlineatus* also has two anal-fin spines (Baldwin and Johnson, 1993: fig. 16C), in the same configuration as those of *Diploprion*, but polarity of the condition for diploprionins is not affected because all other non-diploprionin epinephelins have three anal-fin spines, including the

sister group of *Grammistes*, *Pogonoperca punctata*. Support of the three spines may vary among grammistin epinephelines (Baldwin and Johnson, 1993), but a first anal-fin pterygiophore that supports two supernumerary spines and a third spine in serial association is primitive for all epinepheline tribes. A first anal-fin pterygiophore that bears two supernumerary spines and serially supports a soft ray is cladistically diagnostic of *Diploprion*.

5. *Ascending processes of premaxillae fit into groove in frontal*.—Katayama (1960) noted that *D. bifasciatum* has a concavity between the frontals at the posterior end of the mesethmoid into which the ascending processes of the premaxillae fit. *Diploprion drachi* also has this concavity, but it is lacking in other diploprionins and outgroups.

6. *Long pelvic fin*.—In *D. bifasciatum* and *D. drachi*, the length of the pelvic fin is greater than 30% SL. The pelvic fin is shorter in other diploprionins and outgroups, its length less than 23% SL.

***Aulacocephalus*+*Diploprion*.** *Aulacocephalus* Temminck & Schlegel contains a single species, *A. temmincki* Bleeker, widely distributed in the Indo-Pacific (South Africa, Mauritius, Natal, southern Japan, Korea, northeastern China, Taiwan, Thailand, Rapa, Réunion, Kermadec Islands, and New Zealand—Katayama, 1960; Randall, 1986). A second species, *A. schlegeli* Günther, was described from Mauritius (Isle de France) but considered a synonym of *A. temmincki* by Katayama (1960). We have compared specimens of *A. temmincki* from the western Pacific with MCZ specimens of *A. schlegeli* from Mauritius and concur with Katayama's (1960) synonymy. Despite its widespread distribution, *Aulacocephalus* is relatively rare in collections. Larvae are unknown.

*Aulacocephalus* appears to be intermediate between *Belonoperca* and *Diploprion* in several features, including numbers of dorsal-fin rays (10 in *Belonoperca*, 12 in *Aulacocephalus*, usually 15 in *Diploprion*), anal-fin rays (7–8, 9, 12) and pectoral-fin rays (13–14, 15, 16–18), and in body depth (21–29% SL, 30–37, 40–45). However, *Aulacocephalus* is clearly more closely related to *Diploprion* than to *Belonoperca*, as indicated by the large number of derived features shared by the two:

7. *Ventral flange on lacrimal and second and third infraorbitals* (Fig. 6).—In the outgroups, the lacrimal and second and third infraorbitals are relatively slender bones, and the outer (ventral) margin of the infraorbital series roughly parallels the inner, semicircular margin (as in *Grammistes sexlineatus*, Fig. 6E). The same is true for *Belonoperca* except, as

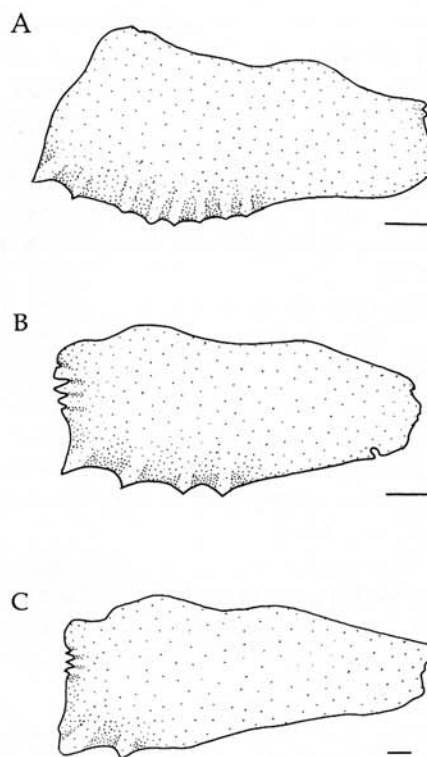


Fig. 9. Interopercle, right side. A) *Belonoperca chabanaudi*, USNM 217873, 67.5 mm SL; B) *Diploprion bifasciatum*, USNM 218889, 70.0 mm SL; C) *Aulacocephalus temmincki*, USNM 64640, 124 mm SL.

