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Larvae and relationships of epinepheline serranids (Teleostei: Percoidei)

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Baldwin, Carole Christine, Ph.D.

The College of William and Mary, 1992

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LARVAE AND RELATIONSHIPS OF EPINEPHELINE SERRANIDS (TELEOSTEI: PERCOIDEI)

A Dissertation
Presented to
The Faculty of the School of Marine Science
The College of William and Mary in Virginia

In Partial Fulfillment
Of the Requirements for the Degree of
Doctor of Philosophy

by
Carole Christine Baldwin
1992

This dissertation is submitted in partial fulfillment of

the requirements for the degree of

Doctor of Philosophy

Carole C. Baldwin

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DEDICATION

I dedicate this work to my family, especially my twin sister, Camille; brothers, David and Gary and their families; and parents, David and Alexandra. None of them understands precisely what systematic ichthyologists strive to accomplish, but they have faithfully supported me throughout my educational career.

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I thank all members of my advisory committee for their valuable criticism of my work. Additionally, I thank J. M. Brubaker (VIMS) for being an enthusiastic and challenging member of my advisory committee despite feeling like a serranid out of water; J. A. Musick (VIMS) for recommending me to the administration for the curatorial assistantship, which not only provided financial support but invaluable experience in the care and maintenance of fish collections as well as an opportunity to teach; J. E. Olney (VIMS), a non-evaluating member of my advisory committee but one who provided direction, criticism, logistical and moral support and cautioned me to avoid "tunnel vision," setting an example in his own research by integrating studies of ecology and evolutionary history of fishes; W. D. Anderson, Jr. (College of Charleston), my outside committee member and co-advisor of my committee for the Master of Science Degree at the College of Charleston, whose meticulousness in both his research and writing have given me a lasting appreciation for the necessity of accuracy in scientific studies; and, G. David Johnson, a true mentor, whose excitement about the potential significance of early life history stages of marine fishes in phylogenetic studies and, especially, his enthusiasm for putting together "pieces of the evolutionary puzzle" continue to be a seemingly limitless source of inspiration. Few students have had the opportunity to be trained by either Dr. Anderson or Dr. Johnson. I feel extraordinarily fortunate to have long-standing, positive and productive relationships with both of them.

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ABSTRACT

Morphology is described for larvae of *Diploprion bifasciatus*, *Belonoperca chabanaudi*, *Jeboehlkia gladifer*, and *Grammistes sexlineatus* of the serranid subfamily Epinephelinae. Known larvae of all epinephelines are compared. Larval epinephelines differ in patterns of pigmentation, head spination, sequence of fin formation and morphology of elongate (often spectacularly so!) dorsal-fin spines.Relationships among epinepheline genera are investigated based on phylogenetic analysis of larval and adult morphology. Five monophyletic tribes are cladistically 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 ichthyotoxin grammistin in the Diploprionini and Grammistini, the latter is proposed to be the sister group of the Liopropomini. This hypothesis is based, in part, on previously unrecognized larval features. Larval morphology also provides convincing 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, *Jeboehlkia gladifer* is hypothesized to be 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 this 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. This study demonstrates that ontogeny is valuable in phylogenetic studies as a source of characters, means of assessing homology and aid to identifying heterochrony.

LARVAE AND RELATIONSHIPS OF EPINEPHELINE SERRANIDS (TELEOSTEI: PERCOIDEI)

INTRODUCTION

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* (synonymized 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 *Rypticus* (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 (herein, the term epinephelin refers to the tribe Epinephelini, whereas epinepheline refers to the subfamily); 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.

Larvae of serranids exhibit an array of morphological specializations, presumably associated with survival in the plankton, that have been shown to be useful in elucidating phylogenetic relationships (Leis, 1986; Johnson, 1988; Baldwin, 1990). Among epinephelines, larvae of the monotypic *Niphon* have been described (Johnson, 1988), and larvae of many epinephelin genera are known (see Kendall, 1984, for a review; Leis, 1986). Hubbs and Chu (1934) described and illustrated two juvenile specimens (31 and 49 mm SL) of *Diploprion bifasciatus* (usually erroneously referred to as *bifasciatum* -- e.g., Baldwin et al., 1991, but should be "*bifasciatus*" to agree with the masculine "prion"), but larvae of all genera of the Diploprionini (*Aulacocephalus, Belonoperca* and *Diploprion*) are undescribed. Larvae of *Liopropoma* (includes *Pikea*) are well known (Fourmanoir, 1971; Kendall, 1979, 1984; Kotthaus, 1970); those of the other liopropomins, *Jeboehlkia* and *Rainfordia*, are undescribed. Within the Grammistini, larval *Grammistes* (Fourmanoir, 1976), *Rypticus* (Aboussouan, 1972; Kendall, 1979) and *Pseudogramma* (Kendall, 1979; Leis and Rennis, 1983) have been described and illustrated, and Fourmanoir (1976) illustrated the head and anterior portion of the body of larval *Aporops*. Larvae of the remaining grammistin genera, *Pogonoperca, Grammistops* and *Suttonia*, are unknown.

The initial impetus for Chapter 1 was the rearing of eggs and larvae of *Diploprion bifasciatus* by Patrick L. Colin (formerly of the Motupore Island Research Department, University of Papua New Guinea), and the description of that reared series is a primary purpose of that chapter. In addition I compare the reared larvae with several wild-caught specimens, comment on habitat and spawning behavior of *D. bifasciatus*, describe postflexion larvae of *Belonoperca chabanaudi*, *Jeboehlkia gladifer* and *Grammistes sexlineatus*, compare the morphologies of known larvae of all genera of the subfamily Epinephelinae and briefly discuss the possible functional significance of elongate dorsal spines in larval epinephelines. This study should help others identify larvae of epinepheline serranids and forms the framework for the phylogenetic analysis described in Chapter 2. Information in this chapter recently was published (Baldwin et al., 1991; Baldwin and Johnson, 1991).

The purpose of the second chapter is to examine relationships among epinepheline genera based on cladistic analysis of larval and adult morphology. In doing so, I test Johnson's (1983:784) allocation of genera to the five epinepheline tribes and examine relationships among the tribes. I do not examine relationships within the speciose Epinephelini, nor within the Diploprionini and Liopropomini; however, I propose a generic phylogeny for the tribe Grammistini and explore the possibility that heterochrony has contributed to the evolution of morphological diversity in grammistins. This chapter will appear in the Proceedings of the Percomorph Phylogeny Symposium (convened at the 1990 meetings of the American Society of Ichthyologists and Herpetologists in Charleston, South Carolina).

CHAPTER 1

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

Methods and Materials

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

The following account of collection and rearing of *Diploprion bifasciatus* was summarized from information provided by P. L. Colin (pers. comm., January 1990). Adult *Diploprion bifasciatus* were collected in the vicinity of the Motupore Island Research Station of the University of Papua New Guinea, southeast of Port Moresby. Fishes were captured, by SCUBA divers using multiprong spears, within one half hour of the time spawning would naturally have occurred, placed in individual plastic bags and returned to the laboratory. Gametes were obtained using gentle pressure on the abdomen and mixed in a bowl of seawater. About one hour elapsed between collection and stripping, and the adults were dead or dying at the time of gamete removal. Fishes not already dead were anesthetized with a solution of quinaldine and alcohol in seawater and then rinsed in seawater prior to stripping.

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

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

Reared and wild-caught larvae examined in this study are listed in the Appendix.

Diploprion bifasciatus (Figs. 1-3, Plate 1A)

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

Habitat.--Observations of behavior and collections of adult *D. bifasciatus* were made off the south coast of New Guinea near Port Moresby, Papua New Guinea by P. L. Colin (Pers. Comm., January 1990) and are summarized below. *Diploprion bifasciatus* usually was found in inshore reef areas where water visibility was typically 5-15 m. Generally juveniles were found farther inshore than adults, but individuals less than about 60 mm SL were never seen. Observations and collections of spawning adults were made at two locations in the Bootless Bay area, southeast of Port Moresby. At Lion Island, *D. bifasciatus* usually occurred along a steep reef slope between a shallow, narrow reef fringing the east side of the island and a mud bottom starting about 18-20 m. The slope was approximately 30-45° and covered with coral and gorgonians. *Diploprion bifasciatus* also was collected south of Loloata Island where a shallow reef extends south of the island for about 1 km. The reef drops abruptly from a depth of 1 m via a series of shelves to a mud bottom at 20-27 m. In some areas, a vertical face exists at the lower limit of the reef, and adult *D. bifasciatus* usually were found in such areas. The two collection sites were similar, with vertical relief reaching to a sediment bottom, and in both localities fishes were collected near the reef-mud interface. *Diploprion bifasciatus* inhabited greater depths at Loloata Island, where the reef-mud interface was deeper.

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

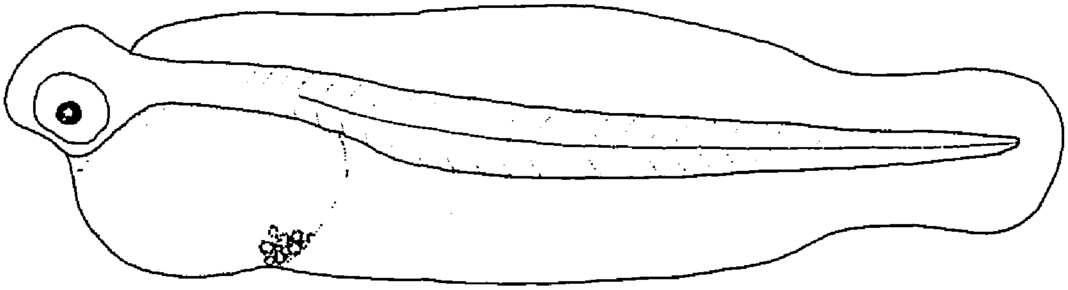
Data are insufficient to comment on the occurrence of seasonal, diel or lunar periodicity in spawning, but the presence of visibly swollen females in late afternoon appears to be a reliable indicator that spawning will occur that evening. Colin (1989) commented on the use of the visible condition of the female as an indicator of daily spawning potential in butterflyfishes (*Chaetodon*).

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

General Development of Larvae.-- Morphometric data and counts are given in Table 1. Recently hatched larvae (1.5 - 2.0 mm NL) have a large ovoid yolk (52.6 - 80.0% NL) with numerous small oil globules at the posterior end; the number of oil globules is approximately the same as noted for early-stage eggs. The body is dorso-ventrally flattened over the yolk, the eyes are unpigmented, the mouth is not formed, median-fin folds are slightly to well developed and the intestine is apparent only as it bends ventrally towards the anus, which is located slightly posterior to midbody (55.0 - 57.9% NL). Before the yolk is completely absorbed (in all specimens by 3.4 mm NL), the body becomes laterally compressed and changes in shape from moderately deep in preflexion larvae (body depth 12.9 - 30.4% NL at pectoral-fin base) to deep in postflexion specimens (body depth 39.7 - 47.5% SL), the intestine coils and shortens slightly (43.3 - 52.2% NL), an inconspicuous swimbladder forms, the eyes become pigmented and the

Figure 1. Preflexion larvae of *Diploprion bifasciatus*: A) USNM 290880-6, 2.8 mm NL, 24 hours post hatch; B) USNM 290882-12, 2.8 mm NL, 48 hours post hatch; C) USNM 290884-8, 3.1 mm NL, 78 hours post hatch.

