

AID TO IDENTIFICATION OF AMERICAN GROUPER LARVAE

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ABSTRACT

The serranid tribe Epinephelini (subfamily Epinephelinae) is represented in American waters by 36 nominal species and 2 undescribed ones in 4 genera, 2 of which are monotypic. Although adult groupers are readily identifiable, specific identification of larvae has proved problematic. Kendall (1979) was able to identify larvae of the four American genera on the basis of meristic data, but found that specific identification was prevented by overlap in ranges of meristic characters among many species and by the apparent absence of any species-specific larval characters. Grouper larvae are characterized by elongate, serrated second dorsal and pelvic fin spines. Comparative examination of the serration patterns of these larval spines shows that they exhibit species and species-group differences. These features in conjunction with frequency distributions of meristic characters and geographic distributions allow identification of larvae of 13 of the 21 American species of *Epinephelus*. The remaining eight can be placed in one of three species groups. Striking morphological differences between larval *E. afer* from the western Atlantic and eastern Pacific suggest that these populations are specifically distinct. Larvae of the genus *Mycteroperca* share diagnostic features, but specific separation remains unresolved.

The serranid subfamily Epinephelinae, as defined by Johnson (1983), comprises five tribes, Nipponini, Epinephelini, Diploprionini, Grammistini and Liopropomini. Of these, the Epinephelini, commonly called groupers, are by far the most speciose, most widely distributed and most important commercially. In his revision of the American groupers, Smith (1971) recognized 35 species in three genera. He did not consider the monotypic genus *Gonioplectrus*, however Kendall and Fahay (1979) suggested that *Gonioplectrus* is closely related to the epinephelines, and Johnson (1983) included it in that tribe. Thus, the tribe Epinephelini is represented in American waters by 36 nominal species in four genera. Two undescribed species of *Epinephelus* are known from the eastern Pacific (R. H. Rosenblatt, personal communication).

Although adults of the American groupers are readily identifiable, characters that aid in specific identification of their larvae have not been described. Kendall (1979) briefly reviewed the history of description of larval groupers worldwide and reiterated the general physiognomy that characterizes them (Fig. 1). Most striking are the elongate, serrated second dorsal and pelvic fin spines. The first and third dorsal spines are much shorter than the second, but also usually bear serrations. Also characteristic of all epinepheline larvae are the long serrated spine at the angle of the preopercle and a large pigment spot on the caudal peduncle that migrates from the ventral midline to a mid-lateral position early in development. Epinepheline larvae are easily recognizable by their possession of the above combination of characters.

Kendall (1979) was able to separate larvae representing the genera *Epinephelus*, *Mycteroperca* and *Paranthias* on the basis of fin ray counts but not by larval morphology. Larvae of the fourth American genus, *Gonioplectrus*, also have unique fin ray counts and differ from all other epinepheline larvae in having a deeper body and the serrated second and third dorsal spines nearly equal in length (Kendall and Fahay, 1979). With the exception of the monotypic *Paranthias* and

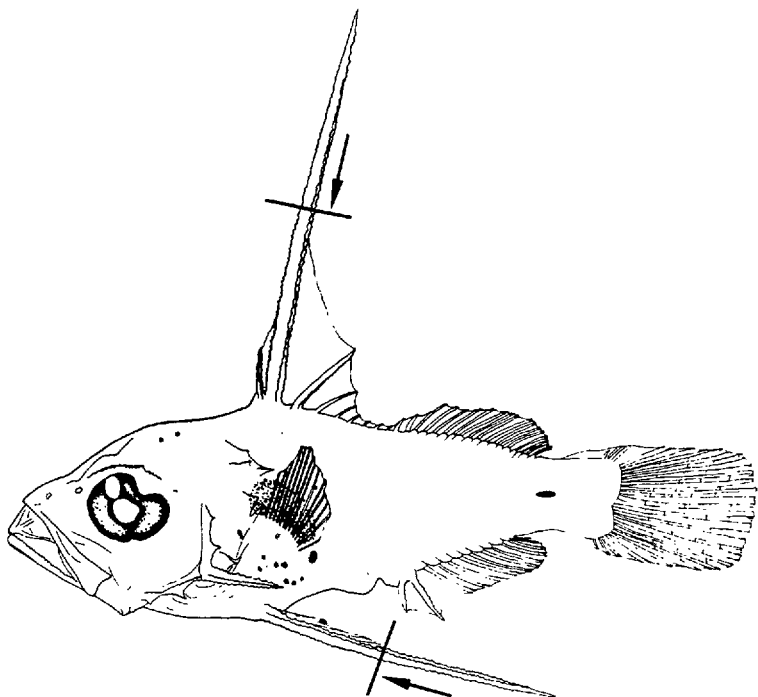


Figure 1. Larva of a member of the *Epinephelus morio* species group, 7.6 mm (from Kendall, 1979, fig. 32). Solid lines and arrows indicate location and orientation of cross-sectional views shown in Figure 3.

Gonioplectrus, Kendall (1979) was unable to positively identify any epinepheline larva to species. There is considerable overlap in ranges of meristic counts among many species of American groupers. In some cases fin ray counts allow placement in one of several species groups, but Kendall found no species or species-group larval characters and concluded "that evolutionary differences within this group are not reflected in larval morphology."

An ongoing investigation of grouper spawning in the South Atlantic Bight, conducted off the coast of South Carolina since 1979 by the MARMAP (Marine Resources Monitoring, Assessment and Prediction) program of the Marine Resources Research Institute, Charleston, South Carolina, has led to further morphological studies of grouper larvae with the goal of improving abilities to identify them. During close examination of large numbers of grouper larvae, it became evident that different patterns of serration are present on the elongate second dorsal and pelvic fin spines. Serrations on these fin spines have been known since the earliest description of epinepheline larvae (Fage, 1918), but the detailed configurations of these serrations have never been investigated. Further study of these serration patterns indicated that they are not due to individual variability, but that they are consistent features characterizing certain species and, more commonly, species groups. The major purposes of this paper are to describe the various types of serrations found on second dorsal and pelvic fin spines of larvae of American groupers and to demonstrate their efficacy for specific identification when combined with typical dorsal, anal and pectoral fin ray counts. Although it is still not possible to identify larvae of all American species of groupers, the

discovery of larval characters diagnostic of species and species groups brings us closer to this goal and may provide additional insight into the evolutionary relationships of these species.

MATERIALS AND METHODS

Material for this investigation came from several sources. Western Atlantic material was collected off South Carolina from February to September, 1979, from the R/V DOLPHIN and R/V ATLANTIC SUN by the MARMAP program of the Marine Resources Research Institute, Charleston, South Carolina. Dr. A. W. Kendall provided western Atlantic material from collections of the R/V DOLPHIN taken by NMFS (National Marine Fisheries Service), Sandy Hook, in 1965–1968 from Cape Cod, Massachusetts, to Palm Beach, Florida. Eastern Pacific material was also supplied by Kendall from the EASTROPAC and CalCOFI programs. Dr. E. D. Houde provided material from neuston net samples in the Gulf of Mexico. Specimens were also examined from collections of the Academy of Natural Sciences (Philadelphia), American Museum of Natural History, California Academy of Sciences, Harbor Branch Foundation, Museum of Comparative Zoology, Natural History Museum of Los Angeles County, Royal Ontario Museum, Scripps Institution of Oceanography, NMFS Southeast Fisheries Center (Beaufort, Panama City and Miami Laboratories), U.S. National Museum of Natural History, University of California at Los Angeles, University of Miami Rosenstiel School of Marine and Atmospheric Science and University of Michigan Museum of Zoology. Over 700 larvae and early juveniles (2.5 mm NL–62.0 mm SL) were examined. Although the majority of the Atlantic specimens came from the South Atlantic Bight, Caribbean and Gulf of Mexico, specimens from as far north as Shinnecock Bay, New York, and as far south as northern Brazil were examined. Eastern Pacific material ranged from Bahia Magdalena, Baja California, to Paita, Peru, and included specimens from the Galapagos Islands and the Gulf of California.

Measurements were made with a calibrated ocular micrometer or with dial calipers. Notochord length (NL) was taken from tip of upper jaw to tip of notochord before and during notochord flexion. Standard length (SL) was taken from tip of upper jaw to posterior margin of hypurals after notochord flexion. All measurements are SL unless otherwise noted. In the species accounts, typical (most frequent) counts are given for dorsal, anal and pectoral fin rays.

Drawings were prepared with the aid of a camera lucida. Second dorsal spines were drawn in situ, but left pelvic spines were removed in order to illustrate them in two views. Although diagnostic features are detectable without staining, spines were frequently stained with alizarin to facilitate illustration. Several whole specimens were cleared and stained for bone and cartilage following the method of Dingerkus and Uhler (1977) as modified by Fritzsche and Johnson (1979).

RESULTS

Identification

Although the ranges of fin ray counts overlap among many epinepheline species, the frequency distributions of these counts (Tables 37–39 in Smith, 1971) provide a valuable tool in species identification. Consulting Table I of Kendall (1977), where only total ranges are given, one would conclude that *Epinephelus niveatus* and *E. drummondhayi* are not separable on the basis of numbers of dorsal fin rays (XI, 14–16 vs. XI, 15–16). However, the frequency distributions of Smith (1971) indicate that 50 of 63 specimens of *E. niveatus* had 14 dorsal soft rays (only two had 16), whereas seven of eight specimens of *E. drummondhayi* had 16 (as did 10 additional specimens we examined). Thus, it is imperative that typical (most frequent) counts, rather than total ranges, be applied in the identification of epinepheline larvae. In this way, larvae can be identified with some degree of certainty (in this study $\geq 80\%$) and frequently co-occurrence of a specific larval feature (e.g., pattern of spine serrations) with the typical counts will validate the specific or species-group identification. Typical dorsal, anal and pectoral (sum of left and right) fin ray counts for all described species of American groupers (excluding *Mycteroperca*) are given in Table 1. This table is based on the frequency distribution tables of Smith (1971) and some additional counts made during the course of this study. Typical counts were arbitrarily considered to be those that encompassed $\geq 80\%$ of the sample counted. Unfortunately Smith's sample size

Table 1. Typical (most frequent) dorsal, anal, and pectoral fin ray counts of American groupers (excluding *Mycteroperca*) based on frequency distribution tables of Smith (1971). Counts given are those that encompassed $\geq 80\%$ of the specimens examined. Pectoral counts are given as the sum of left and right fins. Species are listed in order of increasing number of dorsal spines and dorsal soft rays respectively. Subgenera of Smith (1971) are in parentheses

Species	Ocean	Dorsal	Anal	Pectoral
<i>Gonioplectrus hispanus</i>	A	VIII, 13	III, 7	32
<i>Paranthias furcifer</i>	A&P	IX, 18-19	III, 9	40
<i>Epinephelus</i> (<i>Cephalopholis</i>)				
<i>cruentatus</i>	A	IX, 14	III, 8	32
<i>panamensis</i>	P	IX, 14	III, 8	34
<i>fulvus</i>	A	IX, 15	III, 9	36
(<i>Epinephelus</i>)				
<i>acanthistius</i>	P	IX, 17	III, 9	35-37
<i>nigritus</i>	A&P	X, 14-15	III, 9	36-38
<i>analogus</i>	P	X, 17	III, 8	39-40
<i>niveatus</i>	A&P	XI, 14	III, 9	36
<i>flavolimbatus</i>	A	XI, 14	III, 9	36
<i>mystacinus</i>	A	XI, 14-15	III, 9	37-38
<i>guaza</i>	A	XI, 15-16	III, 8	36
<i>itajara</i>	A&P	XI, 15-16	III, 8	37-38
<i>guttatus</i>	A	XI, 15-16	III, 9	34
<i>drummondhayi</i>	A	XI, 16	III, 9	36
<i>morio</i>	A	XI, 16-17	III, 9	34
<i>striatus</i>	A	XI, 16-17	III, 8	36
<i>adscensionis</i>	A	XI, 16-17	III, 8	36-38
<i>labriiformis</i>	P	XI, 16-17	III, 8	35-39
(<i>Alphesthes</i>)				
<i>afer</i>	A&P	XI, 17-18	III, 9	34
<i>multiguttatus</i>	P	XI, 19	III, 9	35-37
(<i>Dermatolepis</i>)				
<i>inermis</i>	A	XI, 19-20	III, 9	36-38
<i>dermatolepis</i>	P	XI, 18-19	III, 9	38-39

varied considerably among species (6-129 specimens) and this may affect the reliability of some of these counts in representing the true population. We attempted to supplement the smaller samples with additional counts where possible.

