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PHYLOGENY OF THE EPINEPHELINAE (TELEOSTEI: SERRANIDAE)

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ABSTRACT

Relationships among epinepheline genera are investigated based on cladistic analysis of larval and adult morphology. Five monophyletic tribes are delineated, and relationships among tribes and among genera of the tribe Grammistini are hypothesized. Generic composition of tribes differs from Johnson's (1983) classification only in the allocation of *Jeboehlkia* to the tribe Grammistini rather than the Liopropomini. Despite the presence of the skin toxin grammistin in the Diploprionini and Grammistini, we consider the latter to be the sister group of the Liopropomini. This hypothesis is based, in part, on previously unrecognized larval features. Larval morphology also provides evidence of monophyly of the subfamily Epinephelinae, the clade comprising all epinepheline tribes except Niphonini, and the tribe Grammistini. Larval features provide the only evidence of a monophyletic Epinephelini and a monophyletic clade comprising the Diploprionini, Liopropomini and Grammistini; identification of larvae of more epinephelines is needed to test those hypotheses. Within the tribe Grammistini, we propose that *Jeboehlkia gladifer* is the sister group of a natural assemblage comprising the former pseudogrammid genera (*Aporops, Pseudogramma* and *Suttonia*). The "soapfishes" (*Grammistes, Grammistops, Pogonoperca* and *Rypticus*) are not monophyletic, but form a series of sequential sister groups to *Jeboehlkia, Aporops, Pseudogramma* and *Suttonia* (the closest of these being *Grammistops*, followed by *Rypticus*, then *Grammistes* plus *Pogonoperca*). The absence in adult *Jeboehlkia* of several derived features shared by *Grammistops, Aporops, Pseudogramma* and *Suttonia* is incongruous with our hypothesis but may be attributable to paedomorphosis. The generic phylogeny of the Grammistini proposed herein emerges as the single most parsimonious hypothesis largely because of the method chosen for analyzing multistate characters.

Few percoid families have received as extensive systematic treatment as the Serranidae. Since its recognition almost 200 years ago, the family has been expanded, restricted and subdivided, and often has comprised a bewildering array of genera whose affinities to one another were unclear. By restricting it to the subfamilies Anthiinae, Epinephelinae and Serraninae (sensu Jordan and Eigenman, 1890, with some modifications), Gosline (1966) made an important step toward defining the Serranidae as a natural assemblage. Johnson (1983) largely corroborated Gosline's hypothesis, but cladistically refined it, citing four derived features (presence of three opercular spines and absence of the procurrent spur, third preural radial cartilages and posterior uroneural) as evidence of the monophyly of the family.

Furthermore, Johnson (1983) diagnosed a monophyletic subfamily Epinephelinae (as distinct from the Anthiinae, Serraninae and other percoids) based on absence of an autogenous distal radial on the first dorsal-fin pterygiophore. His Epinephelinae differs radically from previous concepts of the subfamily because it includes not only the grouper genera (*Epinephelus, Mycteroperca, Paranthias*, etc.), but *Niphon* (historically considered a serranid but relegated to the Percichthyidae by Gosline, 1966); *Aulacocephalus, Belonoperca* and *Diploprion* (treated as grammistids by Randall et al., 1971; Randall et al., 1980); *Liopropoma* and *Rainfordia* (treated as members of a fourth serranid subfamily, the Grammistinae, by Kendall, 1976); *Pikea* (synonomized with *Liopropoma* by Randall and Taylor, 1988); *Jeboehlkia* (not allocated to a subfamily but considered a close relative of *Liopropoma* by Robins, 1967); *Grammistes, Grammistops, Pogonoperca* and *Ryp-*

ticus (part of the Grammistidae of Gosline, 1960; Schultz, 1966); and *Aporops, Pseudogramma* and *Suttonia* (part of the Grammistidae of Gosline, 1960 and Schultz, 1966, but treated as a separate family, the Pseudogrammidae, by Greenwood et al., 1966).

Johnson (1983) divided his Epinephelinae into five tribes (Niphonini, Epinephelini, Diploprionini, Liopropomini and Grammistini), and commented on their monophyly and interrelationships; however, no cladistic hypothesis of relationships among epinepheline genera exists that would corroborate the hypothesized monophyly of the tribes and describe their intra- and interrelationships.

The purpose of this paper is to examine relationships among epinepheline genera based on cladistic analysis of larval and adult morphology. In doing so, we test Johnson's (1983: 784) allocation of genera to the five epinepheline tribes and examine relationships among the tribes. We do not examine relationships within the speciose Epinephelini, nor within the Diploprionini and Liopropomini; however, we propose a generic phylogeny for the tribe Grammistini and explore the possibility that heterochrony has contributed to the evolution of morphological diversity in grammistins.

Methods and Materials

Examination of osteological features was facilitated by clearing and staining (or by preparing radiographs of) selected specimens. Illustrations were made with the aid of a camera lucida. Photographs were made with an Olympus OM12 35-mm camera attached to a Wild M-5 stereomicroscope. Histological sections of skin were prepared and stained with Sudan Black B following the methods of Luna (1968). The first caudal vertebra is considered the first vertebra with a haemal arch and haemal spine (in all serranids examined, the two or three vertebrae preceding the one with the first haemal spine have what appears to be a very small haemal arch and canal). The first interneural space is that between the first and second neural spines (see discussion in Birdsong et al., 1988). Institutional abbreviations are as defined by Leviton et al. (1985). "Epinepheline" refers to the subfamily Epinephelinae; "epinephelin" refers to the tribe Epinephelini. Johnson's (1983) definition of the subfamily Epinephelinae rendered several previously used taxonomic names obsolete, including "Grammistidae" and "Pseudogrammidae." Nevertheless, for convenience, we frequently refer to genera of the former Pseudogrammidae (*Aporops, Pseudogramma* and *Suttonia*) as "pseudogrammids."

Outgroup Analysis

Monophyly of the Serranidae and Epinephelinae has been hypothesized (Johnson, 1983), but that of the remaining serranid subfamilies, the Serraninae and Anthiinae, is questionable. According to Meisler (1987), serranines (excluding *Acanthistius* which was considered an anthiine by Heemstra and Randall, 1986) share two derived features: anterior portion of second infraorbital bone completely lateral to posterior lacrimal, and supramaxilla lacking. Meisler (1987) also hypothesized that a unique morphology of the spinous dorsal-fin pterygiophores is indicative of the monophyly of the Anthiinae (including *Acanthistius*); Baldwin (1990a) suggested that the absence of a toothplate on the second epibranchial may be a synapomorphy of anthiines; and Anderson et al. (1990) tentatively accepted that character and the presence of 26 vertebrae as autapomorphic for the subfamily. Most of the characters listed above, however, appear in at least some other percoids, and further study is needed to test the hypothesized monophyly of both subfamilies. No cladistic hypothesis exists regarding relationships among the Anthiinae, Epinephelinae and Serraninae, although below we present preliminary evidence linking epinephelines and anthiines (see "Outgroup Relationships").

Character polarity for the Epinephelinae was hypothesized using the outgroup comparison method of Maddison et al. (1984). Johnson (1983, 1988) hypothesized that *Niphon* is the sister group of all other epinephelines. Considering anthiines plus serranines as the first outgroup for the Epinephelinae and other percoids as the second, we corroborate Johnson's hypothesis and thereafter treat *Niphon* as the first and serranines plus anthiines as the second outgroup for the remaining epinephelines. After cladistically elucidating the monophyly and relationships of the five epinepheline tribes, we examine relationships within the tribe Grammistini, polarizing characters on the basis of outgroup comparison with liopropomins and diploprionins (the first and second outgroups for the Grammistini, respectively, based on our original analysis).

Cladistically primitive members of outgroups have more effect on hypotheses of ancestral states for

the ingroup than taxa that originate at higher nodes on the cladogram (Maddison et al., 1984). In Meisler's (1987) phylogeny of the Serraninae, *Chelidoperca* is hypothesized to be the primitive sister group of all other serranines, and *Centropristis, Paralabrax* and a lineage comprising all other serranine genera form an unresolved trichotomy.

No similar hypothesis of generic relationships exists for the Anthiinae, although Roberts (1989) recognized two "groups" within the Anthiinae, one containing *Caesioperca, Caprodon, Ellerkeldia* (relegated to the synonymy of *Hypoplectrodes* by Anderson and Heemstra, 1989), *Lepidoperca, Plectranthias* and *Selenanthias*. He noted that those taxa are characterized only by primitive anthiine characters, including 15 branched caudal-fin rays, three predorsal bones, some posterior dorsal- and anal-fin pterygiophores trisegmental and scales with two rows of cteni. Based on morphology of gill arches, configuration of dorsal-fin pterygiophores and number of vertebrae, Baldwin (1990b, unpubl. data) proposed that *Acanthistius* and *Trachypoma*, formerly treated as a serranine and epinepheline, respectively, may be cladistically primitive anthiines. Other genera considered as "basal anthiines" in her preliminary phylogeny include *Caesioperca, Caprodon, Epinephelides, Giganthias, Hypoplectrodes, Lepidoperca, Othos* and *Plectranthias*. In addition to being characterized by the primitive characters listed above (Roberts, 1989), those taxa lack another derived feature that unites other anthiine genera as a monophyletic group: scales without ctenial bases in posterior field (vs. scales with posterior field filled with bases of old cteni).

Phylogenetic Reconstruction

The character matrix (Table 1) was analyzed using the "Branch and Bound" option of the software package PAUP (Phylogenetic Analysis Using Parsimony, Version 2.4.1, written by D. L. Swofford, Illinois Natural History Survey), an approach that is guaranteed to find all most parsimonious trees. The single most parsimonious tree resulting from the analysis appears in Figure 1 (but see "Discussion"). In the absence of information on patterns or processes of evolution (e.g., gradualism) that could be used to order multiple states of a single character a priori, analysis of multistate characters was conducted in two ways: (1) by treating all multistate characters as unordered in the computerized search for trees (following Swofford, 1985); and (2) by attempting to order them using the iterative functional ingroup/outgroup (FIG/FOG) method of Watrous and Wheeler (1981)—also see Mooi (1989), and the transformation series analysis (TSA) of Mickevich (1982). Additional comments on ordering of multistate characters are provided in the character analysis (see "Monophyly and Interrelationships of Epinepheline Tribes") and in the "Discussion." The tree was rooted using outgroup information ("Other Serranids" in Table 1), and characters were optimized using accelerated transformation (ACCTRAN). Alternative, equally parsimonious hypotheses of character evolution resulting from delayed transformation optimization (DELTRAN) are discussed in the text.

Characters used in this study are described below in the order in which they appear on the cladogram. Discussion of each character is preceded by an italicized description of the derived state. Numbers followed by ′ or ″ indicate multiple states of a single character. Numbers followed by the symbol ® indicate reversal to the primitive state. Unless otherwise noted, descriptions of characters of larval serranids are based on information from Kendall, 1979; Leis, 1986; Johnson, 1988; Baldwin, 1990a; Baldwin et al., 1991; and Baldwin and Johnson, 1991.

Larval epinephelines examined in this study are listed in Baldwin et al. (1991) and Baldwin and Johnson (1991), and anthiine and serranine larvae examined are listed in Baldwin (1990a). Adult (and Juvenile) Material Examined Is Listed Below: EPINEPHELINAE. *Anyperodon leucogrammicus*, USNM 218817 (1, cleared and stained, hereafter abbreviated "cs"); *Aporops bilinearis*, USNM 218920 (3 specimens, cs). *Aulacocephalus temmincki*, USNM 71332 (1, radiograph, hereafter abbreviated "r"); USNM 64640 (1, r). *Bathyanthias roseus*, BMNH 1879.5.14.155 (1, holotype, r). *Belonoperca chabanaudi*, USNM 217813 (1, cs). *Cephalopholis fulva*, USNM 269803 (1, cs). *Diploprion bifasciatus*,[1] USNM 218889 (1, cs); USNM 183096 (3). *Epinephelus guttatus*, VIMS/CBL 3692 (16); *E. morio*, VIMS/CBL 3735 (1). *Grammistes sexlineatus*, USNM 128886 (1, cs). *Grammistops ocellatus*, USNM 218873 (1, cs); USNM 260562 (2). *Jeboehlkia gladifer*, USNM 201422 (1, holotype, r); Indian River Coastal Zone Museum 107:7433 (1, cs). *Liopropoma carmabi*, USNM 198283 (1, cs; 6, r); *L. susumi*, USNM 218726 (1, cs); USNM 285949 (6, r); *L. yoshinoi* USNM 192964 (1, r); *L. maculatum*, USNM 198225 (1, r); *L. pallidum*, USNM 223296 (1, r); *L. collettei*, USNM 285953 (1, r); *L. rubre*, USNM 267787 (1, r); *L. mitratum*, USNM 285942 (1, r); *L. lineata*, USNM 289868 (1, r); *L. mowbrayi*, USNM 274927 (1, r); *L. swalesi*, USNM 209922 (1, r); *L. tonstrinum*, USNM 261544 (1, r); *L. eukrines*, USNM 197499 (1, r). *Niphon spinosus*, USNM 296642 (formerly ZUMT 4916) (1, cs). *Pikea cubensis*, USNM 197669 (1, r); USNM uncat. OREGON 3595 (2, r); OREGON 4843 (1, r); SILVER BAY

[1] W. D. Anderson, Jr., recently has brought to our attention that the spelling of the serranid species *Diploprion bifasciatum* should be *Diploprion bifasciatus* ('us' rather than 'um' to agree with the masculine 'prion').

Table 1. Character matrix for the Epinephelinae. 0, primitive state; 1–3, derived states; 9, state unknown

	Character									
	1–5	6–10	11–15	16–20	21–25	26–30	31–35	36–40	41–45	46–52
Other Serranids	00000	00000	00000	00000	00000	00000	00000	00000	00000	0000000
Niphon	11111	11000	00000	00000	00000	00000	00000	00000	00000	0000000
Epinephelini	11000	00111	11100	00000	00000	00000	00000	00000	00000	0000000
Aulacocephalus	11000	00119	00999	11110	09900	00000	00099	00000	00000	0000000
Belonoperca	11000	00111	00011	11110	00000	00000	00000	00000	00000	0000000
Diploprion	11000	00111	00011	11110	00000	00000	00000	00000	00000	0000000
Liopropoma	11000	00111	00011	00001	11111	10000	00000	00000	00000	0000000
Bathyanthias	11000	00111	00011	00001	11111	10000	00000	00000	00000	0000000
Rainfordia	11000	00119	00999	00001	19911	10000	00099	00000	00000	0000000
Pogonoperca	10000	00119	00999	20001	19900	01111	11399	11000	00000	0000000
Grammistes	11000	00111	00011	20001	11100	01111	11311	11000	00000	0000000
Rypticus	11000	00111	00011	20001	11100	01111	11311	00110	00000	0000000
Grammistops	11000	00119	00999	20001	19900	01111	12299	00111	11000	0000000
Jeboehlkia	11000	00111	00011	00001	21100	01111	19111	00111	00110	0000000
Aporops	11000	00111	00011	00001	21100	01111	12111	00111	11101	1111110
Pseudogramma	11000	00111	00011	00001	21100	01111	12111	00111	11111	1211111
Suttonia	11000	00119	00999	00001	29900	01111	12111	00111	11111	1211111

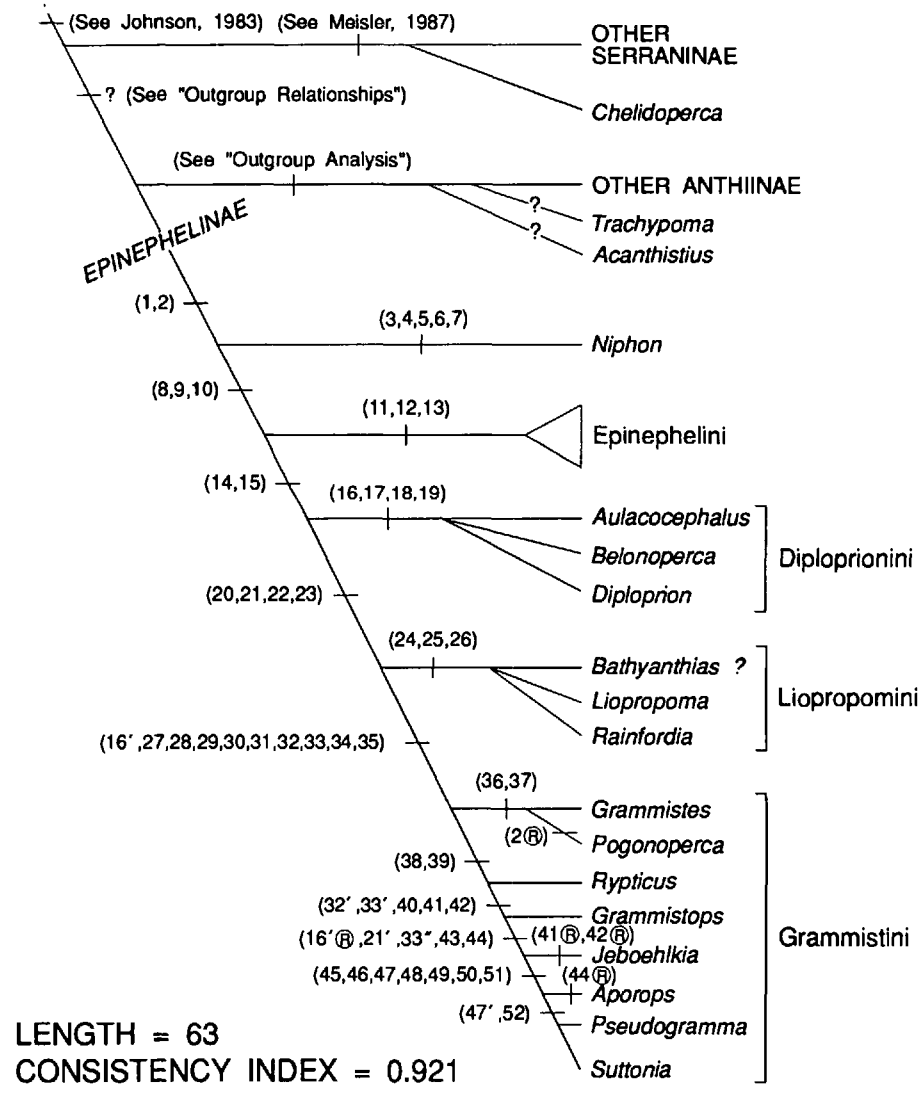

Figure 1. Cladogram showing hypothesized relationships among epinepheline genera. Numbers followed by ' or " indicate multiple states of a single character. Numbers followed by the symbol ® indicate reversal to the primitive state.

2471 (1, r); *P. mexicana atlanticus*, USNM uncat. OREGON 4304 (1, r); USNM uncat. (1, cs). *Plectropomus maculatum*, USNM 218818 (1, cs). *Pogonoperca punctata*, USNM 205492 (1, r). *Pseudogramma gregoryi*, USNM uncat., Belize (1); *P. polyacantha*, USNM 209575 (3, cs); USNM 295992 (41). *Rainfordia opercularis*, USNM 203247 (1, cs). *Rypticus subbifrenatus*, VIMS 05605 (1); *R. nigripinnis*, USNM 294075 (1, cs); *Rypticus* sp., USNM 270278 (1, cs). *Suttonia lineata*, USNM 209705 (2, 1 cs); *S. suttoni*, USNM 285959 (1, r); ROM 61078 (1).

ANTHIINAE. *Acanthistius cinctus*, NMNZ P.19458 (1, cs); *A. serratus*, AMS I. 19602004 (1, cs). *Caesioperca lepidoptera*, NMNZ, P. 19913; *C. rasor*, AMS I. 19211005 (1, cs). *Caprodon longimanus*, NMNZ P.23451 (1, cs). *Epinephelides leai*, AMS I. 4917 (1, r). *Holanthias fuscipinnis*, BPBM 24530 (1, cs). *Hypoplectrodes maccullochi*, AMS I. 15840008, (1, cs); *H. hunti*, NMNZ P. 11765 (1, cs). *Lepidoperca tazmanica*, NMNZ P. 20367, (1, cs). *Luzonichthys earlei*, BPBM 29137 (1, cs). *Nemanthias carberryi*, USNM 218810 (2, cs). *Othos dentex*, AMS I.234006-006 (1, r). *Plectranthias inermis*, USNM, 307792 (1, cs); *P. nanus*, BPBM 22681 (1, cs); *P. wheeleri*, AMS I. 22820810, (1, cs); *P. winniensis*,

USNM 236646, (1, cs). *Pronotogrammus aureorubens*, USNM 185228 (8, 1 cs); *P. martinicensis*, USNM 307793 (1, cs). *Pseudanthias smithvanizi*, AMS I. 20436009 (1, cs). *Rabaulichthys altipinnis*, USNM 307791 (1, cs). *Serranocirrhitus latus*, AMS I. 2262008 (1, cs). *Trachypoma macracanthus*, NMNZ P. 5559 (1, cs); NMNZ P. 11792 (1, cs).