A



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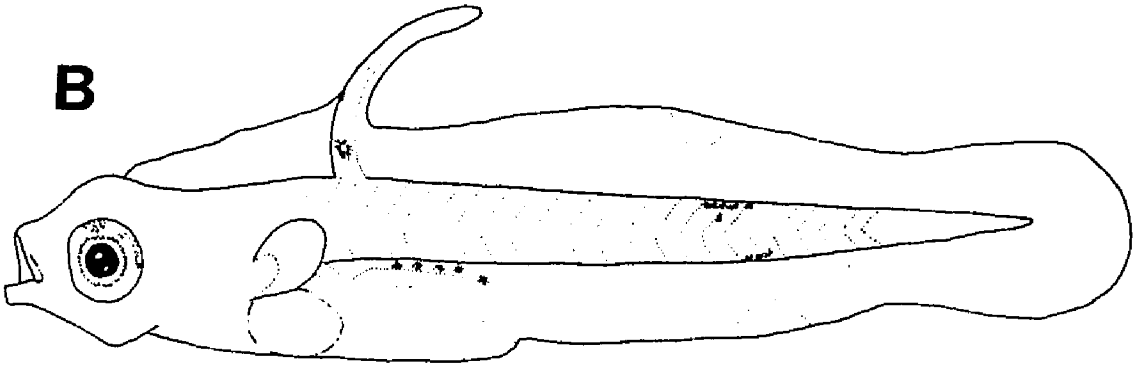

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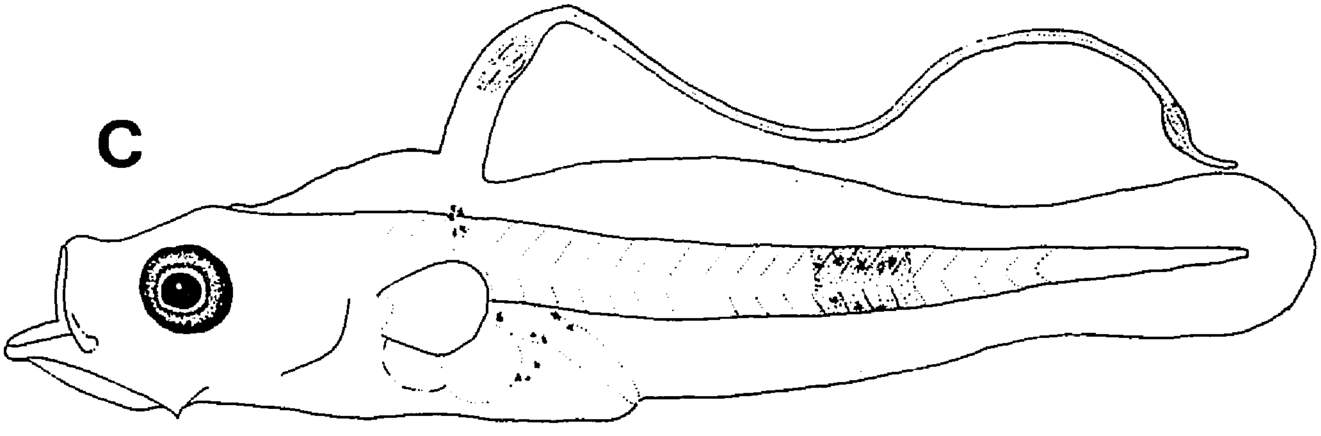


Figure 2. Larva of *Diploprion bifasciatus* undergoing notochord flexion: USNM 290892-2, 6 mm NL, 12 days post hatch.

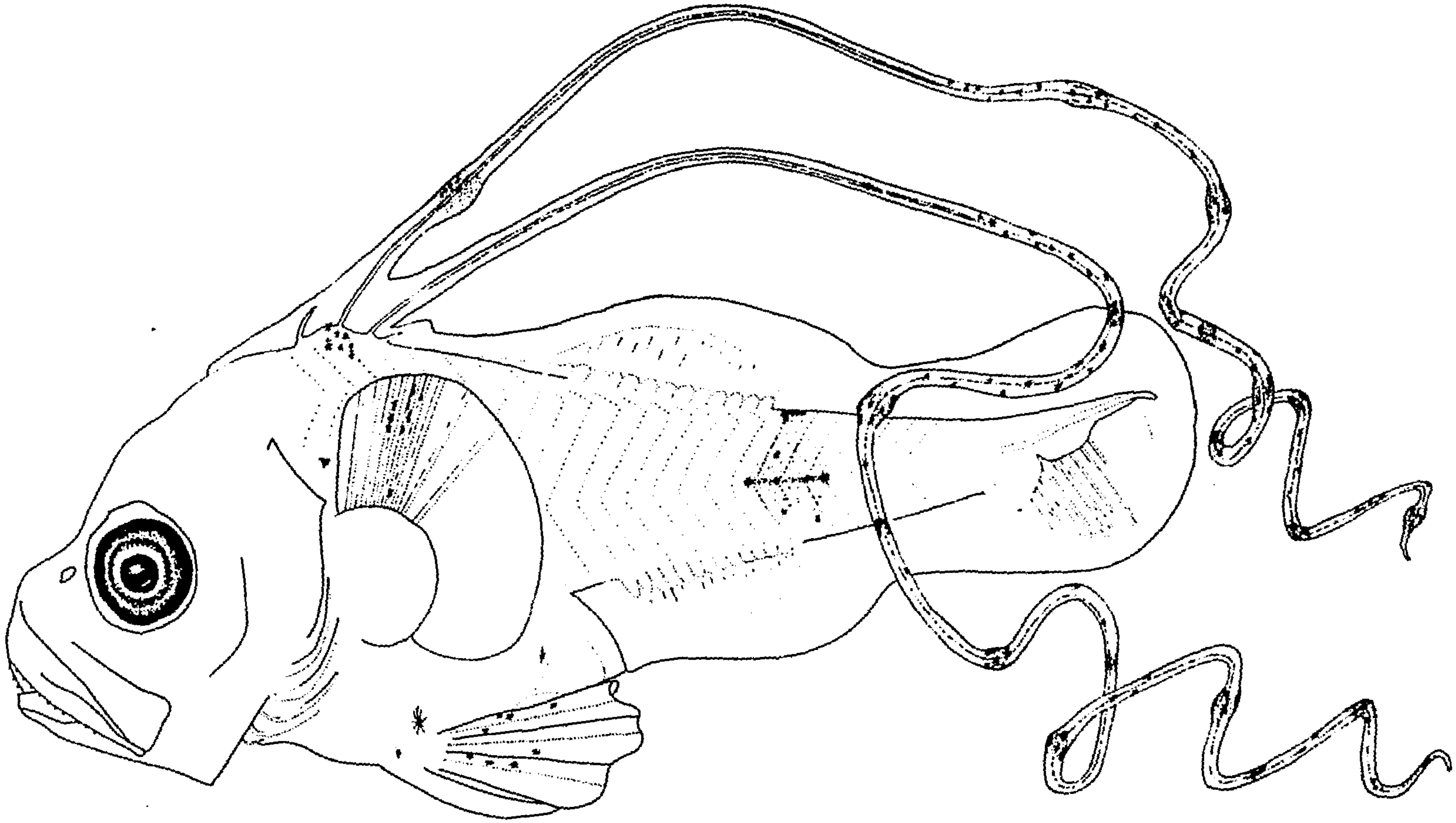


Figure 3. Postflexion larva of *Diploprion bifasciatus*: USNM 290919, 16.2 mm SL, 24 days post hatch.

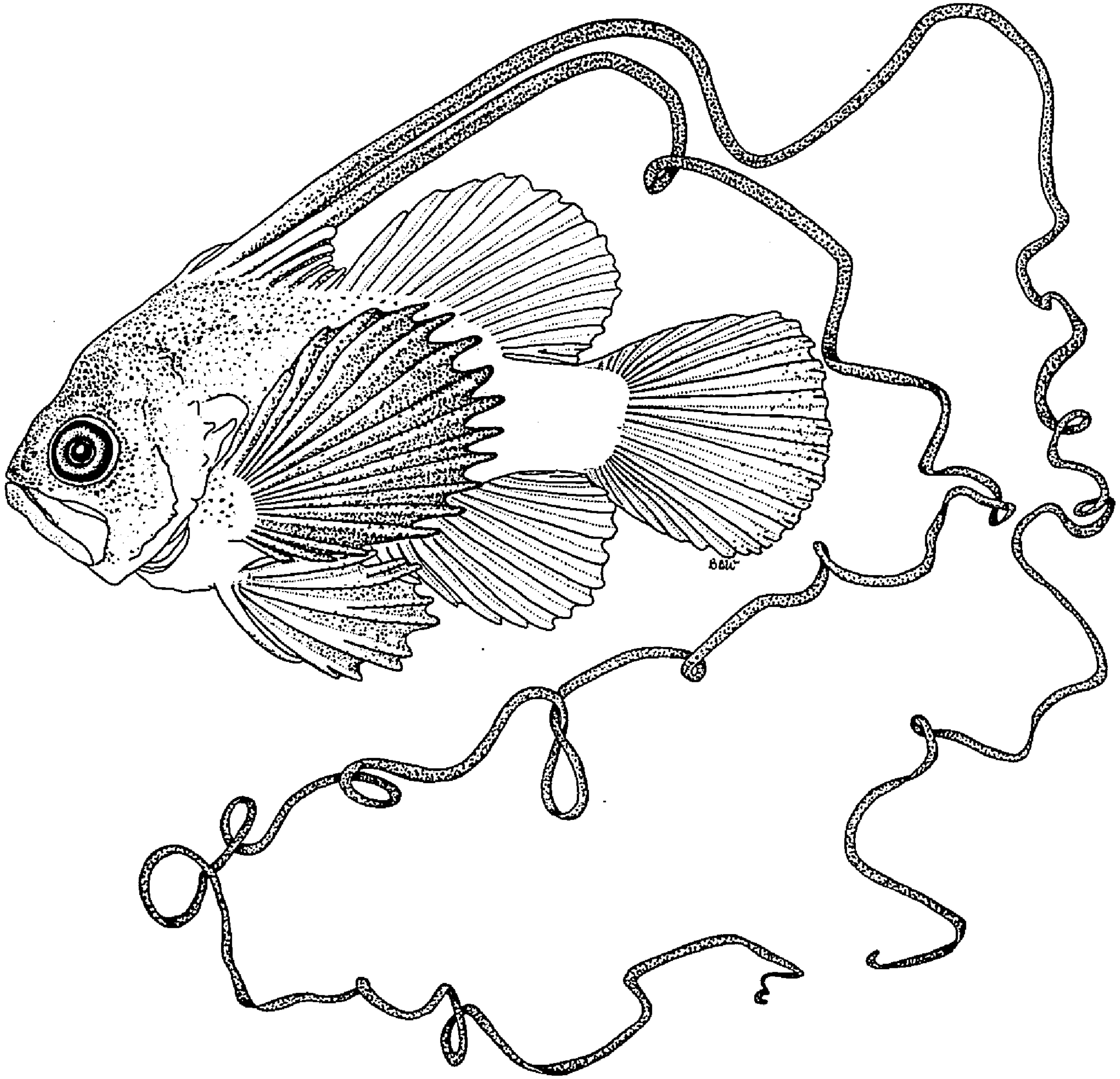


Table 1. Morphometric data and counts of larval *Diploprion bifasciatum*. Body length is in mm; other morphometric values are expressed as %body length. Parentheses enclose the number of specimens measured; where more than one specimen was examined, values are means followed by standard deviation. Values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

Body length	Preanal length	Predorsal length	Snout length	Eye diameter	Body depth at P_1 base	Body depth at anus	Depth caudal peduncle	Head Length
1.5-2.0 (12)	57.0;2.2	-	-	-	-	15.2;0.4	-	-
2.1-3.0	48.0;2.2 (46)	30.5;1.7 (29)	6.9;0.2 (29)	6.9;0.2 (29)	18.4;4.3 (46)	14.6;2.1 (46)	-	22.5;2.4 (42)
3.1-4.0 (39)	48.2;2.0	31.4;1.8	6.8;0.9	7.6;1.4	18.2;2.3	14.3;1.9	-	25.2;1.5
4.1-5.0 (3)	47.1;1.6	31.6;1.1	8.1;1.4	8.1;1.4	22.0;1.3	16.9;0.8	-	27.8;0.1
6.3 (1)	50.0	28.6	9.5	9.5	31.7	25.4	-	
6.6 (1)	48.5	27.3	9.1	9.1	33.3	27.3	-	28.8
7.3 (1)	63.0	38.4	11.0	11.0	39.7	24.7	11.0	37.0
8.8 (1)	56.8	31.8	11.4	11.4	42.0	36.4	14.7	38.6
9.8 (1)	56.1	34.7	13.3	11.2	42.9	32.7	13.3	34.7
10.7 (1)	57.0	31.8	10.3	11.2	44.9	37.4	15.0	35.5
11.0 (1)	58.2	38.2	10.9	10.9	46.4	38.2	14.0	40.9
13.3 (1)	50.4	30.1	9.0	9.8	45.1	39.8	13.8	39.8
15.5 (1)	51.6	32.3	10.3	10.3	45.2	37.4	15.8	41.3
16.2 (1)	52.5	28.4	8.6	10.5	47.5	42.6	15.8	39.5
(Wild-caught specimens)								
5.7 (1)	49.5	40.8	8.7	8.7	34.9	24.8	-	33.5
5.8 (1)	51.4	41.4	10.0	10.0	30.0	22.9	-	35.7
7.1 (1)	56.1	42.1	11.7	9.4	40.9	32.1	-	40.9
10.4 (1)	59.4	39.3	12.8	8.8	36.9	30.5	12.8	41.7
10.9 (1)	55.2	38.3	10.7	9.2	41.4	33.7	13.0	39.8
13.3 (1)	57.9	30.1	10.5	10.5	49.6	40.6	15.0	42.1
31.4 (1)	56.1	30.6	6.1	9.6	45.9	41.4	15.9	35.0

Table 1 (cont.)