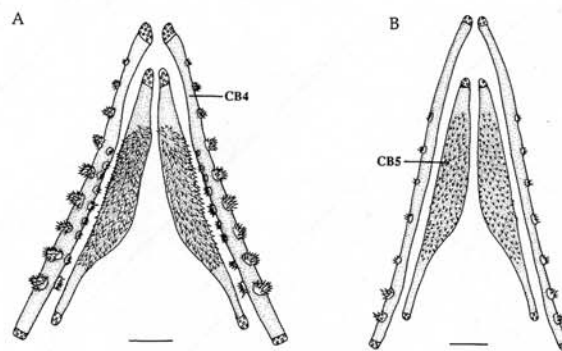


Fig. 10. Fourth (CB4) and fifth (CB5) ceratobranchials, dorsal view. A) *Diploprion bifasciatum*, USNM, 218889, 70.0 mm SL; B) *Belonoperca chabanaudi*, USNM 217873, 67.5 mm SL.

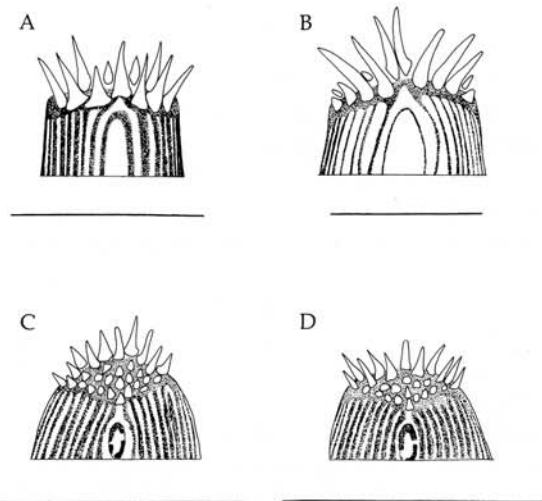
discussed above, the lacrimal is prolonged dorsoanteriorly (Fig. 6A, B). In *Aulacocephalus* and *Diploprion*, there is a well-developed flange of bone below the tubed region of the lacrimal and second and third infraorbitals (second through fifth infraorbitals in *Aulacocephalus*), and thus the outer margin of the an-

terior part of the infraorbital series dips ventrally well below the orbit (Fig. 6C, D).

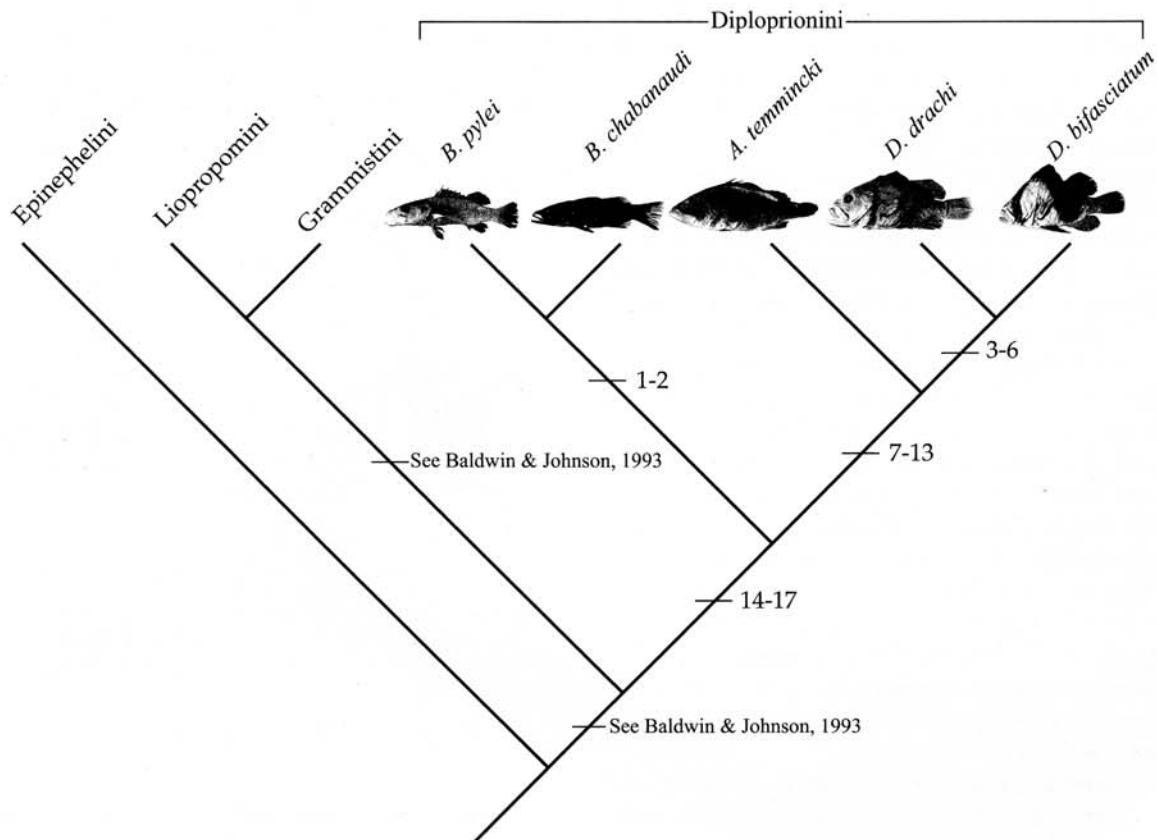
8. *Deep serrations on posterior margin of interopercle* (Fig. 9). — The posterior margin of the interopercle of *Belonoperca* and that of the outgroups is generally smooth (Fig. 9A). *Aulacocephalus* and *Diploprion* have a series of deep serrations on the dorsal portion of the posterior interopercular margin (Fig. 9B, C).