SERRANINAE. *Centropristis philadelphica*. VIMS 7961 (1); *C. striatus*, VIMS/CBL 3810 (1). *Chelidoperca*, USNM 307787 (1, cs). *Diplectrum formosum*, VIMS 2478 (1); *D. biuittatum*, VIMS 3848 (1). *Hypoplectrus indigo*, USNM 302767 (1, cs); *H. unicolor*, VIMS 765 (3). *Schultzea beta*, USNM 89002, (3, cs). *Serranus cabrilla*, USNM 269884 (1, cs).

OTHER PERCOIDEI. *Ambassis moluccas*. USNM 218805 (1, cs). *Apogon moluccensis*, USNM 213380 (1, cs). *Brinkmannella elongata*, USNM 206944, (1, cs). *Centropomus undecimalis*, USNM 306580 (1, cs). *Cheilodipterus quinquelineatus*, USNM 218806 (1, cs). *Datnioides* sp., USNM 269799 (1 cs). *Dicentrarchus labrax*, USNM 218915 (1, cs). *Dinolestes lewini*, USNM 599321 (1, cs). *Epigonus lenimen*, USNM 207732 (1, cs). *Gaterin chrysotaenia*, USNM 290498, (1, cs). *Girella tricuspidata*, USNM 290939 (1, cs). *Glaucosoma hebraicum*, USNM 293442 (1, cs). *Graus nigra*, SIO 65-670 (1, cs). *Howella*, USNM 306589 (1, cs). *Labracoglossa argentiventris*, USNM 290495 (1, cs). *Lates niloticus*, USNM 306732 (1, cs). *Micracanthus strigatus*, SIO 61-146 (1, cs). *Morone americana*, USNM 109851 (1, cs); *M. saxatilis*, VIMS uncat. (1, cs). *Parapriacanthus ransonneti*, USNM 218867 (1, cs). *Perca fluviatilis*, USNM 187747 (1, cs). *Polydactylus sexfilis*, USNM 214123. *Polyprion americanus*, USNM 269542 (1, cs). *Rhomboplites aurorubens*, GMBL 55-1 (1, cs). *Scombrolabrax heterolepis*, USNM 292766 (1, cs). *Scombrops boops*, USNM 49933 (1, cs). *Synagrops* sp., USNM 216483 (1, cs).

OUTGROUP RELATIONSHIPS

Character Analysis

As noted above, relationships among the Anthiinae, Epinephelinae and Serraninae are unresolved. Below, we discuss specific characters of both larval and adult morphology that may indicate a sister-group relationship between the Anthiinae and Epinephelinae.

Distal Radials of Spinous Dorsal-fin Pterygiophores Rest Posteriorly in Groove in Next Proximal-middle Pterygiophore (Figs. 2, 3).—In serranines and most epinephelines, the posteroventral portion of the distal radial of each dorsal-fin pterygiophore is tightly bound to the anterodorsal portion of the next proximal-middle pterygiophore (Fig. 2A, E). The distal radial is loosely connected to its serially associated (i.e., anterior) proximal-middle element, often resting in a groove (Fig. 3A) or on a ledge (Fig. 3E) of this element (although posteriorly, serially associated proximal-middle and distal elements are often widely separated, as in *Liopropoma* and *Aporops*, see character 21).

In *Acanthistius* and anthiines, the anterior margin of the distal radial abuts and is tightly bound to its serially associated proximal-middle element (Figs. 2C, D; 3B, C). More importantly, the distal radial is only loosely bound to the next proximal-middle pterygiophore, and has a keel-like posteroventral margin that can slide back and forth in a groove on the v-shaped anterior ledge of that element (Figs. 2C, D; 3B, C). *Niphon* shares with *Acanthistius* and anthiines this tight connection of the distal radial anteriorly with its serially associated proximal-middle pterygiophore and loose association posteriorly with the grooved ledge of the next proximal-middle element (Figs. 2B, 3D).

Meisler (1987) interpreted the condition observed in *Acanthistius* and anthiines as derived within the Serranidae, particularly because he observed no other percoid in which the distal radial rests posteriorly in a groove in the next proximal-middle element. We have seen a similar condition among percoids only in *Polyprion* and *Girella* and thus concur with Meisler (1987) that the presence of a groove on the v-shaped anterodorsal corner of the proximal-middle element is probably derived within the Serranidae. However, the loose interlocking or overlapping association between the distal radial and its serially associated proximal-middle element in serranines and most epinephelines also appears to be derived, because in most

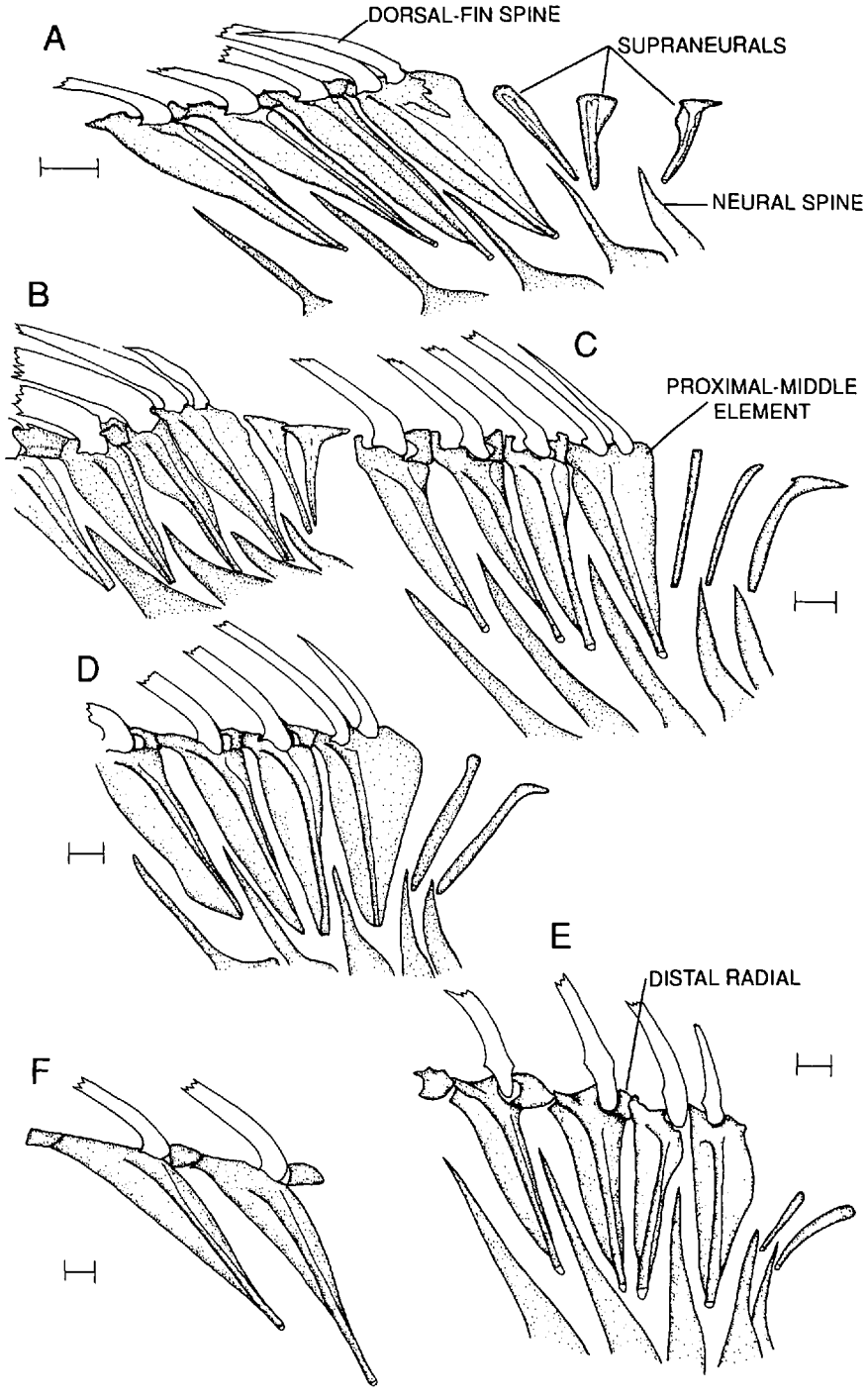

Figure 2. A–E: Anterior spinous dorsal-fin pterygiophores, supraneurals and neural spines in selected serranid fishes, right side. A) *Schultzea beta* (Serraninae), USNM 89002, 160 mm SL; B) *Niphon spinosus* (Epinephelinae), USNM 296642 (formerly ZUMT 4916), 132 mm SL; C) *Acanthistius serratus* (Anthiinae), AMS I. 19602004, 67.0 mm SL; D) *Pronotogrammus martinicensis* (Anthiinae), USNM 307793, 61.0 mm SL; E) *Diploprion bifasciatus* (Epinephelinae), USNM 218889, 70.0 mm SL. F: Fifth and sixth dorsal-fin pterygiophores of *Morone saxatilis* (Moronidae), VIMS uncat., 106 mm SL. Scale bars = 1 mm.

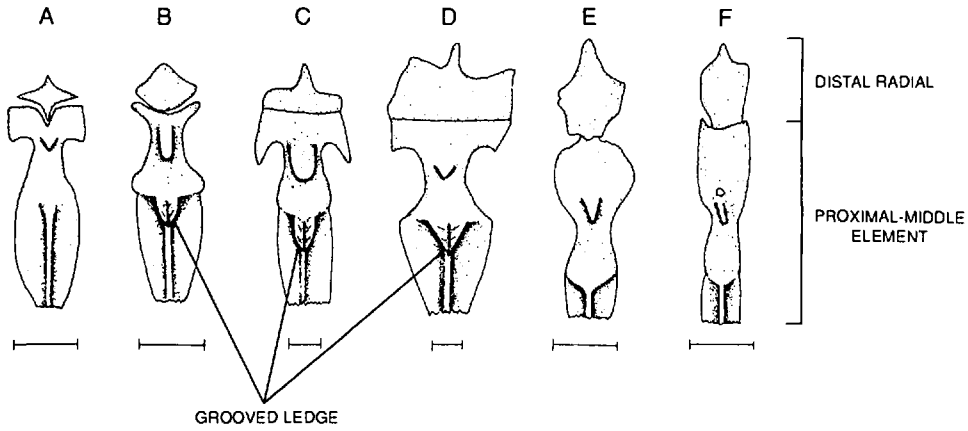

Figure 3. Dorsal view (top of page is posterior) of a single spinous dorsal-fin pterygiophore (distal radial and dorsal spine supernumerarily associated with proximal-middle element removed): A) *Schultzea beta* (Serraninae), third pterygiophore, USNM 89002, 160 mm SL; B) *Acanthistius serratus* (Anthiinae), seventh pterygiophore, AMS I. 19602004, 67.0 mm SL; C) *Holanthias fuscipinnis* (Anthiinae), fifth pterygiophore, BPBM 24530, 91.0 mm SL; D) *Niphon spinosus* (Epinephelinae), third pterygiophore, USNM 296642, 132 mm SL; E) *Diploprion bifasciatus* (Epinephelinae), sixth pterygiophore, USNM 218889, 70.0 mm SL; F) *Morone saxatilis* (Moronidae), sixth pterygiophore, VIMS uncat., 106 mm SL. Scale bars = 1 mm.

percoids we examined, the distal radial is tightly bound to both its serially- and secondarily-associated proximal-middle elements (e.g., as in *Morone saxatilis*, Figs. 2F, 3F).

Even if we assume that the v-shaped groove in *Niphon* and anthiines is derived within the Serranidae, its interpretation is problematic. Because this configuration of pterygiophores is found among epinephelines only in *Niphon*, it is equally likely that (1) the condition evolved in a common ancestor of anthiines and epinephelines and was lost within the latter or (2) it evolved independently in *Niphon* and the anthiine lineage.

Thirteen Dorsal-fin Spines.—Serranines, most anthiines and most epinephelines have 10 or fewer dorsal-fin spines. *Acanthistius* and *Niphon* are unique among serranids in usually having 13 dorsal-fin spines, and *Trachypoma* has 12. Numbers of dorsal-fin spines vary widely among percoids, and in the absence of a sister-group hypothesis for the Serranidae, we are unable to hypothesize the ancestral condition for the family. A high number of dorsal-fin spines could have evolved in an ancestor common to anthiines and epinephelines and been subsequently reduced in both subfamilies, but polarity of this character is equivocal.

Antrorse Preopercular Spines (Fig. 4).—Serranines, most anthiines and most epinephelines lack antrorse preopercular spines. Two or three strong, antrorse spines are present on the lower limb of the preopercle in the cladistically primitive (see "Monophyly and Interrelationships of Epinepheline Tribes") *Niphon* (Fig. 4E) and some epinephelins (e.g., *Plectropomus, Alphestes*), as well as the basal anthiines *Acanthistius* (Fig. 4B), *Trachypoma* (Fig. 4C), *Epinephelides, Hypoplectrodes* (Fig. 4D), *Othos* and *Plectranthias*. Antrorse preopercular spines occur elsewhere among percoids examined only in *Perca*, where they are weak serrations. Thus, antrorse spines appear to be derived within the Serranidae, and may have evolved in an ancestor common to anthiines and epinephelines and been subsequently lost in both subfamilies. Assuming that our designation of genera as

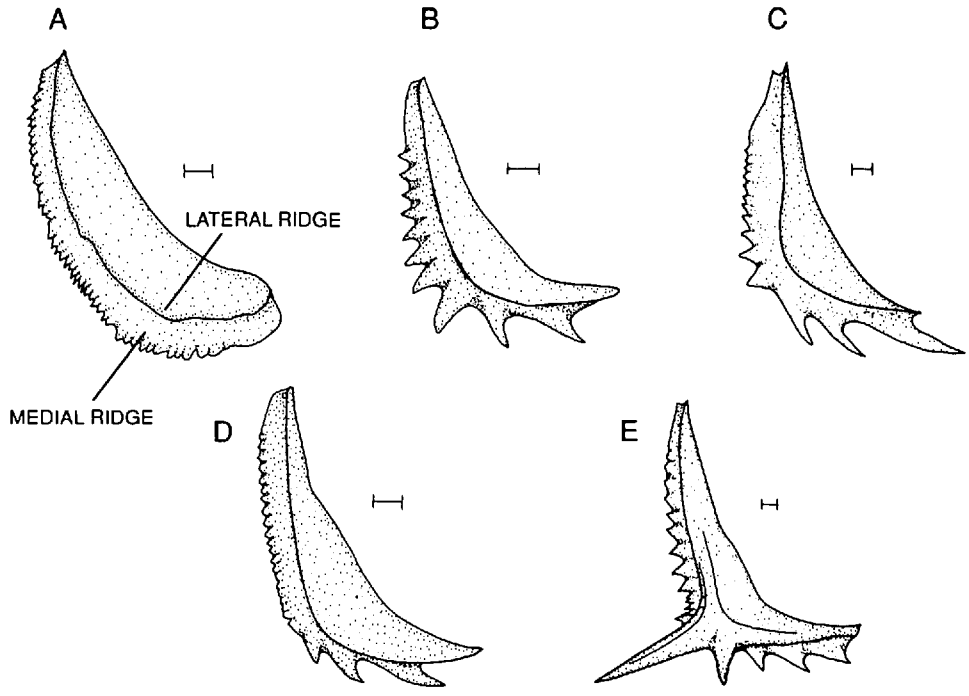

Figure 4. Preopercle, right side. A) *Chelidoperca* (Serraninae), USNM 307787, 78.0 mm SL; B) *Acanthistius serratus* (Anthiinae), AMS I. 19602004, 67.0 mm SL; C) *Trachypoma macracanthus* (Anthiinae), NMNZ P. 11792, 88.0 mm SL; D) *Hypoplectrodes hunti* (Anthiinae), NMNZ P. 11765, 71.5 mm SL; E) *Niphon spinosus* (Epinephelinae), USNM 296642, 132 mm SL. Scale bars = 1 mm.

"cladistically primitive" anthiines and epinephelines is accurate, independent evolution in the Anthiinae and Epinephelinae with subsequent losses in each lineage, or independent evolution in genera that have antrorse spines requires additional steps. With one exception, configuration of antrorse spines and serrations on the preopercle are very similar in basal epinephelines and anthiines. Unlike the others, *Niphon* (Fig. 4E) has an elongate spine at the angle of the preopercle that we believe is autapomorphic. This spine (and the one immediately anterior to it) are lateral to the antrorse spines and appear to be part of the lateral preopercular ridge, whereas the antrorse spines of *Niphon* (Fig. 4E), *Plectropomus* and primitive anthiines (Fig. 4B–D) are part of the medial preopercular ridge.

Larvae with a Single Supraorbital Spine.—Larvae of serranines and some epinephelines (liopropomins and grammistins—see character 22 below) lack supraorbital spination. All known anthiine and other epinepheline larvae have one to several supraorbital spines. A single supraorbital spine is present in basal epinephelines and anthiines including *Niphon, Plectranthias garrupellus* and undescribed larvae tentatively identified in this study as *Acanthistius* and *Hypoplectrodes* (unpubl. data). Early life history information is available for 64 of 92 taxa treated as percoids by Johnson (1984). Of those, 22 families (excluding serranids) have some type of supraorbital spination. Only four, Coryphaenidae, Rachycentridae, Echeneididae and Lobotidae, have a single supraorbital spine resembling the condition in *Niphon* and primitive anthiines, and three (Coryphaenidae, Rachycentridae and Echeneididae) are part of the monophyletic "carangoids" (Johnson, 1984). Thus, only if lobotids or carangoids are the sister group of the Ser-

ranidae is the polarity of this character equivocal. Lacking evidence to support that relationship, we consider the presence of a single supraorbital spine as derived within the Serranidae, specifically in an ancestor common to anthiines and epinephelines.

Discussion of Outgroup Relationships

We are unaware of any character shared by all anthiines and epinephelines that is lacking in serranines, but *Niphon* and at least cladistically primitive anthiines share several. Two characters, configuration of dorsal-fin pterygiophores and presence of 13 dorsal-fin spines, are uninformative because we are unable to assess their polarity, and they occur among epinephelines only in *Niphon* (rendering the hypothesis that they evolved independently in anthiines and epinephelines as likely as one that infers common ancestry). Assuming that the identification of the serranid sister group would not change our hypotheses of polarity, two characters, single supraorbital spine in larvae and antrorse preopercular spines in adults, are more convincing as synapomorphies of anthiines and epinephelines. Because supraorbital spines occur among epinephelines in more taxa than *Niphon*, it is more parsimonious to hypothesize a single evolutionary step in a common ancestor of the two subfamilies than independent acquisition in the two lineages. Nevertheless, identification of larvae of more "basal" anthiines is needed to test this hypothesis. The strongest evidence of a possible sister-group relationship between the Anthiinae and Epinephelinae is the configuration of spines and serrations on the preopercle, particularly, the presence of two or more antrorse spines on the lower limb. Although patterns of preopercular spination vary considerably among percoids, the pattern of primitive epinephelines and anthiines appears to be unique. Only the presence of a similar pattern in an as yet unidentified serranid sister group could alter the interpretation of this character as a synapomorphy of anthiines plus epinephelines.

Our preliminary findings suggest a sister-group relationship between the Anthiinae and Epinephelinae, but further investigation, including an analysis of generic relationships among anthiines, is needed.