Species of *Mycteroperca* are not included in this table because frequency distributions of all fin ray counts are too similar to allow separation by typical counts. Larvae of the genus *Mycteroperca* are easily distinguished from other epinephelines by the following combination of features: higher number of anal soft rays (10-13, usually 11, vs. 7-10, usually 8 or 9), characteristic spine morphology (Table 2) and presence of a cleithral pigment spot. Because no species-specific morphological differences were identified, the species of *Mycteroperca* are not treated here.

Adult fin ray complements are present in groupers fairly early in development and can generally be used in identification of larvae by 6-7 mm. The characteristic dorsal and pelvic spine morphology is present at about 5 mm and is in some cases retained beyond 30 mm. Juvenile pigmentation is usually not present until at least 20 mm and may appear considerably later. Thus, fin ray counts and spine morphology provide a means of identification from about 5-6 mm to 20-30 mm, or until species-specific pigmentation has developed in the juvenile.

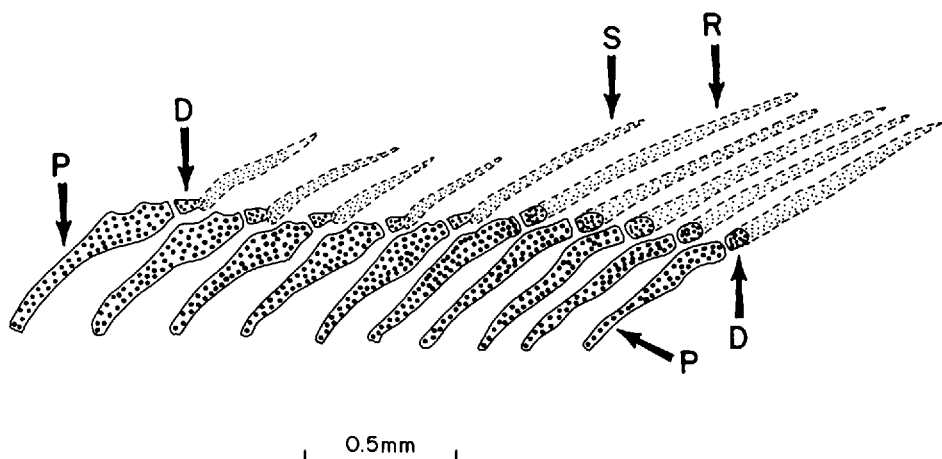


Figure 2. Left lateral view of middle portion of dorsal fin of a 7.6 mm *Mycteroperca* sp. showing cartilaginous pterygiophores (large stipples) and developing fin rays (small stipples). Note difference in shape and position of distal pterygiophore elements supporting spines and soft rays. D, distal radial; P, proximal radial; R, first soft ray; S, last dorsal spine.

Kendall (1979) noted that a complete distinction between spines and soft rays is difficult in epinepheline larvae because the last two dorsal spines and last anal spine develop initially as soft rays and may not completely transform to spines until about 20 mm. This presents no problem with anal fin ray counts since the adult complement of spines is invariably three and the remaining elements can be counted as soft rays. On the other hand, the adult complement of dorsal spines cannot be assumed (because it varies specifically) and counting of untransformed spines as soft rays will result in misidentification. Fortunately, it is possible to identify those elements that will eventually become spines by the nature and position of the distal radials of the pterygiophores supporting them (Fig. 2). The distal radials supporting the dorsal spines are typically somewhat flattened or triangular in comparison to the more spherical distal radials supporting the soft rays. Furthermore, their dorsal margins lie somewhat below a line drawn tangent to the dorsal margins of the succeeding soft-ray distal radials. In addition, the bases of all spines articulate with only the posterior portion of their corresponding distal elements, whereas soft-ray bases lie directly over their associated distals, and eventually embrace them laterally. These consistent features allow an accurate spine and soft-ray count as soon as all elements are present.

Larval Spines

In all epinepheline larvae, the first three to four dorsal spines bear serrations and the second spine is considerably elongate. The manner in which these spines are supported is described by Johnson (1983). This spine complex develops prior to formation of the more posterior spines and soft rays and is first evident as a small opaque area in the anterior portion of the dorsal fin fold (~2.5 mm NL). By ~3.5 mm NL, the first three spines are developing within this area and the second is notably elongate. It is the second, elongate spine that develops species and species-group specific serrations (hereinafter referred to as spinelets). The spine itself is chevron-shaped in cross-section, with the apex of the chevron

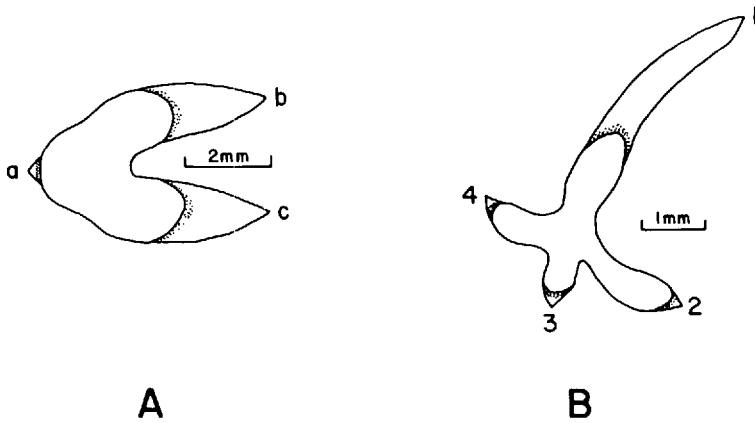


Figure 3. A, Transverse section (see Fig. 1) of the second dorsal spine of a 16.0 mm *Mycteroperca* sp., dorsal view: a, spinelet on apex ridge; b and c, spinelets on posterolateral wings. B, Transverse section (see Fig. 1) of the left pelvic spine of a 14.0 mm *Mycteroperca* sp., posterior view: 1, dorsomedial (primary) ridge, showing enlarged recurved spinelet; 2, ventromedial ridge and spinelet; 3, ventrolateral ridge and spinelet; 4, dorsolateral ridge and spinelet. (Numbers in succeeding pelvic spine illustrations correspond to these.)

pointing anteriorly (Fig. 3A). Spinelets are borne along the margin of the apex and the margins of the posterolaterally-directed wings. The apex spinelets are generally small bumps or simple spine-like projections. The wing margin spinelets are usually larger and may consist of straight, curved (toward the tip of the spine), recurved (toward the base of the spine), or bifurcated spine-like projections, the shape and size of which vary along the length of the spine. Dorsal spines are illustrated in left lateral view, showing the spinelets of the apex and left posterolateral wing. Spinelets of the right wing are essentially identical to those of the left.

Pelvic spine buds appear at 2.5 mm NL and by 5–6 mm SL the spines are well-developed, elongate and bear diagnostic spinelets. In cross-section, each pelvic spine consists of a central core with four ridges of varying dimensions projecting at approximately right angles to one another (Fig. 3B). For reference, ridges of the left pelvic spine are numbered clockwise (in posterior view) beginning with the dorsomedial ridge. (Ridges of the right pelvic spine would be numbered counterclockwise.) Each ridge bears spinelets along its margin, although it is generally those of the first (hereafter referred to as the primary ridge) that exhibit diagnostic features. Spinelets on the lateral wings of the second dorsal spine and the primary ridge of the pelvic spine are usually similar for individual specimens, but diagnostic characteristics tend to be better developed in the pelvic spine. Left pelvic spines are illustrated in ventromedial and ventrolateral view so that the spinelets of all four ridges can be shown.

Due to the scarcity of larval epinepheline material in museum and larval collections, it was not possible to obtain complete developmental series of most species. For seven species, no specimens <10 mm were seen and three species were only represented by specimens ≥ 20 mm. Where more complete series were examined (e.g., *E. cruentatus*, 5.2–20.5 mm and *E. itajara*, 6.2–17.4 mm), it was evident that although minor changes in spinelet configuration do occur with growth, the salient features are detectable from as early as 5–6 mm until the spines begin

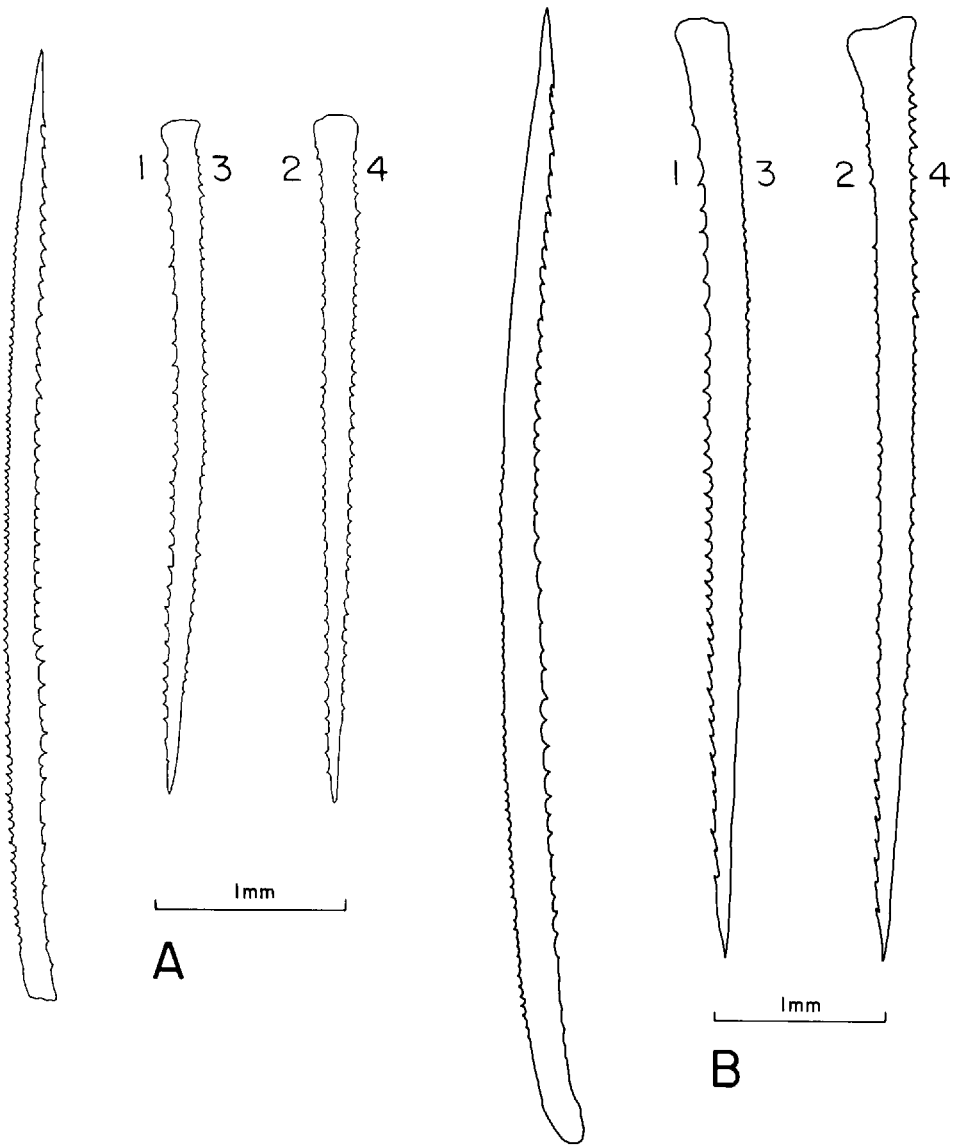


Figure 4. *Epinephelus morio/drummondhayi/guttatus*, second dorsal spine (left lateral view) and left pelvic spine (ventromedial and ventrolateral views): A, 9.0 mm specimen; B, 14.4 mm specimen.

to regress (≥ 20 mm). Where specimens were available, spines from individuals of two size classes (5–10 mm and 10–20 mm) were illustrated.