9. *Two rows of tooth plates on fourth ceratobranchial* (Fig. 10). — *Belonoperca* and the outgroups have two rows of tooth plates on the first three ceratobranchials (on the lateral and medial edges) but a single row on the lateral edge of the fourth (Fig. 10B). *Aulacocephalus* and *Diploprion* have two rows of tooth plates on the first through fourth ceratobranchials (Fig. 10A).

10. *Well-developed fourth pharyngobranchial cartilage*. — Typically in percoids, the fourth pharyngobranchial is a small (reduced relative to more prim-



**Fig. 11.** Diploprionin scales, posterior field. A) *Diploprion drachi*, USNM 205489, 110 mm SL; B) *Aulacocephalus temmincki*, USNM 64640, 124 mm SL; C) *Belonoperca chabanaudi*, USNM 217873, 67.5 mm SL; D) *B. pylei*, USNM 345848, 61.9 mm SL.



**Fig. 12.** Hypothesized relationships among diploprionins. Numbers correspond to characters in text and Table 3. Autapomorphies of terminal taxa not included on tree. Photographs of fishes, from left to right: *Belonoperca pylei* BPBM 37615, 68.0 mm SL, *B. chabanaudi* USNM 338448, 113 mm SL, *Aulacocephalus temmincki* USNM 71332, 151 mm SL, *Diploprion drachi* USNM 205489, 110 mm SL, *D. bifasciatum* USNM 228044, 107 mm SL. Tree length=21, CI=1.0, RI=1.0.



itive teleosts) cartilage (Johnson 1984). Loss or reduction of this cartilage also characterizes *Belonoperca* and most outgroups, but *Diploprion* and *Aulacocephalus* have a well-developed fourth pharyngobranchial cartilage. The liopropomin serranid *Pikea* also has a prominent fourth pharyngobranchial cartilage (this study), presumably as an independent acquisition.

11. *Scales lacking radial rows of cteni* (Fig. 11).—Ctenoid scales ("ct" of Johnson, 1984, "ctenoid" of Roberts, 1993) of percoids typically have a marginal row of complete cteni and numerous submarginal rows of truncated cteni (bases of formerly marginal cteni). The bases and complete cteni form radial rows from the anterior edge of the posterior field to the posterior margin of the scale. *Belonoperca* (Fig. 11C, D) and most outgroups have typical ctenoid scales (some groupers and grammistins have scales without cteni on various areas of the body, the liopropomin *Rainfordia* has a single row of marginal cteni much like a goby, and *Jeboehlkia* and the pseudogrammin genera have radial rows of complete cteni—see Baldwin and Johnson, 1993). In *Aulacocephalus* and *Diploprion* (Fig. 11A, B), radial rows of cteni and ctenial bases do not develop; rather, cteni are added only in secondary positions on either side of an existing ctenus. The first (most central) ctenus may have another posterior to it, but a radial arrangement does not occur elsewhere.

12. *Articular and ascending processes of premaxilla large* (Fig. 7).—In most epinephelins, including *Belonoperca*, the articular and posterior maxillary processes of the premaxilla are approximately equal in height (or the articular process is slightly shorter), and the ascending premaxillary process never extends greatly beyond the dorsal margin of the articular process (Fig. 7A, B). In *Aulacocephalus* and *Diploprion*, the articular process is larger (in height) than the posterior maxillary process (slightly larger in *Aulacocephalus*, considerably so in *Diploprion*), and the ascending process of the premaxilla extends dorsally well beyond the dorsal margin of the articular process (Fig. 7C, D).

13. *Deep head*.—As noted under Character 1, a shallow head is primitive for diploprionins, the ratio of head length/head depth at mid-orbit >2.0 in *Belonoperca* and most outgroups (certain groupers and soapfishes have deeper heads). Head depth is greatest in *Diploprion*, but in both *Aulacocephalus* and *Diploprion*, the ratio of head length/head depth at mid-orbit is <2.0 (1.5–1.6 in *Aulacocephalus*, 1.1–1.3 in *Diploprion*).

