A

B

C

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Redescription of *Gracila albomarginata* (Fowler and Bean) and *Cephalopholis polleni* (Bleeker) with Comments on the Generic Limits of Selected Indo-Pacific Groupers (Pisces: Serranidae: Epinephelinae)

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ABSTRACT.— Redescriptions, complete synonymies and new distribution records are given for *Gracila albomarginata* and *Cephalopholis polleni*; our generic classification of *C. polleni* contradicts that of recent authors who assigned the species to *Gracila*, which now becomes monotypic. The utility and phylogenetic importance of selected characters are evaluated as the basis for continued recognition of the epinepheline genera *Aethaloperca*, *Cephalopholis* and *Gracila*. Scale morphology and neurocrania of several epinephelines are illustrated and compared. [*Aethaloperca*, *Cephalopholis*, *Epinephelinae*, fishes, *Gracila*, groupers, Indo-Pacific, osteology, scale morphology, Serranidae, systematics]

This study evolved as an outgrowth of our efforts to determine the proper placement of *Cephalopholis albomarginatus* Fowler and Bean and *Epinephelus polleni* Bleeker within the current generic classification of groupers (tribe Epinephelini). We have concentrated our focus on *Cephalopholis*, *Aethaloperca* and *Gracila*, three poorly defined nominal genera that several authors have uncritically considered to be closely related. Smith (1954) recognized *Aethaloperca* Fowler (type species: *Perca rogaa* Forsskal) as a valid genus "closely related" to *Cephalopholis* Schneider (type species: *C. argus* Schneider). He also assigned *C. albomarginatus* to *Aethaloperca*, although it does not have a deep and compressed body, one of three characters he mentioned to distinguish the genus. Most sub-

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PLATE I. A, *Gracila albomarginata*, juvenile, Marshall Is., Kwajalein (D. S. Johnson); B, *G. albomarginata*, adult, Maldive Is., Malé (J. Randall); C, *Cephalopholis polleni*, 149 mm SL, BPBM 21166, Philippines, Mactan Is. (J. Randall).

sequent workers have recognized *Aethaloperca* as monotypic or as a synonym of *Cephalopholis*. Randall (1964) erected another monotypic genus, *Gracila*, for *C. albomarginatus*, stating that while it does not properly belong in *Cephalopholis*, it fits no better in *Aethaloperca*. Katayama (1974) recognized a second nominal species of *Gracila*, *G. okinawae* (a synonym of *E. polleni*). The primary character used by subsequent authors to justify allocation of *polleni* to *Gracila* rather than *Cephalopholis* is its truncate caudal fin (versus rounded in *Cephalopholis*, excluding *Aethaloperca*), a character that we believe has little value as an indicator of relationships. As discussed in the section on relationships, we have found no further evidence to suggest that *polleni* is more closely related to *Gracila albomarginata* than to species of *Cephalopholis*, and we thus retain *polleni* in the latter genus.

MATERIALS AND METHODS

Specimens examined for this study are deposited in the following institutions: AMNH, American Museum of Natural History, New York City; ANSP, Academy of Natural Sciences of Philadelphia; BM(NH), British Museum (Natural History), London; BPBM, Bernice P. Bishop Museum, Honolulu; CAS, California Academy of Sciences, San Francisco; MCZ, Museum of Comparative Zoology, Harvard University, Cambridge; MNHN, Museum National d'Histoire Naturelle, Paris; RMNH, Rijksmuseum van Natuurlijke Historie, Leiden; ROM, Royal Ontario Museum, Toronto; RUSI, J. L. B. Smith Institute of Ichthyology, Grahamstown, South Africa; UG, University of Guam; USNM, National Museum of Natural History, Smithsonian Institution, Washington, D. C.; WAM, Western Australian Museum, Perth. Counts and measurements follow those outlined by Randall and Ben-Tuvia (1983). Caudal concavity is the distance between vertical lines passing through the tips of the shortest middle caudal rays and the longest ray of the dorsal lobe of the caudal fin, with the fin in its normal spread condition. Following the method described by Hughes (1981), each scale illustrated in Fig. 1 was cleaned rapidly in a 1.5% solution of cold sodium hypochlorite using a small paintbrush to remove the epithelial tissue and sheath of connective tissue encasing the posterior field. Cleaned scales were glued to small glass cover slips, which were then mounted on aluminum specimen stubs and goldcoated for SEM examination. In addition to the specimens used to illustrate Figs 2-5, the following cleared and stained material was examined: *Aethaloperca rogaa*, ANSP 111164 (1); *Cephalopholis* argus, ANSP 140189 (2), ANSP 140193 (1); *C. boenack*, ANSP 145570 (4); *C. formosa*, ANSP 158515 (4); *C. fulva*, ANSP 112814 (3); *C. leopardus*, ANSP 140225 (2), ANSP 145561 (2); *C. nigripinnis*, ANSP 111179 (2); *C. pachycentron*, ANSP 145079 (2); *C. spiloparaea*, ANSP 109334 (2); *C. urodeta*, ANSP 130165 (1); *Gracila albomarginata*, BPBM 20310 (1).

SYSTEMATIC TREATMENT

The generic classification of the approximately 170 species that constitute the serranid tribe Epinephelini (*sensu* Johnson, 1983) remains inadequate, and this study has done little to alleviate the problem. Although several genera (e.g., *Variola*, *Plectropomus*, *Cromileptes*) can be clearly diagnosed with unique characters, the majority of species (ca. 100) are placed in the poorly diagnosed genus *Epinephelus*, which, to date, is distinguished from the next largest genus, *Cephalopholis* (ca. 30 species), primarily by number of dorsal spines (XI versus IX). Most students of Atlantic and eastern Pacific groupers have followed Smith (1971) in treating *Cephalopholis* as a subgenus of *Epinephelus*, while those

who study Indo-Pacific species consider *Cephalopholis* distinct from *Epinephelus* (Randall and Ben-Tuvia 1983, Leis 1986).

Specific outgroups for the Epinephelini have been identified (Johnson 1983, Johnson 1988), so that a species-level cladistic analysis is possible; however, given the number of species involved, this is unlikely to be forthcoming in the forseeable future. Furthermore, based on our admittedly incomplete knowledge of the limited, and yet seemingly capricious osteological and other morphological variability within the Epinephelini, we doubt that a well-corroborated, largely resolved cladogram would result. In dealing with classificatory questions like those raised here, we are largely forced to work within the existing phenetic classification, although some characters can be interpreted cladistically. Below we discuss character states that vary among epinephelin* serranids and their potential for providing useful phylogenetic information, with particular reference to the current concepts of the monotypic genera *Gracila* and *Aethaloperca*, their relationship to *Cephalopholis*, and the generic allocation of the species *polleni*. The distribution of these character states among selected grouper genera is summarized in Table 1.

1. *Dorsal-fin spines.*— As noted above, the two most speciose epinephelin genera are distinguished by number of dorsal spines. All species of *Cephalopholis* have nine dorsal spines, while most species of *Epinephelus* have 11 (with the exception of three eastern Pacific species, *E. acanthistius*, with nine, and *E. analogus* and *E. nigritus*, with 10). Johnson (1988) argued, based on outgroup comparison, that the primitive number of dorsal spines for the Epinephelini is eight or nine and that 10 or more spines is derived. Dorsal spine number in *Gracila*, *Aethaloperca* and *Cephalopholis* is phylogenetically uninformative; species assigned to these genera all share the primitive state, nine spines.

2. *Shape of caudal fin.*— As a matter of convenience several authors have considered a rounded caudal fin to be diagnostic of *Cephalopholis* (*sensu stricto*), in contrast to the truncate fin which characterizes *C. polleni*, *Gracila* and *Aethaloperca*. A rounded caudal fin is not unique to *Cephalopholis*, and among species of *Epinephelus* caudal fin shape exhibits a continuum from slightly emarginate through truncate to rounded. Caudal-fin shape also varies within the outgroups, and we are thus unable to polarize this character.

3. *Scale morphology.*— McCully (1961) described a basic difference in the configuration of the scalelets in the posterior field of the scales among epinephelin genera. With one exception (*Plectropomus*), he noted that *Cephalopholis* and all genera with fewer than 10 dorsal spines, have scales in which the first scalelet is usually fused to the structures anterior to it. In contrast, in *Epinephelus* and other genera with 10 or 11 dorsal spines (except *Alphestes* and *Dermatolepis*, whose scales are distinct from all other epinephlins), the first scalelet is rarely fused to the main body of the scale. Our observations (Fig. 1) bear this out. Furthermore, the fused condition characterizes the first (Diploprionini + Grammistini + Liopropmini) and second (Niphonini) outgroups for the Epinephelini and thus we interpret the unfused condition as derived for *Epinephelus* and the genera that share it. *Aethaloperca* and *C. polleni* have the primitive fused *Cephalopholis* condition. *Gracila albomarginata* exhibits the derived state in which the first scalelet is usually free.