Monophyly of the Epinephelinae

1. *First dorsal-fin pterygiophore lacks an autogenous distal radial and, in larvae, serially supports an elongate spine.*—In most percoids, including serranine and anthiine serranids, the pterygiophores of the spinous dorsal fin comprise a proximal-middle element that is tightly or loosely bound to a separate small distal radial (Fig. 2A, C, D, F). In all epinephelines, the first dorsal-fin pterygiophore lacks a separate distal radial (Fig. 2B, E; Johnson, 1983: fig. 7), a modification that probably serves no special function in adults but may be related to support of an elongate dorsal-fin spine in larvae. Elongate dorsal-fin spines are uncommon among known larvae of percoids, and are lacking in serranines. Most anthiine larvae also lack elongate dorsal-fin spines, but several western Atlantic species (*Anthias nicholsi, Hemanthias vivanus, Plectranthias garrupellus*) have an elongate third dorsal-fin spine. All known larvae of the Epinephelinae have at least one elongate dorsal-fin spine. The elongate element (or the first if more than one elongate element is present) is serially associated with the first dorsal-fin pterygiophore and may be the first (e.g., *Rypticus*), second (e.g., *Epinephelus, Diploprion, Liopropoma, Pseudogramma*) or third (*Niphon*) spine depending on the number of spines (none, one or two, respectively) borne in supernumerary association with the first pterygiophore (see Johnson, 1988, for discussion of serial and su-

pernumerary association of pterygiophores and fin rays). In anthiines, the elongate spine (the third) also is borne in serial association with the first dorsal-fin pterygiophore (anthiines have two supernumerary spines). However, the first pterygiophore is modified in epinephelines but unmodified in anthiines, and we are unable to determine if the conditions in the two subfamilies should be considered homologues. Possibly, the presence of an elongate dorsal-fin spine supported by a modified first dorsal pterygiophore is an autapomorphy of the Epinephelinae, and an elongate spine in larval anthiines evolved one or more times independently; alternatively, an elongate spine could have evolved in an ancestor common to epinephelines and anthiines, been lost in most anthiines and retained in epinephelines where it becomes extremely elongate, receiving additional support through a modification of the serially associated pterygiophore. Absence of an elongate spine in larvae tentatively identified in this study as the cladistically primitive anthiines *Acanthistius* and *Hypoplectrodes* (unpubl. data) supports the former hypothesis. In either scenario absence of an autogenous distal radial on the first dorsal-fin pterygiophore is a uniquely derived feature of the Epinephelinae.

2. *Supraneurals (predorsal bones) two or fewer.*—Serranines and cladistically primitive anthiines have three supraneurals, the primitive percoid complement (Johnson, 1984). Many anthiines and all epinephelines except *Pogonoperca* have only two supraneurals. If anthiines with three supraneurals form a monophyletic group, loss of one supraneural could be considered a synapomorphy of the Anthiinae plus Epinephelinae with a reversal in the former. However, preliminary investigations of anthiine phylogeny do not support monophyly of the cladistically primitive anthiines (Roberts, 1989; this study), and thus it is more parsimonious to hypothesize independent losses of the posterior supraneural in the two subfamilies. Johnson (1983) noted that the presence of a tiny supraneural bone in *Pogonoperca* in the usual position of the third supraneural is best interpreted as secondary, because *Pogonoperca* is a member of the Grammistini.

Monophyly and Interrelationships of Epinepheline Tribes

Niphonini

Johnson (1983, 1988) aligned the monotypic *Niphon* Cuvier and Valenciennes with the Epinephelinae, and accorded it tribal status on the basis of several characters, treated cladistically below, that we interpret as autapomorphies:

3. *Pattern of supraneurals, anterior dorsal-fin pterygiophores and neural spines 0+0/2/1/1/.*—Serranids typically have one supraneural anterior to the first neural spine, the first dorsal-fin pterygiophore in the second interneural space and two pterygiophores in the third interneural space (as in *Schultzea beta,* 0/0+0/2/1+1/, Fig. 2A; *Acanthistius serratus,* 0/0/0+2/1+1/, Fig. 2C; *Pronotogrammus martinicensis,* 0/0/2/1+1/, Fig. 2D; and *Diploprion bifasciatus,* 0/0/1/1+1/, Fig. 2E). *Niphon* is unique among serranids in having two supraneurals anterior to the first neural spine, the first pterygiophore in the first interneural space and only one pterygiophore in the third interneural space (Fig. 2B). The pattern in *Niphon* is derivable from the serranine (0/0+0/2/1+1) or primitive anthiine (0/0/0+2/1+1/) condition via loss of the posterior supraneural (characteristic of all epinephelines) and an anterior shift in the second supraneural and first two pterygiophores.

4. *Dorsal-fin rays XIII,11.*—Among serranids, 13 dorsal-fin spines characterize only *Niphon* and *Acanthistius,* a genus usually considered a serranine but relegated to the Anthiinae by Heemstra and Randall (1986). Pending a resolution of rela-

tionships among serranid subfamilies, we tentatively recognize the presence of 13 dorsal-fin spines as an autapomorphy of *Niphon* and note that the combination of 13 dorsal-fin spines and 11 soft rays is unique among serranids to *Niphon* (*Acanthistius* has 14–17 soft rays).

5. *Vertebrae 30.*—Serranids typically have 24 (serranines and most epinephelines) or 26 (most anthiines) vertebrae, although one epinepheline genus, *Aporops,* has 28. The presence of 30 vertebrae is unique among serranids to *Niphon.*

6. *Lacrimal serrate.*—Johnson (1983: fig. 2A) noted that the ventral margin of the lacrimal in *Niphon* is serrate. Among serranids, we have observed a serrate lacrimal only in the anthiine, *Caesioperca rasor,* which has serrations on the dorsal margins of all infraorbitals, clearly a non-homologous condition.

7. *Preopercle with enlarged spine at angle.*—A large spine at the angle of the preopercle is a common feature of many percoid larvae (including *Niphon*) but is rare in adults. Its presence in adult *Niphon* (see Fig. 4E) is autapomorphic.

Epinephelini + Diploprionini + Liopropomini + Grammistini

Johnson (1983, 1988) hypothesized that *Niphon* is the sister group of all other epinephelines. The following derived characters, analyzed by Johnson (1988) and briefly reviewed below, support this hypothesis:

8. *First supernumerary dorsal-fin spine absent.*—In *Niphon,* serranines, anthiines and many percoids, two supernumerary spines are present on the first dorsal-fin pterygiophore (Fig. 2A–D), whereas in all other epinephelines there is never more than one (Fig. 2E, also see Fig. 10).

9. *The two supraneurals are reduced in size.*—As noted (character 2), presence of two supraneurals is autapomorphic for the Epinephelinae. In the outgroups, supraneurals are robust, dorso-ventrally elongate structures, and the dorsal portion of at least the anteriormost is usually expanded anteriorly (Fig. 2A–D). In other epinephelines, the supraneurals are substantially shorter, and neither is typically expanded (Fig. 2E, also see Fig. 10).

10. *The spine serially associated with the first dorsal-fin pterygiophore is extremely elongate in larvae and encased in a fleshy sheath.*—In larvae of most other serranids, the spine serially associated with the first pterygiophore, though sometimes produced relative to other dorsal spines, is usually less than one-half the body length and is not covered in a fleshy sheath. In known larvae of all epinephelines except *Niphon,* this spine is covered at least initially in a fleshy sheath and is extremely elongate, usually reaching well over half the length of the body.

Epinephelini

As defined by Johnson (1983), the tribe Epinephelini includes *Anyperodon* Günther, *Cromileptes* Swainson, *Epinephelus* Bloch (including the subgenera *Epinephelus, Promicrops, Cephalopholis, Dermatolepis* and *Alphestes,* most of which are accorded generic status by researchers of Indo-Pacific fishes), *Gonioplectrus* Gill, *Gracila* Randall, *Mycteroperca* Gill, *Paranthias* Guichenot, *Plectropomus* Oken, *Triso* (Randall, Johnson and Lowe—erected for *Trisotropis dermopterus* because *Trisotropis* Gill is a junior synonym of *Mycteroperca* Gill, and *T. dermopterus* is distinct from *Mycteroperca*—see Randall et al., 1989), and *Variola* Swainson. Adult features that support the monophyly of the Epinephelini are unknown. The following characters of larvae, initially noted by Johnson (1983) but treated cladistically below, are autapomorphies of the tribe:

11. *Elongate second dorsal- and pelvic-fin spines with robust serrations* (Fig. 5).—Serrate fin spines are lacking in larval serranines, most anthiines and all

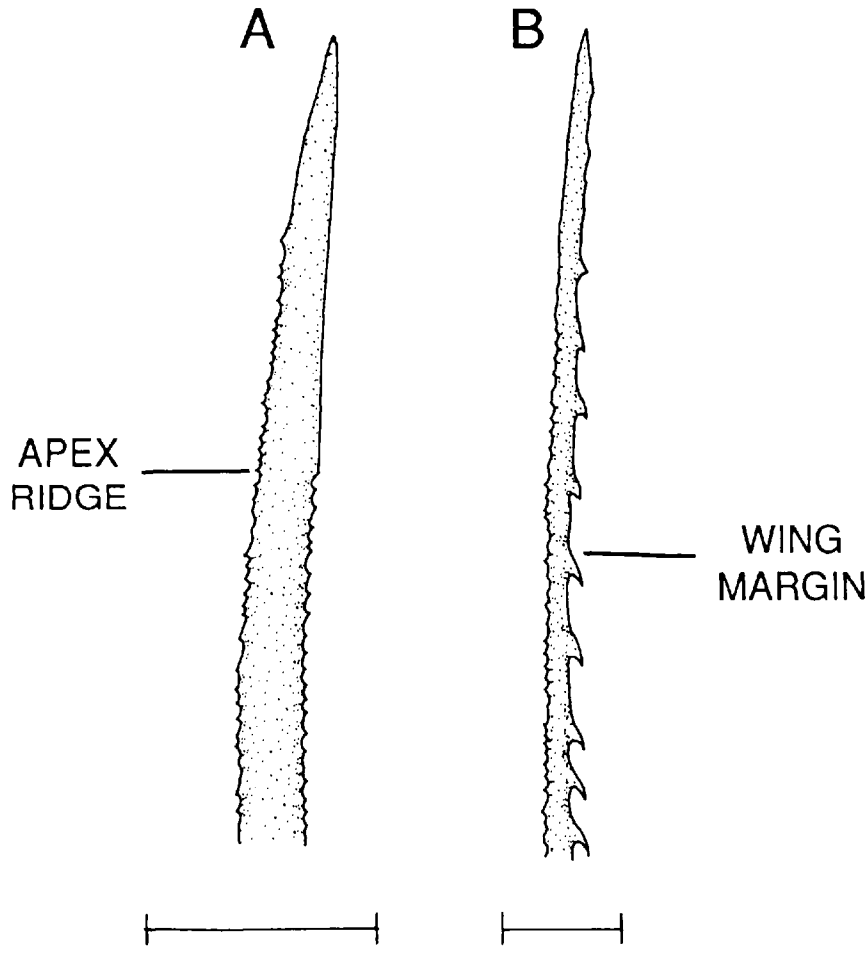

Figure 5. Serrate dorsal-fin spines of two serranid larvae, left lateral view. A) *Hemanthias vivanus* (Anthiinae), third dorsal spine, MCZ, MOC 10–89,1, 6.1 mm SL; B) *Epinephelus cruentatus* (Epinephelinae), second dorsal spine, redrawn from Johnson and Keener (1984), 6.5 mm SL. Scale bars = 0.5 mm.

epinephelines except the Epinephelini. Baldwin (1990a) noted the presence of serrations on the pelvic- and sometimes dorsal- and anal-fin spines in the anthiines, *Hemanthias vivanus, Pronotogrammus aureorubens* and *P. eos,* one of several characters she interpreted as synapomorphic for those species. Johnson and Keener (1984) described and illustratcd patterns of serrations on fin spines of grouper larvae from American waters. They noted that serrations on the anterior margin (apex ridge) of the anterior dorsal-fin spines are small bump-like projections, whereas those on the posterolateral margins (wing margins) are robust and sometimes curved or bifurcate (Fig. 5B). When present, serrations on fin spines in anthiines are feeble, and those of the posterolateral margins are not more prominent than those of the apex (Fig. 5A). Similar differences are apparent in the patterns of serrations on pelvic and anal-fin spines. Because *Niphon* and primitive anthiines lack serrate fin spines, it is most parsimonious to hypothesize independent evolution of serrate fin spines in epinephelines and anthiines. Dif-

ferences in configuration of the serrations in the two subfamilies corroborate the hypothesis that they are nonhomologous, independently derived conditions.

12. *Elongate preopercular spine serrate.*—Known serranid larvae bear spines on the preopercle. In serranines and most epinephelines, the spine at the angle of the preopercle is not serrate, although it may be robust (as in diploprionins and grammistins, as defined herein) or even elongate (as in *Niphon*). Development of a large serrate spine at the angle of the preopercle is characteristic of all known larvae of the Epinephelini. Such a spine also is consistently present in anthiines except in Indo-Pacific larvae tentatively identified as *Acanthistius, Caesioperca, Caprodon,* and *Plectranthias* (unpubl. data), taxa that appear to be cladistically primitive members of the Anthiinae. Outgroup comparison indicates that the presence of an elongate, serrate spine at the angle of the preopercle is derived within the Epinephelini.

13. *Pigment spot on midventral caudal peduncle migrates dorsally to midlateral position.*—The presence of a single melanophore on the midventral margin of the caudal peduncle just posterior to the termination of the anal fin is a common feature among serranid and other percoid larvae, but only in epinephelins does this melanophore migrate dorsally to a midlateral position (Leis, 1986). Leis (1986) noted that this migration does not occur in larvae of four species of *Plectropomus* examined by him, and we only tentatively include this character as a synapomorphy of epinephelins, pending further investigation of other larval *Plectropomus.* As suggested by Leis (1986), this character may best be interpreted as a synapomorphy of all epinephelins exclusive of *Plectropomus.*

Diploprionini + Liopropomini + Grammistini

14. *The elongate dorsal-fin spine(s) in larvae are filamentous.*—When present, elongate dorsal-fin spines in larvae of epinephelins, *Niphon* and anthiines are robust. In larval diploprionins, liopropomins and grammistins, elongate dorsal-fin spines are thin, flexible and sometimes encased in elaborately ornamented sheaths. Baldwin et al. (1991) noted that these often spectacularly elongate, filamentous dorsal-fin spines probably have a different function than the robust spines of *Niphon* and epinephelins, but concluded that further study of the filaments is needed before a plausible functional explanation can be hypothesized.

15. *Larvae lack elongate spine at angle of preopercle.*—Serranines have poorly developed preopercular spination, but epinephelins, *Niphon* and anthiines have an elongate (often serrate) spine at the angle of the preopercle. Although preopercular spines in larval diploprionins, liopropomins and grammistins are often robust, none is elongate relative to the others. Outgroup comparison indicates that the absence of an elongate preopercular spine in larvae is a derived condition within the Epinephelinae.

Diploprionini

Johnson (1983) assigned *Aulacocephalus* Temminck and Schlegel, *Belonoperca* Fowler and Bean and *Diploprion* Kuhl and van Hasselt to his tribe Diploprionini; those genera share the following derived features:

16. *Epidermis with mucous cells that contain the skin toxin grammistin* (Fig. 6).—Randall et al. (1971) and Randall et al. (1980) discovered the presence of a unique mucous cell in the epidermis of *Aulacocephalus, Belonoperca, Diploprion, Grammistes, Grammistops, Pogonoperca* and *Rypticus* that contains the ichthyotoxin grammistin (Fig. 6A). This toxin is a hemolysin that is positive to Dragendorff reagent, negative to biuret and ninhydrin reagents, produces a positive

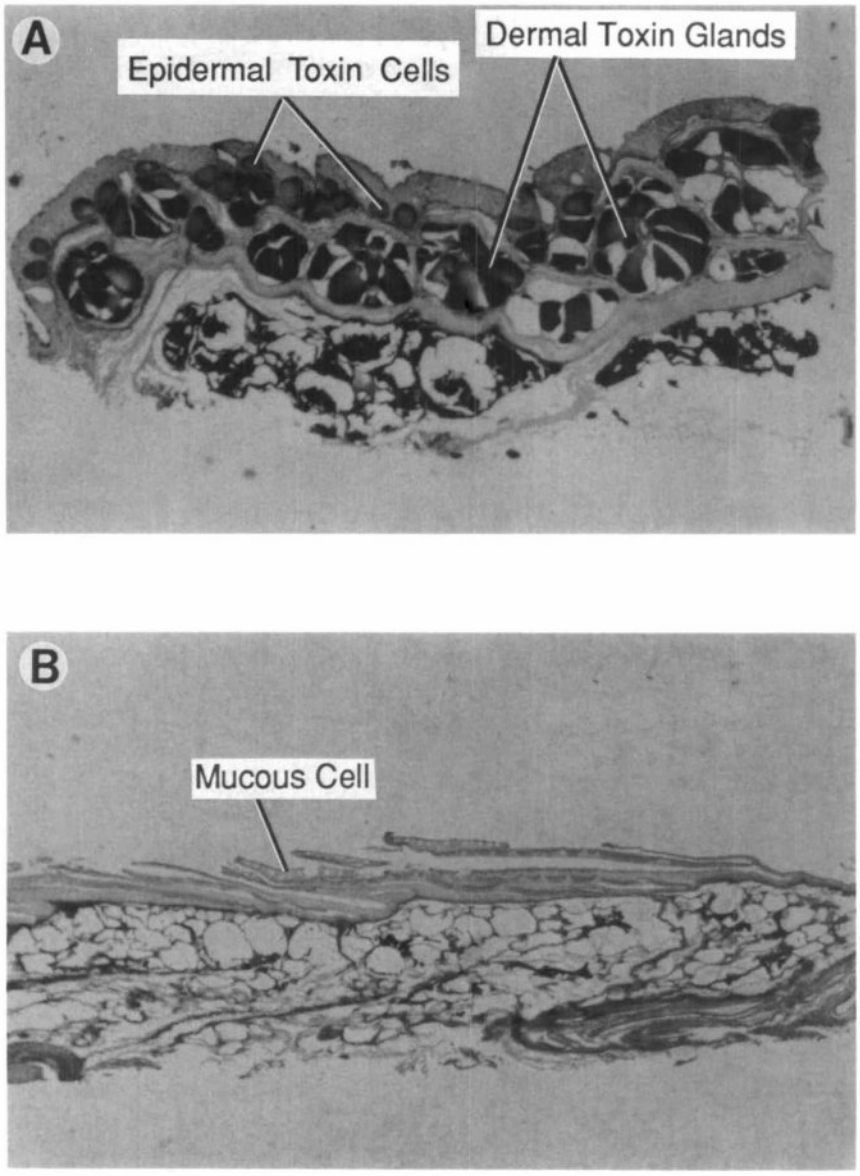

Figure 6. Photomicrograph of histological sections (Sudan Black B preparations) of skin taken from near base of anal fin. A) *Grammistops ocellatus*, USNM 260562, 55.5 mm SL; B) *Suttonia lineata*, USNM 209705, 49.6 mm SL. Note the small, darkly stained epidermal toxin cells and large dermal toxin glands in the soapfish, *Grammistops*.