Relative lengths of second dorsal and pelvic spines differ significantly among species. Again, due to lack of complete series, frequent broken spines, and small numbers of specimens, it was not possible to statistically quantify allometric changes in spine lengths. It is clear, however, that certain species are characterized by extremely long spines throughout the larval periods whereas other species develop relatively short spines. Ranges of dorsal spine lengths as percentage standard length are given for most species in the species accounts.

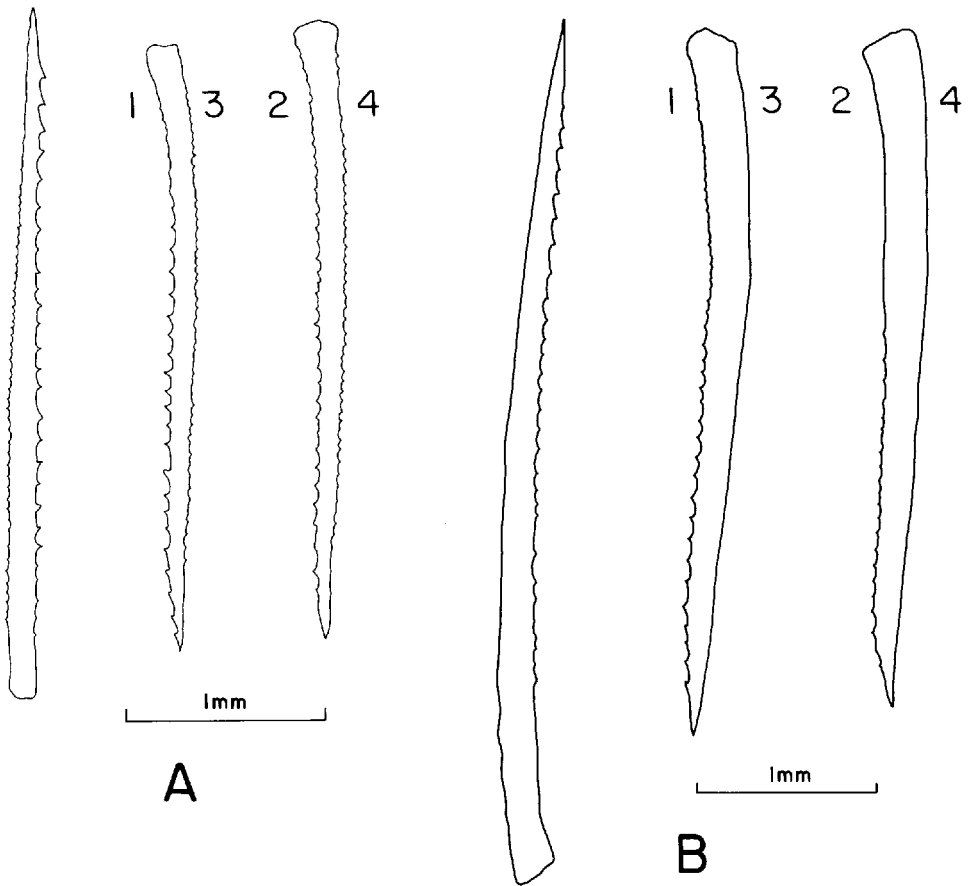


Figure 5. *Epinephelus striatus/adscensionis*, second dorsal spine (left lateral view) and left pelvic spine (ventromedial and ventrolateral views): A, 10.0 mm specimen; B, 17.6 mm specimen.

Species Accounts

In the accounts that follow, second dorsal and pelvic spinelet configurations are characterized for each species or species group, beginning with the most generalized configurations. Table 2 summarizes the major diagnostic features.

Epinephelus morio, *E. guttatus* and *E. drummondhayi*

Larvae of these three western Atlantic species (*Epinephelus morio* group) were not separable. *Epinephelus morio* and *E. guttatus* share similar fin ray counts (D XI, 15–17; A III, 9; P₁, 34). *Epinephelus drummondhayi* differs only by a slightly higher total number of pectoral fin rays (36). All specimens examined with these counts had similar body form, relative spine lengths and spinelet morphology. Second dorsal and pelvic spines are of the generalized type in which all spinelets are simple, straight, and relatively small (Fig. 4). With the exception of Atlantic specimens of *E. afer* (see account of *E. afer*), fin ray counts distinguish members of the *E. morio* group from all other species with spines of this type.

Approximately 90 larval specimens ranging in size from 3.5 mm NL to 14.4

mm SL were examined. In 10 specimens (6.3–13.8 mm) the second dorsal spines were 46–67% SL. A 25.9 mm specimen of *E. morio* showed juvenile pigmentation and had no traces of larval spination. Although it is possible that all specimens examined of this type with 34 total pectoral fin rays were either *E. morio* or *E. guttatus*, it seems more likely that both species were seen, considering the geographic coverage and number of specimens examined. Several specimens from the South Atlantic Bight had 36 total pectoral fin rays and were probably *E. drummondhayi*, but they differed in no obvious way from specimens with 34.

Epinephelus striatus and *E. adscensionis*

The two western Atlantic species, *E. striatus* and *E. adscensionis*, share identical fin ray counts (D XI, 16–17; A III, 8; P₁ 36–38). These counts allow separation of their larvae from all other western Atlantic species with the exception of *E. itajara*, which has a distinctive larval spine morphology and *E. guaza*, known in the western Atlantic only from the southern hemisphere. Second dorsal and pelvic spines of larval *E. striatus* and *E. adscensionis* are reminiscent of the *E. morio* group in which all spinelets are simple, straight and quite small (Fig. 5). The spines appear somewhat shorter and the spinelets more widely spaced, but positive separation of the *E. striatus* and *E. morio* groups is possible only after development of a full complement of anal fin rays.

The smallest specimen examined was 10.5 mm (second dorsal spine 40% SL), and most of the approximately 200 specimens were 20–30 mm (second dorsal spine 17–21% SL). Onset of spinelet resorption occurred as early as 19 mm; however, characteristic spinelet morphology was evident in all but a few of the 200 specimens.

Epinephelus labriformis

Epinephelus labriformis is known only from the eastern Pacific. Fin ray counts (D XI, 16–17; A III, 8; P₁ 35–39) distinguish it from all other Pacific epinephelines except *E. itajara*. Thirty specimens were examined (12.1–44.0 mm), only two of which were less than 20 mm. Based on the specimens examined, juvenile transformation occurs late in this species. Although most specimens were transformed by 30 mm, five specimens (30.1–36.3 mm) still had elongate dorsal and pelvic spines (second dorsal spine 40–48% SL) with distinct spinelets, and the smallest transformed specimen was 24.1 mm. The second dorsal spine is of the generalized type, bearing simple straight spinelets along the wing margins and a single row of very small spinelets at the apex (Fig. 6A). The primary ridge of each pelvic spine bears a series of slightly enlarged curved spinelets along about three-fourths of its length. These are reduced to simple spinelets along the distal one-fourth of this ridge. The remaining pelvic ridges bear smaller, alternately curved and straight spinelets. These larval spine configurations readily distinguish *E. labriformis* from *E. itajara*.

Epinephelus analogus

Epinephelus analogus occurs only in the eastern Pacific and is distinguished from other Pacific species by the following counts: D X, 17; A III, 8; P₁ 39–40. Two specimens (26.2 and 32.4 mm) were examined, both of which retained elongate second dorsal (44–46% SL) and pelvic spines. The wing margins of the dorsal spine and the primary ridge of the pelvic spine bear small, straight spinelets

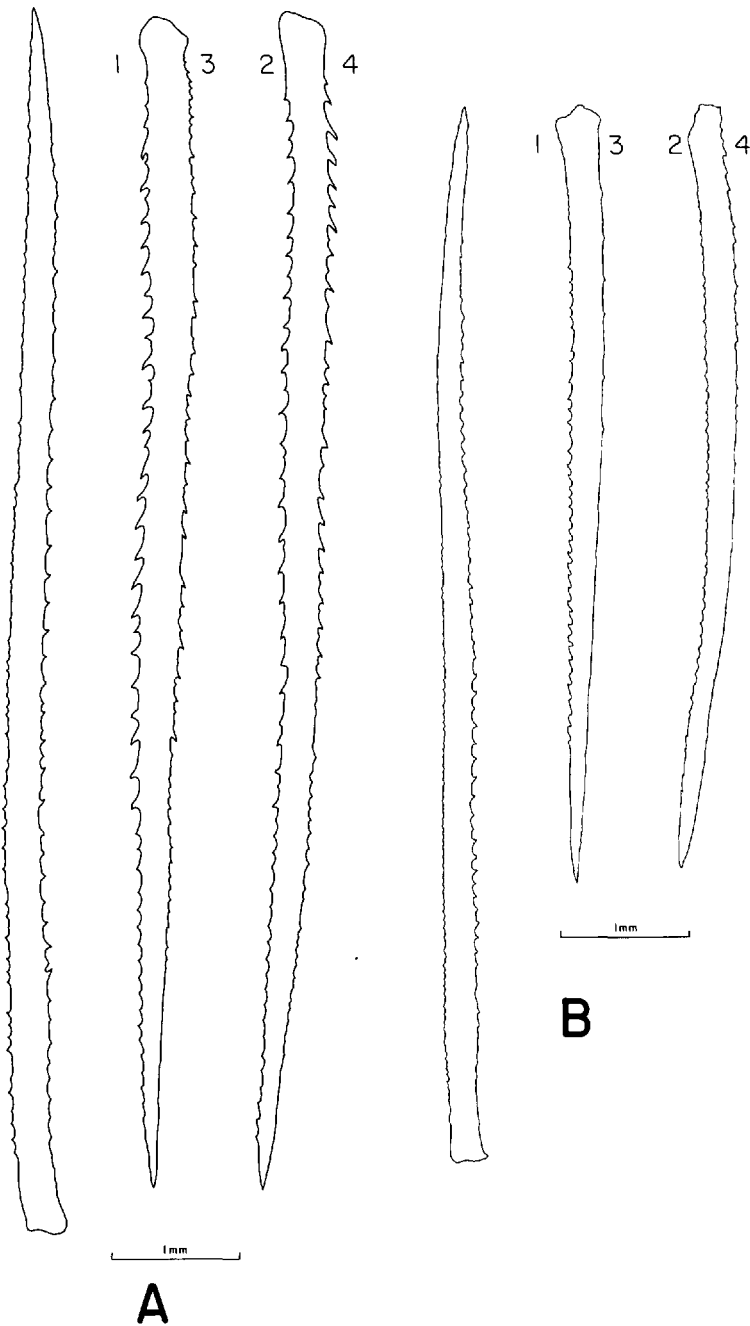


Figure 6. A, *Epinephelus labriformis*, second dorsal spine (left lateral view) and left pelvic spine (ventromedial and ventrolateral views), 12.1 mm specimen. B, *Epinephelus analogus*, second dorsal spine (left lateral view) and left pelvic spine (ventromedial and ventrolateral views), 26.2 mm specimen.

which become slightly recurved near the tip (Fig. 6B). These recurved spinelets were more pronounced in the 32.4 mm specimen. Spinelets are poorly developed on the remaining pelvic ridges, apparently as the result of resorption.

Epinephelus niveatus and *E. flavolimbatus*

Epinephelus niveatus (eastern Pacific and western Atlantic) and *E. flavolimbatus* (western Atlantic) share identical fin ray counts (D XI, 14; A III, 9; P₁ 36); these counts separate them from all other American groupers. Six larval specimens (4.0–19.0 mm) of *E. niveatus*/*E. flavolimbatus* from the western Atlantic were examined (second dorsal spine 65–86% SL). In addition, two transforming (23.5 and 24.8 mm) and five fully transformed (26.0–31.3 mm) juveniles of *E. niveatus* were examined as well as six juvenile *E. flavolimbatus* (29.1–33 mm). Pacific material of *E. niveatus* consisted of five specimens (9.0–33.2 mm) all of which retained elongate larval spines with characteristic spinelets.