Body	Length of	Length of	Length of	Yolksac	Dorsal	Anal	Pectoral	Pelvic	Caudal fin	
length	P_1 fin	D spine II	D spine III	length	fin	fin	fin[a]	fin	Principal	Procurrent
1.5-2.0 (17)	-	-	-	60.1;7.7	-	-	-	-	-	-
2.1-3.0	13.3;1.7 (23)	35.8;26.0 (29)	-	14.5;9.1 (45)	0-I,-	-	-	-	-	-
3.1-4.0	15.4;1.5 (27)	118.9;69.4 (38)	7.6;5.3 (7)	4.3;2.0 (17)	I-II,-	-	-	-	-	-
4.1-5.0 (3)	13.2;2.3	130.8;7.3	35.4;7.1	-	II,-	-	-	-	-	-
6.3 (1)	19.0	69.8	76.2	-	IV,-	-	8	I,5	3 + 3	-
6.6 (1)	21.2	166.1	224.4	-	IV,-	-	9	I,5	4 + 4	-
7.3 (1)	31.5	186.3	230.1	-	VIII,15	II,12	18	I,5	9 + 8	2 + 2
8.8 (1)	39.8	127.3+	102.3+	-	VIII,14	II,12	18	I,5	9 + 8	2 + 2
9.8 (1)	42.9	285.7	391.8	-	VIII,15	II,13	18	I,5	9 + 8	3 + 4
10.7 (1)	44.9	-	-	-	VIII,15	II,12	17	I,5	9 + 8	4 + 4
11.0 (1)	48.2	261.8	392.7	-	VIII,15	II,12	17	I,5	9 + 8	6 + 6
13.3 (1)	46.6	228.6	457.1	-	VIII,14	II,12	18	I,5	9 + 8	6 + 5
15.5 (1)	46.5	343.2	760.0	-	VIII,14	II,12	18	I,5	9 + 8	7 + 5
16.2 (1)	50.6	500.6	876.5	-	VIII,15	II,12	17	I,5	9 + 8	8 + 7
(Wild-caught specimens)										
5.7 (1)	7.3	34.9+	27.7+	-	II,-	-	-	I,3	-	-
5.8 (1)	7.1	30.0+	24.3+	-	II,-	-	-	I,4	-	-
7.1 (1)	11.7	40.9+	23.4+	-	V,16	II,12	15	I,5	6 + 6	-
10.4 (1)	32.1	54.6+	46.6+	-	VIII,16	II,12	17	I,5	9 + 8	4 + 4
10.9 (1)	30.6	72.0+	64.3+	-	VIII,16	II,12	17	I,5	9 + 8	5 + 5
13.3 (1)	43.6	78.2+	12.0+	-	VIII,15	II,12	17	I,5	9 + 8	7 + 7
31.4 (1)	34.1	63.7	22.9	-	VIII,15	II,12	17	I,5	9 + 8	9 + 8

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

mouth opens. The eye is round, and its horizontal diameter remains approximately equal to or slightly larger than the length of the snout throughout development. The mouth increases in relative size ontogenetically, the maxilla reaching to or nearly to the anterior margin of the eye before flexion, to a point just posterior to the middle of the eye after flexion. A prominent rostral cartilage appears after flexion. Scales are lacking in all specimens examined.

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

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

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

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

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

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

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

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

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

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

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

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

The exact sequence of completion of fins could not be determined solely from the reared material because specimens in the critical size range (between 6.3 and 7.3 mm) are not available. Combining information from reared and wild-caught material, the sequence of completion appears to be pelvic-anal-soft dorsal and pectoral-spinous dorsal-caudal.

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

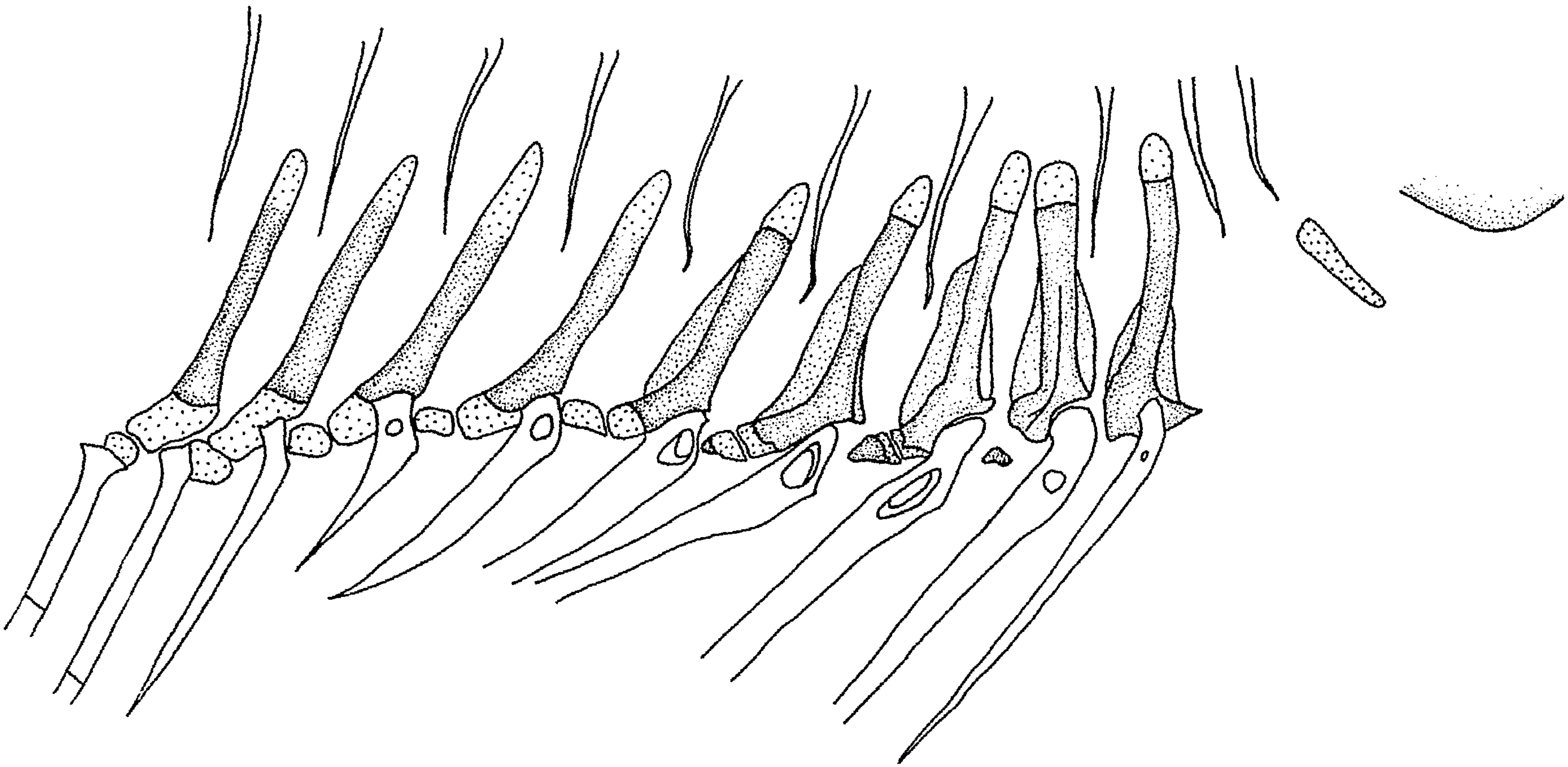
Other dorsal-fin spines begin developing during flexion, the first and fourth spines appearing before those more posterior. In a 7.3-mm SL specimen, the second, third and fourth dorsal-fin spines have paired lateral fossae near the bases, whereas the other spines do not. In an 11.0-mm SL specimen, all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

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

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

The caudal fin is the last fin to complete development. The notochord is undergoing flexion in 6.3 to 7.1-mm specimens, and flexion is complete in a 7.3-mm specimen. Three to six principal caudal-fin rays are present in both the upper and lower lobes of the caudal fin in flexion specimens, but no procurrent rays are evident. In a 7.3-mm SL specimen, all principal

Figure 4. Spinous dorsal fin of an 11.0 mm SL larva of *Diploprion bifasciatus*.



caudal-fin rays (9 + 8) are present, and there are four procurrent rays. Adult *D. bifasciatus* have 17 procurrent caudal-fin rays (9 + 8). It is difficult to count procurrent rays in whole postflexion specimens because the rays are surrounded by thick tissue. A cleared and stained specimen of 11.0 mm SL has six procurrent rays both dorsally and ventrally.

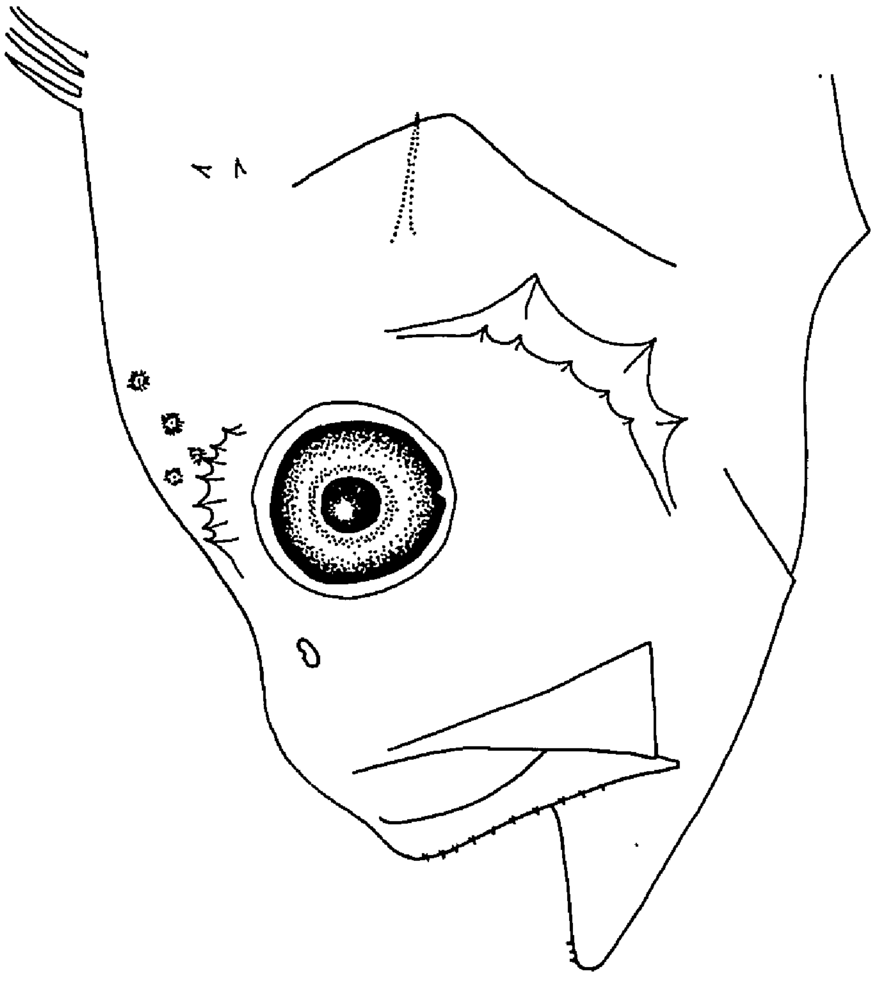
Comparison with Wild-caught Larvae.--Several wild-caught specimens were available for comparison with the reared material. Morphometric data and counts of the wild-caught specimens are given at the bottom of Table 1. In general, reared and wild-caught specimens are similar morphometrically, but in preflexion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

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

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

Head spination in the wild-caught larvae is more conspicuous than in the reared material (Fig. 5). Head spines of reared larvae are difficult to observe in whole specimens, but those of

Figure 5. Head spination in a wild-caught larva of *Diploprion bifasciatus* (CSIRO,AS05/83, 7.8 mm SL).