(black) reaction to the histological stain Sudan Black B and tastes bitter (Randall et al., 1971). The skin of liopropomins and *Pseudogramma* and its allies was not investigated histologically, but taste tests for grammistin performed on the latter by Randall et al. (1971) were negative. We have examined histological sections of the skin of *Pseudogramma* and *Suttonia* stained with Sudan Black B and find no evidence of epidermal toxin cells (Fig. 6B). The presence of grammistin in the epidermis is a derived feature within the Epinephelinae; it is lacking in other

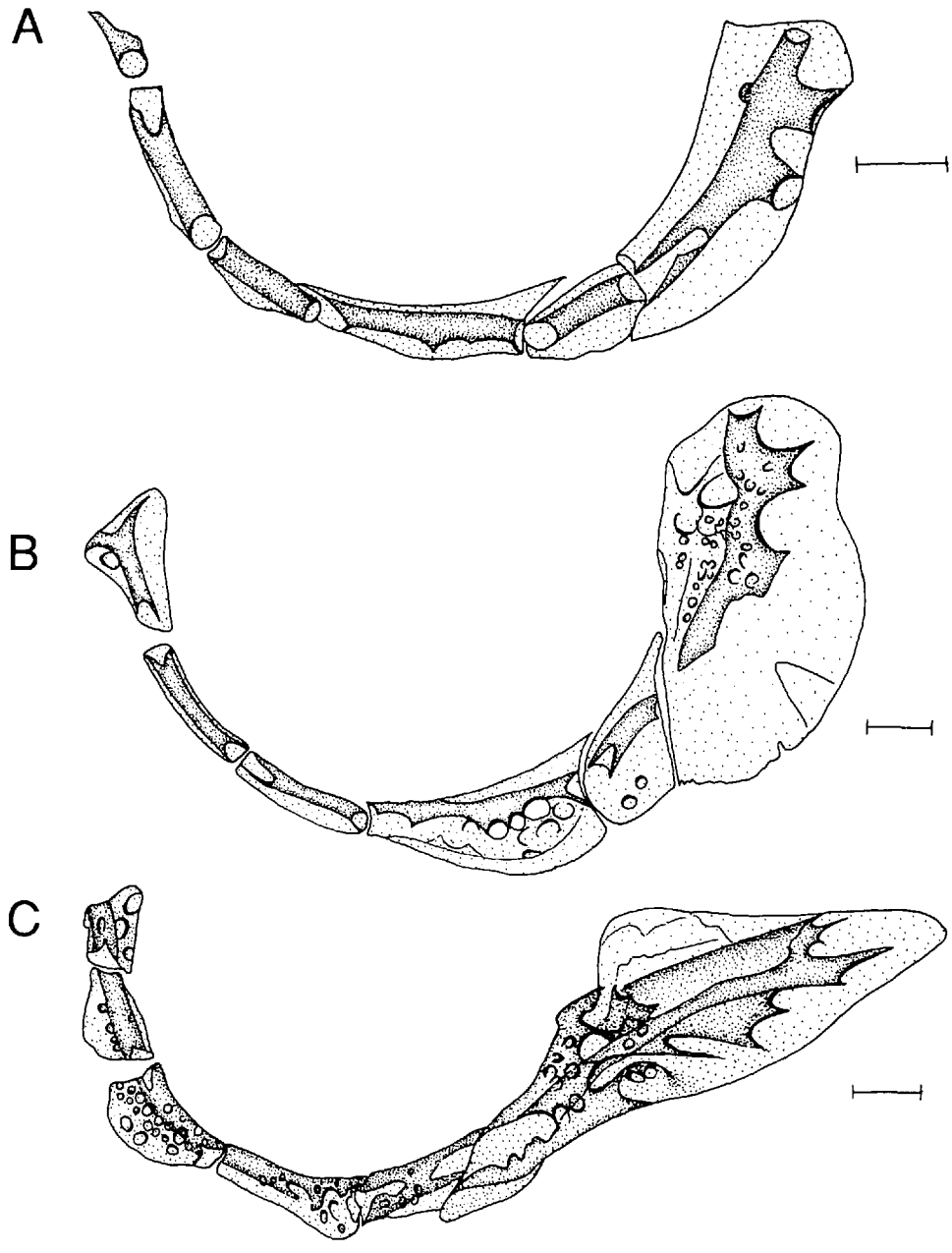

Figure 7. Infraorbital series, right side. A) *Grammistes sexlineatus*, USNM 218886, 68.0 mm SL; B) *Diploprion bifasciatus*, USNM 218889, 70.0 mm SL; C) *Belonoperca chabanaudi*, USNM 217813, 67.5 mm SL. Scale bars = 1 mm.

serranids and is not known to occur in other percoids. The distribution of epidermal grammistin suggests a sister-group relationship between diploprionins and the so-called "soapfishes" (*Pogonoperca, Grammistops, Grammistes* and *Rypticus*) of the tribe Grammistini (together, the "Grammistidae" of Randall et al., 1971). An analysis of the chemistry of grammistin in diploprionins and soapfishes that

Figure 8. Base of spinous dorsal fin of *Diploprion bifasciatus*, USNM 183096, 209 mm SL.

might yield information useful in assessing homology of the substance in the two groups is beyond the scope of this study. Oshima et al. (1974) noted considerable differences between diploprionins and soapfishes in the behavior of the toxin in column chromatography, countercurrent distribution and thin layer chromatography. Their results may indicate nonhomology of epidermal grammistin. However, as discussed below (character 16′) soapfishes not only have grammistin in epidermal cells but in large dermal glands (Fig. 6A). If dermal grammistin is chemically different from epidermal grammistin, then differences might be expected in elution and distribution patterns in taxa that have only epidermal grammistin and those that have both epidermal and dermal toxins. In the absence of an assessment of homology and lacking information that would allow us to order this character (e.g., state "1" in Table 1, in which grammistin occurs only in the epidermis must precede state "2," in which epidermal and dermal grammistin are present), it is most parsimonious (although intuitively unsatisfactory) to hypothesize independent acquisition of the skin toxin in the Diploprionini and Grammistini, with the addition of dermal toxin glands in soapfishes, and a reversal in the ancestor of *Pseudogramma* and relatives. The alternative hypothesis, that grammistin evolved in a common ancestor of diploprionins and grammistins, requires an additional reversal, in the Liopropomini. We are confident that the presence of grammistin does not indicate a sister-group relationship between diploprionins and soapfishes because, as described below, liopropomins share at least four derived features with grammistins that are lacking in diploprionins, and the affinities of the soapfishes lie with the "pseudogrammid" genera.

17. *Neurocranium and infraorbitals rugose* (Fig. 7).—In other epinephelines, serranines and anthiines, the neurocranium and infraorbital bones generally are smooth in appearance. In *Aulacocephalus, Belonoperca* and *Diploprion,* bones of the neurocranium (particularly the frontals) and infraorbitals (Fig. 7) have numerous small, semicircular, round or oblong concavities that impart a texture of rugosity (Johnson, 1983).

18. *Bases of dorsal and anal fins covered with ridges of tissue* (Fig. 8).—In the outgroups and other epinephelines, skin at the bases of dorsal and anal fins is smooth. In diploprionins, the skin at the bases of those fins is rimpled, forming a series of elevated ridges (Fig. 8).

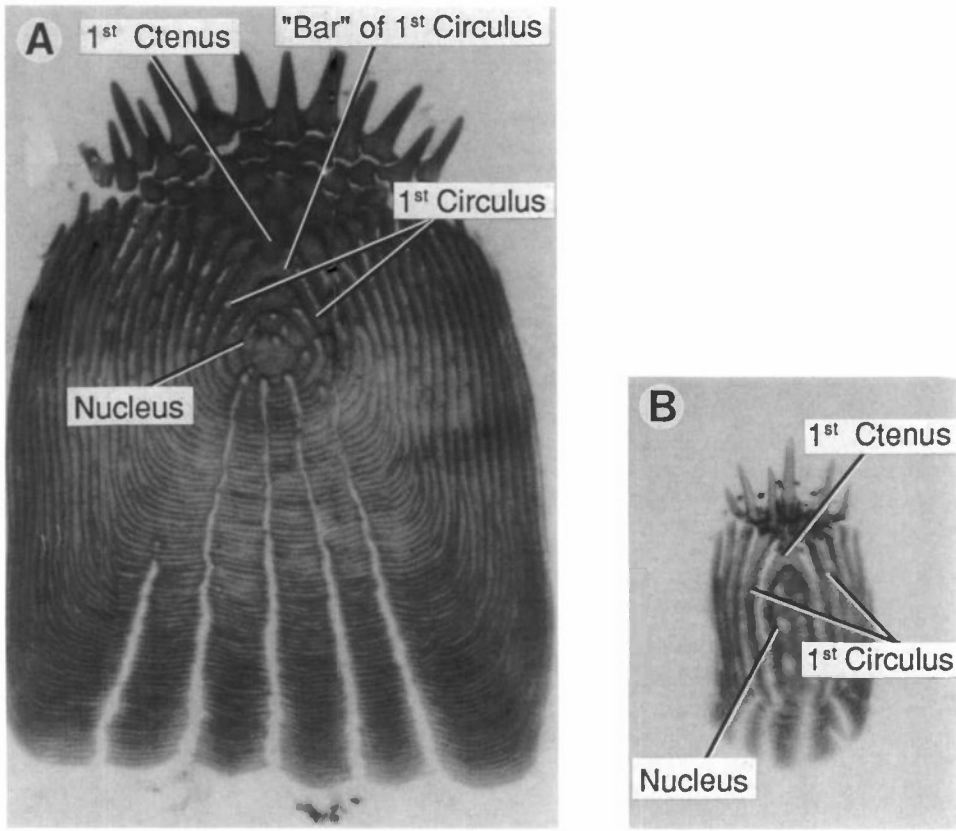

Figure 9. Photomicrographs of scales. A) *Belonoperca chabanaudi*, USNM 217813, 67.5 mm SL; B) *Acanthistius serratus*, AMS I. 19602004, 67.0 mm SL.

19. *First circulus of scales forms a bar that projects posteriorly along the midline and, in regenerated scales, functions as the first ctenus* (Fig. 9).—McCully (1961) believed that a similar scale morphology was indicative of a close relationship among *Acanthistius, Aulacocephalus* and *Diploprion*, and placed those taxa in his tribe Diploprionini. Our examination of serranid scales and McCully's (1961) descriptions and illustrations indicates that *Aulacocephalus, Diploprion* and *Belonoperca*, a genus not examined by McCully, share the unique morphology of the first circulus described by McCully (Fig. 9A), but that *Acanthistius* does not. In most serranids, the first circulus either is closed posteriorly and has no bar originating from it (see Fig. 19A, B), or it is open posteriorly such that the two free ends abut the posterior edge of the scale plate (Fig. 9B; also see Figs. 13, 19C–E). We have not examined scales of all species of *Acanthistius*, but those of *A. cinctus* and *A. serratus* (Fig. 9B) have the first circulus open. The bar-like structure in the posterior field of scales of *Acanthistius*, although similar in appearance to the "bar" of diploprionins, is actually the first ctenus and extends from the nucleus, rather than from the first circulus. Thus, we agree that the presence of a bar projecting from the first circulus (and functioning as the first ctenus in regenerated scales, McCully, 1961) is a derived feature within the Serranidae, but believe it diagnoses a Diploprionini that includes *Aulacocephalus, Belonoperca* and *Diploprion* and excludes *Acanthistius*.

Liopropomini + Grammistini

Despite the apparent absence of the skin toxin grammistin in liopropomins, it is most parsimonious to hypothesize a sister-group relationship between the Liopropomini and Grammistini on the basis of the following shared features:

20. *First dorsal-fin pterygiophore thin and curved* (Fig. 10).—In other epinephelines and the outgroups, the first dorsal-fin pterygiophore has well-developed laminar flanges along its length (see Fig. 2). It is oriented either vertically or angled such that the dorsal (distal) portion of the pterygiophore is more posterior than the ventral portion, and it is always straight (see Fig. 2). In *Liopropoma* (Fig. 10A), *Rainfordia* and the grammistins (e.g., *Aporops*, Fig. 10B), the first pterygiophore is slender along its entire length, having lost most or all of the laminar flanges, and it is usually curved such that the distal portion of the pterygiophore is far posterior of the proximal. Outgroup comparison indicates that the condition in liopropomins and grammistins is derived.

21. *Distal radials of third through last spinous dorsal-fin pterygiophores separated from serially associated proximal-middle elements, the latter reduced posteriorly to a blunt spine* (Fig. 10).—The serially associated proximal-middle and distal elements of the anteriormost dorsal-fin pterygiophores in most serranids are very closely associated (see Figs. 2, 10A). Posteriorly, the distal radials remain tightly bound to their serially associated proximal-middle elements in *Niphon* and anthiines (presumably the primitive percoid condition, see "Outgroup Relationships") but loosely bound in serranines and most epinephelines. In liopropomins (e.g., *Liopropoma*, Fig. 10A) and grammistins (e.g., *Aporops*, Fig. 10B), however, the distal radials of at least the third through last pterygiophores become widely separated from their serially associated proximal-middle element (Johnson, 1983). Presumably because it no longer serves to support the distal radial, the posterior portion of the proximal-middle element loses its articular surface and is reduced to a small, backward projecting blunt spine. Similar reductive modifications of proximal-middle elements occur in many other percoids (e.g., *Ambassis, Brinkmannella, Centropomus, Graus*), but outgroup comparison suggests that the presence of an articulation between proximal-middle elements and serially associated distal radials is the primitive condition for the Epinephelinae. Loss of this articulation is considered synapomorphic for the Liopropomini and Grammistini.

22. *Larvae lack supraorbital spination.*—Although absent in larval serranines, supraorbital spines are present in known larvae of all diploprionins, epinephelins, *Niphon* and anthiines, and may represent a synapomorphy of the Anthiinae plus Epinephelinae (see "Outgroup Relationships"). Absence of supraorbital spination in larval Liopropomini and Grammistini is considered a secondary loss and is indicative of a sister-group relationship between those tribes.

23. *Pelvic fins develop late.*—In most serranid larvae, the pelvic fin is one of the first fins to complete development (Johnson, 1984), whereas in larval liopropomins and grammistins, it is the last.

Liopropomini

Johnson (1983) placed *Jeboehlkia* Robins, *Liopropoma* Gill, *Pikea* Steindachner and *Rainfordia* McCulloch in the tribe Liopropomini. *Bathyanthias* Günther (type species *B. roseus*) was not included in his list of epinephelines because Schultz (1958) placed this genus in the synonymy of *Liopropoma* based on its possession of nine dorsal-fin spines. However, Robins (1967) regarded *Bathyanthias* as a synonym of *Pikea*, noting that *B. roseus* greatly resembles *P. mexicana* Schultz. *Pikea* is now considered a synonym of *Liopropoma*, but according to Randall and

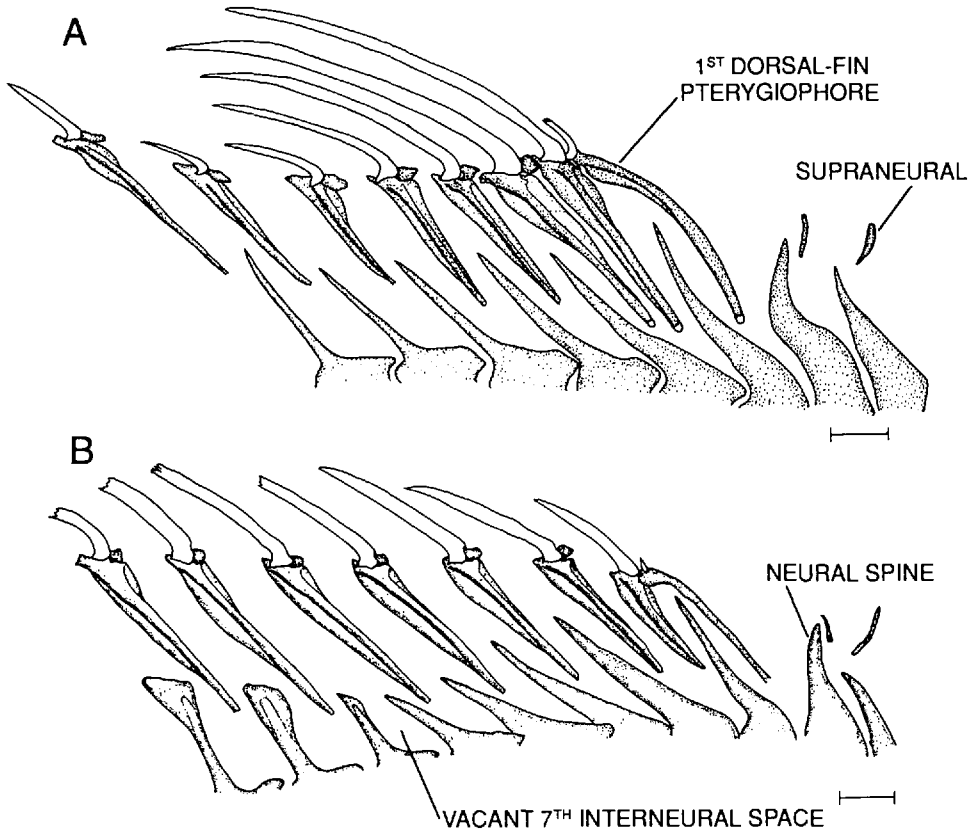

Figure 10. Spinous dorsal-fin pterygiophores and anterior neural spines, right side. A) *Liopropoma susumi*, USNM 218726, 48.0 mm SL; B) *Aporops bilinearis*, USNM 218920, 50.0 mm SL. Scale bars = 1 mm.

Taylor (1988), two Atlantic species of *Pikea*, *P. mexicana* and *P. cubensis* Schultz, do not belong in *Liopropoma*. As noted by Randall and Taylor (1988), there is thus the possibility that *Bathyanthias* Günther is a valid genus and, perhaps, should include *P. mexicana* and *P. cubensis* which, at present, have no generic allocation.

Our examination of a radiograph of the holotype of *B. roseus* (BMNH 1879.5.14.155) indicates that this species has eight, rather than nine, dorsal-fin spines. Thus, *B. roseus* is identical to *P. mexicana* in number of dorsal-fin spines as well as other features, including numbers of dorsal-fin soft rays (14), pectoral-fin rays (15) and pored lateral-line scales (47 in *B. roseus*, Robins, 1967; 46 or 47 in *P. mexicana*, Schultz, 1958). In his original description of *B. roseus*, Günther (1880) described the pigmentation as "uniform rose-colour, with two faint lighter longitudinal bands." Schultz (1958) did not provide a description of the color in living specimens of *P. mexicanus*, but Robins et al. (1986) noted that the head and body are pale red with two longitudinal yellow lines of pigment on the head.

Further study is needed to resolve the taxonomy of these species, but we note the possibility that *P. mexicana* Schultz, 1958, is a junior synonym of *B. roseus* Günther, 1880. For purposes of this paper, we tentatively consider *Bathyanthias* as a valid genus that may include *P. mexicanus* and *P. cubensis*.

Robins (1967) described *Jeboehlkia gladifer* from a single mature female, 40.1

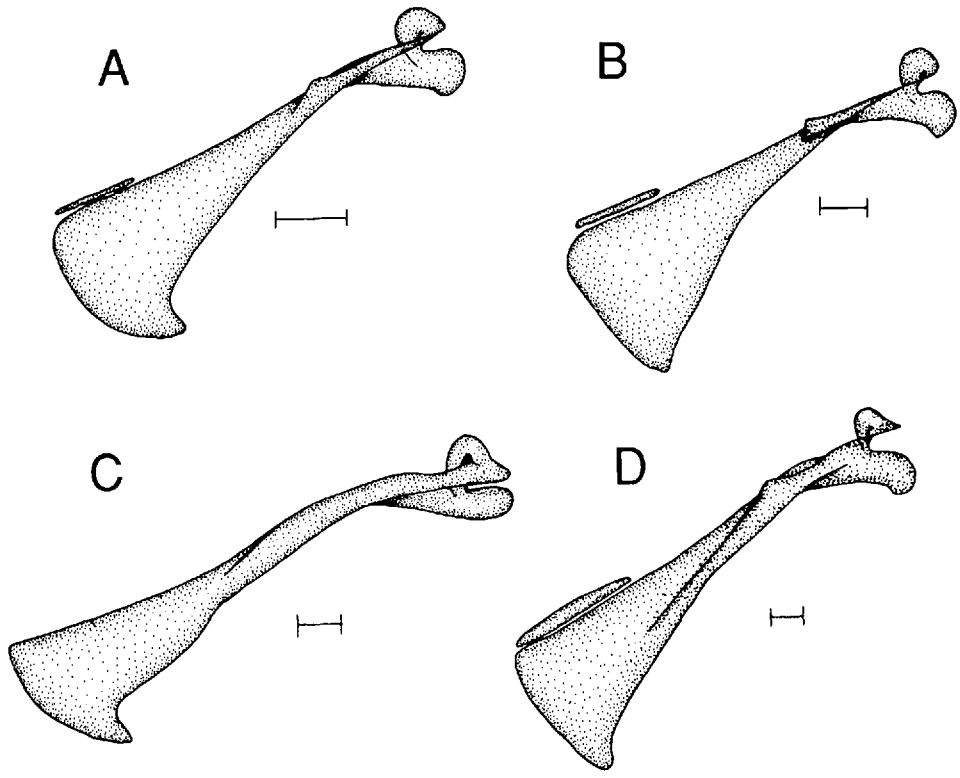

Figure 11. Maxilla, right side. A) *Liopropoma susumi*, USNM 218726, 48.0 mm SL; B) *Jeboehlkia gladifer*, Indian River Coastal Zone Museum 107:7433, 55.0 mm SL; C) *Rainfordia opercularis*, USNM 203247, 98.0 mm SL; D) *Pikea mexicana*, USNM uncat., 103 mm SL. Scale bars = 1 mm.

mm SL, and noted that it greatly resembles *Liopropoma*. Johnson (1983) included *Jeboehlkia* in his Liopropomini, but did not examine the holotype. Our examinations of the holotype of *J. gladifer* (USNM 201422), a cleared and stained adult specimen and the single known larval specimen (Baldwin and Johnson, 1991) suggest that the affinities of *Jeboehlkia* do not lie with the liopropomins, but with the more specialized grammistins. *Jeboehlkia* lacks most of the following characters diagnostic of the Liopropomini, now redefined to include only *Liopropoma*, *Rainfordia* and, possibly, *Bathyanthias*.