4. *Neurocranium.*— Internal osteological features of epinephelins have never been studied comprehensively, and any conclusions based on skull characters would be tentative because character states have not been docu-

* Epinephelin refers only to members of the tribe Epinephelini in constrast to epinepheline which applies to the entire subfamily.

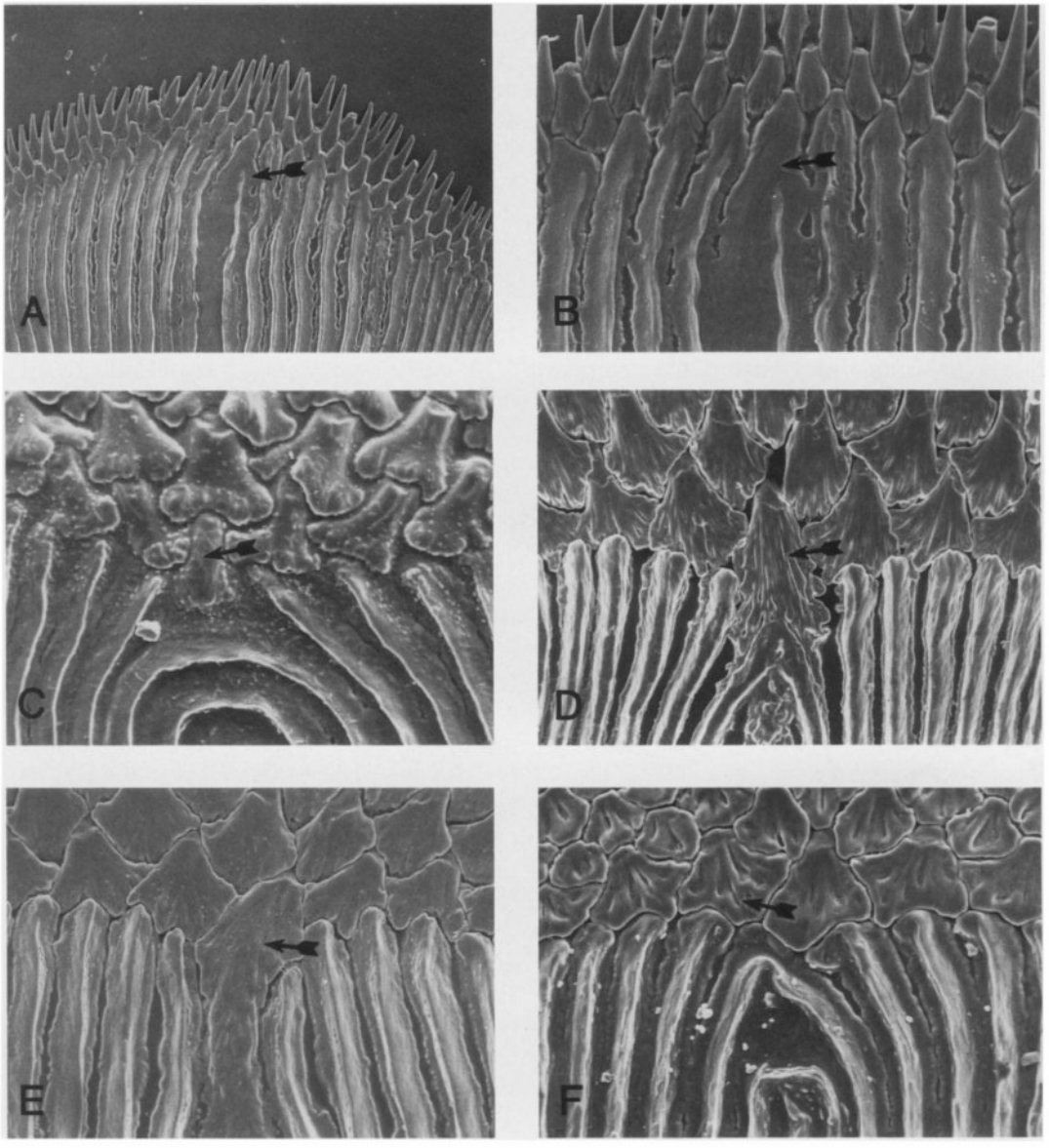

FIG. 1. Scanning electron micrographs of ctenoid scales (from area between lateral line and base of spinous dorsal fin, just above tip of the pectoral fin) of selected epinephelin species, posterior field toward top; first scalelet indicated by arrow. A, *Liopropoma susumi;* posterior end of scale showing all scalelets in posterior field. BL. Closeups showing region of first scalelet B, *Liopropoma susumi;* C, *Niphon spinosus;* D, *Cephalopholis argus;* E, *C. sexmaculatus;* F, *Epinephelus fasciatus.*

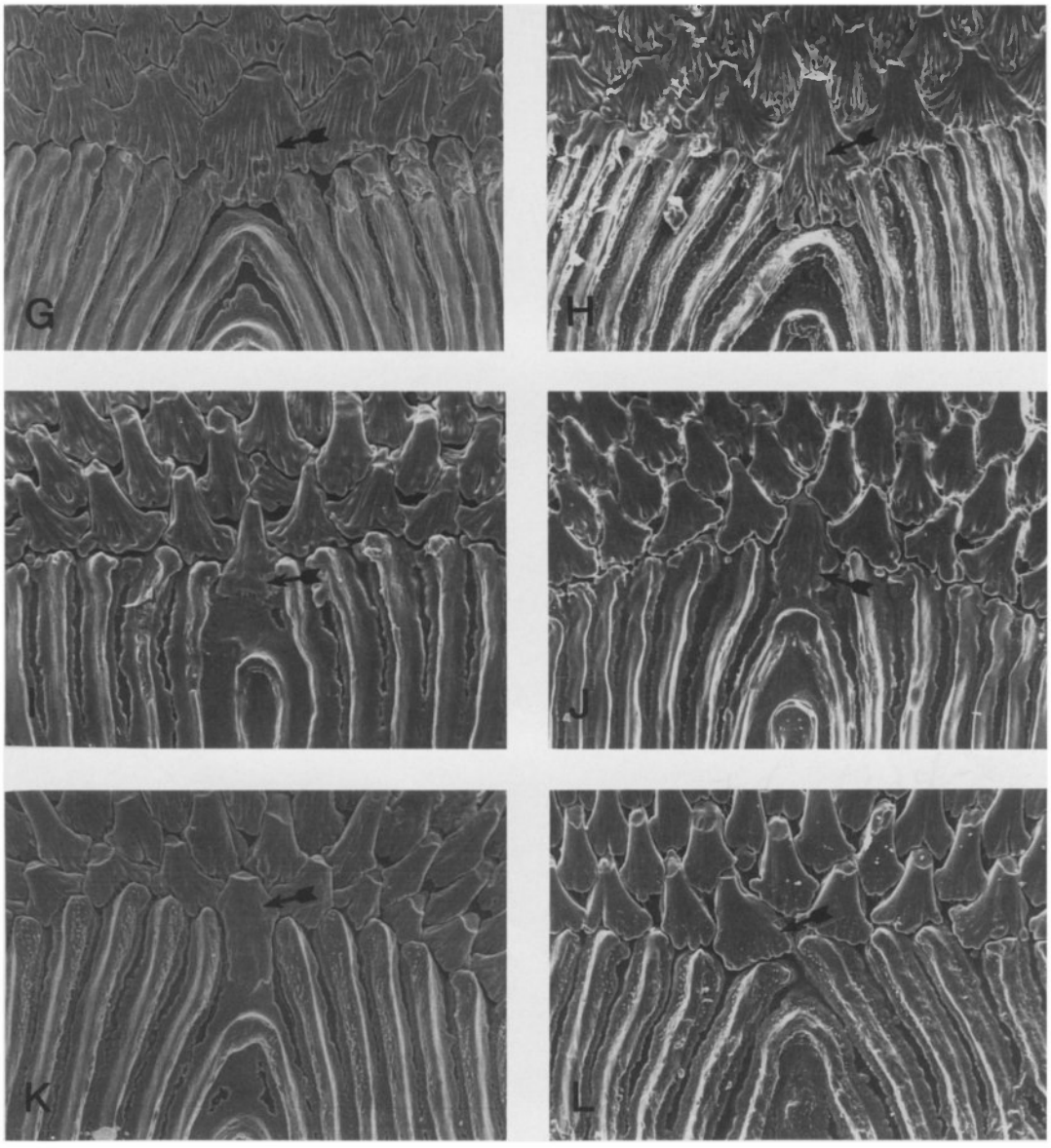

FIG. 1. (Continued). **G**, *Epinephelus hexagonatus;* **H**, *E. summana;* **I**, *Cephalopholis igarashiensis*; **J**, *Aethaloperca rogaa*; **K**, *Cephalopholis polleni*; **L**, *Gracila albomarginata.*