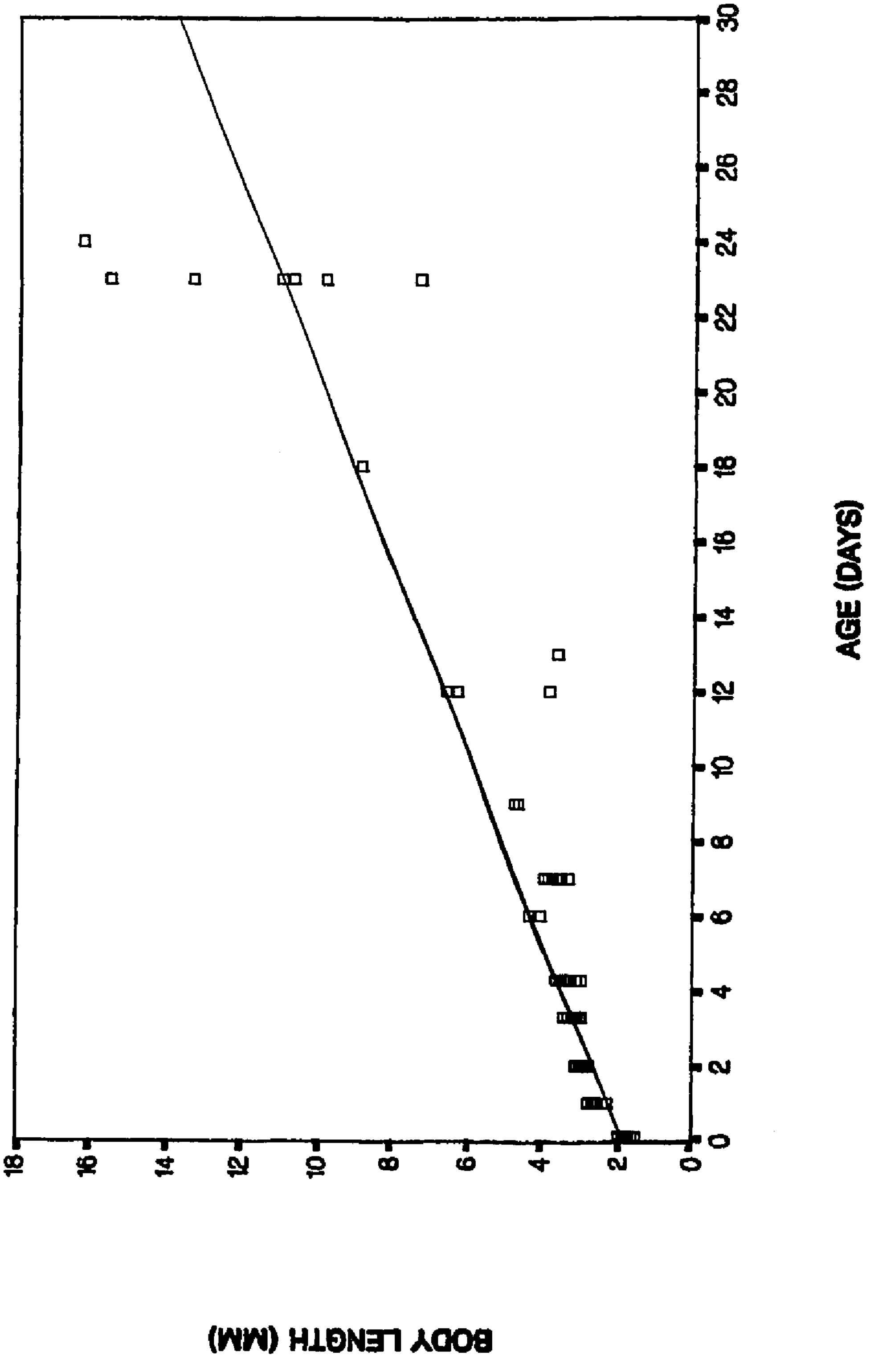
the wild-caught larvae are larger and can be seen clearly in whole specimens. Additionally, more supraorbital spines are present in the wild-caught larvae (five to eight vs. four in most reared specimens). The small differences in meristics and spination between the reared and wild-caught specimens could be due to the small sample size examined, the rearing process (see Blaxter, 1984 and Hunter, 1984) or, possibly, variation between populations of *D. bifasciatus* in New Guinea (locality adults were collected for obtaining gametes) and the northwest continental shelf of Australia (locality most wild-caught larvae were obtained).

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

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

Observations of Living Larvae.-- At 24 h post hatch (2.3-2.8 mm NL), larvae had numerous chromatophores. Orange chromatophores were present on the tip of the snout, anterior portion of each eye, anterior part of brain, anterior and posterior margins of the yolk sac, at

Figure 6. Regression of body length on age, showing growth in reared specimens of *Diploprion bifasciatus*.



BODY LENGTH (MM)
0
2
4
6
8
10
12
14
16
18
AGE (DAYS)
0
2
4
6
8
10
12
14
16
18
20
22
24
26
28
30

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

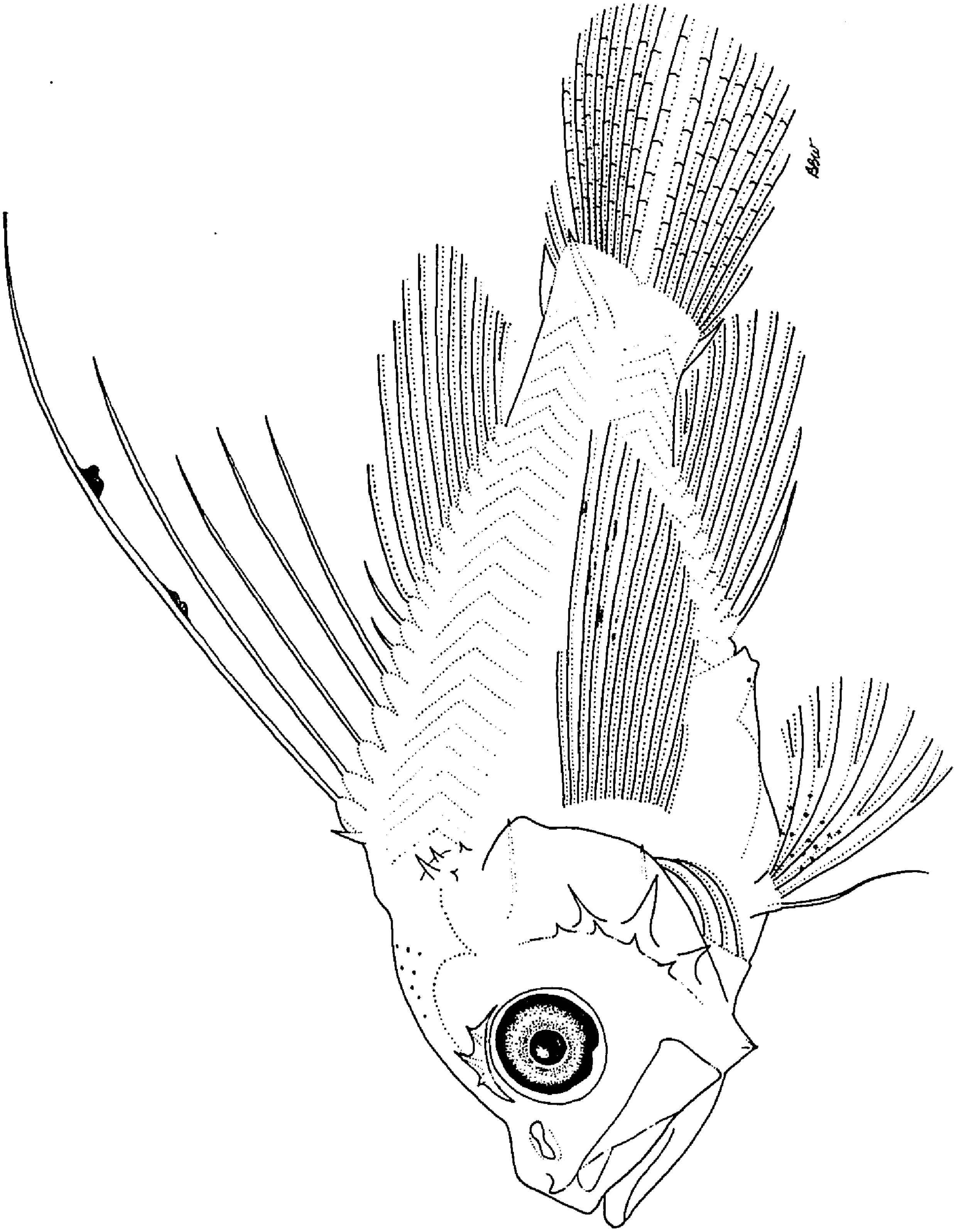
Larvae were not reared through metamorphosis. At 23- and 24-d post hatch, when rearing was terminated, the larvae were actively feeding and appeared to be growing well.

Belonoperca chabanaudi (Fig. 7)

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

The following description is based on four wild-caught specimens, ranging in size from 6.9 to 11.8 mm SL. The identifications of larval *Belonoperca* are based on comparisons of meristic

Figure 7. Postflexion larva of *Belonoperca chabanaudi*: ZMUC P43671, 6.9 mm SL; dorsal fin drawn from USNM 309607, 11.8 mm SL.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features of larvae and adults (see Leis and Rennis, 1983:73); particularly diagnostic is the combination of dorsal-, anal- and pectoral-fin rays. Morphometric data and counts are given in Table 2.

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

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

In the smallest specimen (6.9 mm SL), a group of very faint melanophores extends ventrally from the base of the eighth dorsal soft ray to just below midbody. The anterior portion of the trunk lacks pigment. Several melanophores are present on the upper rays of the pectoral fin and on the proximal portion of the pelvic fin. Anal and caudal fins are without pigment. There are several small melanophores on each frontal bone. In larger specimens, the number of melanophores on the frontals increases, and no pigment is evident on the trunk and pelvic fin, but possibly it has faded.