24. *Prominent, anteriorly directed, hook-like process extends from posteroventral corner of maxilla* (Fig. 11).—In most other epinephelines, serranids and percoids, the posteroventral portion of the maxilla lacks projections. *Jeboehlkia* and *Pseudogramma* have a very small, almost ventrally directed maxillary process (Fig. 11B) that bears little resemblance to the large, anteriorly directed, hook-like process of *Liopropoma* (Fig. 11A) and *Rainfordia* (Fig. 11C). A prominent maxillary hook is not evident in the radiograph of the holotype of *B. roseus*, but the process is weakly developed in *P. cubensis* and *P. mexicana* (Fig. 11D). A well-developed maxillary hook may be indicative of a sister-group relationship between *Liopropoma* and *Rainfordia*.

25. *Subocular shelf extends from more than one infraorbital* (Fig. 12).—In most percoids, the subocular shelf is a thin flange of bone that extends medially from the third infraorbital (Fig. 12A). This shelf may extend anteriorly and posteriorly over the second and fourth infraorbitals, but those bones do not bear separate

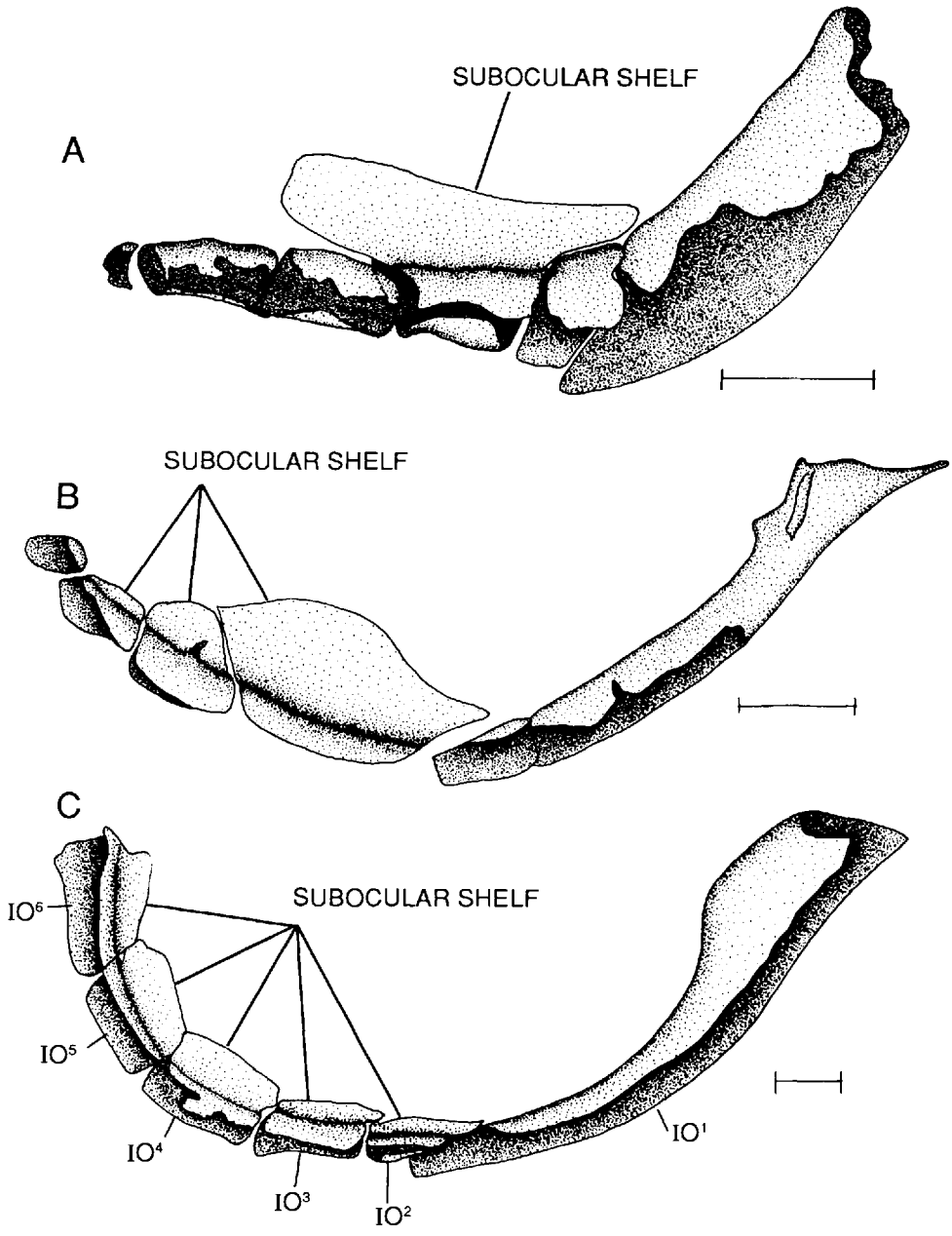

Figure 12. Infraorbital series (IO) showing subocular shelf, right side, dorso-lateral view (series flattened beneath a glass microscope slide for illustration). A) *Aporops bilinearis*, USNM 218920, 48.0 mm SL; B) *Liopropoma carmabi*, USNM 198283, 43.5 mm SL; C) *Rainfordia opercularis*, USNM 203247, 98.0 mm SL. Scale bars = 1 mm.

shelves. In *Pikea mexicana* and *Liopropoma*, the shelf comprises three flanges of bone, a large extension from the third infraorbital and smaller ones from the fourth and fifth (Fig. 12B). *Rainfordia* has separate shelves extending from the second through sixth infraorbitals (Fig. 12C). Meisler (1987) noted the presence

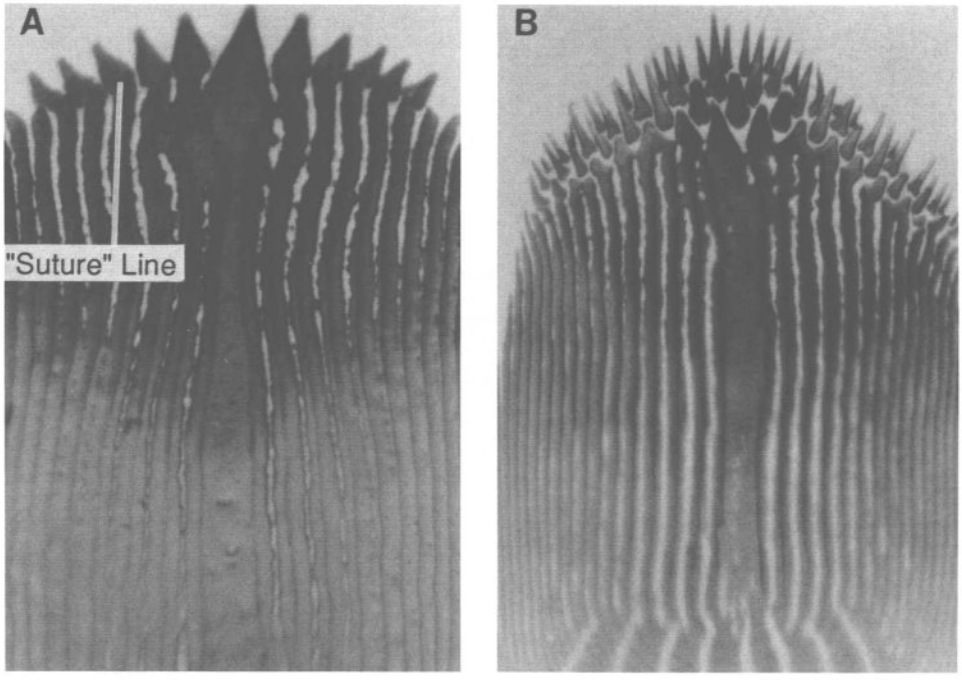

Figure 13. Photomicrograph of liopropomin scales. A) *Rainfordia opercularis,* USNM 203247, 98.0 mm SL; B) *Liopropoma carmabi,* USNM 198283, 43.5 mm SL.

of a "tripartite" subocular shelf extending from the third through fifth infraorbitals in *Diplectrum* and three species of *Serranus* and considered this modified shelf a synapomorphy of those taxa. We are aware of no other features indicative of a close relationship between those serranines and liopropomins and consider the states in the two subfamilies as independently derived.

In *Jeboehlkia,* a large subocular shelf is all that remains of the third infraorbital, and all other infraorbitals, except the lacrimal, are lost. This condition is unlike that of any serranid examined, and thus provides no clues as to the affinities of *Jeboehlkia.*

26. *Scales with cteni fused to open ends of at least medialmost circuli* (Fig. 13).—Johnson (1984) distinguished between two types of ctenoid scales, one in which cteni are projections of the scale plate (his "Ct'"), and "true" ctenoid scales in which cteni are separate entities bound by connective tissue to the scale plate (Roberts, 1993). Superficially, the ctenoid scales of some liopropomins appear to be the former because at least some of the cteni are continuous with the circuli (lateral ridges of McCully, 1961). A close examination of the ends of circuli in liopropomins, however, particularly the more lateral elements, often will reveal a small suture line that suggests the origin of the condition is via fusion of cteni to the ends of open circuli (Fig. 13). Our attempts to document this fusion developmentally were unsuccessful, however, because cteni already are "fused" to circuli in the smallest larvae (ca. 15–17 mm SL) on which we could find scales.

Despite the fact that differences exist among liopropomins in morphology of scales (those of *Rainfordia* bear only a single row of cteni (Fig. 13A); those of *Liopropoma* (Fig. 13B), *Pikea mexicana* and *P. cubensis* have more than one row but differ from one another substantially in size) the presence of cteni that are

continuous with ends of circuli is a unique feature that infers a common ancestry for the liopropomins.

Cteni on scales of *Jeboehlkia* are not fused to circuli. As discussed below (character 43), *Jeboehlkia* shares with *Pseudogramma* and its relatives another derived configuration of cteni.

Grammistini

The remaining epinepheline genera, *Aporops* Schultz, *Grammistes* Bloch and Schneider, *Grammistops* Schultz, *Jeboehlkia* Robins, *Pogonoperca* Günther, *Pseudogramma* Bleeker (includes *Rhegma* Gilbert), *Rypticus* Cuvier and *Suttonia* Smith form the monophyletic Grammistini based on their shared possession of numerous derived features.

16′. *Skin with epidermal cells and dermal glands containing the skin toxin grammistin.* —Randall et al. (1971) described large, dermal toxin-secreting glands in *Grammistes, Grammistops* (Fig. 6A), *Pogonoperca* and *Rypticus,* but noted that grammistin is lacking in the dermis of other epinephelines, including diploprionins, which are known to have grammistin in epidermal mucous cells. The presence of dermal toxin glands is a uniquely derived feature that implies monophyly of the soapfishes; however, as discussed below, *Rypticus* and *Grammistops* share several derived characters with the "pseudogrammid" genera that are lacking in *Grammistes* and *Pogonoperca,* and thus it is most parsimonious to hypothesize the evolution of dermal toxin glands in the ancestor of the Grammistini, with a reversal within the tribe.

27. *Procurrent caudal-fin rays fewer than 10.* —Serranines, anthiines and other epinephelines have 10 or more (most have 13–28) procurrent caudal-fin rays, whereas grammistins have six to nine.

28. *Soft dorsal fin with all except anteriormost pterygiophore trisegmental.* —All epinephelines except some members of the tribe Epinephelini have some trisegmental pterygiophores (in which the middle element is separate from the proximal) in the posterior portion of the soft dorsal fin, and they are present primitively in serranines (e.g., *Chelidoperca,* Meisler, 1987) and anthiines (e.g., *Acanthistius,* some *Plectranthias, Othos*; this study). Thus, presence of trisegmental pterygiophores appears to be a primitive serranid feature that has been lost independently in some serranines and anthiines. In all non-grammistin serranids, the number of trisegmental pterygiophores is always at least two fewer than the total number of soft dorsal-fin pterygiophores because at least the first and second pterygiophores are bisegmental (e.g., 10 of 12 are trisegmental in *Liopropoma carmabi,* 10 of 15 in *Diploprion bifasciatum*). In grammistins, usually all except the first pterygiophore of the soft dorsal fin are trisegmental (e.g., 12 of 13 in *Grammistes* and *Pogonoperca punctata,* 24 of 25 in *Rypticus* sp., 11 of 12 in *Grammistops,* eight of nine in *Jeboehlkia,* 19 of 20 in *Pseudogramma polyacantha,* 23 of 24 in *Aporops* and 21 of 22 in *Suttonia*). We consider the large number of dorsal trisegmental pterygiophores in grammistins to be a derived condition within the Epinephelinae.

29. *Seventh interneural space vacant* (Figs. 10, 14).—In other epinephelines, serranines and anthiines, a pterygiophore supernumerarily supporting a dorsal-fin spine inserts into the seventh interneural space (as in *Liopropoma,* Fig. 10A). In grammistins (e.g., *Aporops,* Fig. 10B) there is no spinous dorsal-fin pterygiophore between the seventh and eighth neural spines. Although absence of an element in the seventh interneural space could be the result of loss of a dorsal spine (grammistins have eight or fewer dorsal spines whereas some epinephelines

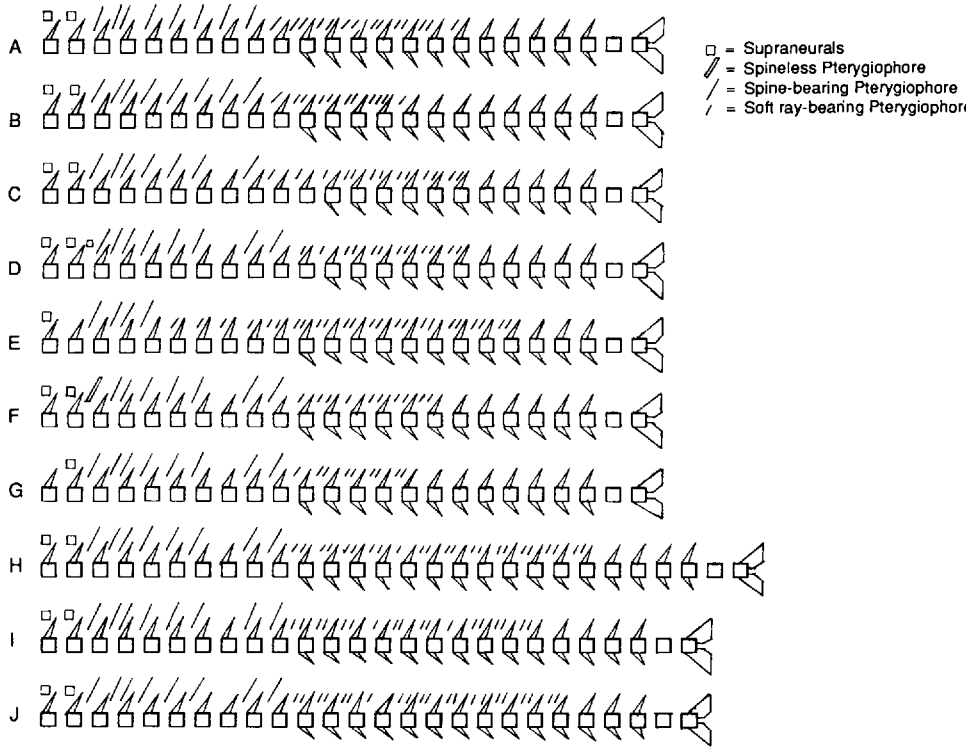

Figure 14. Schematic of interdigitation patterns of neural spines and dorsal-fin pterygiophores, left side. A) *Diploprion*; B) *Liopropoma*; C) *Grammistes*; D) *Pogonoperca*; E) *Rypticus*; F) *Grammistops*; G) *Jeboehlkia*; H) *Aporops*; I) *Pseudogramma*; J) *Suttonia*.

have nine or more) or the insertion of an extra precaudal vertebra (conceivable at least in *Grammistes* and *Pogonoperca* which have 11 precaudal vertebra whereas other epinephelines have 10), we believe the condition in grammistins results from neither of these but from a posterior shift of the pterygiophore that normally occupies the seventh interneural space. In liopropomins and diploprionins (the appropriate outgroups for the Grammistini), the pterygiophores supernumerarily supporting the seventh and eighth dorsal-fin spines (the seventh and eighth pterygiophores) insert into the seventh and eighth interneural spaces, respectively (Fig. 14A, B). In grammistins, the pterygiophores that supernumerarily bear the seventh (*Grammistes*) or seventh and eighth dorsal spines (the seventh or seventh and eighth pterygiophores, respectively) insert into the eighth or eighth and ninth interneural spaces, and the seventh interneural space is vacant (Fig. 14C–J). Although loss of the seventh pterygiophore (and spine) in *Diploprion* and *Liopropoma* (Fig. 14A, B) yields the condition observed in *Grammistes* (seven dorsal-fin spines, none supported by pterygiophores in the seventh and ninth interneural spaces, Fig. 14C), this hypothesis requires that a new pterygiophore (and spine) form in the ninth interneural space in other grammistins. Insertion of an additional precaudal vertebra also is less parsimonious, because it can only explain the condition in *Pogonoperca* (eight dorsal spines, 11 precaudal vertebrae, Fig. 14D). None of the scenarios described above can explain the condition in *Rypticus* (Fig. 14E), wherein there are only three or four spines.

In grammistins, but not other epinephelines, the sixth and seventh neural spines

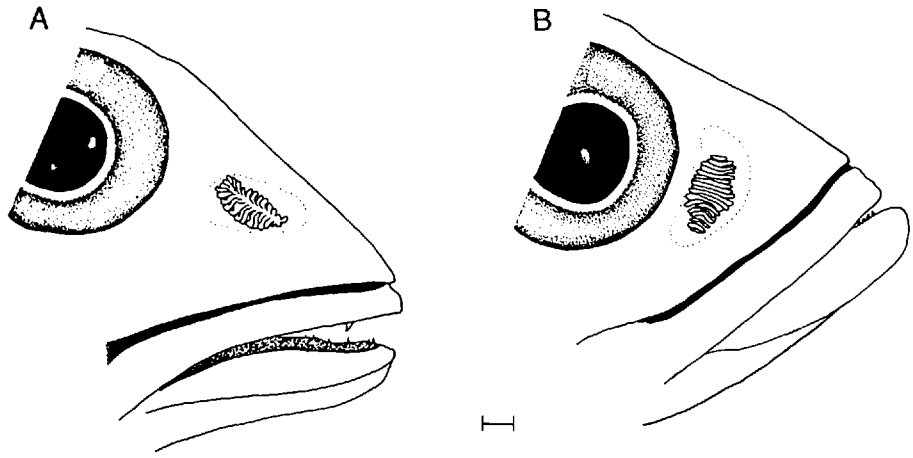

Figure 15. Nasal organ (overlying tissues removed). A) *Epinephelus guttatus*, CBL 3692, 65.0 mm SL; B) *Grammistops ocellatus*, USNM 260562, 73.0 mm SL. Scale bar = 1 mm.

are greatly inclined posteriorly (Fig. 10B). But the eighth neural spine is oriented more vertically, and the posteriorly inclined seventh neural spine comes close to contacting it, leaving little space for insertion of a pterygiophore. Reduction in size of the seventh interneural space could be associated with the hypothesized posterior shift of the seventh pterygiophore.