**Summary of Relationships.** Relationships among diploprionins supported by our data are depicted in Figure 12, character numbers on the tree corresponding to derived features described in the preceding section on relationships. A character matrix used in analyzing phylogenetic relationships with the "Branch and Bound" option of PAUP (Swofford, 1991) is given in Table 3. Our data suggest that the diploprionin genera *Belonoperca* and *Diploprion* are mono-

**Table 3.** Character matrix used in constructing cladogram in Fig. 12

	Character			
	1–5	6–10	11–15	16–19
<i>Plectropomus</i>	00000	00000	00000	0000
<i>Liopropoma</i>	00000	00000	00000	0011
<i>Grammistops</i>	00000	00000	00000	0211
<i>Belonoperca pylei</i>	11000	00000	00011	1110
<i>Belonoperca chabanaudi</i>	11010	00000	00011	1110
<i>Aulacocephalus temmincki</i>	00000	01111	11111	11?0
<i>Diploprion bifasciatum</i>	00121	11111	11111	1110
<i>Diploprion drachi</i>	00121	11111	11111	11?0

Outgroups for the Diploprionini are the Epinephelini, Liopropomini, and Grammistini, represented by *Plectropomus*, *Liopropoma*, and *Grammistops*, respectively. For descriptions of characters 14–19, included here to establish monophyly of the Diploprionini and outgroup relationships, and for additional characters supporting outgroup relationships, see Baldwin and Johnson (1993). 1. prominent anterodorsal projection of lacrimal extending onto snout absent (0), present (1); 2. ascending process of premaxilla straight (0), curved posteriorly (1); 3. vomerine teeth in single patch (0), two patches (1); 4. three anal-fin spines (0); two, one supernumerary and one serial on first pterygiophore (1); two, both supernumerary on first pterygiophore (2); 5. ascending processes of premaxilla not extending to frontals (0), fit into groove in frontals (1); 6. pelvic fin <ca. 23% SL (0), >ca. 30% SL (1); 7. well-developed flanges on lacrimal and second and third infraorbitals absent (0), present (1); 8. deep serrations on posterior margin of interopercle absent (0), present (1); 9. fourth ceratobranchial with one row of toothplates (0), two rows (1); 10. fourth pharyngobranchial cartilage small or absent (0), well developed (1); 11. scales with radial rows of cteni/ctenial bases (0), without radial arrangement of cteni/ctenial bases (1); 12. articular and posterior maxillary processes of premaxilla nearly equal in height (0), articular process appreciably larger (1); 13. head shallow, head depth  $\geq 2.0$  in head length (0); head deep, depth 1.1–1.6 in length (1); 14. neurocranium and circum-orbitals smooth (0), rugose (1); 15. ridges of tissue on bases of dorsal and anal fins absent (0), present (1); 16. bar extending posteriorly from first circulus of scales absent (0), present (1); 17. grammistin absent (0), in epidermal cells (1), in epidermal cells and dermal glands (2); 18. spine at angle of preopercle in larvae elongate (0), not elongate (1); 19. first dorsal-fin pterygiophore robust and straight (0), thin and curved (1).

phyletic and that *Belonoperca* is the sister group of *Diploprion* plus *Aulacocephalus*. We did not identify any derived features unique to *Aulacocephalus* (other than the color pattern of *A. temmincki*—blue or purple with yellow stripe along dorsal margin of body from snout to base of caudal fin—see Masuda et al., 1984: pl. 125), but we retain it as a monotypic genus because it is intermediate in phylogenetic position between *Belonoperca* and *Diploprion* and lacks the diagnostic features of those genera. The absence of homoplasy in the data set is unusual, but a small number of characters were identified as informative in this study, and some characters that might have been interpreted as homoplastic (e.g., the presence of two anal-fin spines in *Belonoperca* and *Diploprion*) were determined to be structurally non-homologous prior to the computer analysis.

Although multiple branching in the phylogenetic reconstruction (Fig. 12) makes it difficult to select a diploprionin species that might most closely resemble the ancestral diploprionin, clearly *Diploprion*, with unusual epinepheline features such as a very deep body, two anal-fin spines, very long ascending premaxillary processes, etc., is highly specialized with respect to *Aulacocephalus* and *B. pylei*, as is *B. chabanaudi*, with a single supernumerary spine on the first anal-fin pterygiophore and five elongate dorsal spines in the larval stage. Based on collection data from museum specimens, *B. chabanaudi* and *Diploprion* appear to inhabit shallower depths than *Aulacocephalus* and *B. pylei*, possibly suggesting that evolution of the group involved shoreward radiation from a deep-reef form.

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