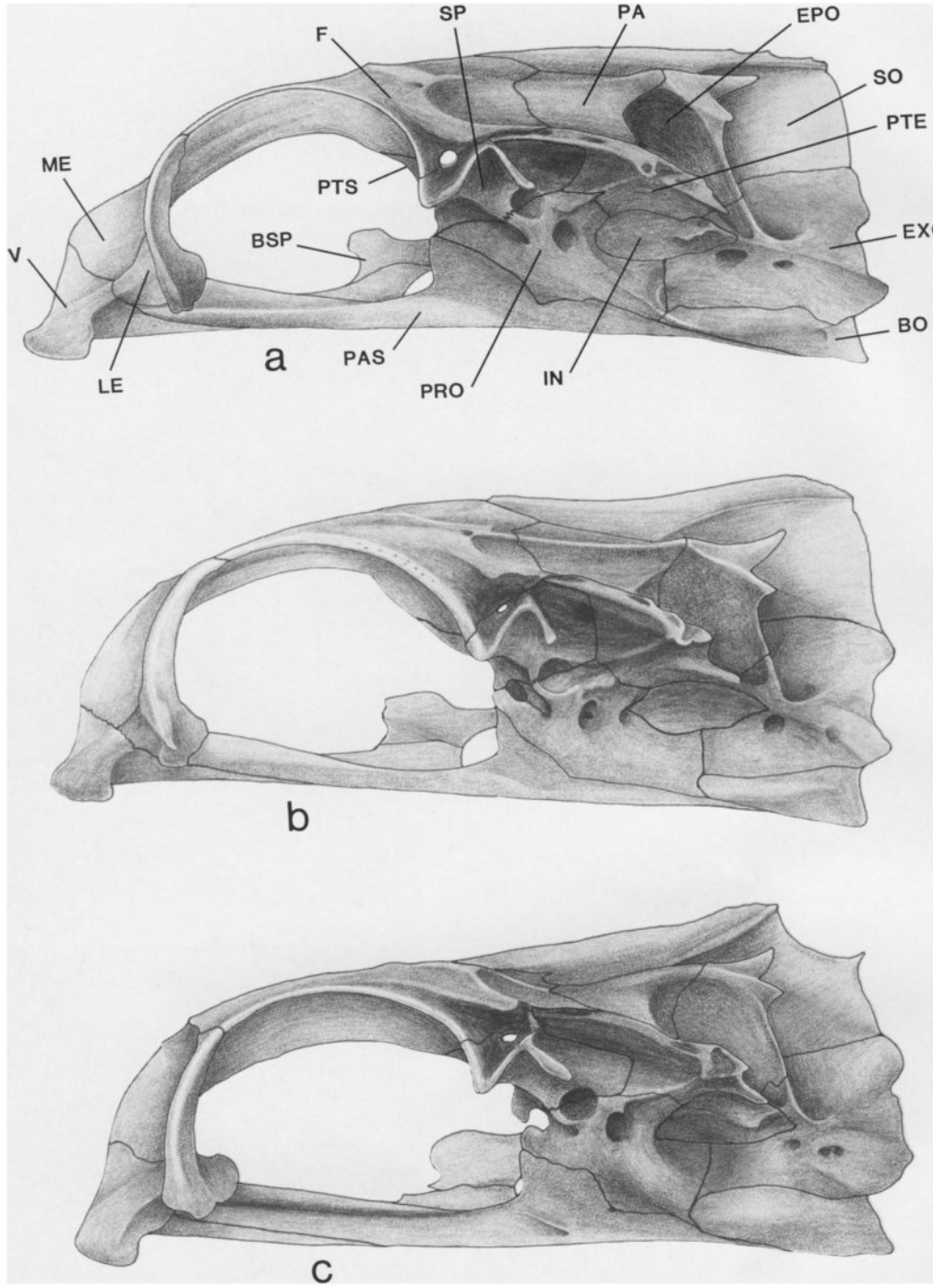

FIG. 2. Neurocrania in lateral view: **a**, *Cephalopholis argus*, 130 mm SL, ANSP 131785; **b**, *Cephalopholis polleni*, 129 mm SL, ANSP 131185; **c**, *Gracila albomarginata*, 143 mm SL, BPBM 16261. Abbreviations: BO, basioccipital; BSP, basisphenoid; EPO, epioccipital; EXO, exoccipital; F, frontal; IN, intercalar; LE, lateral ethmoid; ME, mesethmoid; PA, parietal; PAS, parasphenoid; PRO, prootic; PTE, pterotic; PTS, pterosphenoid; SO, supraoccipital; Sp, sphenotic; V, vomer.

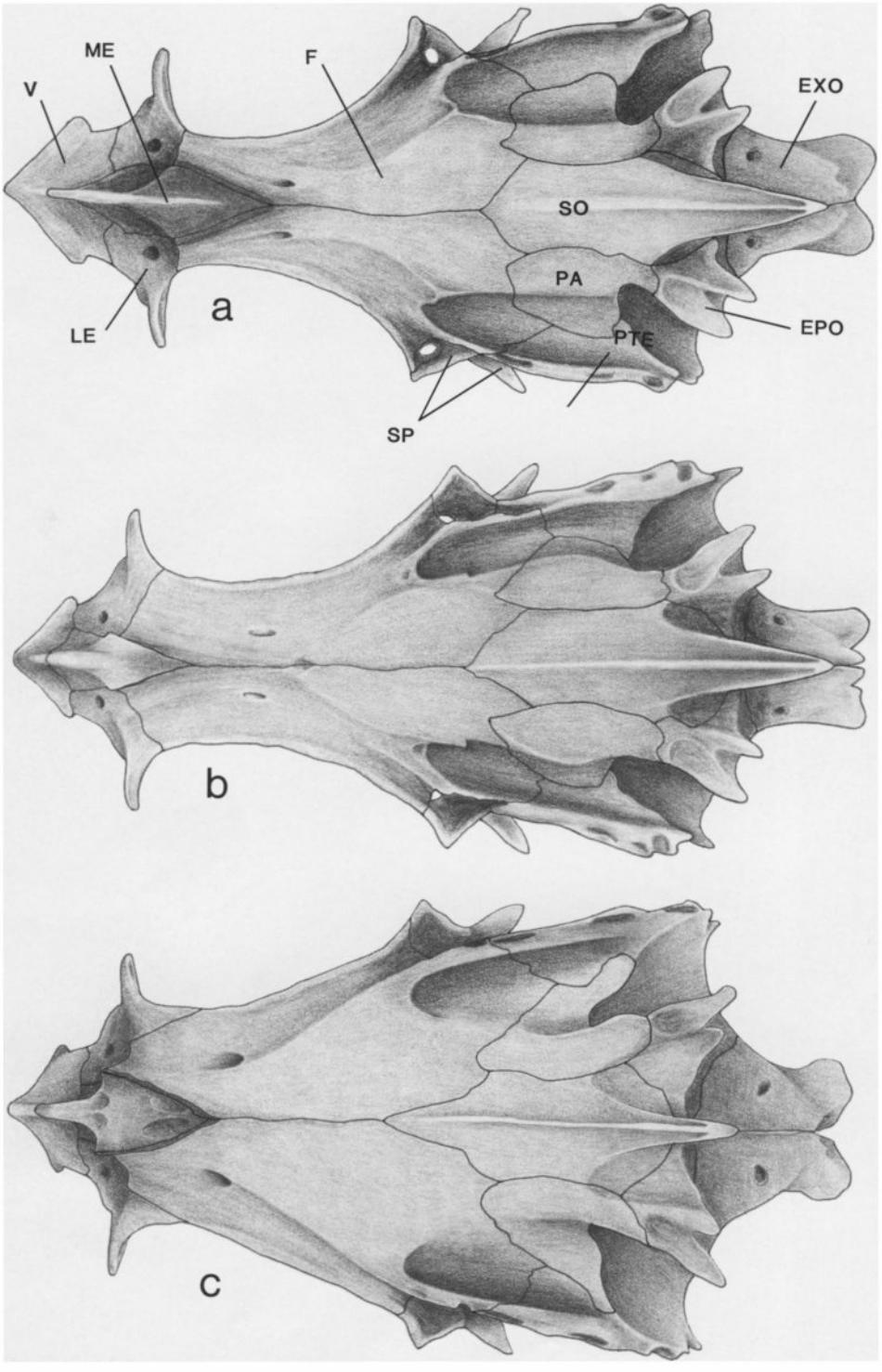

FIG. 3. Neurocrania in dorsal view: **a**, *Cephalopholis argus;* **b**, *Cephalopholis polleni;* **c**, *Gracila albomarginata.* Data as in Fig. 2.