30. *Nasal organ comprised of a single row of horizontally-oriented lamellae* (Fig. 15).—In non-grammistin serranids, the nasal organ is round to oval in shape (if oval, the long axis of the organ is oriented essentially anterior to posterior), and has lamellae radiating in rosette fashion from a central point or line (Fig. 15A). Gosline (1960) noted the presence of an enlarged, elongate nasal rosette in *Pseudogramma*, and Johnson (1983) considered an elongate rosette as indicative of relationship between liopropomins and grammistins. Our investigations reveal that the nasal organ in all grammistins, but not liopropomins, is dorsoventrally elongate, usually somewhat ovoid in shape, and consists of a stack of horizontally-oriented lamellae that are essentially parallel to one another (Fig. 15B).

31. *Second anal-fin pterygiophore straight, not bending posteriorly* (Fig. 16).—In other serranids, the proximal-middle radial of the second anal-fin pterygiophore is straight proximally and bends posteriorly near the distal extremity (Fig. 16A, B). In the Grammistini, the second anal-fin pterygiophore is straight throughout its entire length (Fig. 16C–F). Superficially, this condition appears to result from loss of the middle element of the second pterygiophore, but it may also be explained by a straightening (and possibly shortening) of the middle element.

32. *Preopercle with 1–3 spines* (Fig. 17).—Adults of other epinephelines and the outgroups typically have numerous spines or serrations on the posterior margin of the preopercle (Figs. 4, 17A). Among grammistins, fewer spines (two or three in *Grammistes*, *Pogonoperca* and *Rypticus*, one in *Grammistops* and *Pseudogramma* and its relatives—Fig. 17B, also see Fig. 23) usually are present. Liopropomins either lack preopercular spines (some *Liopropoma*) or have few (*Rainfordia*) or many (*Bathyanthias*) weakly developed serrations. These conditions are different from that of grammistins which have a reduced number of generally well-developed spines. *Jeboehlkia* is unique among adult grammistins in having approximately seven preopercular spines, including three or four antrorse spines on the lower limb (Fig. 18A). Considering the distribution of other characters, it

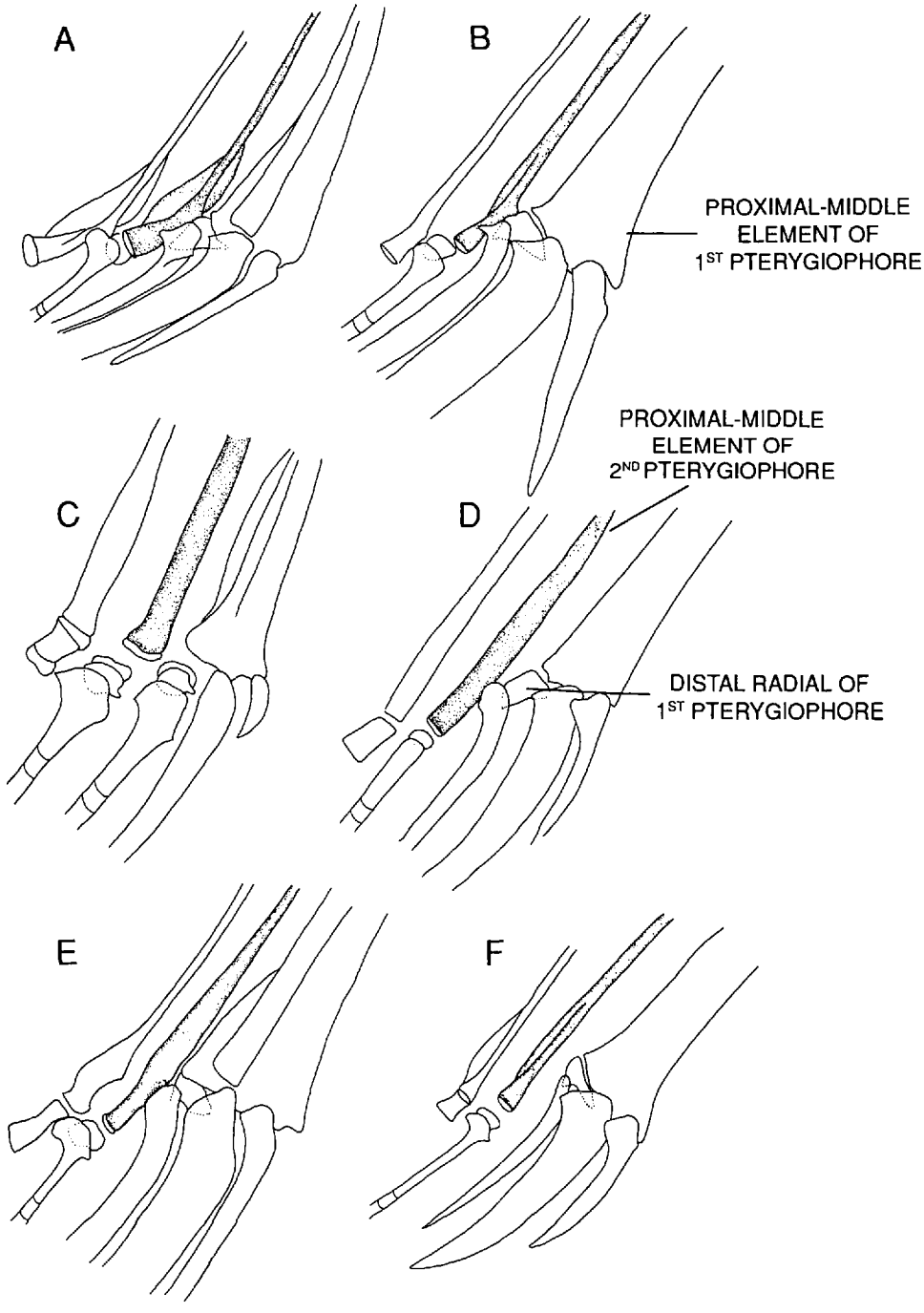

Figure 16. Anal-fin spines and pterygiophores, right side. Proximal-middle element of second anal-fin pterygiophore stippled. A) *Schultzea beta*, USNM 89002, 160 mm SL; B) *Liopropoma susumi*, USNM 218726, 48.0 mm SL; C) *Grammistes sexlineatus*, USNM 218886, 68.0 mm SL; D) *Grammistops ocellatus*, USNM 218873, 91.0 mm SL; E) *Jeboehlkia gladifer*, Indian River Coastal Zone Museum 107:7433, 55.0 mm SL; F) *Aporops bilinearis*, USNM 218920, 50.0 mm SL.

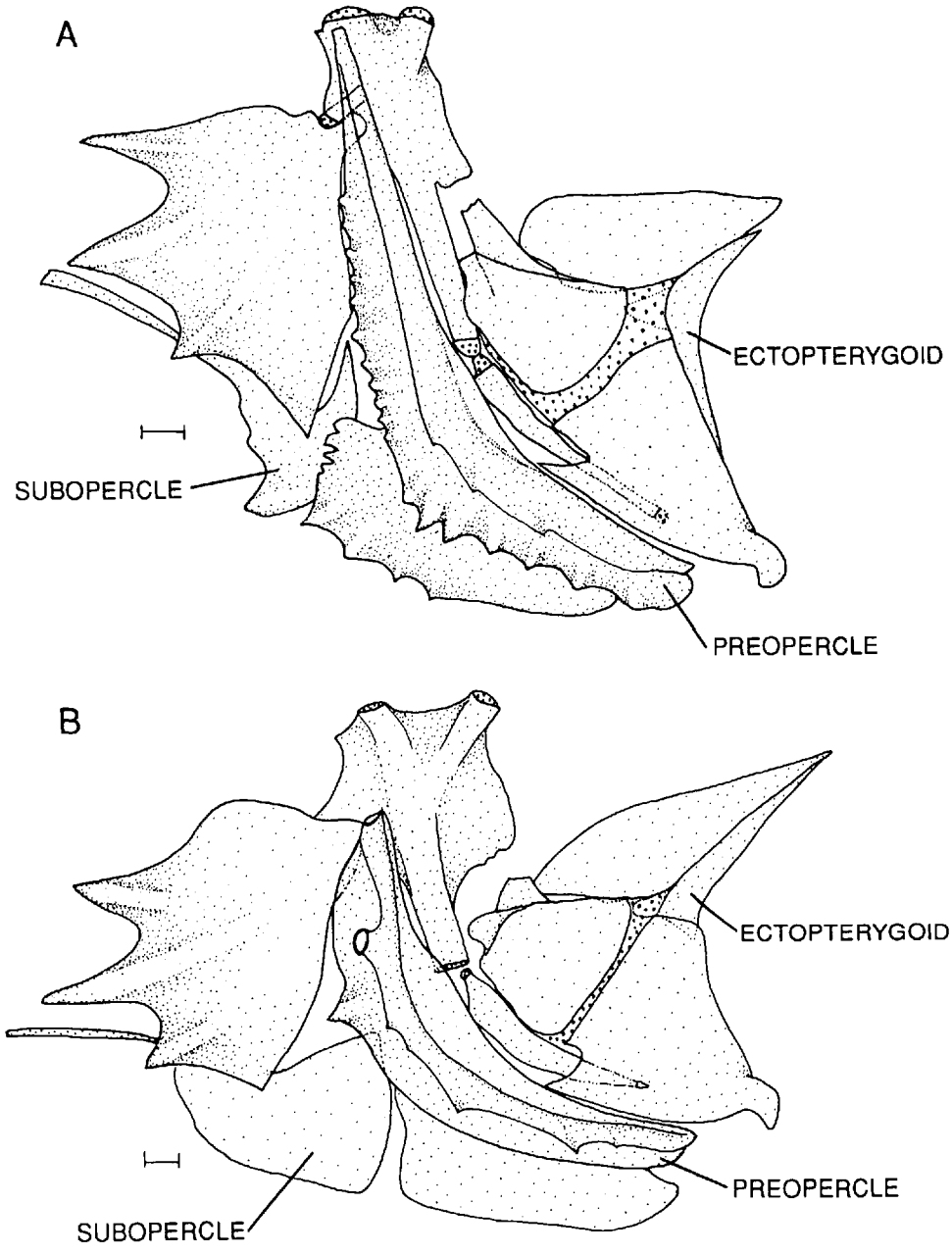

Figure 17. Suspensorium, right side. A) *Diploprion bifasciatus*, USNM 218889, 70.0 mm SL; B) *Grammistops ocellatus*, USNM 218873, 91.0 mm SL. Scale bars = 1 mm.

is most parsimonious to hypothesize a reduction in number of preopercular spines in the ancestral grammistin with a reversal, or possibly a truncation of ontogeny (see discussion below), in *Jeboehlkia*.

Adults of *J. gladifer* are small (the holotype is a mature female of 40.1 mm SL—see Robins, 1967), and have an elongate dorsal-fin spine, a character present

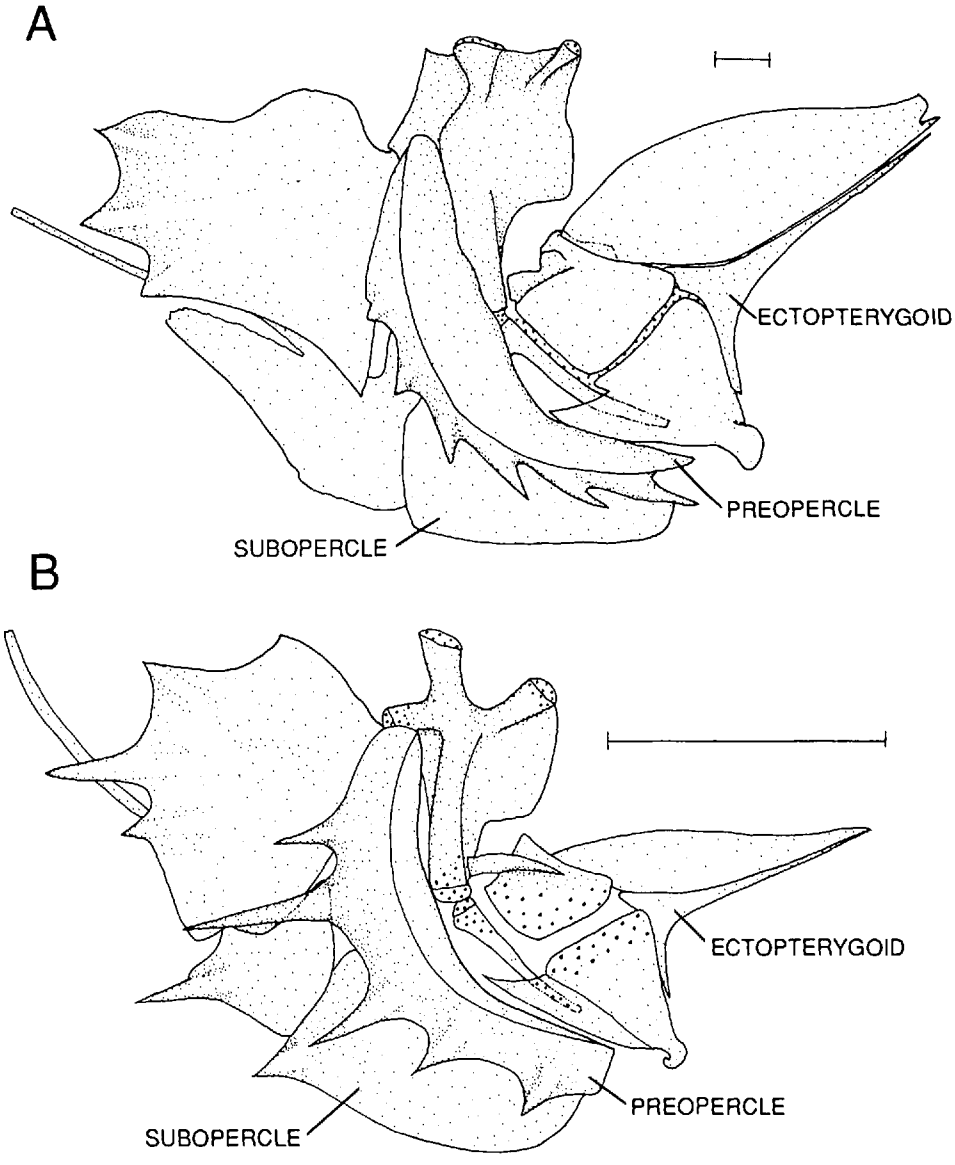

Figure 18. Suspensorium, right side. A) *Jeboehlkia gladifer*, Indian River Coastal Zone Museum 107: 7433, 55.0 mm SL; B) *Pseudogramma gregoryi*, MCZ 79302, 10.8 mm SL.

in all known epinepheline larvae, but not in adults. The presence of an elongate spine in adult *Jeboehlkia* can be interpreted as a truncation of the ontogenetic trajectory of other epinephelines; i.e., a result of paedomorphosis. Our investigation of the ontogeny of other grammistin genera suggests that several aspects of the morphology of adult *Jeboehlkia* may be paedomorphic, including the presence of a large number of spines on the preopercle.

Known larvae of all grammistins (*Grammistes, Rypticus, Jeboehlkia, Aporops* and *Pseudogramma*) have five or six well-developed spines on the medial ridge of the preopercle (as in *Pseudogramma gregoryi*, Fig. 18B). These spines typically disappear in the transformation to the juvenile stage, after which any spination

on the preopercle of the adult begins to form. Adults of *Grammistes, Pogonoperca* and *Rypticus* share the derived condition of two or three preopercular spines (character 32), and *Grammistops* shares with "pseudogrammids" the derived condition of a single preopercular spine (see character 32′, Fig. 17B). In *Jeboehlkia,* however, larval spines apparently are never resorbed. A complete ontogenetic sequence is needed to confirm this, but the preopercular spines in adult *Jeboehlkia* (Fig. 18A) are identical in number and very similar in configuration to those of larval *Jeboehlkia* (see Baldwin and Johnson, 1991: fig. 1), and their presence may be the result of retention of the larval condition in adults. The apparent reversal in number of preopercular spines in *Jeboehlkia,* then, may be explained by truncation of the ontogenetic sequence of other grammistins. Because we suspect that a high number of preopercular spines in adult *Jeboehlkia* is due to paedomorphosis, we do not know what the adult complement of spines would be if truncation were not involved; accordingly, in the character matrix (Table 1), character 32 for *Jeboehlkia* is coded as missing. This reduces the length of the tree by one step (removes a reversal or an autapomorphy) but does not affect the topology. Any placement of *Jeboehlkia* within the Grammistini, including as the sister group of all other members, requires a paedomorphic step in *Jeboehlkia* to explain the large number of preopercular spines. Retention of the primitive (outgroup) condition cannot explain the condition in *Jeboehlkia* because it is not homologous with the outgroup condition. In liopropomins, the sister group of the Grammistini, known larvae bear few poorly developed preopercular spines (Kendall, 1979; Baldwin et al., 1991), and as mentioned above, adults either lack preopercular spines or bear few to many small serrations. This growth pattern is different from that of *Jeboehlkia* in which six or seven strong, well-developed spines are present in both larvae and adults. Similarly, in the Diploprionini, the second outgroup for the Grammistini, two or three strong (*Belonoperca*) or weak (*Diploprion*) preopercular spines in larvae are not retained in adults; rather, the posterior preopercular margin in adults becomes covered with small spines or serrations (see Fig. 17A).