Second dorsal and pelvic spines of *E. niveatus* and *E. flavolimbatus* (Fig. 7) are similar to those of *Mycteroperca* (Fig. 15B). Wing margins of the second dorsal spine bear large recurved spinelets along most of their length with a series of smaller straight spinelets proximally. In most specimens < 10 mm, there is a single row of small straight spinelets at the apex (Fig. 7A). In larger specimens an additional row of similar spinelets develops along either side of the primary apex row (Fig. 7B), distinguishing this type of spine from that of *Mycteroperca*. These secondary rows are sometimes incomplete but may extend along almost the entire length of the spine as they do in *E. mystacinus* (Fig. 8A) and *E. cruentatus* (Fig. 10). The primary ridge of the pelvic spine resembles the second dorsal spine wing margins in bearing large recurved spinelets along most of its length. The remaining pelvic ridges bear small straight spinelets, those near the base of ridge 4 being slightly enlarged.

Epinephelus mystacinus

Epinephelus mystacinus apparently occurs only in the western Atlantic. Although Seale (1940) reported a 40 mm juvenile from the Galapagos Islands (identification confirmed by Smith, 1971, and by us), the collection locality is questionable (R. H. Rosenblatt, personal communication), and no additional specimens have been reported from the Pacific. Fin ray counts of *E. mystacinus* (D XI, 14–15; A III, 9; P₁ 37–38) are similar to those of *E. niveatus* and *E. flavolimbatus*, but differ in that the latter two species rarely have 15 dorsal soft rays and typically have only 36 pectoral rays. Smith (1971) included *E. mystacinus* in his *E. niveatus* group. A single larval specimen (20.0 mm) was available, collected off Florida by the Harbor Branch Foundation from their Johnson-Sea-Link submersible. Fin ray counts (D XI, 15; A III, 9; P₁ 38) indicate that it is most likely *E. mystacinus*. Furthermore, it differs from *E. niveatus* and *E. flavolimbatus* in pelvic spine morphology. This specimen showed no evidence of spine or spinelet resorption (second dorsal spine 75% SL).

The second dorsal spine is like that of *E. niveatus* and *E. flavolimbatus* in having large recurved spinelets along most of the length of the wing margins and three parallel rows of simple straight spinelets at the apex (Fig. 8A). The primary ridge of the pelvic spine also resembles these two species in bearing large recurved spinelets along most of its length. However, the second pelvic ridge differs in bearing, along the distal one-half of its length, large recurved spinelets similar to those of the primary ridge. Enlarged recurved spinelets on the second pelvic ridge

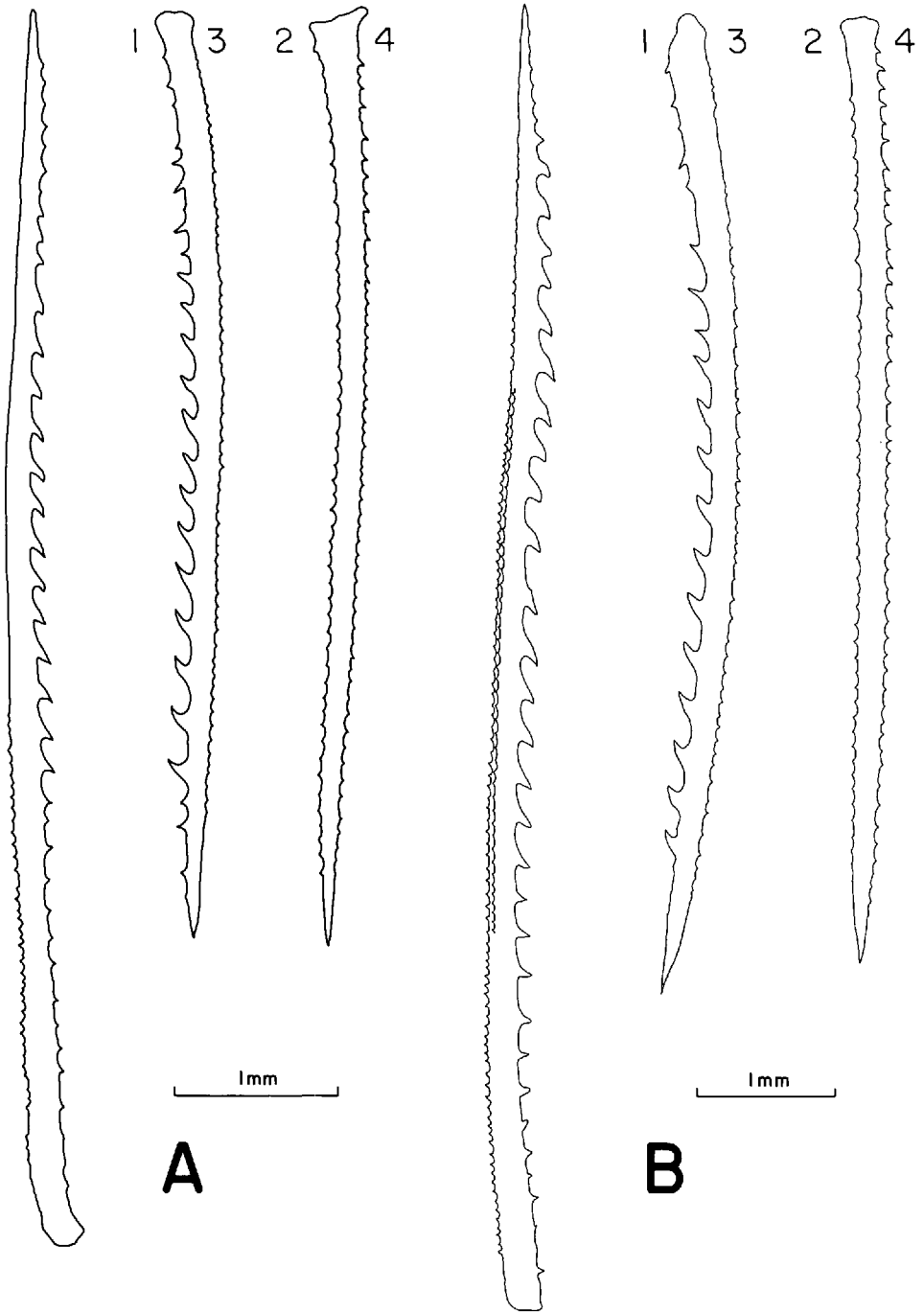


Figure 7. *Epinephelus niveatus/flavolimbatus*, second dorsal spine (left lateral view) and left pelvic spine (ventromedial and ventrolateral views): A, 8.7 mm specimen; B, 13.1 mm specimen.

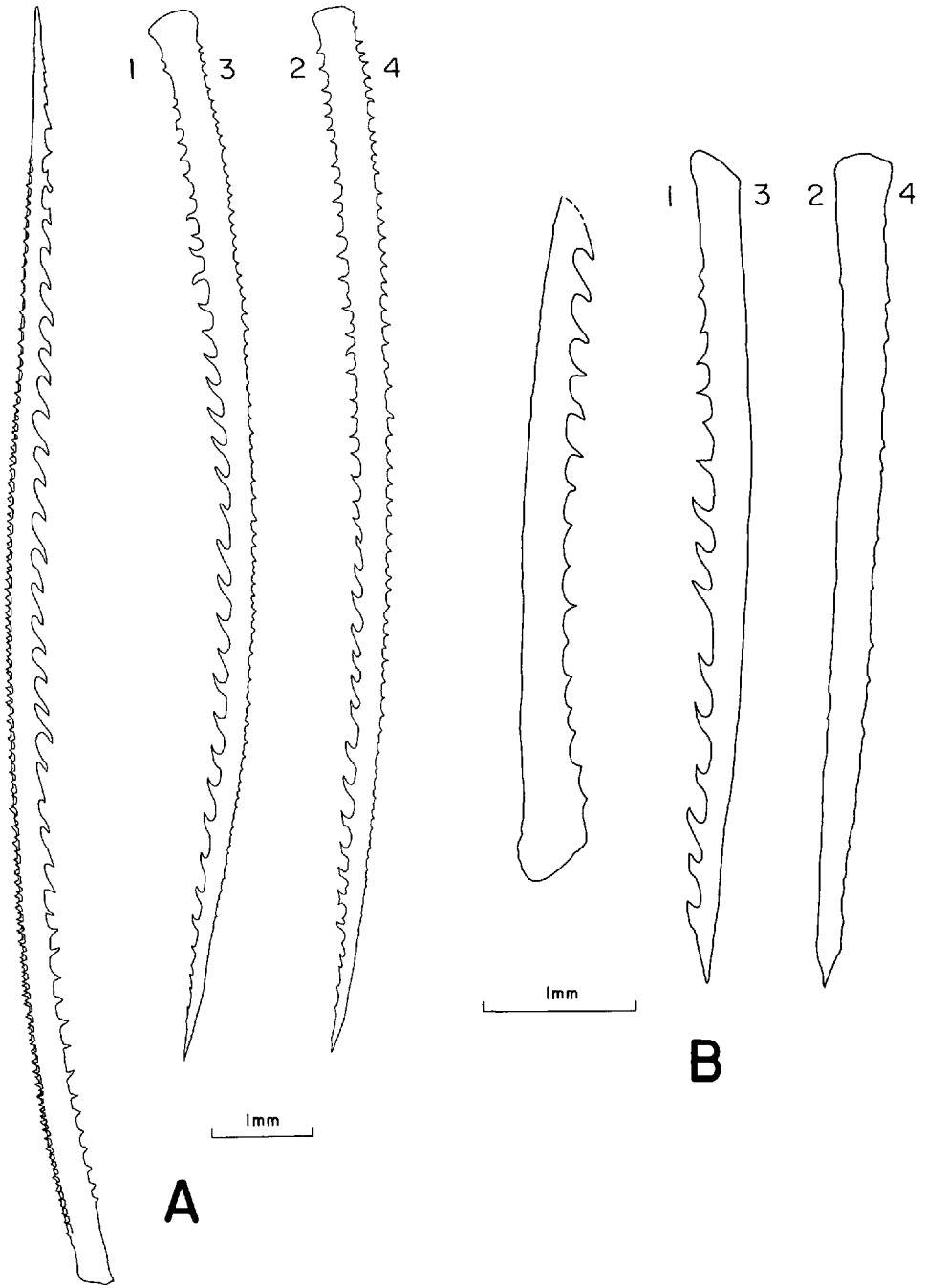


Figure 8. A, *Epinephelus mystacinus*, second dorsal spine (left lateral view) and left pelvic spine (ventromedial and ventrolateral views), 20.0 mm specimen. B, *Epinephelus acanthistius*, second dorsal spine (broken, left lateral view) and left pelvic spine (ventromedial and ventrolateral views), 25.0 mm specimen.

were seen elsewhere only in *E. itajara* and in a specimen tentatively identified as *E. nigrilus*. Spinelets of the remaining pelvic ridges are similar to those of *E. niveatus* and *E. flavolimbatus*.

Epinephelus nigrilus

Epinephelus nigrilus occurs in both the eastern Pacific and western Atlantic and is distinguished from other epinephelines by the following counts: D X, 14–15; A III, 9; P₁ 36–38. Based on fin ray counts, a single Atlantic specimen (9.1 mm) was tentatively identified as *E. nigrilus*. Second dorsal and pelvic spines of this specimen (not illustrated) were damaged, preventing complete characterization of the spinelets. Large, very widely-spaced, recurved spinelets were present along the primary ridge of the left pelvic spine and several similar spinelets were detectable on ridge 2, suggesting a configuration similar to that of *E. mystacinus* and *E. itajara* (Figs. 8A, 9). The second dorsal spine was broken near the base.

Epinephelus acanthistius

Epinephelus acanthistius occurs only in the eastern Pacific and is distinguished from other eastern Pacific epinephelines by the following counts: D IX, 17; A III, 9; P₁ 35–37. Nine specimens were examined, ranging in length from 22.2–27.1 mm. Second dorsal (17.3–26.7% SL) and pelvic spines showed some evidence of resorption particularly at the tips, but spinelets were easily characterized. Spinelet morphology of *E. acanthistius* (Fig. 8B) is reminiscent of that seen in *E. niveatus* and *E. flavolimbatus* (Fig. 7), and Smith (1971) considered *E. acanthistius* to be a member of the *E. niveatus* species group. Wing margins of the second dorsal spine bear simple straight spinelets proximally, but distally these become large, broad-based recurved spinelets. The relative extent of the recurved spinelets was impossible to determine due to resorption of an unknown distal portion of the second dorsal spine. Although spinelets of the apex ridge were mostly resorbed, rudiments in this area suggest the existence of both primary and secondary ridges, as in *E. niveatus*. The primary ridge of the pelvic spine bears large recurved spinelets along most of its length. Spinelets on the remaining pelvic ridges are poorly developed, apparently as the result of resorption.