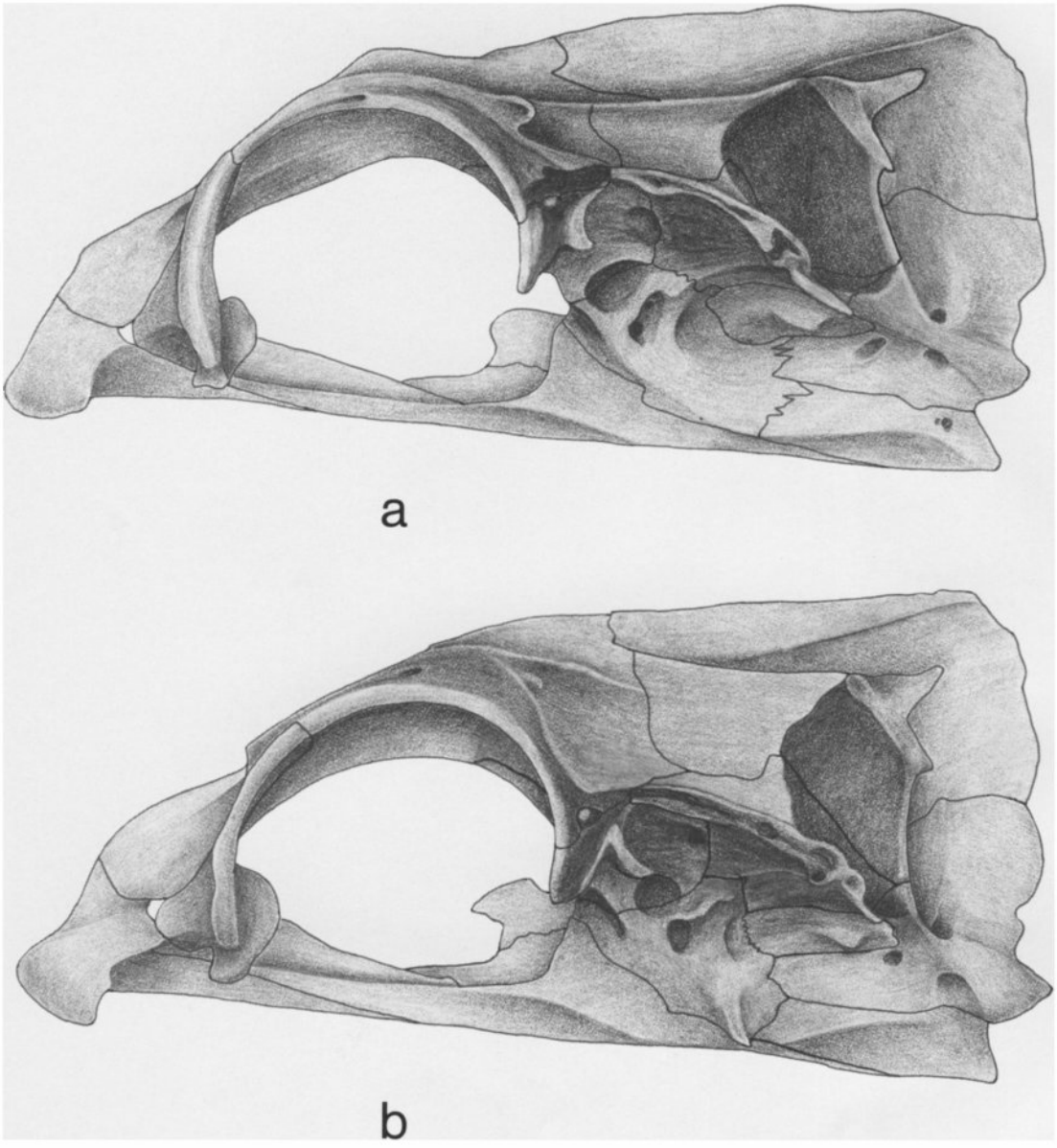

FIG. 4. Neurocrania in lateral view: **a**, *Cephalopholis igarasiensis*, 148 mm SL, BPBM 19177; **b**, *Aethaloperca rogaa*, 138 mm SL, USNM 279148.

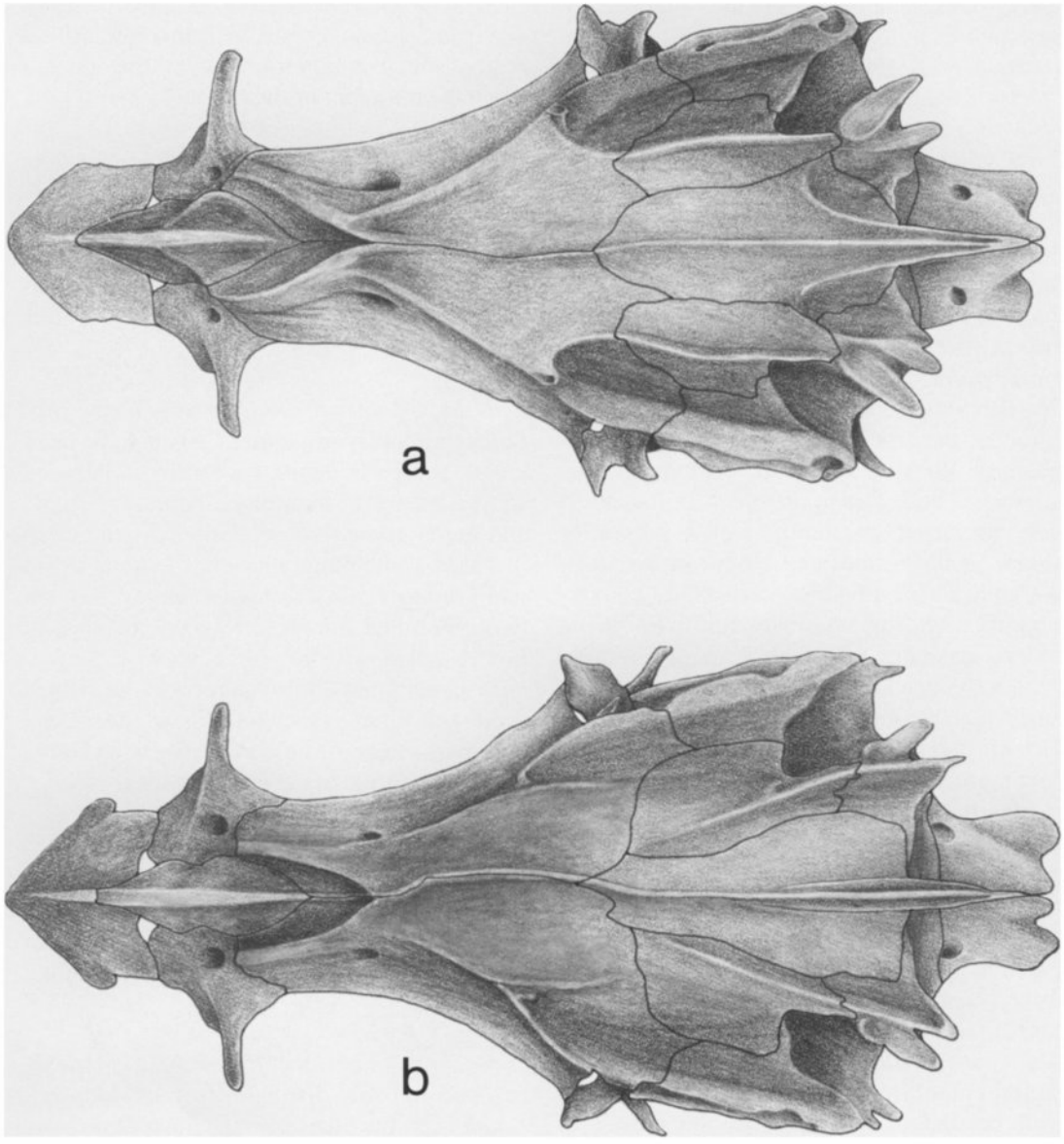

FIG. 5. Neurocrania in dorsal view: a, *Cephalopholis igarasiensis;* b, *Aethaloperca rogaa.* Data as in Fig. 4.

mented for the majority of species. Katayama's (1959) work on the serranid fishes of Japan provides the most extensive survey of skeletal features in the Epinephelini, based on many of the Japanese species in the genera *Cephalopholis, Epinephelus,* Variola, *Plectropomus* and *"Trisotropis."* Although Katayama identified features that distinguish those epinephelins he examined as a group from other serranids, he demonstrated no consistent differences that characterize each genus, particularly *Cephalopholis* and *Epinephelus*. Smith (1971) noted differences in the neurocrania of American epinephelins involving the relative development of a mesethmoid pit and transverse wall between the anterior ends of the frontals and the orientation of the frontoparietal crests. These differences do not serve to distinguish *Epinephelus* and *Cephalopholis*; Smith noted that the transverse ethmoid wall is present or absent in the former and absent in the latter and that the frontoparietal crests are convergent in both. Our examination of Indo-Pacific species indicates that these features are difficult to characterize and appear to be continuously variable among species of both genera. The same is true of the transverse ridges connecting the anterior ends of the frontoparietal crests used by Gill (1865) to diagnose the genus *Petrometopon* (treated by Smith as a synonym of *Cephalopholis*). The neurocrania of *Gracila, Aethaloperca* and several species of *Cephalopholis*, including *polleni*, are illustrated in Figs 2-5. The most distinctive among these is that of *Gracila* with its deep, cancellous mesethmoid pit, discontinuous frontoparietal crests, broad supraorbital laminae and blunt frontopterotic ridges that extend well beyond the midpoint of the orbit. In *Aethaloperca* and *C. igarashiensis*, there is a shallow, noncancellous mesethmoid depression, well-developed frontoparietal crests (disjunct in *Aethaloperca*) and relatively narrow supraorbital laminae. The cranium of *C. polleni* exhibits none of the distinctive features that characterize *Gracila* and resembles more closely that of *C. argus,* which also lacks a cancellous mesethmoid pit, and has continuous frontoparietal crests, a narrow interorbital region and frontopterotic ridges that do not reach the midpoint of the orbit.