33. *Scales without cteni and with radii in all fields* (Fig. 19).—Scales of most serranids are ctenoid and have radii only in the anterior field (see Fig. 9). *Grammistes* (Fig. 19A), *Pogonoperca* and *Rypticus* have cycloid scales with radii in all fields. The scales of *Grammistops* (Fig. 19B) are similar but have a few poorly developed cteni in the posterior field with radii confined to anterior and lateral fields. This condition appears to be morphologically intermediate between the cycloid scales of *Grammistes, Pogonoperca* and *Rypticus* (Fig. 19A) and scales of *Jeboehlkia, Aporops, Pseudogramma* and *Suttonia* (Fig. 19C–E), which have well developed cteni in the posterior field and only a few radii penetrating the lateral fields. Intuitively, cycloid scales of the soapfishes might appear to represent the most derived state in an ordered, linear character transformation from a primitive ctenoid condition. In such a scenario, the ctenoid scale of the ancestral grammistin ("0" in Table 1) becomes the ctenoid scale of *Pseudogramma* and relatives ("1" in Table 1) by the addition of a few lateral radii. The number of lateral radii increases in *Grammistops* ("2") concomitant with a reduction in number of cteni. Finally, lateral radii occupy all fields in other soapfishes ("3"), and cteni are lost. However, as noted below (see character 43), configuration of cteni in *Pseudogramma* and relatives is different from that of grammistin outgroups. Thus, two steps (addition of radii and change in configuration, reduction or loss of cteni) are required to produce any of the three derived character states ("1," "2" or "3") from the outgroup condition. In the absence of ontogenetic information that might order the character states (i.e., cycloid scales of soapfishes are not preceded on-

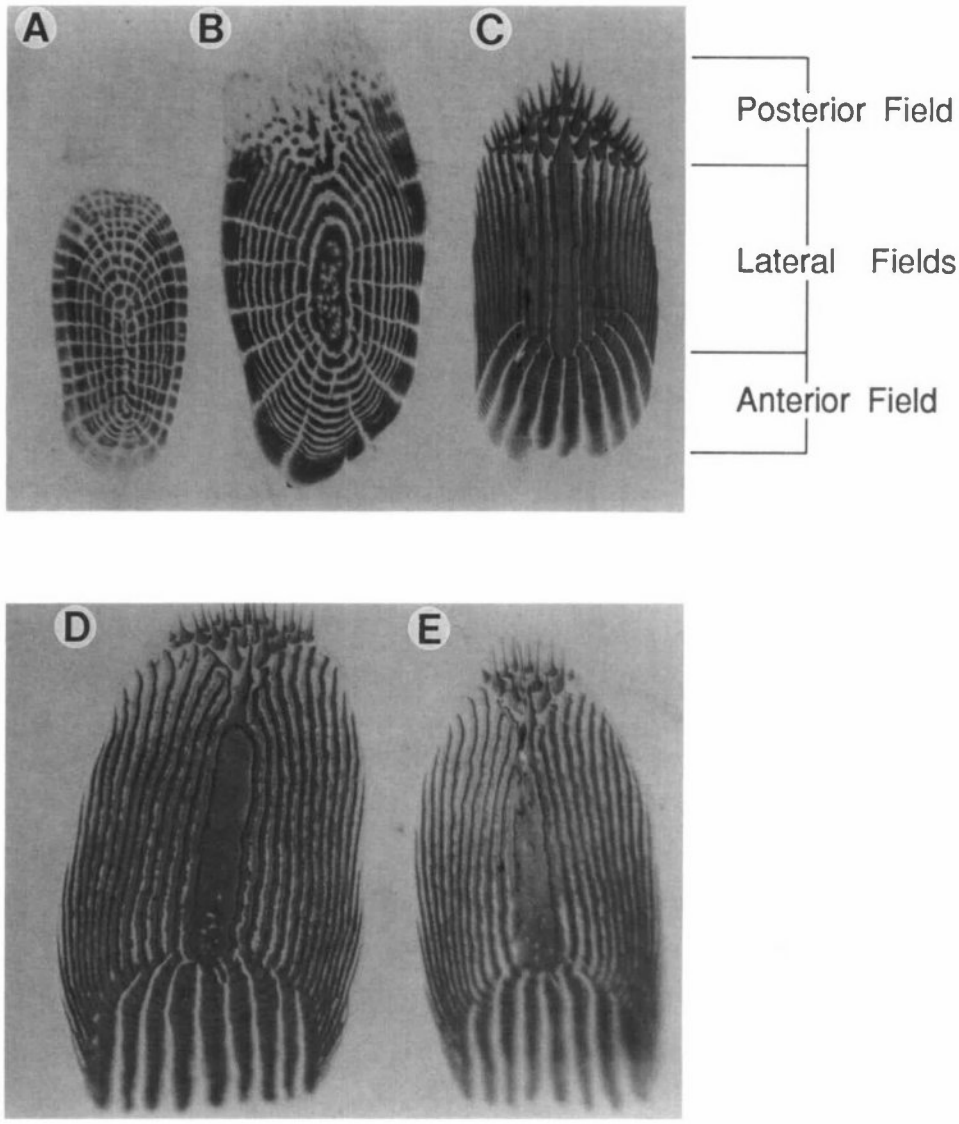

Figure 19. Photomicrographs of grammistin scales. A) *Grammistes sexlineatus*, USNM 218886, 68.0 mm SL; B) *Grammistops ocellatus*, USNM 218873, 91.0 mm SL; C) *Pseudogramma polyacantha*, USNM 209575, 33.0 mm SL; D) *Aporops bilinearis*, USNM 218920, 50.0 mm SL; E) *Jeboehlkia gladifer*, Indian River Coastal Zone Museum 107:7433, 55.0 mm SL.

togenetically by ctenoid scales), and without proof that evolution must proceed incrementally (i.e., loss of a few cteni must precede loss of all cteni), it is just as likely that "0" transforms to "2" and then to "1" and "3" or that "0" → "3" → "2" → "1." The distribution of other characters (see "Phylogeny of the Grammistini" below) suggests that *Grammistes, Pogonoperca* and *Rypticus* are cladistically primitive members of the Grammistini. Thus, the presence of small, cycloid scales ("3") is a synapomorphy of the Grammistini, and the conditions in *Grammistops* ("2," character 33′), *Jeboehlkia* and *Pseudogramma* and its relatives ("1," character 33″) are interpreted as successive steps in the transformation of this character towards a novel (vs. primitive) ctenoid condition.

34. *Larvae without melanophores on frontal bones.*—Known larvae of non-grammistin serranids usually have one to several melanophores on each frontal, the number often increasing with increasing size of the larva. Absence of frontal pigment in larval grammistins is derived.

35. *Larvae without spines on lateral preopercular ridge.*—In known larvae of all other serranids, the lateral ridge of the preopercle bears two to several very small spines (Baldwin, 1990a: fig. 3). Absence of those spines is diagnostic for larvae of the Grammistini.

Phylogeny of the Grammistini

The following characters are synapomorphies within the Grammistini, an hypothesized phylogeny of which appears in Figure 1. Polarity for the Grammistini was established using liopropomins and diploprionins as the first and second outgroups, respectively.

Grammistes + *Pogonoperca*

36. *Precaudal vertebrae 11.*—The number of caudal vertebrae varies considerably among serranids, but the presence of 10 precaudal vertebrae is a conservative feature within the family. *Grammistes* and *Pogonoperca* share the derived condition of 11 precaudal vertebrae, found elsewhere among serranids only in some anthiines.

37. *Ventral tip of lower jaw with fleshy flap.*—Randall et al. (1971) noted the presence of a large fleshy protuberance at the tip of the chin in *Pogonoperca punctata* and a similar but smaller flap in the same location in the monotypic *Grammistes.* Courtenay (1967) described a similar fleshy tab in some *Rypticus,* but in all species we examined, only a very slight thickening of tissue on the tip of the lower jaw is discernible that does not resemble the fleshy flap in *Grammistes* and *Pogonoperca.*

Rypticus + *Grammistops* + *Jeboehlkia* + *Aporops* + *Pseudogramma* + *Suttonia*

38. *Second supernumerary dorsal-fin spine reduced or absent.*—As noted previously (character 8), all epinephelines except *Niphon* have lost the first supernumerary dorsal-fin spine. The second supernumerary dorsal-fin spine is well developed in epinephelins, diploprionins, liopropomins, *Grammistes* and *Pogonoperca,* but is reduced to a nubbin or lost in all other grammistins (as in *Aporops,* Fig. 10B).

39. *Parapophyses of last precaudal vertebra fuse posteriorly and then bifurcate ventrally* (Fig. 20).—In other serranids, parapophyses usually project ventrolaterally, and contact one another only in posterior precaudal vertebrae via a bony bridge (labelled "ventral bridge" in Fig. 20A). In all grammistins except *Grammistes* and *Pogonoperca,* the parapophyses of the last precaudal vertebra are directed more ventrally than ventrolaterally, and the posterior edges of the parapophyses fuse proximally to form a posteriorly curved shield-like structure (Fig. 20B–E). The parapophyses are separate from one another distally, and resemble two prongs projecting ventrally from the "shield."

Grammistops + *Jeboehlkia* + *Aporops* + *Pseudogramma* + *Suttonia*

33′. *Scales with fewer lateral radii and some ctenii* (Fig. 19).—The presence of at least a few cteni in the posterior field of *Grammistops* (more in *Jeboehlkia* and the "pseudogrammids") and the reduced number of lateral radii are derived

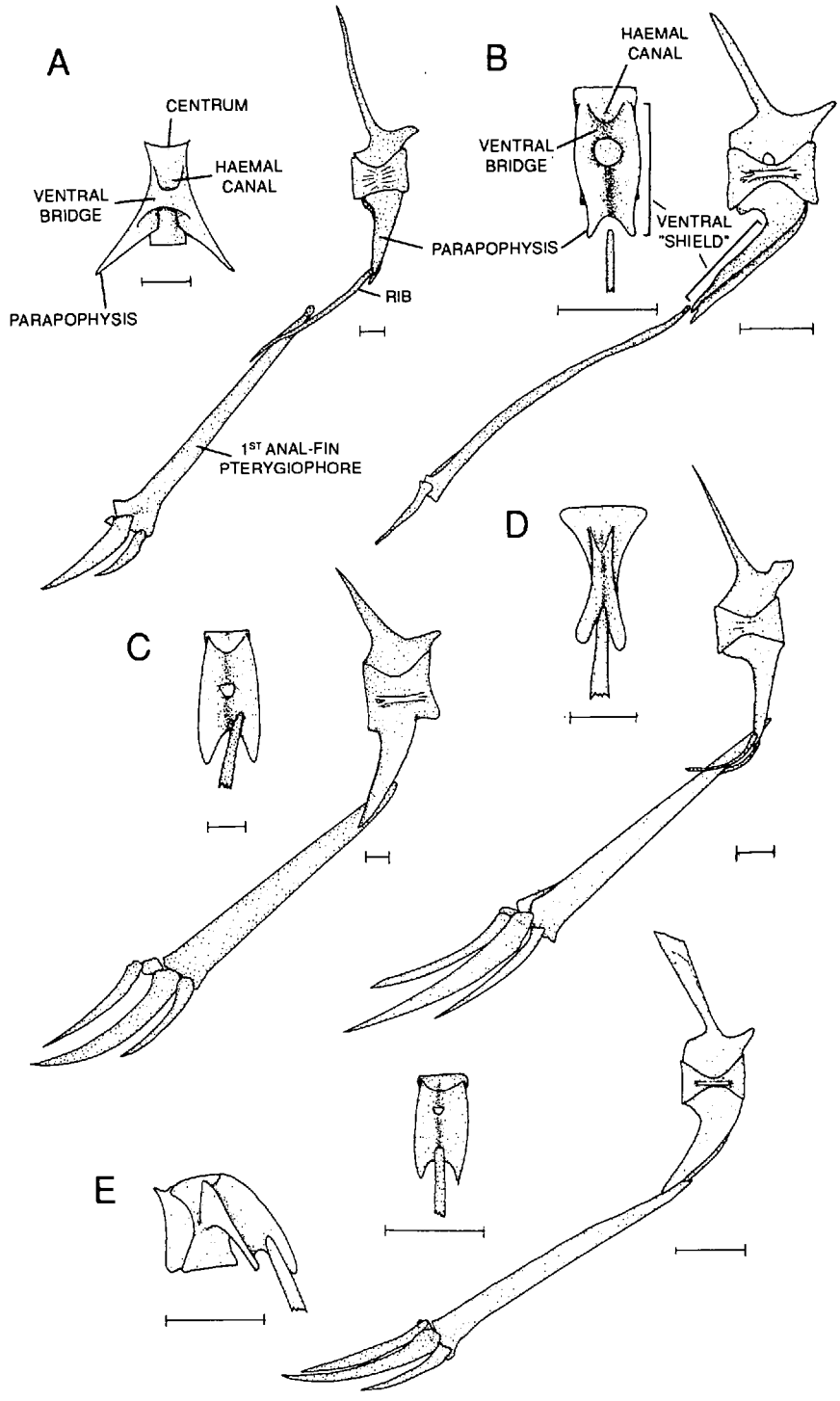

Figure 20. Last precaudal vertebra and first anal-fin pterygiophore. A) *Diploprion bifasciatus*, USNM 218889, 70.0 mm SL; left—ventral view, right—right lateral view; B) *Rypticus* sp., USNM 270278, 37.0 mm SL; left—ventral view, right—right lateral view; C) *Grammistops ocellatus*, USNM 218873, 91.0 mm SL; left—ventral view, right—right lateral view; D) *Jeboehlkia gladifer*, Indian River Coastal

features within the Grammistini, wherein scales are primitively cycloid with radii in all fields (character 33).

40. *First anal-fin pterygiophore tightly associated with modified parapophyses of last precaudal vertebra* (Fig. 20).—In most serranids, the dorsal tip of the first anal-fin pterygiophore does not reach the parapophyses of the last precaudal vertebra (as in *Diploprion bifasciatum*, Fig. 20A). In *Grammistops, Jeboehlkia* and the "pseudogrammids," the dorsal tip of the first anal-fin pterygiophore projects between the two ventral prongs of the modified, shield-like parapophyses of the last precaudal vertebra, seemingly held tightly in place by them (Fig. 20C–E). This arrangement probably strengthens the pterygiophore which, in the "pseudogrammids," supports all three anal-fin spines.

Characters 39 (formation of ventral "shield") and 40 (association between ventral "shield" and first anal-fin pterygiophore) could be interpreted as two states of the same character. In that case it is equally likely that the association of the first pterygiophore with the "shield" evolved in the ancestor of *Rypticus* + *Grammistops* + *Jeboehlkia* + the "pseudogrammids" with a reversal to character 39 in *Rypticus*.

32′. *Preopercle with one spine.*—The presence in adults of a single preopercular spine is unique among epinephelines to *Grammistops* and the "pseudogrammid" genera (Fig. 17B). As discussed above (character 32), the presence of two or three preopercular spines characterizes other soapfishes. Both conditions are derived relative to the Liopropomini and Diploprionini, but we lack information that would order the two states. Based on congruence with other characters, it is most parsimonious to hypothesize that the presence of two or three preopercular spines is the primitive grammistin condition, and that a reduction to a single preopercular spine occurred in the ancestor of *Grammistops* + *Jeboehlkia* + the "pseudogrammids."

As already noted, the presence in *Jeboehlkia* of seven preopercular spines is best interpreted as a truncation of ontogeny.

41, 42. *Ventral limb of ectopterygoid and dorsal limb of subopercle reduced* (Fig. 17).—In most serranids the anterodorsal portion of the subopercle extends dorsally as a pointed projection that lies along the anterior margin of the opercle (Fig. 17A). Additionally, the ectopterygoid usually bends ventrally to run along the anterior margin of the quadrate (Fig. 17A). In *Grammistops, Aporops, Pseudogramma* and *Suttonia* the dorsal limb of the subopercle is shortened, ending bluntly just above the ventral extremity of the opercle, and the ventral limb of the ectopterygoid is much reduced, terminating near the anterodorsal margin of the quadrate (Fig. 17B). Both of these modifications (as well as the presence of a single preopercular spine) are derived conditions that are lacking in *Jeboehlkia* and thus suggest that *Grammistops* is the closest relative of *Aporops, Pseudogramma* and *Suttonia*. However, a sister-group relationship between *Jeboehlkia* and the "pseudogrammids" is supported by their common possession of at least five derived features that are lacking in *Grammistops* (see below). Furthermore, it is possible that the apparent reversals in size of ectopterygoid and subopercular limbs in *Jeboehlkia*, like the apparent reversal in number of preopercular spines (see character 32), are attributable to paedomorphosis.

←

Zone Museum, 107:7433, 55.0 mm SL; left—ventral view, right—right lateral view; E) *Pseudogramma polyacantha*, USNM 209575, 27.0 mm SL; left—ventro-lateral view, center—ventral view, right—right lateral view. In all ventral views, anterior is towards the top of the page. Scale bars = 1 mm.

Larvae of *Grammistops* are unknown, but in larval *Pseudogramma* (Fig. 18B), the ventral limb of the ectopterygoid is considerably longer (relative to the quadrate) than in adults. Thus, the ontogenetic sequence in *Pseudogramma* progresses from a long to a relatively shorter ventral limb. If this ontogenetic sequence was present in the ancestor of *Grammistops* + *Jeboehlkia* + "pseudogrammids," truncation of this trajectory may be responsible for the presence of a long ventral ectopterygoid limb in adult *Jeboehlkia* (Fig. 18A).

A similar scenario could explain the presence of a well-developed dorsal subopercular limb in adult *Jeboehlkia* (Fig. 18A), because the dorsal limb in larval *Pseudogramma* (Fig. 18B) appears to be somewhat larger (relative to the opercle) than in adult "pseudogrammids" and *Grammistops* (Fig. 17B).

Although we suspect that paedomorphosis may be responsible for long ectopterygoid and subopercular limbs in adult *Jeboehlkia,* we do not code those characters (40, 41) for *Jeboehlkia* as "missing," as we did in the case of the preopercular spines (character 32). This is because we cannot actually differentiate the states in *Jeboehlkia* (long limbs) from the outgroup conditions (long limbs). Furthermore, it is not possible to confidently identify the long ectopterygoid and subopercular limbs in adult *Jeboehlkia* as paedomorphic characters because our understanding of the growth trajectories of those bones is inadequate. The mechanism by which *Grammistops* and *Pseudogramma* and its relatives obtain a short ventral ectopterygoid limb and reduced subopercular limb (relative to the quadrate and opercle, respectively) in adults is unknown. The process could involve failure of the limbs to grow following the larval stage (producing a "short" limb relative to the normally growing quadrate or opercle) or resorption or modification of the shape of the bone during ontogeny. In the former, the short ventral ectopterygoid limb in adult *Grammistops* and "pseudogrammids" is best explained by paedomorphosis; i.e., the primitive grammistin trajectory ("long" ventral limb grows to "long" ventral limb—such that the limb maintains approximately the same relation to the quadrate) is truncated. In this case, the presence of a normal ectopterygoid limb in adult *Jeboehlkia* cannot be interpreted as a further truncation of the "pseudogrammid" trajectory (paedomorphosis), but must be considered a reversal. If, however, resorption or some other modification of shape acts on the ventral ectopterygoid limb of "pseudogrammids" following the larval stage (as is the case with the preopercular spination where the adult condition appears following loss of the larval condition), then truncation of that process in *Jeboehlkia* might result in a "normal" ectopterygoid limb. A complete size series of *Pseudogramma* or its relatives that would allow us to assess the growth trajectory of the ectopterygoid is lacking.

Jeboehlkia + *Aporops* + *Pseudogramma* + *Suttonia*

16'®. *Dermal toxin glands absent.*—The large toxin-secreting glands in the dermis of true soapfishes are lacking in other grammistins. Grammistin apparently has been lost in *Jeboehlkia* and the "pseudogrammids." Histological sections of skin from the latter (Fig. 6A) exhibit no positive reaction to the stain Sudan Black B, a histological agent shown by Randall et al. (1971) to be useful in detecting the toxin.

21'. *Separation between proximal-middle and distal elements of dorsal-fin pterygiophores begins with second pterygiophore.*—Separation of the third and all posterior distal radials of the spinous dorsal fin from their serially associated proximal-middle pterygiophores (and the related modification of the articular surface of the latter) is a synapomorphy of the Liopropomini plus Grammistini

(character 21, Fig. 10A). In *Jeboehlkia* and the pseudogrammid genera (e.g., *Aporops*, Fig. 10B), the same separation and modification occur, but separation begins with the second, rather than third, pterygiophore.

33″. *Scales with few or no lateral radii and well-developed cteni* (Fig. 19).—The presence of small, cycloid scales with lateral radii in all fields appears to be the primitive grammistin condition. The presence of only a few lateral radii and well-developed cteni in the posterior field of *Jeboehlkia* and "pseudogrammids" is derived (Fig. 19C–E). The configuration of cteni in those scales (discussed below) is unique among serranids.

43. *Bases of old cteni not present in posterior field* (Fig. 19).—A single row of cteni on the posterior margin of the scale occurs in some anthiines and in the liopropomin, *Rainfordia* (see Fig. 13A). All other serranids have more than one row of cteni or lack them completely. In those with more than one ctenial row, only the outermost row contains "whole" cteni; the more anterior cteni are reduced to small round or rod-like bases (see Fig. 9) either by truncation (McCully, 1961) or resorption (Hughes, 1981). In *Jeboehlkia, Aporops, Pseudogramma* and *Suttonia,* there are no bases of old cteni in the posterior field (Fig. 19C–E); rather, all cteni, including those anterior to the outermost row, are "whole."

44. *Hypurapophysis absent.*—The hypurapophysis is present in all other serranids as well as in *Aporops.* It is equally likely that (1) the hypurapophysis was lost in the ancestor of *Jeboehlkia* + "pseudogrammids" and reappeared in *Aporops* or (2) was lost independently in *Jeboehlkia* and in the ancestor of *Pseudogramma* + *Suttonia.*

Aporops + *Pseudogramma* + *Suttonia*

45. *Vertebrae 26–28.*—Although anthiines have 26 or 27 vertebrae, and *Niphon* has 30, the presence of 24 vertebrae in liopropomins, diploprionins, epinephelins and serranines indicates that 24 is the primitive number for the Grammistini. An increase in vertebral number in *Aporops* (28 vertebrae) and *Pseudogramma* and *Suttonia* (26) is a synapomorphy of those genera. Equally parsimonious is the possibility that the ancestral "pseudogrammid" had 28 vertebrae (with a reduction in the ancestor of *Pseudogramma* and *Suttonia*) or 26 vertebrae (28 being autapomorphic for *Aporops*).

46. *Neural spines 8–10 expanded distally.*—In most serranids, neural spines terminate distally as somewhat slender, pointed projections (see Fig. 10A). In *Aporops, Pseudogramma* and *Suttonia,* the eighth through tenth neural spines are expanded distally such that each resembles an upright oar (see Fig. 10B).