Epinephelus itajara

Epinephelus itajara is known from the eastern Pacific and western Atlantic. The dorsal and anal fin ray counts (D XI, 15–16; A III, 8) are identical to those of *E. guaza*, but *E. itajara* differs from this species in having a higher number of total pectoral fin rays (37–38 vs. 36). Although *E. itajara* may have either 15 or 16 dorsal soft rays, the specimens identified in this study had only 15, distinguishing them from *E. striatus*, *E. adscensionis* and *E. labriformis*, which have 16 or 17. Five specimens, all from the Atlantic, were examined, ranging in size from 6.2–17.4 mm. Second dorsal and pelvic spines of a 9.2 mm (dorsal spine 88% SL) and a 16.9 mm (dorsal spine broken, 29% SL) specimen are illustrated (Fig. 9). Each lateral wing of the second dorsal spine bears, along most of its length, a series of large recurved spinelets, preceded by a shorter series of small straight spinelets near the base of the spine. The pelvic spines are characterized by having enlarged recurved spinelets on both the first and second ridges. These recurved spinelets begin about one-fourth of the spine length from the base and continue to the tip of the spine on both ridges. Large recurved spinelets on the

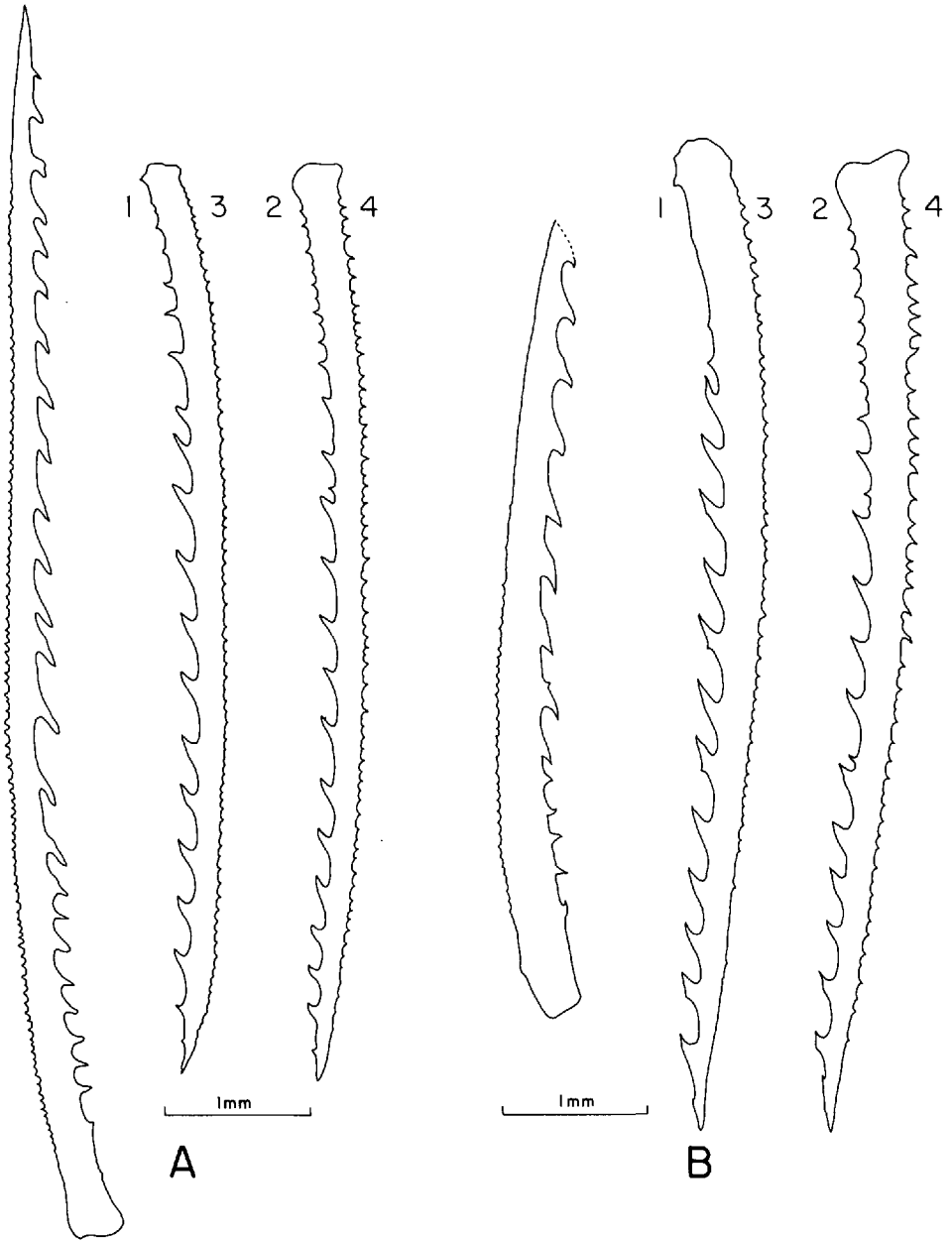


Figure 9. *Epinephelus itajara*, second dorsal spine (left lateral view) and left pelvic spine (ventromedial and ventrolateral views): A, 9.2 mm specimen; B, 16.9 mm specimen (dorsal spine broken).

second pelvic ridge were seen in only two other species, *E. mystacinus* (where they are less extensive) and *E. cf. E. nigrilus*. *Epinephelus itajara* is also characterized by the presence of a pigment spot at the cleithral symphysis, found elsewhere only in *E. cruentatus* and *Mycteroperca*.

Epinephelus guaza

Epinephelus gauza occurs in the eastern and western Atlantic and in the Mediterranean. In the western Atlantic, it is limited to the southern hemisphere. Fin ray counts (D XI, 15–16; A III, 8; P₁ 36) separate it from other Atlantic epinephelines except *E. striatus* and *E. adscensionis*. No specimens were examined from within the range of *E. guaza*.

Epinephelus cruentatus

Epinephelus cruentatus occurs only in the western Atlantic and is distinguished from other Atlantic epinephelines by the following meristics: D IX, 14; A III, 8; P₁ 32. Its larvae appear to be among the most common in Caribbean collections. Forty-six specimens were examined (5.2–20.5 mm). Second dorsal and pelvic spines are extremely elongate in smaller larvae (second dorsal spine 80–105% SL in specimens <10 mm; 20–49% SL in specimens >17 mm), and bear extremely widely-spaced spinelets along their entire length. The second dorsal spine is distinctive in having three parallel ridges of very small straight spinelets along the apex (Fig. 10). Secondary apex ridges occur elsewhere only in Smith's (1971) *E. niveatus* group and in *Gonioplectrus*. Wing margins bear large, recurved spinelets along most of their length, some of which tend to flatten and bifurcate slightly in larger specimens. Spination of the first pelvic ridge is diagnostic, consisting of several enlarged, widely spaced bifurcate spinelets proximally, followed by a series of large recurved spinelets. Bifurcate spinelets were evident in all specimens examined, including those in which regression of the spines had begun (18–20 mm). Bifurcate spinelets occur occasionally in other species (e.g., *E. niveatus*, *E. mystacinus* and *Mycteroperca*), but the consistent presence of several widely spaced in sequence near the spine base is unique to *E. cruentatus*. The remaining pelvic ridges bear very small simple spinelets.

Epinephelus cruentatus is also distinguished by the presence of a small pigment spot at the cleithral symphysis. This spot occurs elsewhere only in *E. itajara* and *Mycteroperca*.

Epinephelus panamensis

Epinephelus panamensis is known only from the eastern Pacific where it is distinguished from other epinephelines by the following meristics: D IX, 14; A III, 8; P₁ 34. No larval specimens of this species were available, but six juveniles (21.3–26.5 mm) were examined. Although regression of the larval spines was nearly complete (second dorsal spine 10.5–23.4% SL), characteristic secondary spination was recognizable at the base of the pelvic spines in three specimens (not illustrated). This consisted of a series of bifurcate spinelets similar to those found in *E. cruentatus*. *Epinephelus cruentatus* and *E. panamensis* were at one time placed in the genus *Petrometopon* Gill. Smith (1971) treated *Petrometopon* as a junior synonym of *Cephalopholis* and relegated the latter to subgeneric status, including the three American species *E. cruentatus*, *E. panamensis* and *E. fulvus*. A close relationship between *E. cruentatus* and *E. panamensis* is supported by the presence of bifurcated larval spinelets in both species; however, as described below, *E. fulvus* does not share this feature.

Epinephelus fulvus

Epinephelus fulvus occurs only in the Atlantic, where it is distinguished from other epinephelines by the following fin ray counts: D IX, 15; A III, 9; P₁ 36.

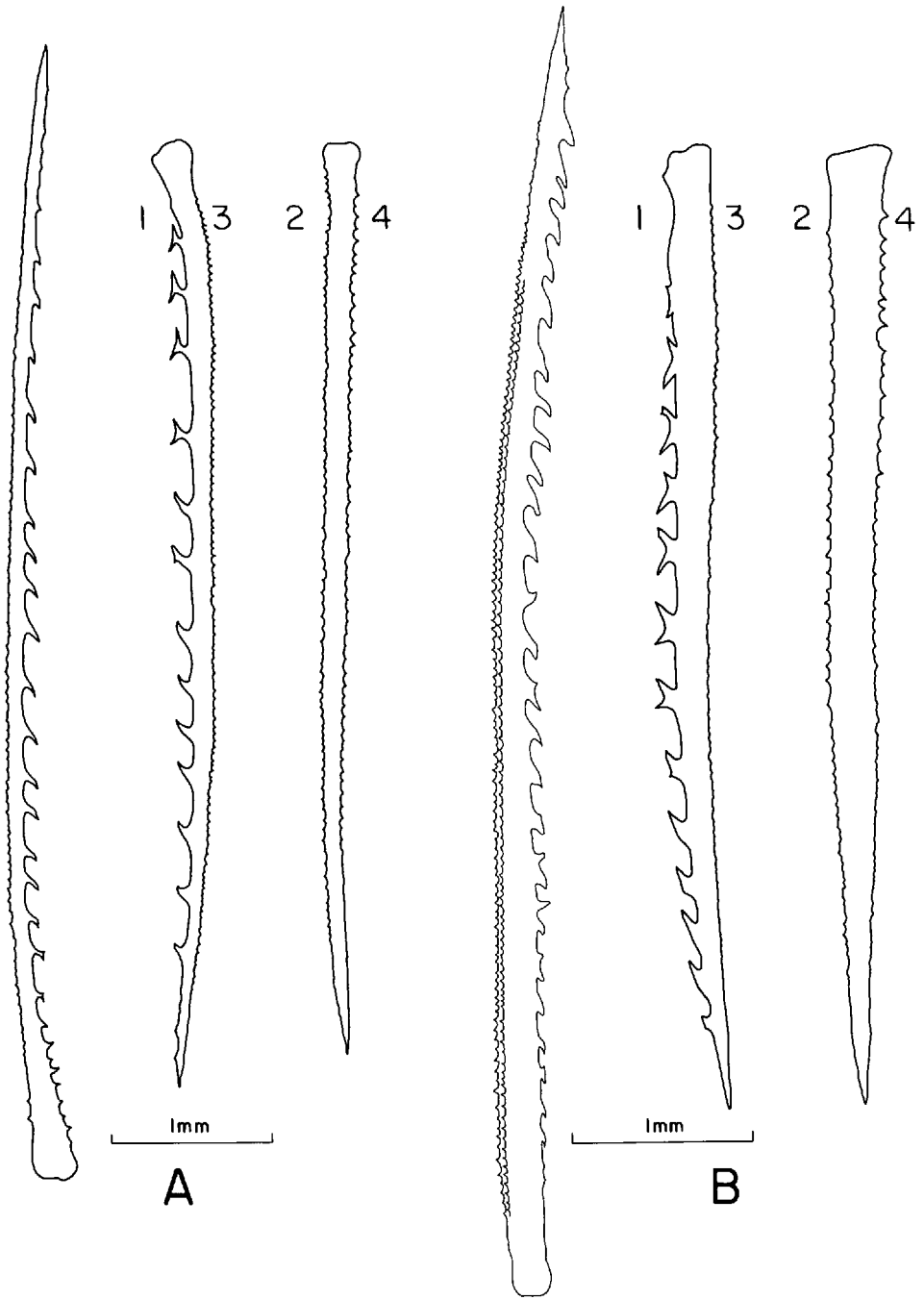


Figure 10. *Epinephelus cruentatus*, second dorsal spine (left lateral view) and left pelvic spine (ventromedial and ventrolateral views): A, 6.5 mm specimen; B, 16.0 mm specimen.