5. *Melanophore pattern in larvae.*— Leis (1986) hypothesized relationships among selected epinephelin genera based on characters of their larvae. The larvae of *Gracila, Aethaloperca,* and *C. polleni* are unknown, and thus larval characters are not applicable to this problem.

6. *Morphometric characters.*— Adult proportional measurements, especially head length and body depth, have been utilized by some authors to partially diagnose *Gracila* and *Aethaloperca*, respectively. As indicated in Table 1, the range of values is quite broad with, in most cases, at least some overlap between nominal intrageneric taxa. In view of this, coupled with a general lack of knowledge concerning the dynamics of growth in these and other epinephelines, we are reluctant to attach any significance to such characters as indicative of generic affinities.

7. *Robustness of fin spines.*— Although difficult to quantify, the slender spines (Fig. 6a) of *Gracila albomarginata* add to the list of derived character states that distinguish it from other epinephelin genera, including *Cephalopholis.*

8. *Shape of pectoral fin.*— An asymmetrical pectoral fin distinguishes *Aethaloperca rogaa* from the other epinephelines contrasted in Table 1 and may represent a derived character state. Even if this surmise is correct, fin shape constitutes an autapomorphy of *Aethaloperca* and is thus uninformative in a phylogenetic context.

Fig. 6. Radiographs to show relative robustness of fin spines: a, *Gracila albomarginata*, ANSP 131744; b, *Cephalopholis polleni*, ANSP 131821.

As outlined above, we know of no derived character that can be used to establish the monophyly of *Cephalopholis*. The case for continued recognition of *Cephalopholis* at the generic level is a problem that goes beyond the scope of this paper; the taxon is maintained herein in the interest of nomenclatural stability and as a matter of convenience. For similar reasons we also advocate the continued recognition of *Aethaloperca*, although with less conviction.

GRACILA Randall 1964

Diagnosis.— An epinephelin serranid genus distinguished by following combination of characters: Dorsal fin IX,14-16; anal fin III,9-10; dorsal and analfin spines relatively slender compared to segmented rays (Fig. 6a); caudal fin truncate to slightly emarginate; pectoral rays 1819, middle rays longest; ctenoid scales with first scalelet usually not fused to structures anterior to it; no antrorse spines on ventral edge of opercle; neurocranium with

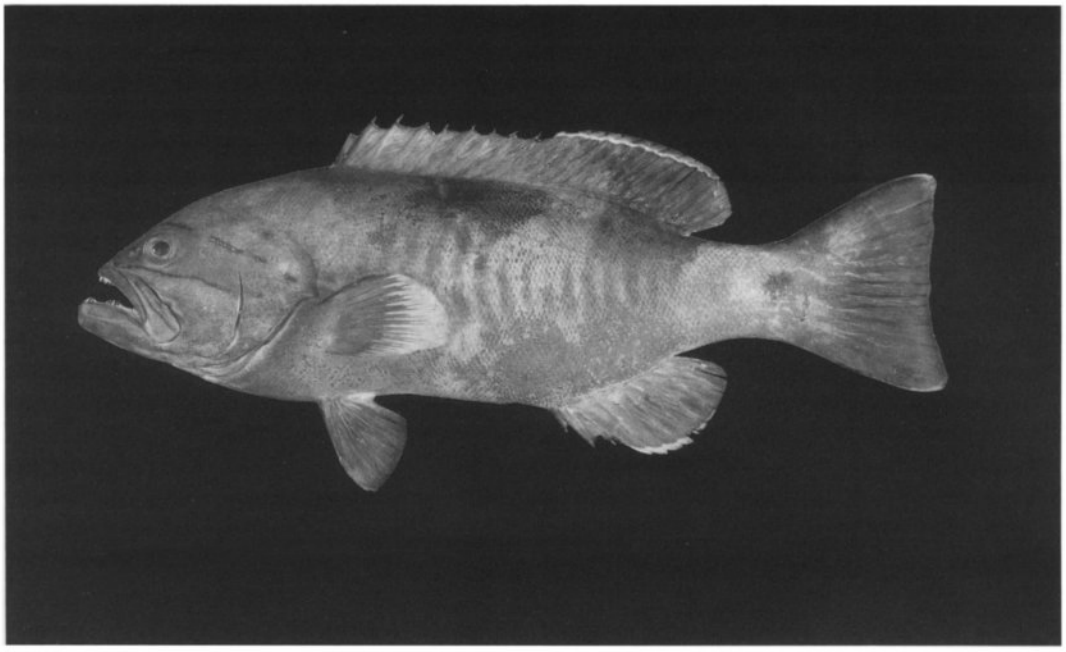

FIG. 7. *Gracila albomarginata*, BPBM 9716, Marshall Is., Majuro, 230 mm SL.

FIG. 8. *Gracila albomarginata*, underwater photograph of adult, Maldive Is., Villingili (J. Randall).

deep, cancellous mesethmoid pit, discontinuous frontoparietal crests, broad supraorbital laminae and blunt frontopterotic ridges that extend well beyond the midpoint of the orbit, figs. 2c, 3c.

Type species.— *Cephalopholis albomarginatus* Fowler and Bean, 1930, by original designation and monotypy.

Gracila albomarginata (Fowler and Bean)
Figs 7-8, Plate IAB

Cephalopholis albomarginatus Fowler and Bean, 1930: 235, fig. 11 (type locality: Danawan Island, vicinity of Sibuko Bay, Borneo; "Allied with *C. polleni* and *C. rogaa*"); Randall, 1964: Redescription; assigned to new monotypic genus *Gracila*).

Aethaloperca albomarginata. Smith, 1954: 925, pl. 33A (new generic allocation; description; distributional records); Smith and Smith, 1963: 15, pl. 12B (listed Seychelles); Postel et al., 1967: 356 (brief description; Reunion).

Gracila albomarginata. Randall, 1964: 282, fig. 1 (redescription; type species of new genus; Society Islands and Tuamotus); Bagnis et al., 1972: 101,unnumbered color photograph (listed from Tahiti and Tuamotus); Katayama, 1974: 101, fig. 2 (description; Naha, Okinawa); Masuda et al., 1975: 212, pl. 45G (brief description; color photograph); Fourmanoir and Laboute, 1976: 65 (brief description; unnumbered color photograph; New Caledonia and Loyalty Islands); Allen and Steene, 1979: 24 (listed Christmas Is., Indian Ocean); Heemstra and Randall, 1984: SERRAN Gracil 1 (occurrence in western Indian Ocean, diagnosis, drawing, comparisons, fishery information); Masuda et al., 1985: 127, pl. 112 EF (brief description; color photograph); Randall, 1985: 470 (listed Society Islands and Tuamotus); Randall, 1986: 192, fig. 22 (briefhdescription; Marshall Islands); Thresher and Colin, 1986: 256 (depth range; Marshall Islands); Heemstra and Randall, 1986: 534, fig. 166.68 & pl. 43 (brief description; color photograph of juvenile); Randall, 1987: 173 (description: behavior); Allen and Steene, 1987: 53, pl. 27, fig. 1 (color photograph, adult, Christmas Is., Indian Ocean); Masuda and Allen, 1987: 115, fig. F (color photograph of 35cm adult).

Description.— Dorsal rays IX,1416 (typically 15); anal rays III,910; pectoral rays 18 or 19; lateralline scales 6674; oblique rows of scales from upper end of gill opening to caudal-fin base 106114; gill rakers 710 + 1416; predorsal bones 2; vertebrae 10+14.

A pair of well-separated, stout canines anteriorly in each jaw, followed by patch of depressible teeth, inner ones largest; canines on dentary smaller, more closely spaced and medial to uppers; side of both jaws with outer row of short, fixed conical teeth that decrease slightly in size posteriorly; medial to this row of teeth is band of depressible villiform teeth (villiform teeth relatively sparse anteriorly); dentary also with inner row of erect, depressible teeth that are longer than their fixed counterparts; vomer with inverted V-shaped band of villiform teeth; palatines with narrow band of villiform teeth; tongue smooth; nostrils subequal, posterior round and simple, anterior oblong, consisting of membranous tube with elevated posterior flap. Preopercular margin finely serrate, with rudiments of larger spines at angle, lower margin smooth and fleshy; marginsjof subopercle and interopercle smooth; middle opercular spine distinctly nearer lower than upper spine; posterodorsal margin of opercular membrane moderately convex. Dorsal and analfin spines relatively slender compared to spines of other epinephelines (Fig. 6a).