47. *Lateral line incomplete or interrupted.*—In other epinephelines the lateral line is complete, but in *Aporops* it is interrupted posteriorly, and in *Pseudogramma* and *Suttonia* it is incomplete, terminating anterior to the caudal peduncle (Gosline, 1960).

48. *Epaxial musculature extends to interorbital* (Fig. 21).—Epaxial musculature terminates anteriorly in most serranids on the supraoccipital crest, well posterior to the interorbital region (Fig. 21A). In the "pseudogrammid" genera, the epaxial musculature covers the supraoccipital dorsally and extends anteriorly to the interorbital region of the frontals (Fig. 21B).

49. *Uppermost pectoral-fin ray reduced to an articular base* (Fig. 22).—In other serranids, the dorsalmost pectoral-fin element is a fully-formed ray with an articular expansion at the base of the medial hemitrich, where it articulates with the scapula (Fig. 21A). In the "pseudogrammids," all that remains of the uppermost pectoral-fin ray is a modified base, which articulates with the scapula an-

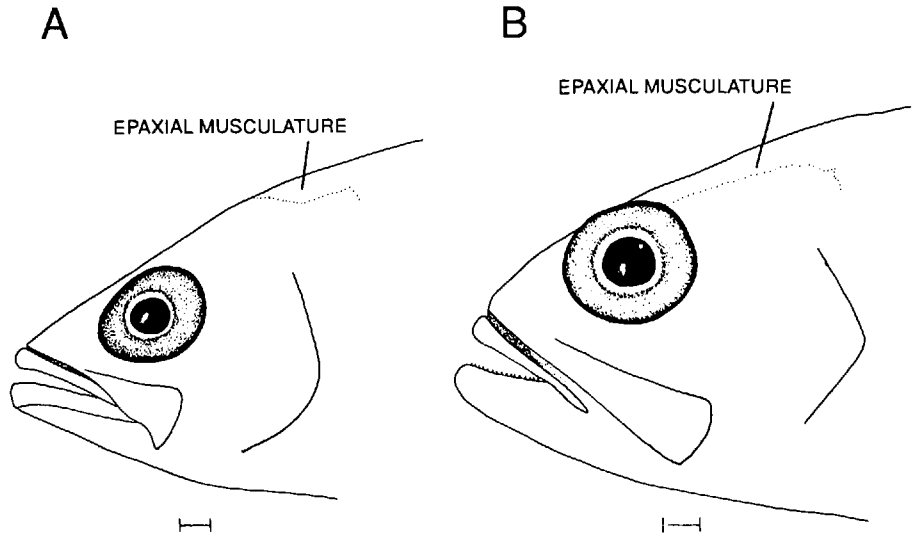

Figure 21. Head, left side, showing anterior extent of epaxial musculature. A) *Liopropoma carmabi*, USNM 198283, 43.5 mm SL; B) *Aporops bilinearis*, USNM 218920, 41.0 mm SL. Scale bars = 1 mm.

teriorly, and rests posteriorly in the branched base of the next pectoral-fin ray (Fig. 22B). This condition is strikingly similar to the "pectoral spur" described by Stiassny (1993) in some atherinomorph fishes. The "spur" in atherinomorphs is a single, unpaired structure, and Stiassny was unable to determine if the element represents a modification of the entire first pectoral-fin ray or only the medial hemitrich. The homology of the "spur" or articular base in "pseudogrammids" with both halves of the uppermost pectoral-fin ray of other serranids is corroborated by examination of its ontogeny. In the pectoral-fin skeleton of an 11.4-mm SL larva of *Pseudogramma gregoryi* (Fig. 22C), a small first pectoral-fin ray is nested within the lateral and medial hemitrichs of the base of the second pectoral

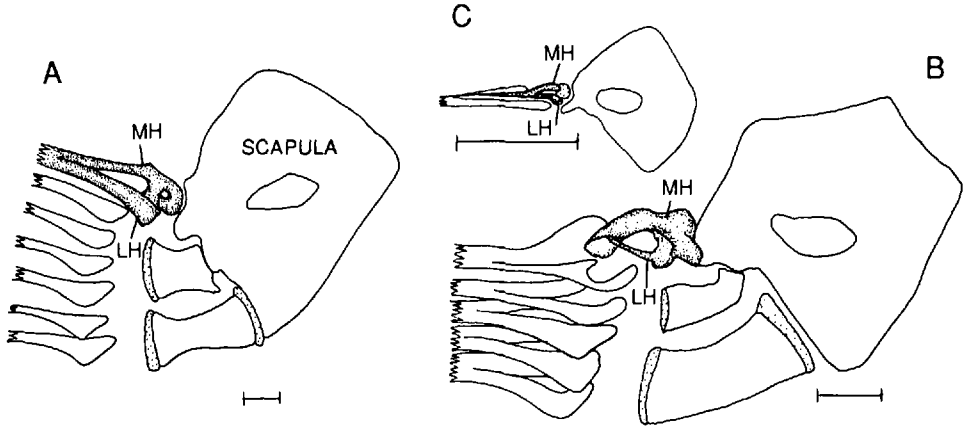

Figure 22. Dorsal portion of pectoral-fin skeleton, right side. First pectoral-fin ray heavily stippled, cartilage lightly stippled. A) *Diploprion bifasciatus*, USNM 21889, 70.0 mm SL; B) *Pseudogramma polyacantha*, USNM 209575, 33.0 mm SL; C) *Pseudogramma gregoryi*, VIMS 08276, 11.4 mm SL. LH—lateral hemitrich; MH—medial hemitrich. Scale bars = 0.5 mm.

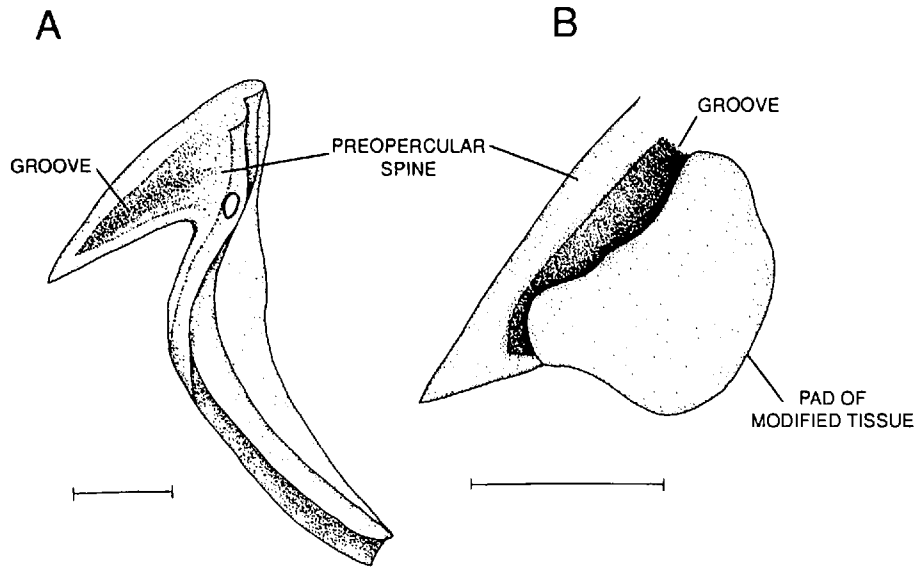

Figure 23. Preopercular spine, right side. A) *Suttonia lineata*, USNM 209705, 39.0 mm SL; B) *Pseudogramma polyacantha*, USNM 295992, 45.0 mm SL (skin covering pad of modified tissue removed). Scale bars = 1 mm.

ray. This first ray comprises a lateral and medial hemitrich, the latter with a cartilaginous head that articulates with the scapula. Both hemitrichs also are visible in adults, although the lateral one is very slender and is apparently fused proximally to the greatly expanded articular head of the medial hemitrich.

50. *Base of preopercular spine covered with pad of modified tissue* (Fig. 23).—As noted previously, *Grammistops* and the "pseudogrammids" have a single preopercular spine (character 32′). Gosline (1960) noted that in "pseudogrammids," there is a pad of glandular-like tissue at the base of this spine (Fig. 23B), which in some species is curved downward, and has a groove that extends the length of the spine (Fig. 23A). Initially we thought this complex might provide a means of delivering a toxin like grammistin. Histological investigation of the glandular tissue revealed a well-defined oblong mass of tissue containing unidentifiable cells that react negatively to the stain Sudan Black B; lying beneath this pad of tissue is what appears to be a muscular sac (Fig. 24). The functional significance of this complex is unknown, but it does not appear to contain grammistin. Nevertheless, it is a synapomorphy of the "pseudogrammid" genera.

51. *First anal-fin pterygiophore supports all three anal-fin spines* (Fig. 16).—In all other serranids with three anal-fin spines, the third spine is supported by both the second anal-fin pterygiophore (supernumerary association) and the first distal radial (serial association—Fig. 16A–E). In the "pseudogrammids," the distal radial of the first pterygiophore becomes widely separated from the second pterygiophore, carrying with it the third anal-fin spine (Fig. 16F).

Pseudogramma + *Suttonia*

47′. *Lateral line incomplete.*—Although it is equally parsimonious to hypothesize that an incomplete lateral line is the primitive "pseudogrammid" condition and that an interrupted lateral line is autapomorphic for *Aporops*, it seems more plausible that a loss of pores in a few scales (resulting in an interruption) preceded

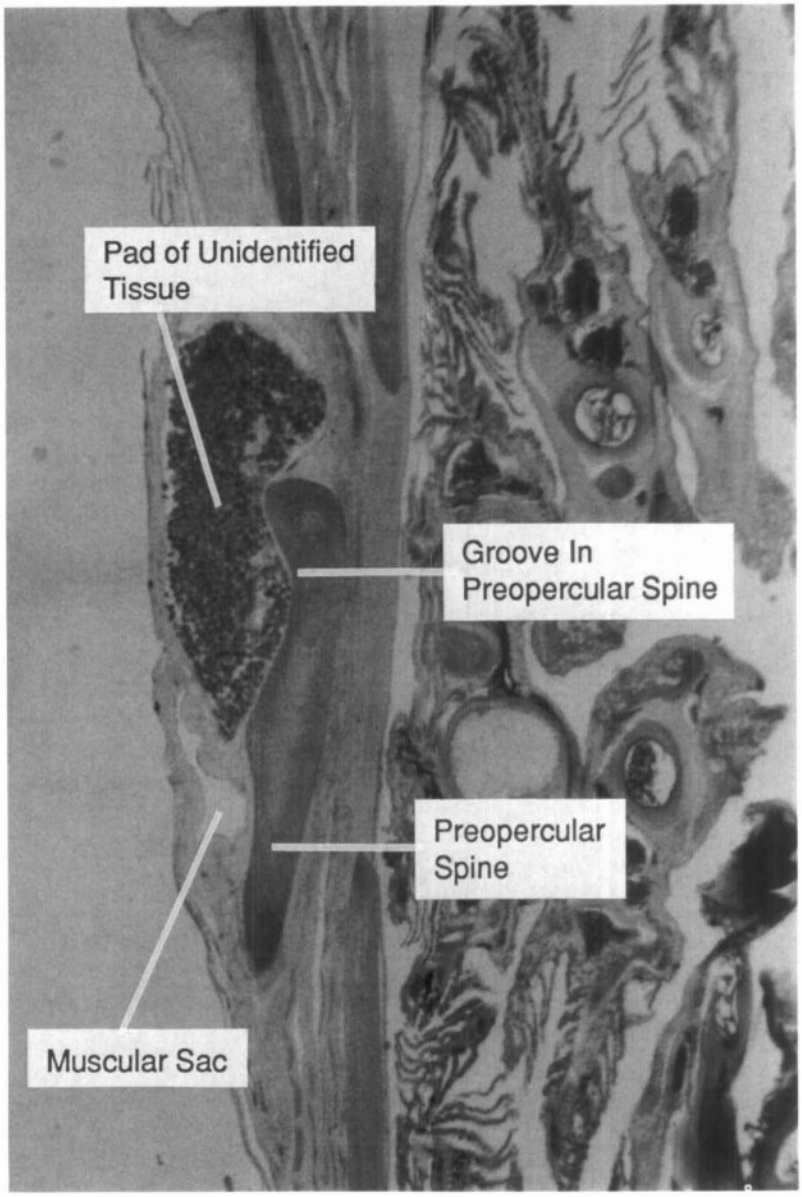

Figure 24. Photomicrograph of cross section (Sudan Black B histological preparation) through head of *Pseudogramma polyacantha*, USNM 295992, 44.5 mm SL.

the loss of pores from many scales (resulting in an incomplete lateral line). The former hypothesis requires that lost pored scales reappear in *Aporops*. It is also equally parsimonious to hypothesize independent origin of an interrupted lateral line in *Aporops* (autapomorphic) and incomplete lateral line in the ancestor of *Pseudogramma* and *Suttonia*. All of the above scenarios yield the same hypothesis of relationships when examined in the context of other characters.

Possibly, an incomplete lateral line in *Pseudogramma* and *Suttonia* is attributable to paedomorphosis (A. Gill, USNM, pers. comm.). If, as in some pseu-

dochromoids, the lateral line in "pseudogrammids" develops from anterior to posterior, ontogenetic truncation could result in failure of the lateral line to develop fully.

52. *Large interorbital lateral-line pores.* —In most serranids, the cephalic lateral line canals that lie between the eyes typically open to the surface of the body via very small, inconspicuous pores. In *Pseudogramma* and *Suttonia,* interorbital pores are uncommonly large and easy to discern (Gosline, 1960).

Discussion

Herein we discuss the monophyly and interrelationships of the five tribes of the subfamily Epinephelinae and propose a generic phylogeny for the tribe Grammistini based on cladistic analyses of larval and adult morphology. Resolution of relationships within the tribes Diploprionini and Liopropomini will require further study as will verification of the monophyly of all polytypic epinepheline genera. A hypothesis of relationships among some genera of the tribe Epinephelini based on larval characters was provided by Leis (1986), but should be expanded to include adult features.

Our hypotheses of generic composition of tribes differ from Johnson's (1983) classification only in the allocation of *Jeboehlkia* to the Grammistini rather than the Liopropomini. Among tribes, we consider grammistins to be most closely related to liopropomins rather than to diploprionins with which they share the presence of the skin toxin grammistin. The Diploprionini comprise the sister group of the Liopropomini + Grammistini, and those tribes + the Epinephelini form the sister group of *Niphon.* All hypotheses of relationships among epinepheline tribes are based, in part, on larval characters, and we note that larval morphology provides the only evidence of a monophyletic Epinephelini and the clade comprising diploprionins, liopropomins and grammistins. The last hypothesis is based in part on the assumption that the as yet undescribed larvae of *Aulacocephalus* and *Rainfordia* have an elongate filamentous dorsal-fin spine (character 14) and lack an elongate spine at the angle of the preopercle (character 15). We are aware that missing data can cause problems in cladistic analyses (Platnick et al., 1991), and note that the only nodes on the cladogram (Fig. 1) affected by deleting all characters that include missing data are the ones supported solely by larval characters (i.e., the Epinephelini and clade comprising diploprionins + liopropomins + grammistins). Identification of larvae of more epinepheline genera is needed to test those hypotheses.

Johnson's (1983) allocation of the soapfishes (*Grammistes, Grammistops, Pogonoperca* and *Rypticus*) and the former pseudogrammid genera (*Aporops, Pseudogramma* and *Suttonia*) to a single tribe (Grammistini) is corroborated in our analysis by ten derived features, eight occurring in all grammistins, two being lost or modified within the tribe. Despite the unique presence of dermal toxin glands in *Grammistes, Grammistops, Pogonoperca* and *Rypticus,* we reject a hypothesis that unites the soapfishes as a natural group, and propose that *Grammistes* + *Pogonoperca* form the sister group of *Rypticus* + *Grammistops* + *Jeboehlkia* + the "pseudogrammid" genera. *Jeboehlkia* lacks three of the five derived characters shared by *Grammistops* and the "pseudogrammids," but it is most parsimonious to consider *Jeboehlkia* as the sister group of the "pseudogrammids." As discussed previously (see characters 32, 41, 42), several aspects of the morphology of adult *Jeboehlkia* that are incongruent with our hypothesis may be attributable to paedomorphosis. *Jeboehlkia* and the "pseudogrammids" are small fishes, relative to most other grammistins, and other features, such as the absence of the skin toxin

grammistin, may be the result of developmental truncation that occurred in the common ancestor of those fishes. Further study, including careful examination of ontogenetic sequences of characters, is needed to test this hypothesis. Finally, *Aporops, Pseudogramma* and *Suttonia,* highly specialized members of the tribe Grammistini, constitute a clade well defined on the basis of seven synapomorphies. We do not elevate them to tribal status because this would render the tribe Grammistini paraphyletic.

The hypothesis of relationships among genera of the tribe Grammistini discussed above and depicted in Figure 1 merits further discussion. It emerges as the single most parsimonious tree only because of the way in which we treated multistate characters. Much has been written about analyzing multistate characters (Mickevich, 1982; Swofford, 1985; Mabee, 1989; Mooi, 1989; Lipscomb, 1990), but there is discordance among proposed methods. In the absence of information that would suggest relationships among character states a priori, we attempted to analyze our multistate data using several different methods, including treating the multistate characters as "unordered" in the computer analysis (see Swofford, 1985) and ordering the multistate characters using a FIG/FOG analysis (Mooi, 1989) and transformation series analysis (TSA) of Mickevich (1982). The last two methods helped only minimally in determining character order because, for most characters, they yielded more than one possible transformation depending on (1) what tree was used initially in the analysis (affected TSA and FIG/FOG) or (2) what characters were polarized first (affected only FIG/FOG). Thus, we were left with the first method, treating multistate characters as "unordered" in the computer analysis, which, despite being criticized by Mickevich (1982) as "nihilistic," we believe to be superior to arbitrarily assigning order. The multistate characters used in this study provide conflicting information concerning grammistin interrelationships, and Swofford's (1985) computerized analysis of unordered character states allowed us to choose among competing hypotheses of character transformation on the basis of congruence with other characters and the principle of parsimony. Although Mickevich (1982) criticized the Fitch (1971) modification of optimization (which is the basis for Swofford's treatment of unordered character states) because it allows one state to transform into any other state without regard to cladogenetic events, it is worth noting that, in this study, all of the transformations produced in the computer analysis of unordered character states were among the transformations resulting from TSA and FIG/FOG analysis.

For those who believe that order among multiple character states can (and should) be determined by morphological similarity (i.e., evolution of traits occurs incrementally, such that e.g., small → medium → large), we note that analyzing the multistate characters used in this study in the order they appear in the character matrix (Table 1, characters 15, 21, 32, 33 and 47) produces two equally parsimonious trees (length = 67, consistency index = 0.866). The topology of one of the trees is identical to that in Figure 1, and the other differs only in the placement of *Rypticus* and *Grammistops* as successive sister groups to *Grammistes* plus *Pogonoperca* (i.e., a monophyletic soapfish assemblage). With the possible exception of character 47 (see "Character Analysis"), we believe that such a priori ordering of characters is not justified by our knowledge of evolutionary process, and note that a tree derived only from the binary characters in the matrix is identical to that in Figure 1 except for the position of *Grammistops* as the sister group of the "pseudogrammids" rather than of *Jeboehlkia* + the "pseudogrammids." Addition of the unordered multistate characters switches the position of *Jeboehlkia* and *Grammistops* by providing an additional three synapomorphies of *Jeboehlkia, Pseudogramma* and its relatives.

In summary, this study provides the first cladistic hypothesis of relationships among epinepheline genera based on larval and adult morphology. It demonstrates the importance of considering ontogenetic data in phylogenetic studies, as a source of characters, as a means of assessing homology, and as an important requirement for identifying heterochrony. It also emphasizes our inadequate knowledge of evolution and the problems that arise accordingly when systematists are confronted with multiple states for a single character. Multistate characters are especially problematic when, as in this study, different hypotheses of phylogeny are obtained when those characters are ordered, unordered or excluded from the analysis. Because we lacked justification to order most of the multistate characters in this study a priori, and because neither FIG/FOG nor TSA provided a single set of transformations for them, we were forced to treat the multistate characters as unordered in our analysis. Although we are aware of no empirical evidence demonstrating that this method produces erroneous results, we acknowledge that the accuracy of our hypothesis of grammistin phylogeny depends, to a large extent, on its validity.

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