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

Body length	Preanal length	Predorsal length	Snout length	Eye diameter	Body depth at P_1 base	Body depth at anus	Depth caudal peduncle	Head Length	Length of P_1 fin
6.9	60.5	37.2	13.0	10.1	39.1	37.7	15.9	39.1	40.6
7.2	58.3	40.3	13.9	9.7	41.7	36.1	15.5	41.2	38.9
8.8	60.2	39.8	15.9	9.1	36.4	34.1	14.8	39.8	44.3
11.8	66.1	38.1	11.9	11.0	40.7	39.0	15.3	43.2	22.9+

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

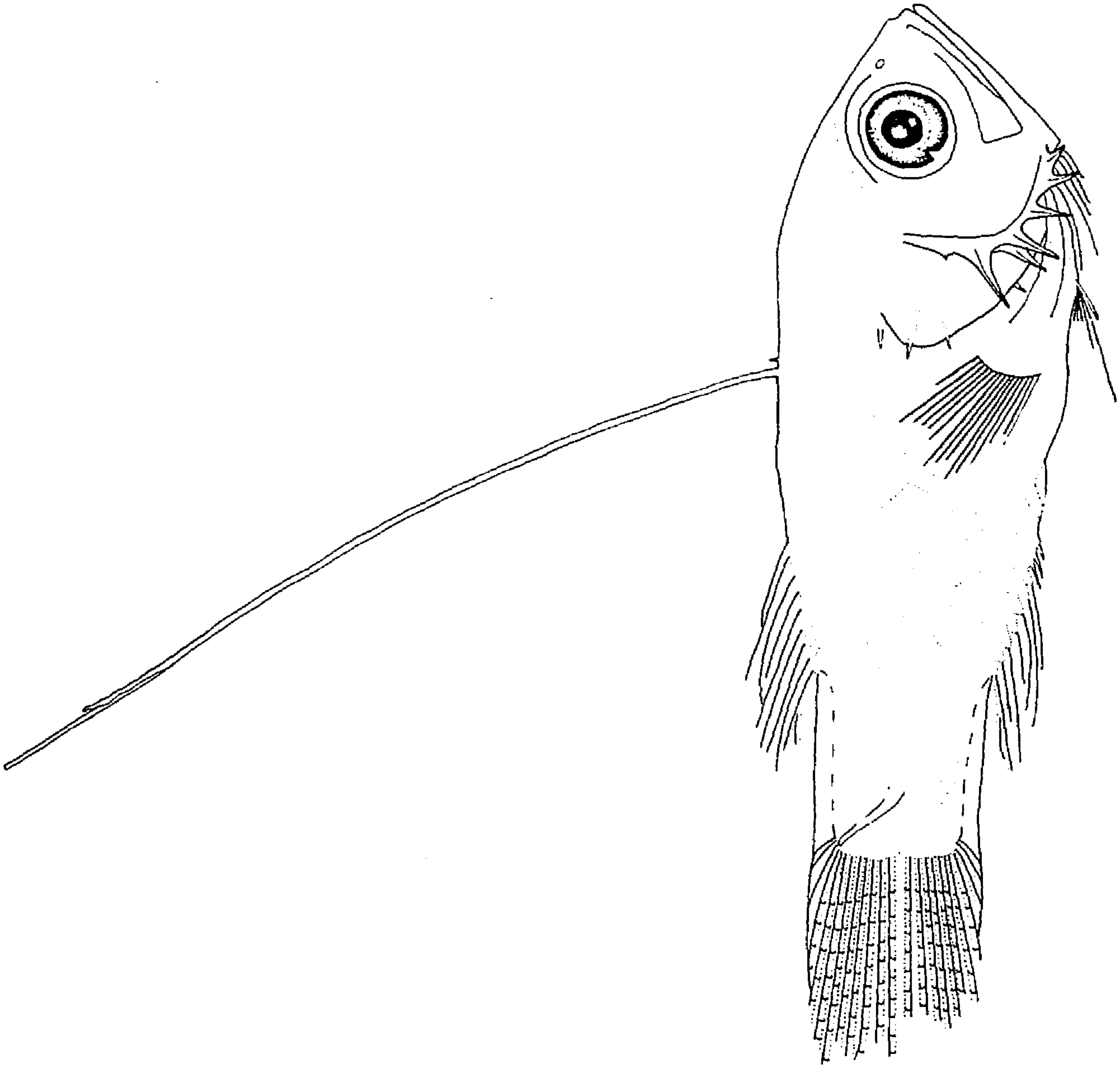
All specimens except the largest (11.8 mm SL) have spines on the supraorbital ridge of the frontal, preopercle, subopercle, posttemporal and supracleithrum. Supraorbital spination consists of two strong spines and sometimes a third weaker spine anteriorly. The medial ridge of the preopercle bears three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

Jeboehlkia gladifer (Figure 8)

Jeboehlkia gladifer Robins, 1967, was described from a single mature female collected at 165 m (90 fms) in the Caribbean Sea. Several additional specimens have been collected recently in similarly deep waters of the Caribbean and western North Atlantic (R. G. Gilmore, pers. comm.). Robins (1967) noted a strong resemblance between *J. gladifer* and the epinepheline genus *Liopropoma*, but accorded the former generic status on the basis of absence of pored lateral line scales. Several features of the holotype, its small size (40.8 mm SL), elongate dorsal-fin spine, produced pelvic-fin rays and large eye appear paedomorphic with respect to other epinephelines (Kendall, 1984).

The following description of larval *Jeboehlkia* is based on a single specimen, 10.2 mm SL, collected between 10 and 300 m in Atlantic slope water off New York (MCZ 81740, Fig. 8). The specimen is in poor condition, lacks pigment (but possibly it is naturally unpigmented) and is bent in half at midbody. It was illustrated (flattened right side up beneath a glass microscope slide) with the aid of a camera lucida. The pectoral fin was drawn from the left side of the body, and myomeres were reconstructed from a combination of vertebrae (partially visible on the damaged right side of the body) and myomeres (partially visible on the left side of the body).

Figure 8. Larva of *Jeboehlkia gladifer*, MCZ 81740, 10.2 mm SL, collected in the western North Atlantic Ocean (40°42.0'N, 65°,00.3'W).



The larva is identifiable as *J. gladifer* on the basis of counts and morphology of fin rays. The holotype (USNM 201422) has the following counts: dorsal-fin rays VIII,9; anal-fin rays III,7; pectoral-fin rays 15; pelvic-fin rays I,5; principal caudal-fin rays 17 and vertebrae 24. The spinous dorsal fin in the larval specimen is incomplete, but the larva clearly has nine soft dorsal-fin rays, a meristic feature unique among Atlantic Epinephelinae to *Jeboehlkia* (see Kendall, 1979, Table 1). Corroborating the identification of this specimen as *Jeboehlkia* is the presence of seven anal-fin soft rays, 15 pectoral-fin rays and a thin, flexible, elongate second dorsal-fin spine. Although Robins (1967) stated that the holotype has seven dorsal-fin spines and that the first spine is the elongate element, an examination of a radiograph of the holotype indicates that the first spine is only an unexposed nubbin and was overlooked by Robins; consequently, there is a total of eight (not seven) dorsal-fin spines. The tiny first spine is the only element borne in supernumerary association with the first dorsal-fin pterygiophore, and the elongate (second) spine in larval *Jeboehlkia* is serially associated with the first dorsal pterygiophore, a hallmark of all known larvae of the Epinephelinae.

The postflexion larva of *J. gladifer* is laterally compressed, moderately deep (body depth at pectoral-fin base 34.5% SL) and has a large head (42.4% SL). The specimen essentially is eviscerated, but the anus is evident just posterior to midbody (56.5% SL). The eye is round, moderately large and greater in diameter than the length of the snout (diameter of eye, 11.0% SL, length of snout, 9.4% SL). The mouth is large, the maxilla reaching just beyond middle of the eye.

The distance between the dorsal and ventral margins of the caudal peduncle is 15.7% SL (between dashed lines on caudal peduncle in Figure 8), but the total depth of the peduncle is greater (18.6% SL between solid lines on caudal peduncle in Figure 8). This disparity is due to the presence of two blade-like sheaths of modified tissue that lie above and below the dorsal and ventral margins of the caudal peduncle, respectively, and extend from the posterior bases of the dorsal and anal fins to the caudal fin. This tissue contains numerous small globules (of fat?). Tissue with a similar appearance covers the procurrent rays of the caudal fin and appears along the lengths of most principal caudal-fin rays, on the rays of the soft dorsal and anal fins and on the head.

The longest ray of the pectoral fin measures 15.1% SL, but all rays appear broken, and the original length of the fin is unknown. Pelvic-fin rays also appear broken, but the first soft ray on the right side and second on the left side are clearly produced. Robins (1967) noted that the first two pelvic soft rays are very elongate in the holotype, and both are probably elongate in intact larvae.

The elongate second dorsal-fin spine is thin, flexible and covered with a sheath of tissue that is torn distally. It measures 105% SL, but is broken, and I am unable to determine its original length.

There is a full complement of soft dorsal- (9), anal- (III,7), pectoral- (15) and principal caudal-fin rays (9+8). Only the first two dorsal-fin spines are visible externally, but four additional tiny spines that have not yet emerged through the skin are apparent in a radiograph of the larva. The procurrent caudal-fin rays are difficult to see, but the specimen appears to have three in both the dorsal and ventral caudal lobes, two fewer than the adult complement of 4+4, as determined from a radiograph of the holotype. The pelvic fin bears one spine and five soft rays, the medialmost two of which are closely approximated. All fin spines are smooth.

There are six prominent smooth preopercular spines, the four on the lower limb becoming increasingly antrorse anteriorly. Robins (1967) noted the presence of three strong antrorse spines on the lower limb of the preopercle in the holotype. My examinations indicate that the three anteriormost antrorse spines in the larval specimen are very similar in morphology and position to those of the holotype and thus provide additional corroborative evidence for the identification of the larval specimen as *J. gladifer*. Antrorse preopercular spines are rare among larval epinephelines (present in some larvae of the epinepheline tribe Epinephelini, Leis

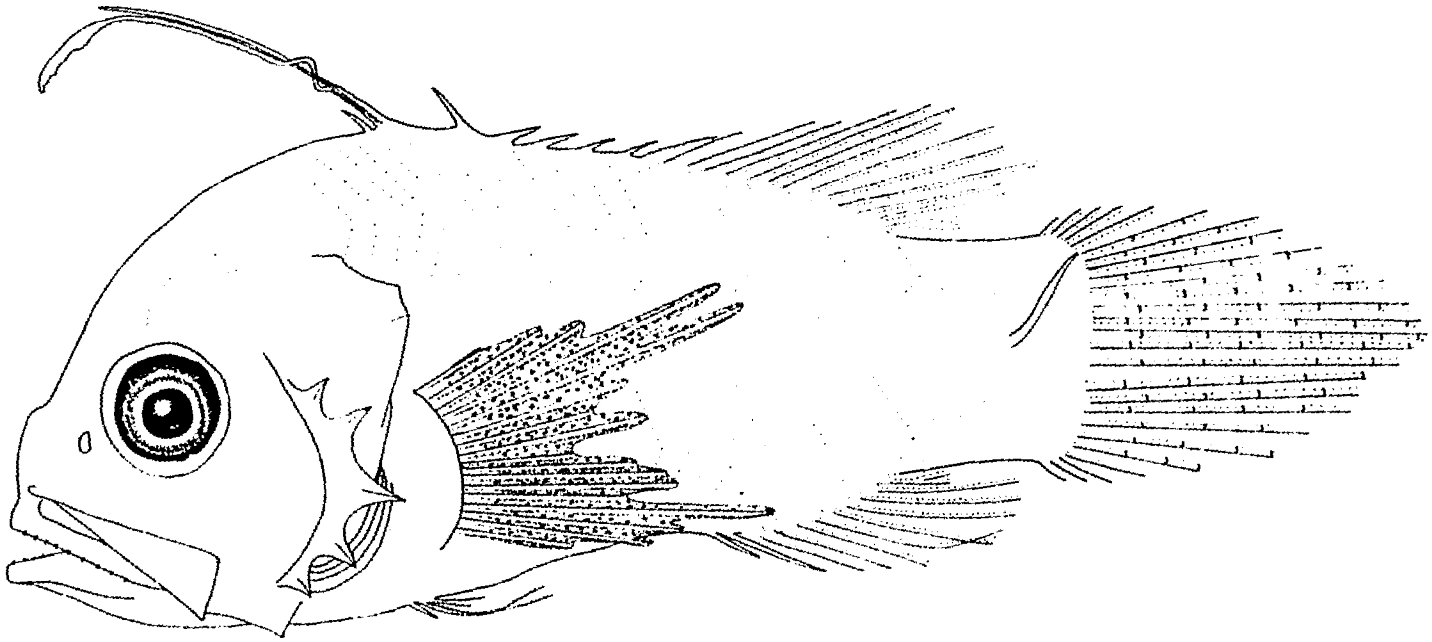
1986), and their presence in larval *J. gladifer*, in combination with other characters, appears diagnostic. The interopercle and supracleithrum each bear one well-developed smooth spine, and a single small spine is present on the subopercle; spines are lacking on the lateral ridge of the preopercle and supraorbital ridge of the frontal. The frontal bones bear a conspicuous "golf ball-like" pattern of very small pits (not illustrated in Figure 8), not nearly so prominent as the raised network of ridges (rugosity) found in some anthiine and epinephelin serranids (see Baldwin, 1990). Scales are lacking and presumably have not yet formed.