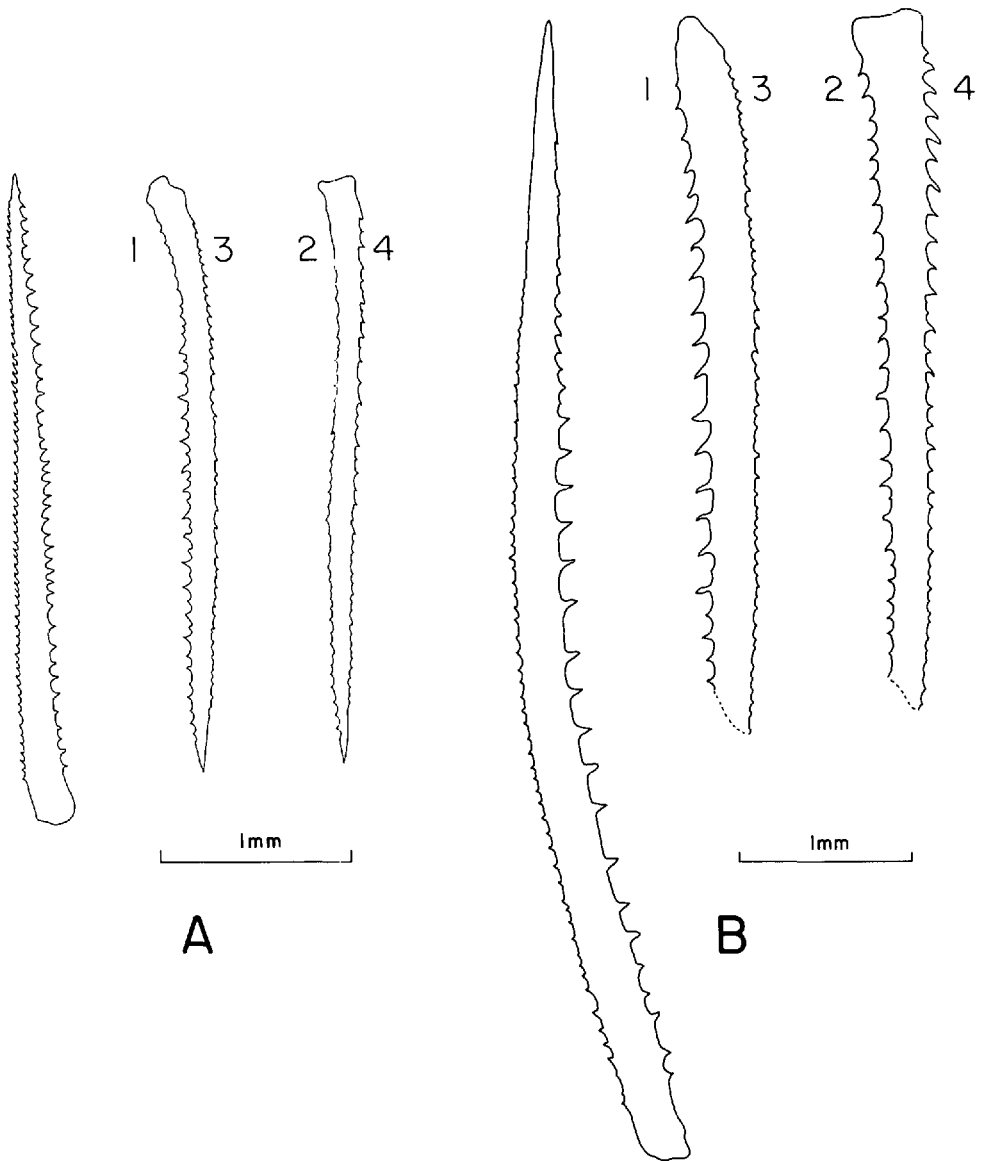


Figure 11. A, *Epinephelus fulvus*, second dorsal spine (left lateral view) and left pelvic spine (ventromedial and ventrolateral views), 8.0 mm specimen. B, *Epinephelus inermis*, second dorsal spine (left lateral view) and left pelvic spine (broken, ventromedial and ventrolateral views), 10.5 mm specimen.

Seven larval specimens were examined (5.5–25.2 mm). In five specimens (5.5–8.4 mm), second dorsal spine lengths were 48–55% SL. Two specimens (24.0–25.2 mm) showed some spine resorption, however, distinct spinelets were still recognizable. In 45 juveniles (22.1–36.7 mm) spinelet resorption was complete and there was some evidence of juvenile pigmentation. Spinelet configuration of *E. fulvus* differs markedly from that of *E. cruentatus* and *E. panamensis*, two

species that Smith (1971) considered to be close relatives of *E. fulvus*. Larvae of *E. fulvus* have second dorsal and pelvic spines of the most generalized type, with all spinelets simple, straight and relatively small (Fig. 11A), a pattern shared with several other species. *Epinephelus fulvus* is readily distinguishable from the others in having only nine dorsal spines. It also appears to differ from these species in having most of the spinelets on the apex ridge of the second dorsal spine curved toward the tip of the spine.

Epinephelus multiguttatus

Epinephelus multiguttatus occurs only in the eastern Pacific and is distinguished from other Pacific species by the following counts: D XI, 19; A III, 9; P₁ 35–37. Seven larval specimens (8.4–31.2 mm) and one juvenile (110 mm) were examined. The length of the second dorsal spine of the smallest specimen was 83% SL and ranged from 24 to 53% in the other specimens (15.2–31.2 mm).

Epinephelus multiguttatus belongs to the subgenus *Alphestes* (Table 1) along with its close relative, *E. afer*, with which it shares a similar body form, small size, antrorse spine at the angle of the preopercle and reduced scale cteni. One feature of the larger larvae of *Alphestes* supports this close relationship. The dorsal and lateral bony surfaces of the neurocranium from mid-orbit to the nape are extremely rugose, giving a pock-marked or honeycombed appearance. Rugosity was not evident in the 8.4 mm specimen but was well-developed in all specimens ≥ 15 mm. Surface rugosity was still evident in a 38.1 mm juvenile *E. afer*; however, in a 62.0 mm specimen, the bone surface was relatively smooth and the honeycombing, while still evident, was mainly subsurface. This feature was not present in larvae or juveniles of any other grouper species examined and apparently characterizes the subgenus *Alphestes*.

Despite the close relationship between *E. multiguttatus* and *E. afer*, larval spine configurations are strikingly different. Second dorsal and pelvic spines of an 8.4 mm and a 15.3 mm specimen of *E. multiguttatus* are illustrated (Fig. 12). The 8.4 mm specimen was illustrated by Kendall (1979, fig. 33) as *Dermatolepis* or *Alphestes*. Wing margins of the second dorsal spine bear a series of somewhat enlarged, widely-spaced, straight spinelets followed distally by smaller, more closely-spaced ones. By 15 mm, the wing margins are distinctive in having several spinelets at approximately mid-length that are notably larger and more broad-based than those on either side of them. A single apex ridge bears small straight spinelets. The primary ridge of the pelvic spine bears a series of elongate, narrow-based, straight or slightly curved spinelets that incline toward the tip of the spine. These develop near the base of the spine, increase in size and then gradually decrease in size and inclination until they become small straight spinelets along the distal one-third of the spine. Spinelets of pelvic ridges 2 and 3 are small and straight. Those of the fourth ridge are slightly enlarged near the base of the spine and incline toward its tip.

Epinephelus afer

Epinephelus afer is represented by populations in the eastern Pacific and western Atlantic. It is distinguished from other American groupers, except *E. morio* and *E. guttatus*, by the following fin ray counts: D XI, 17–18; A III, 9; P₁ 34. Characteristics of the subgenus *Alphestes* are discussed above in the account of its other member, *E. multiguttatus*. Spines of larval *E. afer* from the Pacific differ notably from those of *E. multiguttatus*, and interestingly, those of Pacific *E. afer* show no similarity to those of Atlantic *E. afer* (Fig. 13).

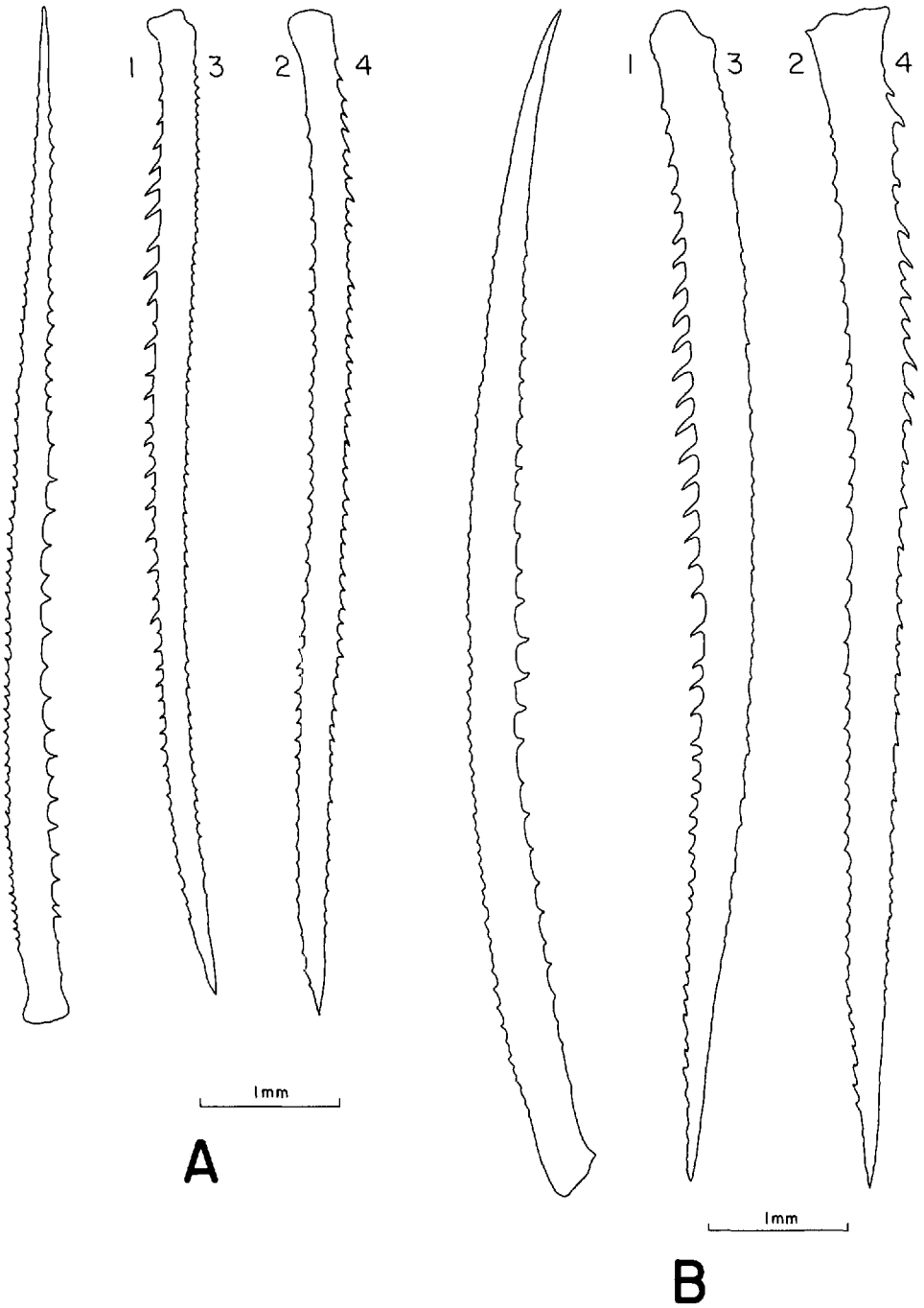


Figure 12. *Epinephelus multiguttatus*, second dorsal spine (left lateral view) and left pelvic spine (ventromedial and ventrolateral views): A, 8.4 mm specimen; B, 15.3 mm specimen.