Scales cycloid on head, breast, abdomen and on body anterodorsally, ctenoid elsewhere; first scalelet of ctenoid scales usually unfused to structures anterior to it (Fig. 1L); head scaled (including maxilla) except for small area above upper lip and edge of opercular membrane; auxiliary scales present on body of adults.

The following proportional measurements are based on 15 specimens, 198-312 mm SL:

Body depth 2.6-3.3 in SL; body width 1.7-2.5 in depth; head small, its length 2.9-3.2 in SL; dorsal profile of head from front of snout to nape moderately convex; snout 3.2-4.5 in head; orbit diameter 5.5-6.8 in head; interorbital space slightly convex, least fleshy width 4.2-5.3 in head; suborbital depth 11.4-15.9 in head; maxilla extending to or beyond (up to 0.5 eye diameters) a vertical at rear edge of orbit, upper jaw length 1.9-2.0 in head; least depth of caudal peduncle 2.3-2.5 in head; interspinous membranes of dorsal fin slightly incised; fifth to seventh dorsal spines longest, 2.9-3.4 in head; sixth to ninth dorsal soft rays longest, 2.1-2.6 in head; dorsal and anal fins rounded posteriorly, longest dorsal rays not reaching vertical at caudal-fin base; second anal spine slightly shorter than third, 3.5-4.3 in head; third anal spine 3.0-3.8 in head; third or fourth anal rays longest, 2.0-2.4 in head; base of dorsal and anal fins somewhat fleshy; caudal fin emarginate in juveniles, 7.7-11.1 m SL (caudal concavity 2.8-4.9 in head) to truncate or slightly emarginate in adults (caudal concavity 6.0-11.5), its length 1.3-1.5 in head; pectoral fins rounded, middle rays longest, 1.5-2.0 in head; tips of depressed pelvic fins not reaching anus (falling short of anus by a distance of 30-65% fin length), their length 1.7-2.0 in head.

Life colors (based on color transparencies of live fish underwater and freshly collected specimens): juveniles (78-130 mm SL) with head and body bright magenta to violet, paler ventrally; bright reddish orange stripe in dorsal and anal fins (more in soft than spinous portion of dorsal fin) and in each caudal lobe, extending forward onto dorsal and ventral edges of caudal peduncle (more so ventrally); middle area of caudal fin, posterior third of soft dorsal and anal fins, and pectoral fin mostly transparent; pelvic fins white. Occasional juveniles are brown instead of violet, but display the same redorange stripes described above.

Color of adults in life: greenish to brownish gray or brown, sometimes with orangish cast (particularly on head), body with 14-20 dark bars on side (varying from dark orangish brown to nearly black) which are about equal in width or slightly narrower than paler interspaces, bars not extending onto back or lower third of body; round dark spot about as large as eye midlaterally on posterior part of caudal peduncle; head with four, narrow, diagonal, approximately parallel, deep blue bands (which may be broken into dashes or spots), first crossing interorbital spacehand ending above middle opercular spine, second from front of snout, passing just under eye, and continuing onto opercle at level of upper pectoralfin base, third from above maxilla to upper part of corner of preopercle, and last along maxilla and extending posteriorly onto lower cheek; occasional individuals with short diagonal blue line on nape; few scattered deep blue spots may be present dorsally on head and anterodorsally on body; opercular membrane, region under maxilla, pectoral axil, and pelvicfin membranes dull reddish orange; iris largely red; upper and lower edges of caudal fin darker than rest of fin; posterior margin of caudal fin (or sometimes just corners) red or magenta; margins of soft portion of dorsal fin orangered with narrow magenta submarginal band; margin of soft portion of anal fin lavender to magenta; (these margins and that of caudal fin fading to whitish in preservative); outer third of pectoral fins orangish. Adults often display large, squarish white area on back, flanked by broad zones of blackish, and white caudal peduncle and fin, thus accentuating the black peduncular spot and dark upper and lower edges of caudal fin (this color phase well illustrated in Fourmanoir and Laboute, 1976: 65, righthand fig. and Allen and Steene 1987, pl. 27, fig. 1). These large white areas may be quickly assumed by the fish and just as rapidly disappear. Figure 8 shows a color variant from the Maldive Islands in which

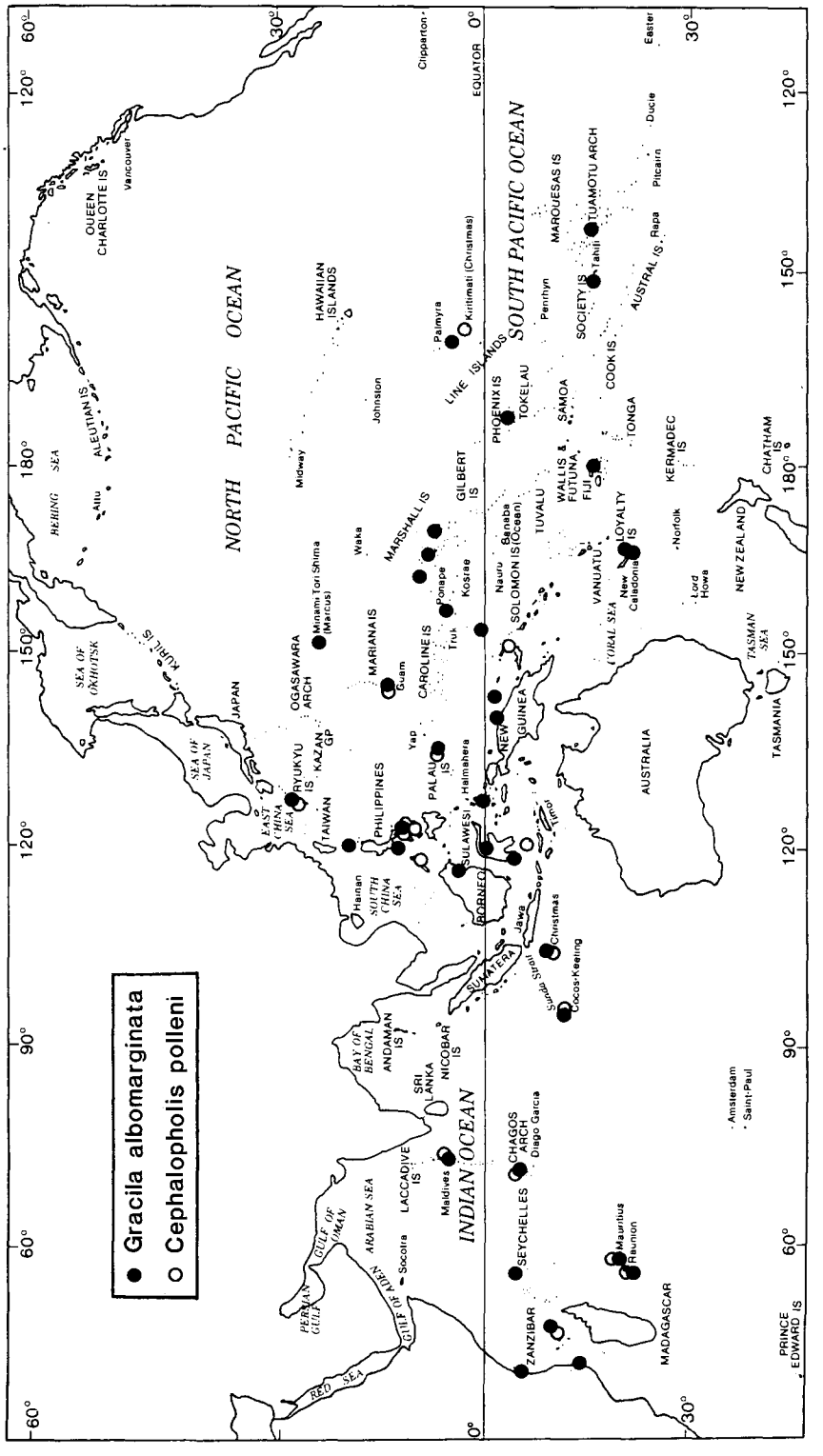

FIG. 9. Distribution of *Gracila albomarginata* and *Cephalopholis polleni* based on specimens examined, field observations and reliable literature records.

there is a broad dark band from snout, enclosing eye, and passing to end of opercle, this band bordered by first two diagonal blue lines on head as described above.

Distribution.— *Gracila albomarginata,* a clear-water, outer reef dwelling species, occurs from east Africa to French Polynesia. Records plotted on distribution map (Fig. 9) for which no specimens are cited are based on the following: East Africa between 3°15'S, including Zanzibar and Pemba Island (Smith, 1954); Seychelles (Smith and Smith, 1963); Tuamotu Archipelago (Randall, 1964); Ryukyu Islands, Okinawa (Katayama, 1974); New Caledonia and Loyalty Islands (Fourmanoir and Laboute, 1976); Christmas Island, Indian Ocean (Allen and Steene, 1979); northern Philippines, Sabtang Island, Duvuck Bay, 20°18'N, 121°51'E (underwater sighting by W. Smith-Vaniz); Marshall Islands, Kwajalein (underwater photograph by D. S. Johnson); and Line Islands, Fanning Island (underwater sighting by J. E. Randall). This species is usually found on exposed reef areas at depths greater than 15 m. The 350 meter maximum depth reported for the species is based on an unverified record of a specimen (BPBM 31632) obtained from a Tahitian fisherman who was using an electric reel to fish in deep water. In a study of deep-reef fishes of Enewetak Atoll, Marshall Islands (Thresher and Colin 1986) observed *G. albomarginata* only between 60-75 m. An actively swimming grouper, *G. albomarginata,* is not inclined to rest on the substrate; it tends to retreat from divers rather than seek shelter on the reef.