Grammistes sexlineatus (Fig. 9)

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

The following description is based on ten larvae (5.5 - 11.4 mm SL) identified by fin-ray counts and morphology of fin spines. *Grammistes* and *Pogonoperca* have similar numbers of fin rays (see Leis and Rennis, 1983:73). Adults are separable on the basis of gross morphology, and presence of seven dorsal spines and two or three anal spines in *Grammistes* (vs. eight and always three, respectively, in *Pogonoperca*). I was unable to positively identify the ten larval specimens as *Grammistes* solely on the basis of meristic features; although they appear to have seven dorsal- and two anal-fin spines, it is possible that an additional spine (or spines) could form indirectly from soft rays as in *Niphon* and epinephelins (see Johnson, 1988). However, in adults of *Pogonoperca*, the eighth dorsal-fin spine is the shortest, whereas in *Grammistes*, the shortest dorsal spine is the seventh. In the larval specimens, the eighth dorsal element is longer than the seventh, and thus probably does not represent the as yet untransformed eighth spine of *Pogonoperca*. Additionally *Pogonoperca* has three anal-fin

Figure 9. Postflexion larva of *Grammistes sexlineatus*: ZMUC P43674, 6.5 mm SL; pectoral fin drawn from right side of specimen.



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

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

Morphometric data and counts are given in Table 3. All specimens are moderately deep (body depth 31.5 - 41.5% SL at pectoral base). The eye is round and its diameter usually is smaller than the length of the snout. The mouth is large, the maxilla reaching a vertical through middle of orbit. The pectoral fin is moderately large, reaching 39.6% SL in an 11.4-mm SL specimen. All specimens examined have the full complements of dorsal-, anal-, pectoral- and principal caudal-fin rays. A 6.5-mm SL specimen has the full complements of pelvic- and procurrent caudal-fin rays, but neither of these fins is complete in a 6.6-mm SL larva nor in smaller specimens.

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

In all specimens the pectoral fin has many small melanophores on all rays, but the density

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

Body length	Preanal length	Predorsal length	Snout length	Eye diameter	Body depth at P_1 base	Body depth at anus	Depth caudal peduncle	Head Length
5.5	57.3	42.3	13.6	8.8	36.2	31.7	18.8	37.7
6.2	60.2	40.2	12.7	9.4	37.5	33.5	18.1	40.2
6.5	55.4	38.5	10.8	9.2	41.5	33.8	18.5	38.5
6.6	57.0	33.9	9.1	9.1	34.8	30.3	16 7	36.4
7.1	59.2	39.4	12.7	8.5	35.2	32.4	18.3	42.3
7.3	damaged	43.8	11.0	8.2	31.5	damaged	damaged	41.1
7.9	60.8	39.2	13.9	7.6	35.4	31.6	15.2	43.0
8.2	57.3	34.1	12.2	8.5	36.6	32.9	17.1	40.2
9.7	56.8	37.9	10.3	8.6	41.3	37.9	15.5	39.6
11.4	57.1	36.6	11.0	8.8	39.6	36.6	16.1	41.0

Body	Length of	Length of	Dorsal	Anal	Pectoral	Pelvic	Caudal fin	
length	P_1 fin	D spine II	fin	fin	fin	fin	Principal	Procurrent
5.5	31.7	28.7+	VII,13	II,9	17	I,4	9 + 8	3 + 3
6.2	33.5	66.9+	VII,13	II,9	17	I,4	9 + 8	4 + 3
6.5	32.3	60.0+	VII,14	II,9	17	I,5	9 + 8	5 + 4
6.6	34.8	24.2+	VII,13	II,9	17	I,4	9 + 8	4 + 4
7.1	29.6	28.2+	VII,13	II,9	17	I,5	9 + 8	5 + 4
7.3	30.1	27.4+	VII,13	II,9	17	I,5	9 + 8	4 + 4
7.9	31.6	27.8+	VII,13	II,9	17	I,5	9 + 8	5 + 4
8.2	30.5	19.5+	VII,14	II,9	17	I,5	9 + 8	5 + 4
9.7	25.8+	15.5+	VII,14	II,9	16	I,5	9 + 8	5 + 4
11.4	39.6	10.3+	VII,14	II,8	17	I,5	9 + 8	5 + 4

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

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

Discussion

Morphological Comparisons of Epinephelinae Larvae.-- With the descriptions of larval diploprionins, larvae of at least some genera of each epinepheline tribe are known. Below, I briefly summarize and compare the morphologies of known larvae of all epinepheline tribes. The comparative information presented here is intended primarily to make it easier for others to identify larval epinephelines; additionally, this information is incorporated in a phylogenetic analysis of the subfamily based on characters of adults and larvae (Chapter 2). A summary of morphological variation in salient features among epinepheline larvae is given in Table 4.

Niphonini: Larval *Niphon* (Fig. 10A) is separable from larvae of all other epinephelines on the basis of a stout but smooth elongate third dorsal spine. Additionally, *Niphon* has a moderately produced pelvic-fin spine, a single supraorbital spine, prominent but smooth preopercular spines, including an enlarged spine at the angle, and small spines on the posttemporal and supracleithrum. Pigment is limited to a patch of melanophores at the posterior base of the anal fin, several melanophores on the frontals in postflexion specimens,

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

GENUS	ELONGATE DORSAL SPINE(S)	MORPHOLOGY ELONGATE SPINE(S)	BODY DEPTH (%SL)	LENGTH PECTORAL FIN (%SL)	HEAD PIGMENT	DORSAL TAIL PIGMENT	VENTRAL TAIL PIGMENT	GUT PIGMENT	FIN PIGMENT
NIPHONINI									
Niphon	3rd	S	30-35[a]	17	+	-	+	+	P_2,C
EPINEPHLINI									
Cephalopholis	2nd	S,Se,EE	36	15	+	-	+	+	D_1,P_2
Epinephelus	2nd	S,Se,EE	35	17	+	-	+	+	D_1,P_2
Gonioplectrus	2nd,3rd	S,Se	51	34	+	(MIDLATERAL)		+	D_1,P_2
Mycteroperca	2nd	S,Se,EE	33-37	15-20	+	-	+	+	D_1,P_2
Paranthias	2nd	S,Se,EE	34	13	+	-	+	+	D_1,P_2
Plectropomus	2nd	S,Se,EE	32-35	14-17	+	-	+	+	D_1,P_2,C
DIPLOPRIONINI									
Belonoperca	2nd-6th	EE,F	39-42	40-44	+	+	-	-	D_1,P_2,P_1
Diploprion	2nd,3rd	EE,F	40-47	32-51	+	+	+	+	D_1,P_2,P_1
LIOPROPOMINI									
Liopropoma	2nd,3rd	EE,F	23-32	14-26	+	-	-[b]	+	D_1
GRAMMISTINI									
Aporops	2nd	EE,F	ND	ND	ND	ND	ND	ND	ND
Jeboehlkia	2nd	EE,F	34.5	15.1	ND	ND	ND	ND	ND
Grammistes	2nd	EE,F	32-42	30-33	-	-	-	-	D_1,P_2,P_1
Pseudogramma	2nd	EE,F	20-29	15-35	-	-	-	+	D_1,P_1
Rypticus	1st	EE,F	24-31	37-45	-	-	-[c]	+	D_1,P_1

[a] Measured at base of pelvic fin; all other measurements in this category made at pectoral-fin base.

[b] One specimen, 11.5 mm SL, with spot on ventral caudal peduncle

[c] One specimen, 5.9 mm SL with several spots along ventral caudal peduncle

Table 4 -- (cont.)

GENUS	SUPRAORBITAL SPINES	LARGE SPINE AT ANGLE OF PREOP	MEDIAL PREOP SPINES	LATERAL PREOP SPINES	OTHER HEAD SPINES	PRECOCIOUS (≤ 4 mm NL) FIN DEVELOPMENT	SEQUENCE[a] OF FIN COMPLETION
NIPHONINI							
Niphon	1	+	4	3	iop,pt,scl	ant. D_1,P_2	$P_2-(D_1-D_2-A)-P_1$
EPINEPHELINI							
Cephalopholis	1 to many	+	2-13	1	iop,sb,pt,scl	ant.D_1,P_2	ND
Epinephelus	1 to many	+	5	1	iop,sb,pt,scl	ant. D_1,P_2	ND
Gonioplectrus	many[b]	+	7	ND	pt,scl	ND	ND
Mycteroperca	1 to many	+	5-10	1	iop,sb,pt,scl	ant. D_1,P_2	$(P_2-D_1-A)-D_2-P_1$
Paranthias	many[b]	+	5	1	iop,sb,pt,scl	ND	ND
Plectropomus	1-4	+	5-7	1-2	iop,sb,pt,scl	ant. D_1,P_2	$(P_2-D_1-A)-D_2-P_1$
DIPLOPRIONINI							
Belonoperca	2-3	-	3	3-4	sb,pt,scl	ND	ND
Diploprion	4	-	3-4	3	pt	ant. D_1	$P_2-A-(D_2-P_1)-D_1$
LIOPROPOMINI							
Liopropoma	-	-	5-6	3-5	iop,sb	ant. D_1	$(D_2-A-P_1)-D_1-P_2$
GRAMMISTINI							
Aporops	-	-	5	none	none	ND	ND
Jeboehlkia	-	-	6	none	iop,sb,scl	ND	$(D_2-A-P_1)(D_1-P_2)$
Grammistes	-	-	4-5	none	none	ND	P_2 last
Pseudogramma	-	-	5	none	iop,sb	ant. D_1,P_1	$P_1-(D_1-D_2)-A-P_2$
Rypticus	-	-	3	none	none	ant. D_1,P_1	P_1first,P_2last

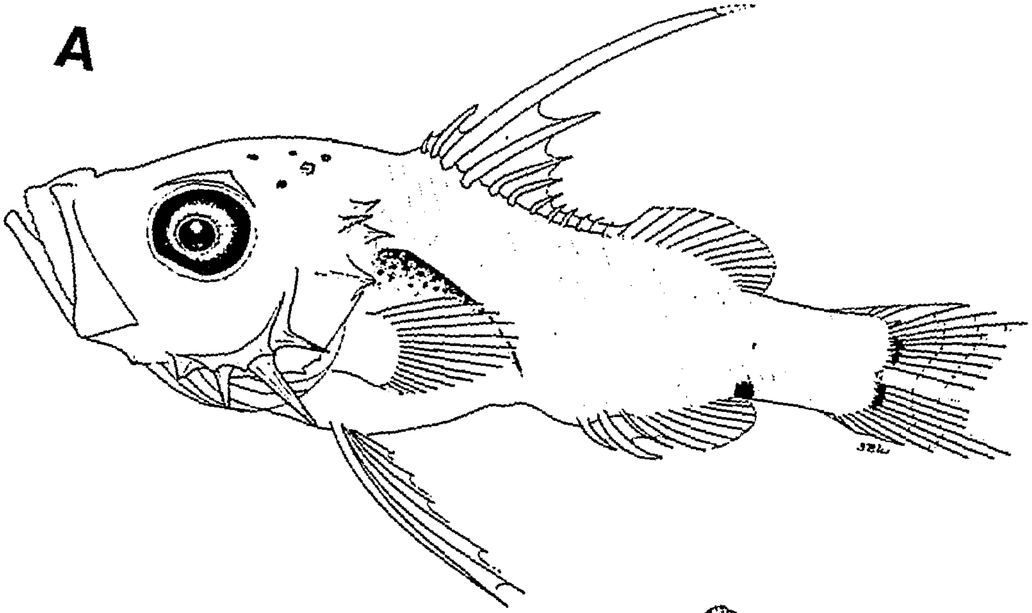
---

[a] Parentheses indicate sequence is variable or unknown.