Pacific material consisted of four larval (16.2–23.0 mm), two transforming (25.2–29.1 mm) and one fully transformed (25.9 mm) specimens. The cranial rugosity that characterizes the subgenus *Alphestes* was well-developed in all these specimens. The second dorsal spine is quite long (79–96% SL in the four larvae) and bears a series of very large, closely-spaced recurved spinelets along most of the length of the wing margins (Fig. 13A). These are preceded, near the base of the spine, by several narrow curved spinelets. A single apex ridge bears small straight spinelets. The primary pelvic ridge also bears large, closely-spaced recurved spinelets along most of its length, preceded at the base by several fairly long but narrow spinelets that curve toward the spine tip. The spinelets of ridges 2 and 4 also curve toward the spine tip. Those of ridge 3 are quite small, of ridge 2 somewhat larger, and of ridge 4 notably enlarged.

Atlantic material consisted of 17 larval (10.5–19.5 mm), five transforming (27.0–28.5 mm) and three fully transformed (33.2–62.0 mm) specimens. Cranial rugosity was evident in the larvae by 13.5 mm, but was fully developed only in the transforming and juvenile specimens. Second dorsal and pelvic spines of a 17.0 mm specimen (Fig. 13B) differ dramatically from those of Pacific specimens (Fig. 13A). The spines are shorter (second dorsal spine 25–59% SL in the larvae, 18–23% SL in the transforming individuals) and have no enlarged recurved spinelets. The second dorsal spine is reminiscent of those of the *E. morio* and *E. striatus* species groups, although the wing margin spinelets tend to be somewhat more widely spaced and curved toward the spine tip. Spinelets of all pelvic ridges are small and straight with those along the proximal one-half of the fourth ridge being slightly enlarged and inclined toward the tip of the spine. Atlantic specimens of *E. afer* are distinguished from those of the *E. morio* group by the presence of cranial rugosity. In addition, most specimens examined had 18 dorsal soft rays (typical count for *E. morio* group 15–17).

The Pacific population of *E. afer* was originally described as a separate species, *Alphestes fasciatus*, by Hildebrand (1946). Smith (1971) concluded that Pacific *A. fasciatus* was indistinguishable from Atlantic *E. afer* and treated the former as a junior synonym of the latter. Striking differences in larval spination between the two populations suggest that they are specifically distinct. These populations warrant further taxonomic study.

Epinephelus inermis

Epinephelus inermis occurs only in the western Atlantic. Fin ray counts (D XI, 19–20; A III, 9; P₁ 36–38) distinguish it from all other Atlantic groupers. Five larval specimens (6.8–10.5 mm; second dorsal spine 63–66% SL) were examined. Second dorsal and pelvic spines most closely resemble those of *E. multiguttatus*. Wing margins of the second dorsal spine bear fairly large, widely-spaced straight spinelets along about three-quarters of their length, followed distally by smaller, slightly recurved ones (Fig. 11B). A single apex ridge bears small, straight spinelets. Spinelets of the primary pelvic ridge are large, fairly narrow and slightly curved toward the spine tip. Ridges 2 and 4 bear smaller narrow spinelets that also curve slightly toward the spine tip, those of the fourth ridge being enlarged proximally. Ridge 3 bears small straight or slightly curved spinelets.

Epinephelus inermis, along with its close Pacific relative, *E. dermatolepis*, belongs to the subgenus *Dermatolepis*, which is characterized by a deep, strongly compressed body and by lack of strong cteni on the scales. Smith (1971) considered the subgenus *Dermatolepis* to be most closely related to the subgenus *Alphestes*. Species of these subgenera share similar fin ray counts, but larger larvae

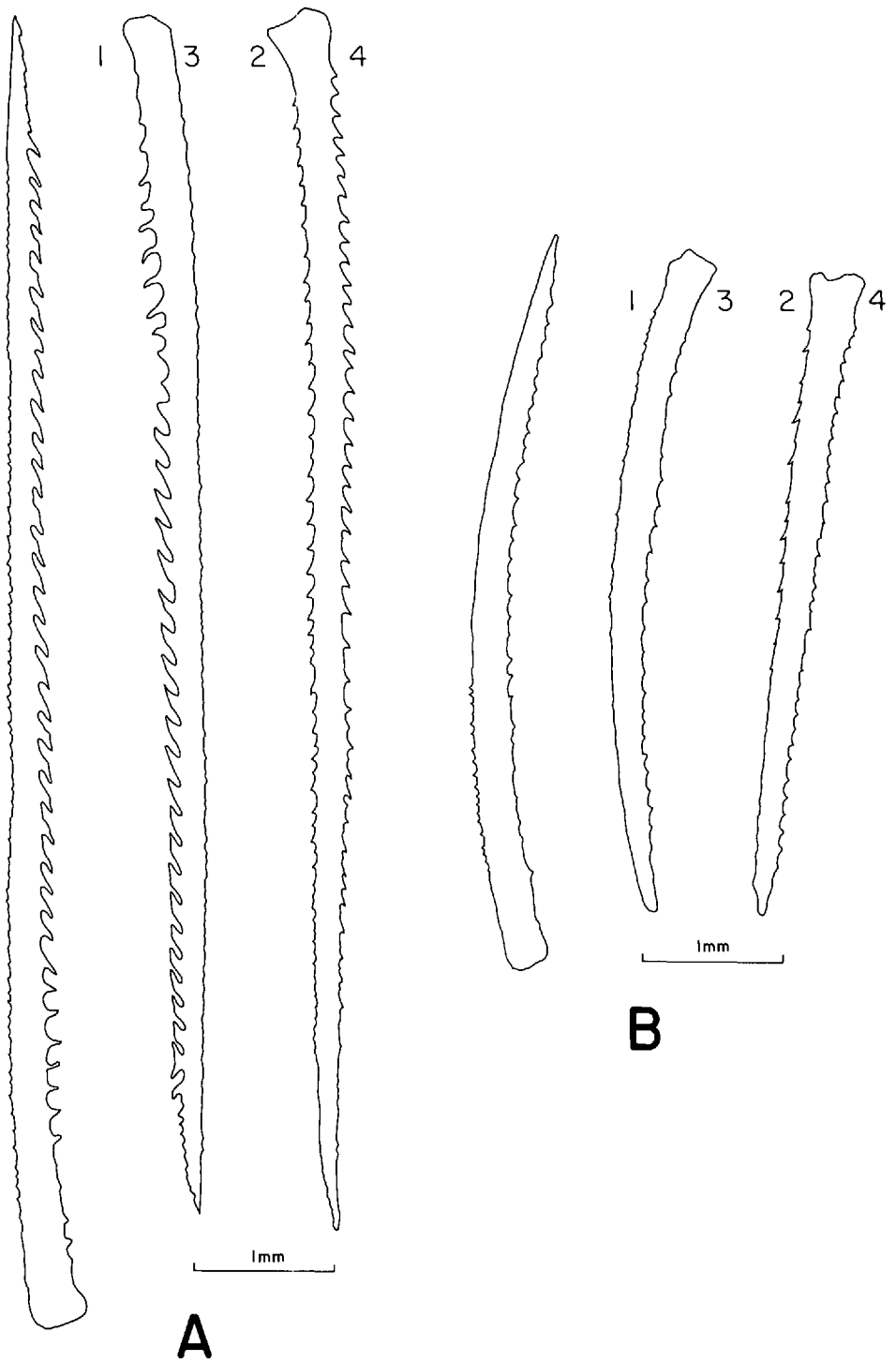


Figure 13. *Epinephelus afer*, second dorsal spine (left lateral view) and left pelvic spine (ventromedial and ventrolateral views): A, Pacific specimen, 16.2 mm; B, Atlantic specimen, 17.0 mm.

of *Alphestes* are readily distinguished by cranial rugosity. Cranial surfaces were smooth in all specimens of *Dermatolepis* examined.

Epinephelus dermatolepis

Epinephelus dermatolepis occurs only in the eastern Pacific. No larval specimens with the typical fin ray counts of this species (D XI, 18–19; A III, 9; P₁ 38–39) were examined. All Pacific larvae examined with counts close to these exhibited the cranial rugosity that characterizes the subgenus *Alphestes*. A 23.0 mm fully transformed juvenile *E. dermatolepis* showed no traces of this rugosity.

Paranthias furcifer

Paranthias furcifer occurs in the eastern Pacific and western Atlantic. Fin ray counts distinguish it from all other American species of groupers (D IX, 18–19; A III, 9; P₁ 40). Five larval specimens from the Pacific (7.7–15.8 mm; second dorsal spine 77–80% SL, excluding broken spine of 15.8 mm specimen) and three from the Atlantic (7.2–7.6 mm; second dorsal spine 54–72% SL) were examined. The 8.6 mm Pacific specimen was illustrated by Kendall (1979). Second dorsal (79% SL) and pelvic spines of this specimen are shown in Figure 14A. Wing margins of the dorsal spine and the primary ridge of the pelvic spine bear a series of long, relatively thin curved spinelets along approximately three-fourths of their length. These spinelets curve toward the tip of the spine and frequently alternate with much shorter, straight spinelets. The apex ridge of the dorsal spine bears, along approximately one-third of its length, narrow-based, slightly elongate spinelets which become simple, small spinelets distally. Pelvic ridges 2, 3 and 4 bear small spinelets that curve slightly toward the spine tip, the spinelets on ridge 4 being enlarged near the base of the spine. In the 15.8 mm specimen, the curved spinelets of the primary pelvic ridge are well-developed, but there is no evidence of the smaller simple spines between them (one smaller specimen also lacked these).

Second dorsal and pelvic spines of the three Atlantic specimens of *P. furcifer* (Fig. 14B) are shorter than those of Pacific specimens and have a notably different spinelet configuration. Wing margins of the second dorsal spine and the primary ridge of the pelvic spine bear small, straight, widely-spaced spinelets along most of their lengths. These spinelets differ from those of the Pacific *P. furcifer* specimens in being considerably shorter, broader and straight rather than curved, although those of the primary pelvic ridge are inclined (not curved) toward the tip of the spine. These differences, although not so striking as those seen in *Epinephelus afer*, seem to offer morphological evidence for taxonomic separation of the Atlantic and Pacific populations of *P. furcifer*.