Material Examined.— Total of 47 specimens 78-312 mm SL from 37 collections. ALDABRA: MNHN 54.131 (1, 272), Calypso. REUNION: BPBM 20054 (1, 204), 20 Oct 1973; MNHN 1965-1 (1, 312). MAURITIUS: BPBM 16317 (1, 89), 16 m, 12 Nov 1973; BPBM 16350 (1, 125), 23 m, 22 Nov 1973; BPBM 20310 (1, 111 C&S), Grand Baie, 35 m, 30 Nov 1973; RUSI 5694 (3, 84-89), Apr 1976. CHAGOS ARCHIPELAGO: ROM 36647 (1, 287), Solomons, 05°21'34"S, 72°12'24"E, sta. WE 79-92, 5-7 m, 23 Mar 1979. MALDIVE ISLANDS: CAS 61349 (1, 275), Malé. COCOS-KEELING ISLANDS: ANSP 131743 (1, 269), Turk Reef, sta. 28, 6-12 m, 9 Mar 1974; ANSP 131744 (1, 266), Turk Reef, sta. 50, 27-46 m, 21 Mar 1974. BORNEO: USNM 89985 (295, holotype of *Cephalopholis albomarginatus*), Danawan Is., vicinity of Sibuko Bay, Albatross, 27 Sep 1909; USNM 183856 (1, 230), Sipadan Is., ca. 04°07'N, 118°50'E, "Albatross", 28 Sep 1909. SULAWESI: USNM 122254 (1, 224), Gulf of Tomini, "Albatross", 25 May 1844; USNM 183854 (1, 233), Birabirahan Is., ca. 05°09'S, 119°36'E, Albatross, 31 Dec 1909; USNM 183857 (1, 215), Binang Unang Is., 0°04'S, 121°36'E, "Albatross", 17 Nov 1904; USNM 183858 (1, 206), Buka Buka Is., 0°42'S, 121°44'E, "Albatross", 20 Nov 1909; USNM 183860 (1, 232), W. of Malibagu Point, ca. 0°23'N, 123°59'E, "Albatross", 21 Nov 1909. INDONESIA: USNM 183853 (2, 225), Halmahera, Gane, 0°45'S, 128°13'E, "Albatross", 1 Dec 1909; USNM 183855 (1, 224), Makyan Is., 0°21'30"N, 127°16'45"E, "Albatross", 28 Nov 1909; USNM 183859 (1, 227), Dodinga Bay, Maitara Is., 0°43'N, 127°22'E, "Albatross", 26 Nov 1909. PHILIPPINES: USNM 99780 (2, 118-125), no precise locality, "Albatross"; USNM 183852 (1, 264), Luzon, Port Maricaban Reef, 13°39'N, 120°50'E, "Albatross", 21 Jul 1908; USNM 149319 (1, 145), Cebu market, "Albatross"; USNM 183851 (1, 234), Mindoro, Sablayan Bay, "Albatross", 12 Dec 1908. IRIAN JAYA: AMNH 16557 (1, 221), Tanamerah Bay, 80 km W. of Hollandia, 1944. PAPUA NEW GUINEA: USNM 272105 (1,198), Hermit Is., PechahI., 01°35'24"S, 145°0'36"E, 33 m. FIJI: BPBM 30946 (1, 268), Vanua Balavu, Nuku Cikobia Is., 28 May 1986. MARCUS ISLAND (MINAMI TORI SHIMA): BPBM 7061 (1, 79), 12 m, 6 Sep 1968. GUAM (?): BPBM 17648 (1, 305), ca. 1966. BELAU (PALAU IS.): CAS 62442 (1, 239), Aulong, 5 Sep 1955. KAPINGAMARANGI ATOLL: CAS 62441 (1, 262), 8 Jul 1954. POHNPEI (PONAPE): USNM 272471 (1, 243). MARSHALL ISLANDS: ANSP 138972 (1, 78), Enewetak, 8 m, 8 May 1978; BPBM 12210 (1,

FIG. 10. *Cephalopholis polleni:* above, BPBM 31502, Indonesia, Bonerate Group, 41 mm SL; below, WAM P.26116007, Christmas Is., 62 mm SL.

262), Enewetak, 24 m, 3 Feb 1972; BPBM 12794 (1, 287), Enewetak, 12 m, 6 Apr 1972; BPBM 9716 (2, 221-226), Majuro, Laura I., 12 m, 31 Mar 1970; BPBM 22704 (1, 67), Majuro, 34 m, 24 Aug 1979. PHOENIX ISLANDS: BPBM 16261 (1, 143 C&S), Canton Is., 16 Dec 1973; CAS 39601 (1, 130), Canton Is., 9 m, Feb 1977. SOCIETY ISLANDS: BPBM 31632 (1, 270), Tahiti, 350 m, 6 Jul 1985; CAS-SU uncat. (1, 257), Tetiaroa, 16 Feb 1957.

CEPHALOPHOLIS Schneider 1801

Diagnosis.— An epinephelin serranid genus distinguished by following combination of characters: Dorsal fin IX,14-17; anal fin III,8-10; dorsal and analfin spines relatively robust compared to segmented rays (Fig. 6b); caudal fin usually rounded (truncate to slightly emarginate in *C. polleni*); pectoral rays 16-18, middle rays longest; ctenoid scales with first scalelet fused to structures anterior to it; no antrorse spines on ventral edge of opercle; neurocranium (see text discussion). Type-species: *Cephalopholis argus* Schneider, 1801, by monotypy.

Cephalopholis polleni (Bleeker)

Fig. 10, Plate Ic

Epinephelus polleni Bleeker, 1868: 336 (type locality: Reunion); Bleeker and Pollen, 1874: 19, pl. 7 (description, color illustration); Sauvage, 1891:

81, pl. 8, fig. 3 (description); Boulenger, 1895: 182 (description; Mauritius).

Plectropoma lineatum Steindachner *in* Bliss, 1883: 45 (type locality: Mauritius).

Cephalopholis virgatus Fourmanoir, 1954: 214 (type locality: Comoro Is., Anjouana); Fourmanoir, 1957: 148, pl. 8B (description); Morgans, 1982: 8 (synonymized with *C. polleni*).

Aethaloperca polleni. Postel et al., 1967: 357, fig. 5 (brief description).

Gracila okinawae Katayama, 1974: 101, fig. 2 (type locality: Naha, Okinawa); Masuda et al., 1975: 212, pl. 45H (brief description; color photograph); Allen and Steene, 1979: 24 (synonymized with *G. polleni*).

Gracila polleni. Allen and Steene, 1979: 24 (listed Christmas Is., Indian Ocean); Schroeder, 1980: 158, fig. 148 (brief description; color photograph; Sulu Archipelago); Shepard and Myers, 1981: 60 (listed Guam; photograph). Heemstra and Randall, 1984: SERRAN Gracil 2, pl. 7, upper left fig. (color photograph, occurrence in western Indian Ocean, diagnosis, drawing, comparisons, fishery data); Masuda et al., 1985: 127, pl. 112G (brief description; color photograph); Heemstra and Randall, 1986: 534, fig. 166.69 & pl. 43 (brief description; color photograph); Randall, 1987: 174 (description; distribution); Allen and Steene, 1987: 53, pl. 27, fig. 2 (color photograph of 30cm adult, Christmas Is., Indian Ocean).

Cephalopholis polleni. Morgans, 1982: 8 (brief description, compiled).

Description.— Dorsal rays IX,15; anal rays III,9; pectoral rays 17-18; lateralline scales 66-72; oblique rows of scales from upper end of gill opening to caudal-fin base 112-124; gill rakers 78 + 14-17; predorsal bones 2; vertebrae 10+14.

A pair of well-separated canines anteriorly in each jaw, followed by a patch of depressible teeth, the inner ones largest; canines on dentary smaller, more closely spaced and medial to uppers; side of both jaws with outer row of erect, fixed, conical teeth that decrease slightly in size posteriorly; upper jaw with medial band of depressible villiform teeth; lower jaw with one or two inner rows of erect, depressible teeth, outermost longer than their fixed counterparts; vomer with inverted V-shaped band of villiform teeth; palatines with narrow band of villiform teeth; tongue smooth; nostrils subequal, posterior round and simple, anterior oblong and consisting of membranous tube with elevated posterior flap. Preopercular margin with slight indentation above angle and finely serrated; subopercle and interopercle both finely serrated; middle opercular spine nearer lower than upper spine; posterodorsal margin of opercular membrane moderately convex. Dorsal- and anal-fin spines relatively robust compared to segmented rays (Fig. 6b).