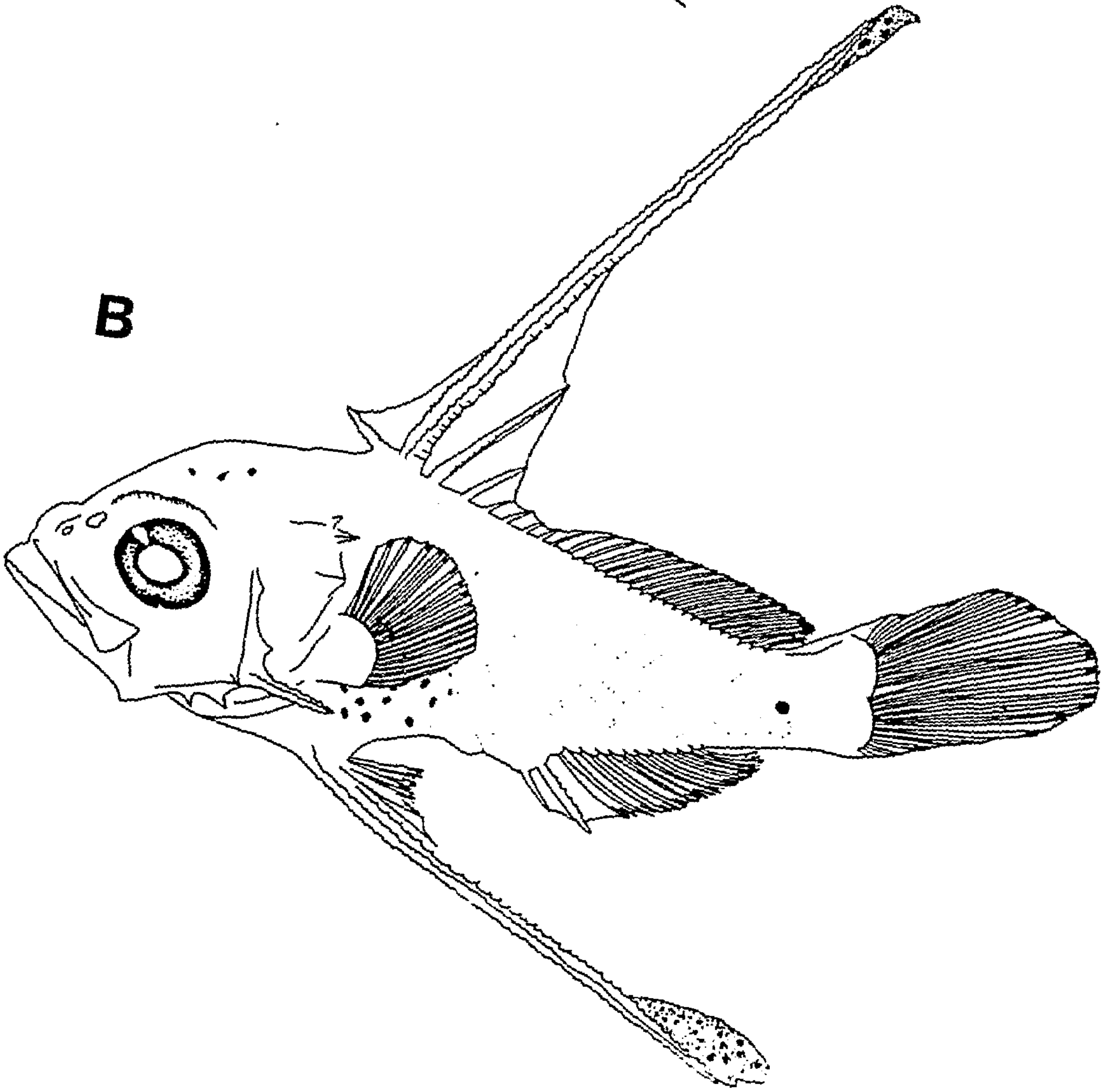
[b] It is unknown if the supraorbital ridge in these taxa, like that of *Cephalopholis*, *Epinephelus*, *Plectropomus* and *Mycteroperca* initially forms as a single spine.

Figure 10. A) Larva of *Niphon spinosus*, 7.0 mm SL (from Johnson, 1988); B) Larva of *Paranthias furcifer*, 8.6 mm (from Kendall, 1979).

A



B



two vertical bars of pigment on the proximal base of the caudal fin and a dense cap of melanophores covering the swimbladder and posterior portion of the gut.

Epinephelini: Epinephelin larvae (e.g., *Paranthias furcifer*, Fig. 10B) can be distinguished from known larvae of other serranids by the extremely elongate, strongly serrate second dorsal- and pelvic-fin spines that give these larvae a kite-shaped appearance. *Gonioplectrus* has a much deeper body than other epinephelins (see Table 4) and also has elongate, stout, serrate third dorsal- and second anal-fin spines (Kendall and Fahay, 1979). Head spination of epinephelins comprises one to several supraorbital spines or a low serrate supraorbital ridge, well developed preopercular spines (spine at angle enlarged and serrate), sometimes small spines on the interopercle and subopercle and small serrate spines on the posttemporal and supracleithrum. Tail pigment generally is limited to melanophores at the ventral midline or midbody laterally. The pelvic and caudal fins may have one to several melanophores, the sheath surrounding the elongate second dorsal-fin spine in preflexion larvae usually has melanophores distally, postflexion larvae have several melanophores on the frontals and there is a dense dorsal cap of melanophores on the posterior portion of the gut and swimbladder.

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

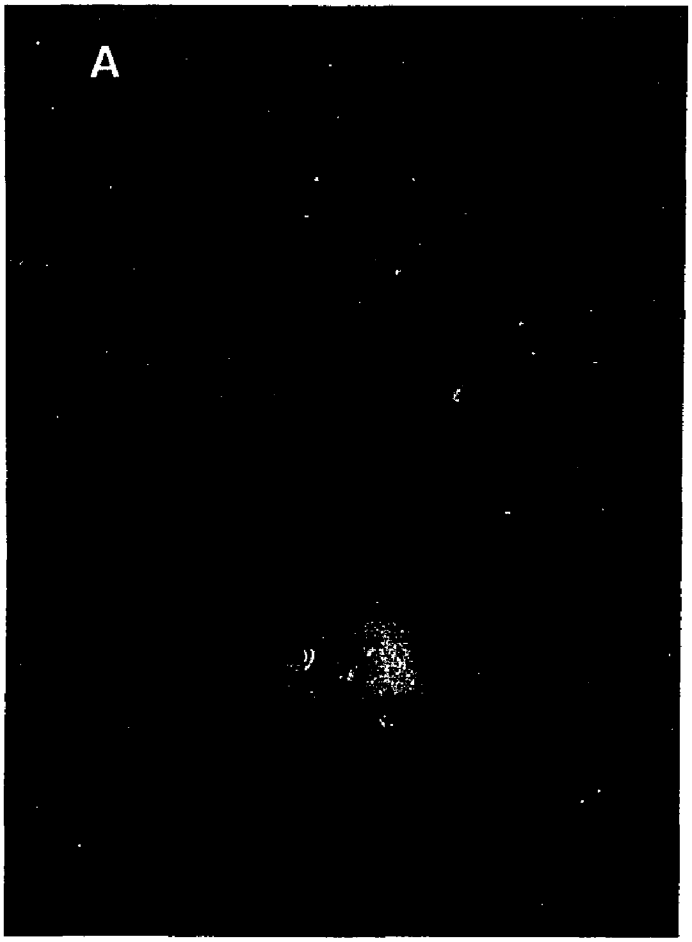
Belonoperca resembles *Diploprion* in lacking stout fin spines and having a large pectoral fin, but differs in having more prominent head spines. *Belonoperca* can be distinguished from known larvae of other serranids by the presence of five elongate dorsal-fin spines (second through sixth) that are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

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

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

Jeboehlkia was regarded as a close relative of *Liopropoma* by Robins (1967) and included in Johnson's (1983) tribe Liopropomini, but several aspects of the morphology of larval *Jeboehlkia gladifer* are inconsistent with those hypotheses. The presence in larval *Jeboehlkia*

Plate 1. A) In vivo photograph of larval *Diploprion bifasciatus*; B) In situ photograph of larval *Liopropoma* (photographs by G. R. Harbison).


A


B

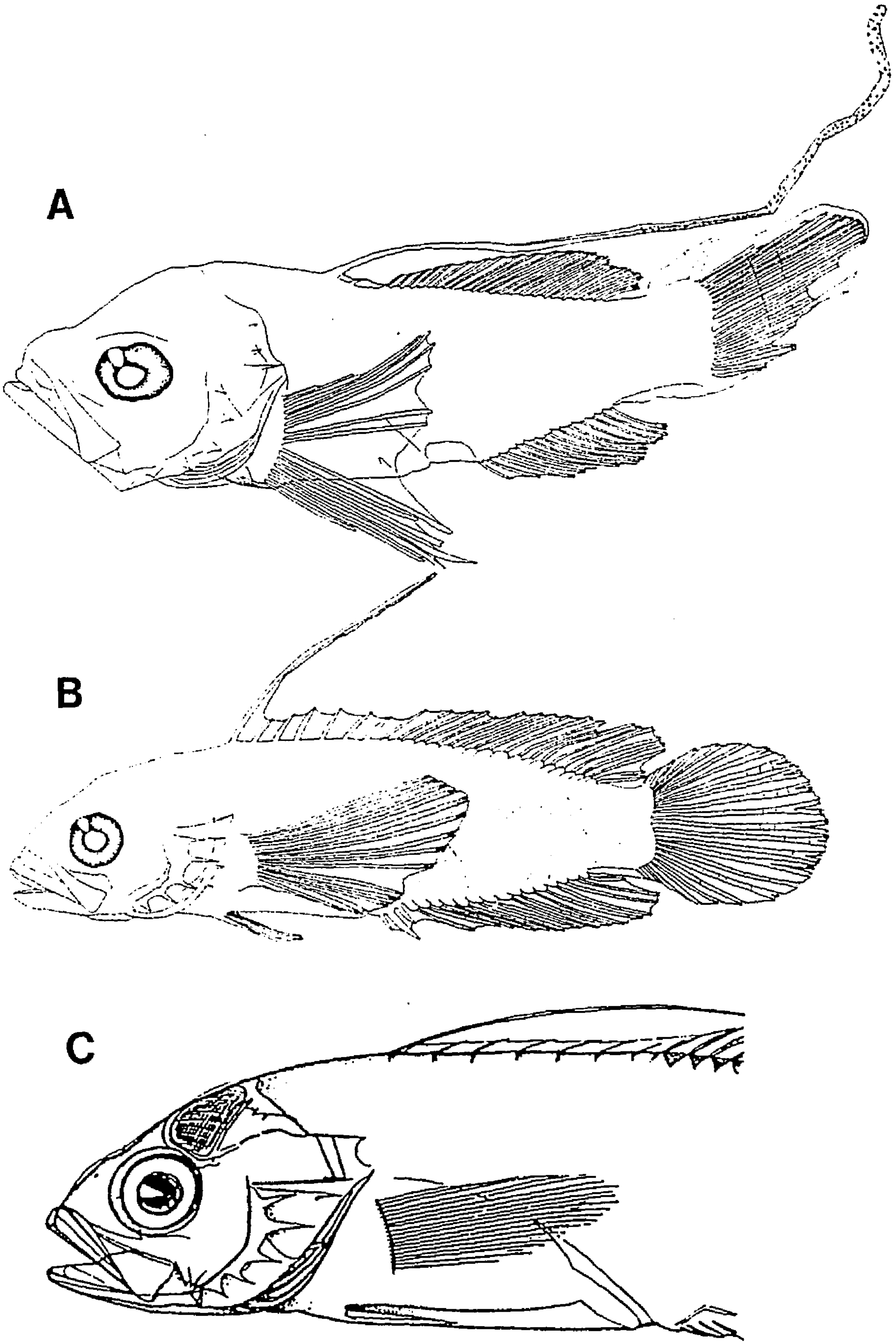
of a single (vs. two in *Liopropoma*) elongate filamentous dorsal-fin spine, robust (vs. weak) spines on the medial preopercular ridge and absence (vs. presence) of spines on the lateral preopercular ridge suggest affinities with Johnson's (1983) Grammistini. Below (Chapter 2), I explore in more detail the relationship of *Jeboehlkia* to other Epinephelinae.

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

Rypticus (Fig. 11A) has a produced dorsal spine that is very similar to that of *Grammistes* except that the first spine is the modified element in *Rypticus*. The first dorsal-fin pterygiophore in *Rypticus* lacks supernumerary spines; thus, the first dorsal spine is serially associated with the first pterygiophore and homologous to the second dorsal spine of *Grammistes*, which has the first spine in supernumerary association with the first pterygiophore. The pectoral fin completes development before all other fins and is quite large and pigmented. The pelvic fin is last to form. Head spination and pigmentation are similar to that of *Grammistes*, except that *Rypticus* has three (vs. five) spines on the medial preopercular ridge.

Pseudogramma (Fig. 11B) has a produced second dorsal-fin spine. The elongate spine has been called the first by some authors, but the first (supernumerary) spine actually is exceedingly small and thus easily overlooked. As in *Grammistes* and *Rypticus* the pectoral fin is large and precocious, the pelvic fin is the last fin to complete development, the medial

Figure 11. A) Larva of *Rypticus* sp., 6.6 mm SL (from Kendall, 1979); B) Larva of *Pseudogramma gregoryi*, 10.2 mm SL (from Kendall, 1979); C) Anterior portion of larva of *Aporops* sp., 12 mm (from Fourmanoir, 1976).