Gonioplectrus hispanus

The monotypic genus *Gonioplectrus* occurs only in the western Atlantic and is distinguished from other species of American groupers by the following counts: D VIII, 13; A III, 7; P₁ 32. Two larval specimens of *G. hispanus* (13.4 and 14.0 mm) were examined. Dorsal and pelvic spine illustrations (Fig. 15A) are based on the 13.4 mm specimen described and illustrated by Kendall and Fahay (1979). As Kendall and Fahay noted, *G. hispanus* differs from other epinepheline larvae in having a deeper, more robust body and in having the third dorsal spine nearly as long as the second (second dorsal spine 36.0–38.6% SL, third dorsal spine 26.0–28.6% SL). In addition, the dorsal and pelvic spine morphology is diagnostic. The

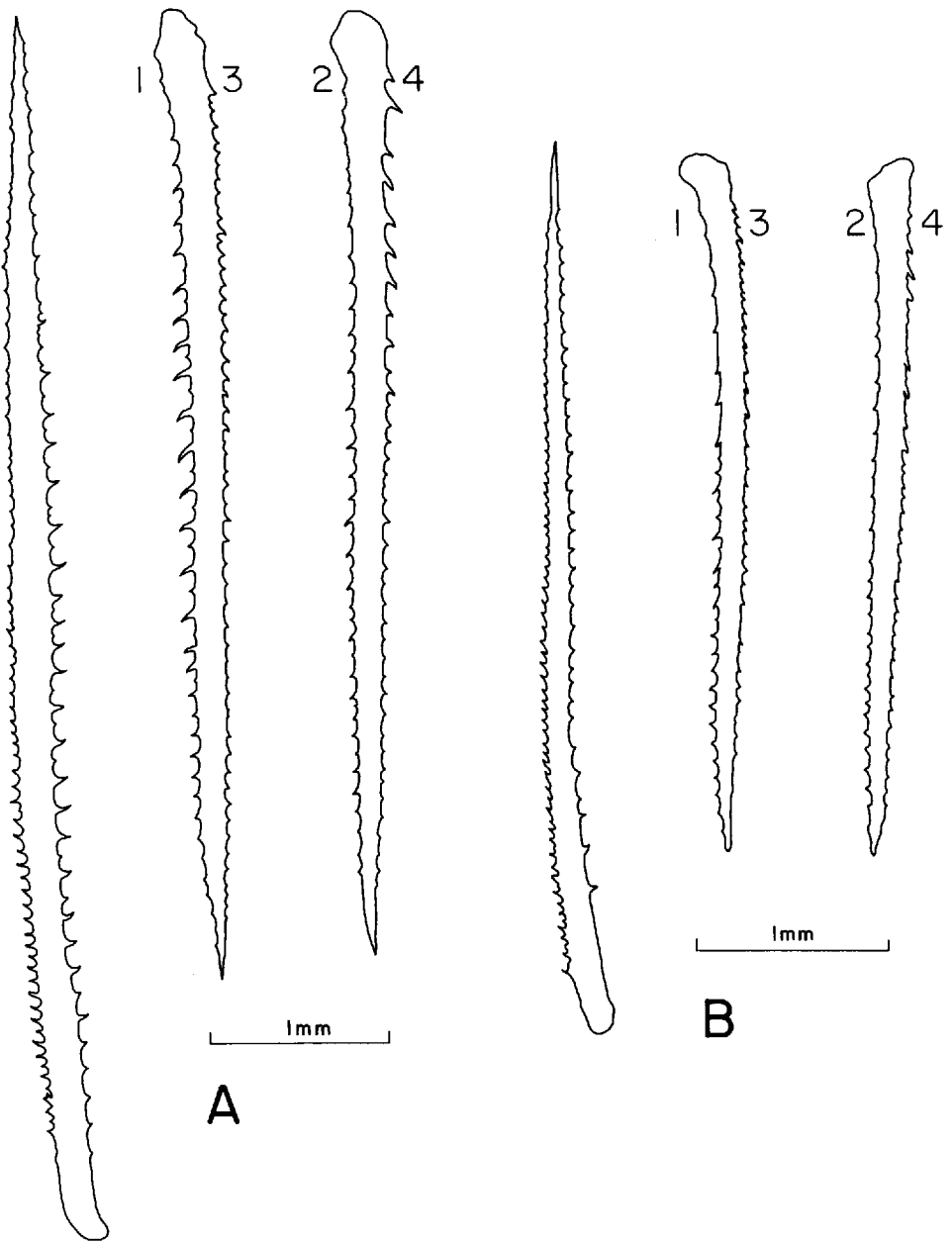


Figure 14. *Paranthias furcifer*, second dorsal spine (left lateral view) and left pelvic spine (ventromedial and ventrolateral views): A, Pacific specimen, 8.6 mm; B, Atlantic specimen, 7.6 mm.

stout second dorsal spine has small bump-like spinelets along the primary apex ridge, and a ridge bearing similar secondary spination extends along each side of the apex.

Small straight spinelets occur along the lateral wings. Most significantly, the

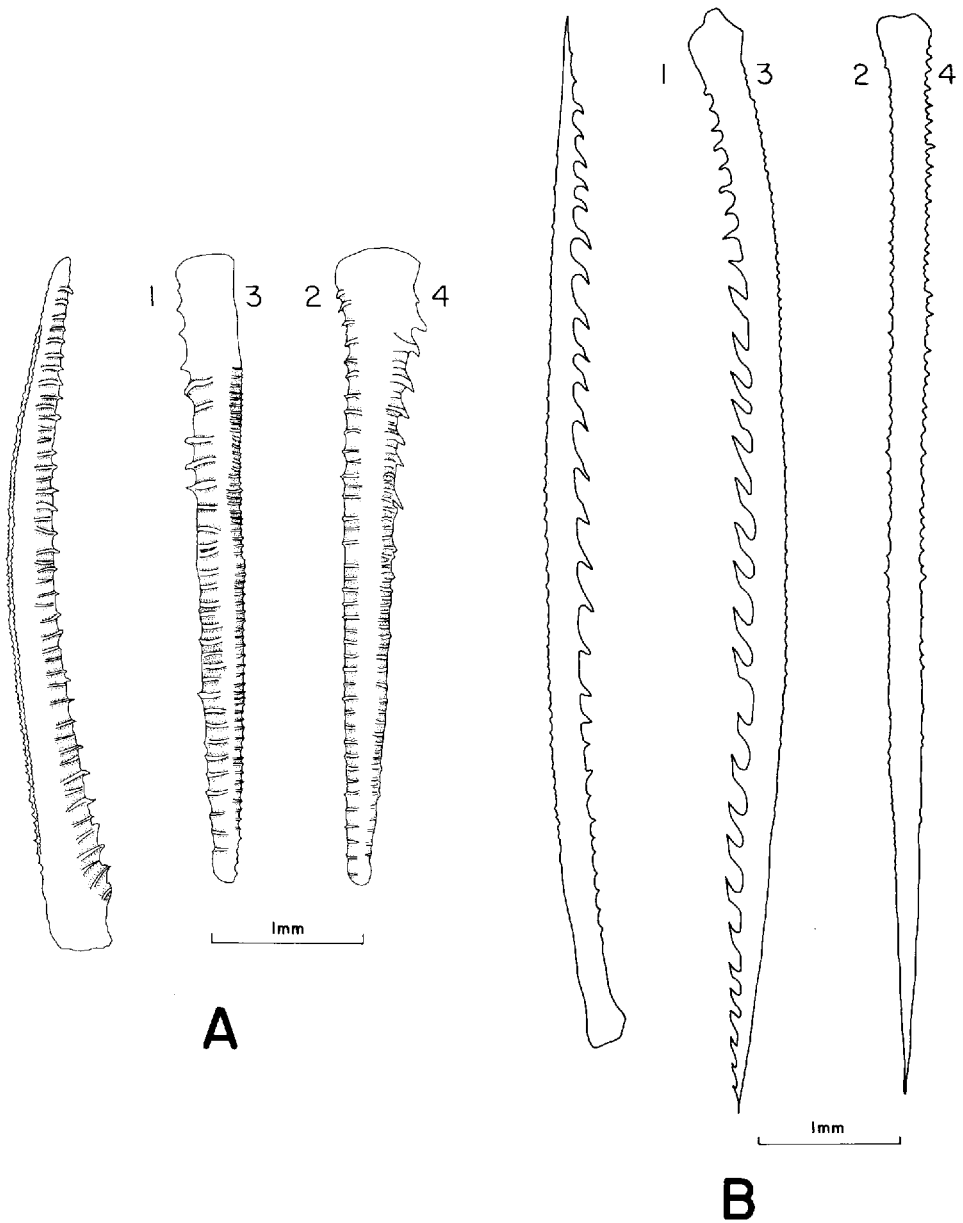


Figure 15. A, *Gonioplectrus hispanus*, second dorsal spine (left lateral view) and left pelvic spine (ventromedial and ventrolateral views), 13.4 mm specimen. B, *Mycteroperca*, second dorsal spine (left lateral view) and left pelvic spine (ventromedial and ventrolateral views), 16.0 mm specimen.

bases of these spinelets extend anteriorly as raised ridges beyond the lateral wing margins. These rounded ridges extend one-half to three-quarters the distance to the apex margin and give the spine a furrowed appearance. The configuration of the third dorsal spine, unlike other epinephelins, is identical to that of the second. The pelvic spines are relatively stout, with ridges 1, 2, and 4 bearing small straight

spinelets that become enlarged and slightly curved near the base of the spine. Ridge 3 bears small, bump-like spinelets (like those on the primary apex ridge of the dorsal spine). The bases of all pelvic spinelets extend as raised ridges toward the medial (central) portion of the spine giving the same furrowed effect present on the second and third dorsal spines.

Mycteroperca

The genus *Mycteroperca* is represented by eight species in the Atlantic and five in the Pacific, with none common to both oceans. The genus is distinguished from other epinephelins by having 10–13 (usually 11) anal soft rays, but extensive overlap of fin ray counts precludes identification of most *Mycteroperca* species using typical counts. Separation of their larvae was not possible. Several hundred larval *Mycteroperca* (3.5 mm NL–24.0 mm SL) were examined. All specimens possess a pigment spot at the cleithral symphysis (also present in *E. cruentatus* and *E. itajara*) and exhibit similar dorsal and pelvic spine configurations, reminiscent of those of *E. niveatus* and *E. flavolimbatus*. Wing margins of the second dorsal spine and the primary ridge of the pelvic spine bear large recurved spinelets along most of their lengths (Fig. 15B). Those of the second dorsal spine are preceded near the base by small straight spinelets and those of the pelvic spine are preceded by a series of narrow curved spinelets. The single apex ridge of the second dorsal spine bears small straight spinelets as do ridges 2, 3 and 4 of the pelvic spine.

DISCUSSION

Larvae of all epinepheline species examined exhibit consistent morphological configurations of the spinelets borne along the elongate second dorsal and pelvic fin spines. In some cases these spinelet configurations are species specific, but more often they characterize several species. Spinelet morphology, in conjunction with typical dorsal, anal and pectoral fin ray counts, allows generic identification of American epinepheline larvae at sizes as small as 4–5 mm and identification of 13 of the 21 American species of *Epinephelus* by 5–6 mm.

Although there have been no direct observations of the function of stiff elongate fin spines in grouper larvae, it is probable that they serve as a deterrent to predation. They bear no obvious sensory structures and are too inflexible to be brought near the mouth for use in feeding. The several fold increase in effective size afforded a larva with fully erected dorsal and pelvic spines must significantly reduce the likelihood of successful predatory attacks by smaller animals.

The function of ornamentation on the spines of larval groupers is less obvious, particularly in light of the specific differences exhibited. A simple, unadorned spine would appear best adapted for predator avoidance, whereas the recurved or bifurcate spinelets that characterize the spines of many larval groupers would seemingly increase the chances of a successful predatory attack by essentially hooking the predator. Differences in spinelet configurations could relate to species recognition, as suggested by Moser (1981) for larval pigment patterns, but the relative transparency of the spines and lack of accentuating pigment makes this improbable. In the absence of direct observational or experimental evidence, the function, if any, of these spinelets remains obscure.

The utility of larval spinelet morphology in evaluating evolutionary relationships within the tribe Epinephelini is also unclear. For the most part, the distribution of spinelet patterns is congruent with the species groups of Smith (1971, fig. 41), but notable exceptions are found in the subgenera *Cephalopholis* and *Alphestes*. Of the three species Smith included in *Cephalopholis*, two, *Epinephelus*

cruentatus and *E. panamensis*, have large recurved and bifurcate spinelets, whereas the spinelets of *E. fulvus* are small and straight (Figs. 10 and 11A). Smith noted, however, that *E. fulvus* appears more closely related to Indo-Pacific and eastern Atlantic species. More perplexing are the strikingly different spinelet patterns seen within *Alphestes*. Here, the distinctive body form, small size, antrorse preopercular spine, modified scales and neurocranial rugosity shared by the constituent species offer strong evidence for monophyly of the subgenus. Despite this, *Epinephelus multiguttatus* and Pacific *E. afer* possess distinctive and dissimilar larval spines, while Atlantic *E. afer* (considered conspecific with Pacific *E. afer* by Smith) have spines reminiscent of the *E. morio* group. Although larval spine and spinelet morphology undoubtedly reflects the evolutionary history of epinepheline serranids, meaningful interpretation of the significance of the various patterns exhibited awaits more comprehensive studies of serranid phylogeny.

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