Scales cycloid on head, breast, abdomen and on body anterodorsally, ctenoid elsewhere; first scalelet of ctenoid scales usually fused to structures anterior to it (Fig. 1K); head scaled except for area between anterior nostril and upper lip, and edge of opercular membrane; maxilla naked or with few embedded scales; auxiliary scales absent on body of adults.

The following proportional measurements are based on 13 specimens, 149-241 mm SL. Body depth 2.7-3.1 in SL; body width 1.9-2.5 in depth; head length 2.6-2.9 in SL; dorsal profile of head from front of snout to nape slightly convex; snout 3.6-4.4 in head; orbit diameter 4.9-5.9 in head; interorbital space slightly convex, least fleshy width 5.0-7.1 in head; suborbital depth 10.0-12.2 in head; maxilla extending to vertical at rear edge of orbit, upper jaw length 1.9-2.1 in head; least depth of caudal peduncle 2.5-3.0 in head; interspinous membranes of dorsal fin deeply incised; fourth to seventh dorsal spines longest, 2.7-3.5 in head; sixth to ninth dorsal soft rays longest, 2.2-2.7 in head; dorsal and anal fins rounded posteriorly, longest dorsal rays not reaching vertical at caudal-fin base; second and third anal spines subequal, the second 2.5-3.2 in head; third or fourth anal rays longest,

1.9-2.5 in head; base of dorsal and anal fins somewhat fleshy; caudal fin truncate to slightly emarginate, its length 1.6-1.9 in head; pectoral fins rounded, middle rays longest, 1.5-1.9 in head; pelvic fins reaching to or slightly behind anus, their length 1.5-2.1 in head.

Life colors (based on color transparencies of live fish underwater and freshly collected specimens): smallest juvenile (BPBM 31502, 41 mm SL) yellowish brown, shading to yellow on caudal peduncle and on snout, and to lavender ventrally on head, breast, and abdomen; faint blue band from lower edge of eye to upper pectoralfin base and conspicuous black spot on snout; base of caudal fin bright yellow, continuing as broad band in each caudal lobe (upper and lower margins of caudal fin pale bluish white, tips of lobes orange); central area of caudal fin hyaline with whitish rays; spinous portion of dorsal fin suffused with yellow; remaining fins pale.

Color of adults, based on underwater photographs taken by J. E. Randall at depths of 46-52 m in Indonesia and Christmas Island (Kiritimati), Line Islands: head green anteriorly and on nape, shading on rest of head and anterodorsal body to yellowish brown and on remainder of body to yellow with dark-edged stripes of bright violet, purple, or blue of about same width as yellow interspaces (stripes usually slightly irregular and increasing in number with growth from six in the 62 mm juvenile of Fig. 10 to 14 or more in adults; on some individuals stripes posterodorsally on body angle upward as they pass posteriorly, extending into base of soft dorsal fin); head with three prominent violet to blue stripes, one above eye, one through eye, and one just below eye, these crossing forehead; four narrower, more diagonal stripes of same color, one above maxilla across cheek, one on maxilla and continuing onto lower cheek, one on edge of upper lip, and one on edge of lower lip; black streak along upper edgehof maxillary groove; dorsal yellowish brown region of head, nape, and anterodorsal part of body with few scattered short violet to blue lines (some curved) or elongate spots; iris with inner ring of yellow; median fins yellow with blue stripes which may be irregular or broken into spots; exposed leading edge and tip of dorsal spines blue, outer edge of interspinous membranes often red; margin of soft portion of dorsal and anal fins blue, usually with submarginal red band; upper and lower edges of caudal fin blue, posterior margin often red; pectoral fins with blue and yellow rays and clear membranes; pelvic fins yellow with blue lateral margin.

Remarks.— None of the three junior synonyms (*Plectropoma lineatum*, *Cephalopholis virgatus* and *Gracila okinawae*) was compared with *C. polleni* when first proposed. Although we have not examined the types of the latter two nominal species, the descriptions and original or subsequently published illustrations of the types are unmistakable. According to Bauchot et al. (1984), the two syntypes of *C. virgatus* are both deposited in the collection IRSM, Station oceanographique de Nossi-Be.

Distribution.—Although infrequently encountered, *Cephalopholis polleni* is wide-ranging on Indo-Pacific reefs where it occurs from the Comoro Islands eastward to Kiritimati in the Line Islands. Records plotted on the distribution map (Fig. 9) for which no specimens were examined are based on the following: Comoro Islands, Anjouana (Fourmanoir 1954); Ryukyu Islands, Okinawa (Katayama 1974); western Sulu Archipelago (Schroeder 1980); and Maldive Islands, Malé, underwater sighting by R. E. Pyle. Day's (1888: 781) record of the species (as *"Serranus polleni"*) from Madras, India is based on a misidentification of *Cephalopholis formosa* (Shaw).

A relatively deep-dwelling species, *C. polleni* is usually found lurking in or near caves

on dropoffs at depths exceeding 35 m. This grouper, in contrast to *Gracila albomarginata*, tends to seek shelter on the reef rather than flee when closely approached.

Material Examined.— Total of 27 specimens, 39-339 mm SL from 23 collections. REUNION: RMNH 5511 (204 mm SL, holotype of *Epinephelus polleni*; BPBM 20055 (1, 158.5), 20 Oct 1973; MNHN 1965-2 (1, 249), 1965. MAURITIUS: BM(NH) 1842.4.25.73 (1, 275, dry mount); BM(NH) 1866.10.28.6 (1, 232); MCZ 5712 (241, holotype of *Plectopoma lineatum*), Nicolas Pike Coll., Agassiz No. 167; MNHN 7425 (1, 339), Lienard. CHAGOS ARCHIPELAGO: ROM 36636 (1, 168), Peros Banhos, 05°27'03"S, 71°48'57"E, sta. WE79-54, 42 m, 6 Mar 1979. COCOS-KEELING ISLANDS: ANSP 131785 (1, 175 C&S), Turk Reef, sta. 60, 67-73 m, 26 Mar 1974; ANSP 131821 (1, 183), Turk Reef, sta. 47, 36-49 m, 20 Mar 1974; ANSP 131822 (3, 161-174), Turk Reef, sta. 57, 51-58 m, 25 Mar 1974. CHRISTMAS ISLAND: WAM P.26115-001 (1, 204) and WAM P.26116-007 (1, 62), Northwest Point, 35-45 m, 67 Jun 1978. INDONESIA: BPBM 31502 (2, 39-41), Kakavia Is., Bonerate Group, 06°53'40"S, 122°13'30"E, 11 m, 9 Oct 1986. PHILIPPINES: BPBM 21166 (1, 149), Mactan Is., 10°18'N, 123°58'E, 27 m, 24 Aug 1977; BPBM 22606 (1, 167), Cebu City market, 3 Aug 1978; USNM 222113 (1, 149), Pamilacan Is., 09°29'20"N, 123°55'00"E, sta. SP 78-41, 21 Jun 1978. NEW BRITAIN: BM(NH) 1981.12.24.1 (1, 186) Nodup (near Rabaul), 40 m, 15 Jul 1975; BM(NH) 1981.12.24.2 (1, 184) Nodup, 50 m, 15 Aug 1975. BELAU (PALAU IS.): BPBM 13831 (1, 161), Augulupelu Reef, 38-46 m, 26 Jan 1972. GUAM: UG 6183 (1, 169). KIRITIMATI (CHRISTMAS IS.): BPBM 31888 (1, 75), 53 m, 16 Jul 1987; BPBM 31944 (2, 96-122), 52 m, 3 Aug 1987.

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TABLE 1. Distribution of selected character states in certain genera and species of Epinephelinae.

	Epinephelus spp.	*Cephalopholis* spp.	*Cephalopholis*		*Gracilia albomarginata*	*Aethaloperca rogaa*
			igarashiensis	*polleni*		
Dorsal-fin spines	11*	9	9	9		9
Caudal fin	emarginate to rounded	rounded	rounded	truncate to slightly emarginate	*juveniles:* emarginate *adults:* truncate or slightly emarginate	truncate
First scalelet	free	fused	fused	fused	free	free
Mid-ventral melanophores in larvae	large, single	small, series	?	?	?	?
Head length in SL	2.2 - 2.8	2.3-2.8	2.3 - 2.4	2.6 - 2.9	2.9 - 3.2	2.5 - 2.7
Body depth in SL	2.5 - 3.7	2.6-3.2	2.0 - 2.3	2.7 - 3.1	2.6 - 3.3	2.1 - 2.5
Pectoral fin shape	symmetrical, middle rays longest	like *Epinephelus*	like *Epinephelus*	like *Epinephelus*	like *Epinephelus*	asymmetrical, fifth or sixth ray longest
Thickness of fin spines	robust	robust	robust	robust Fig. 6b	slender Fig. 6a	robust

* Except 10 in *E. analogus* and *E. nigritus*; and 9 in *E. acanthistius*