A
B
C

preopercular ridge bears five spines and external pigment is limited to the pectoral fin and sheath surrounding the elongate dorsal spine.

Aporops (Fig. 11C) is very similar morphologically to *Pseudogramma.* Fourmanoir's (1976) illustration of the anterior portion of a larval *Aporops* shows the elongate body and tiny first dorsal-fin spine, thin elongate second dorsal spine, moderately large pectoral fin, incompletely formed pelvic fin and five spines on the preopercle.

Function of Elongate Fin Spines.-- The functional significance of elongate dorsal-fin spines in larval epinephelines is unknown. It seems likely that the robust pungent spines of the Niphonini and Epinephelini function to discourage potential predators, but the thin, flexible, filamentous spines of the other tribes may have different functions. In some ways, they resemble the elongate dorsal appendage (vexillum) of carapids. Govoni et al. (1984) analyzed in detail the vexillar structure and were unable to determine its explicit function. They suggested that it may have multiple functions, including predator deception (because the vexillum is pigmented and adorned with fleshy tabs), sensation (because it is innervated, although they found no free neuromasts, chemoreceptors or free nerve endings) and hydrodynamic effects (because of in situ observations of vexillar movement and the increased surface area it affords the larva). I have not examined the elongate filaments of epinephelines histologically, but it would be interesting to compare the microstructures of these appendages to the carapid vexillum. Below, I review some of the possible functions of the spectacularly elongate dorsal spines of larval epinephelines.

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

In summary, the adaptive significance of the elongate, filamentous dorsal spines of epinephelines is unknown, but the advantages these filaments convey to the larvae must outweigh the disadvantages, particularly the high cost, in terms of energy expenditure, of dragging the filaments through the water. Further study of the elongate filaments, including in situ observations and laboratory experiments, are necessary before a single, more definitive, functional explanation can be hypothesized.

CHAPTER 2

PHYLOGENY OF THE EPINEPHELINAE (TELEOSTEI: SERRANIDAE)

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, I 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 (1990) 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 I 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, I 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, I 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 my 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). For example, a state present in Niphon and cladistically primitive anthiines and serranines would be considered primitive for the remaining epinephelines, regardless of its absence in cladistically "more advanced" anthiines or serranines. 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.

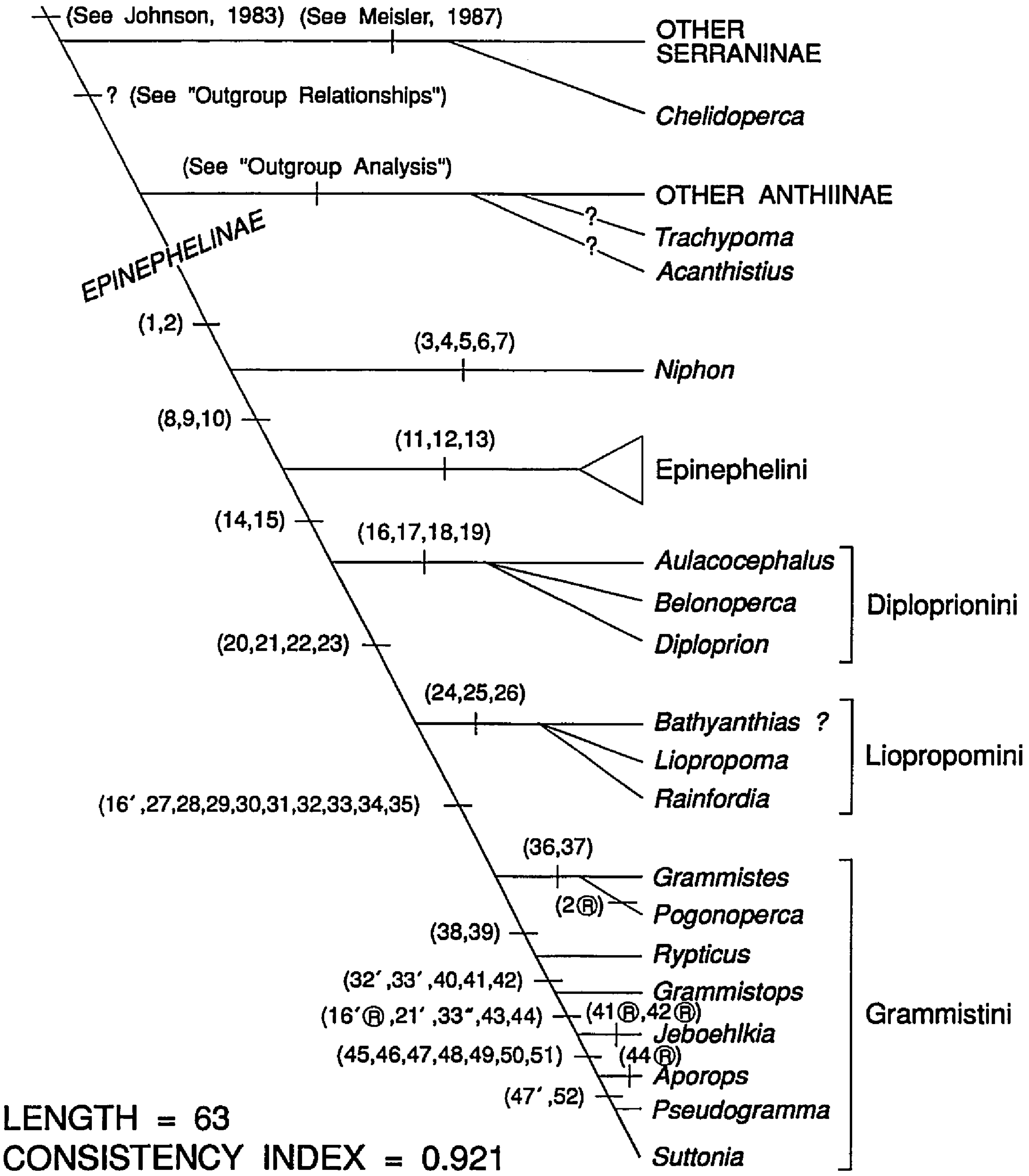
No similar hypothesis of generic relationships exists for the Anthiinae, although Roberts (1989) recognized two "groups" within the Anthiinae, one containing *Caesioperca*, *Caprodon*, *Ellerkeldia* (relegated to the synonymy of *Hypoplectrodes* by Anderson and Heemstra, 1989), *Lepidoperca*, *Plectranthias* 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 (1990a, 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 my 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 apparently 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 5), 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 12 (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

Table 5. Character matrix for the Epinephelinae. 0, primitive state; 1-3, derived states; 9, state unknown.

	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 12. 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.


(See Johnson, 1983)
(See Meisler, 1987)
OTHER SERRANINAE
Chelidoperca
? (See "Outgroup Relationships")
(See "Outgroup Analysis")
OTHER ANTHIINAE
?
Trachypoma
?
Acanthistius
EPINEPHELINAE
(1,2)
(3,4,5,6,7)
Niphon
(8,9,10)
(11,12,13)
Epinephelini
(14,15)
(16,17,18,19)
Aulacocephalus
Belonoperca
Diploprion
Diploprionini
(20,21,22,23)
(24,25,26)
Bathyanthias ?
Liopropoma
Rainfordia
Liopropomini
(16′,27,28,29,30,31,32,33,34,35)
(36,37)
Grammistes
(2Ⓡ)
Pogonoperca
(38,39)
Rypticus
(32′,33′,40,41,42)
Grammistops
(16′Ⓡ,21′,33″,43,44)
(41Ⓡ,42Ⓡ)
Jeboehlkia
(45,46,47,48,49,50,51)
(44Ⓡ)
Aporops
(47′,52)
Pseudogramma
Suttonia
Grammistini
LENGTH = 63
CONSISTENCY INDEX = 0.921

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, 1990; and the information in Chapter 1 (see Baldwin et al., 1991; Baldwin and Johnson, 1991).

Anthiine and serranine larvae examined are listed in Baldwin (1990). Larval and adult epinephelines (and other percoids) examined are listed in Appendix A.

Outgroup Relationships

Character Analysis.-- As noted above, relationships among the Anthiinae, Epinephelinae and Serraninae are unresolved. Below, I 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

Figure 13. 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.

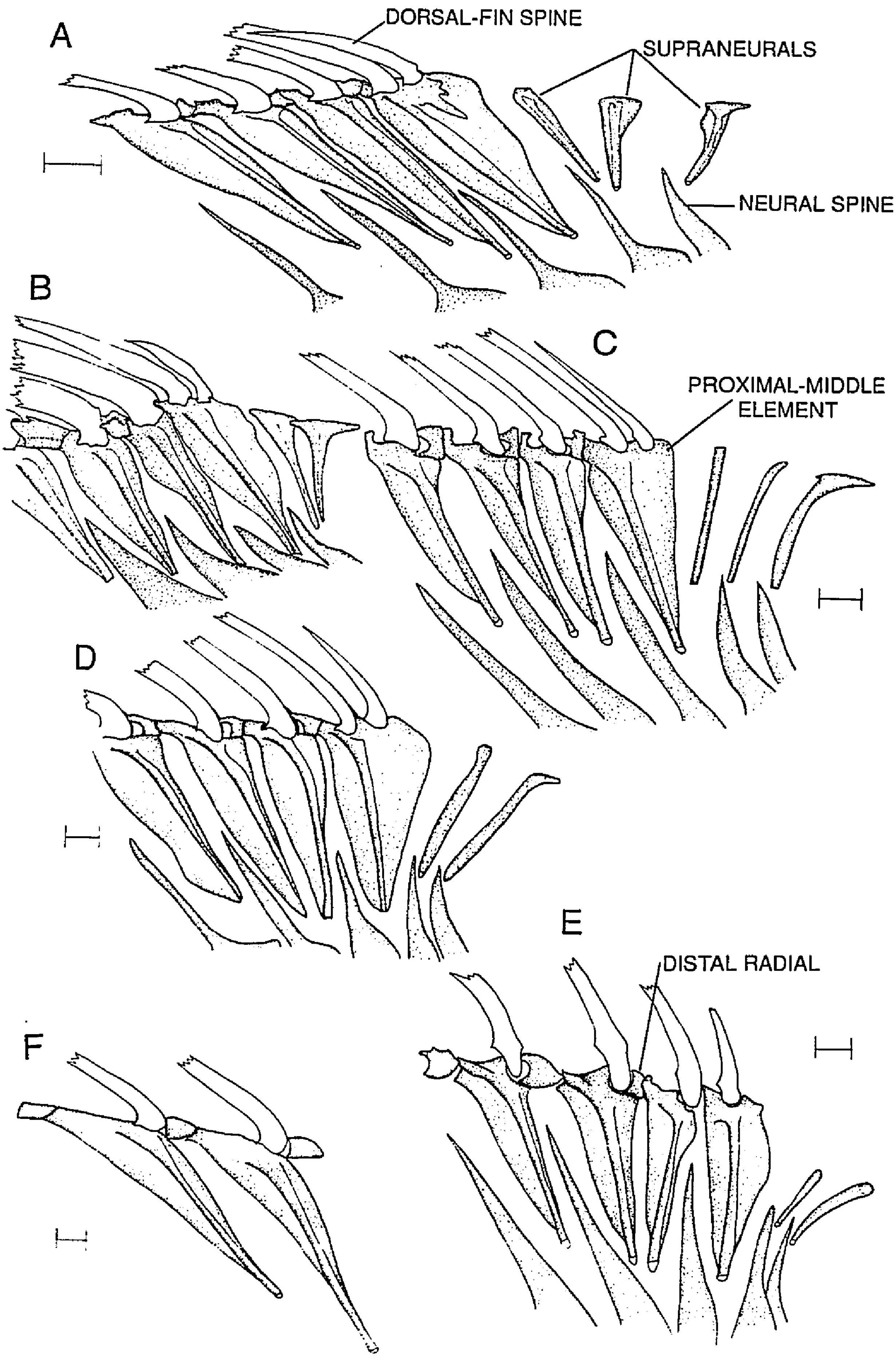
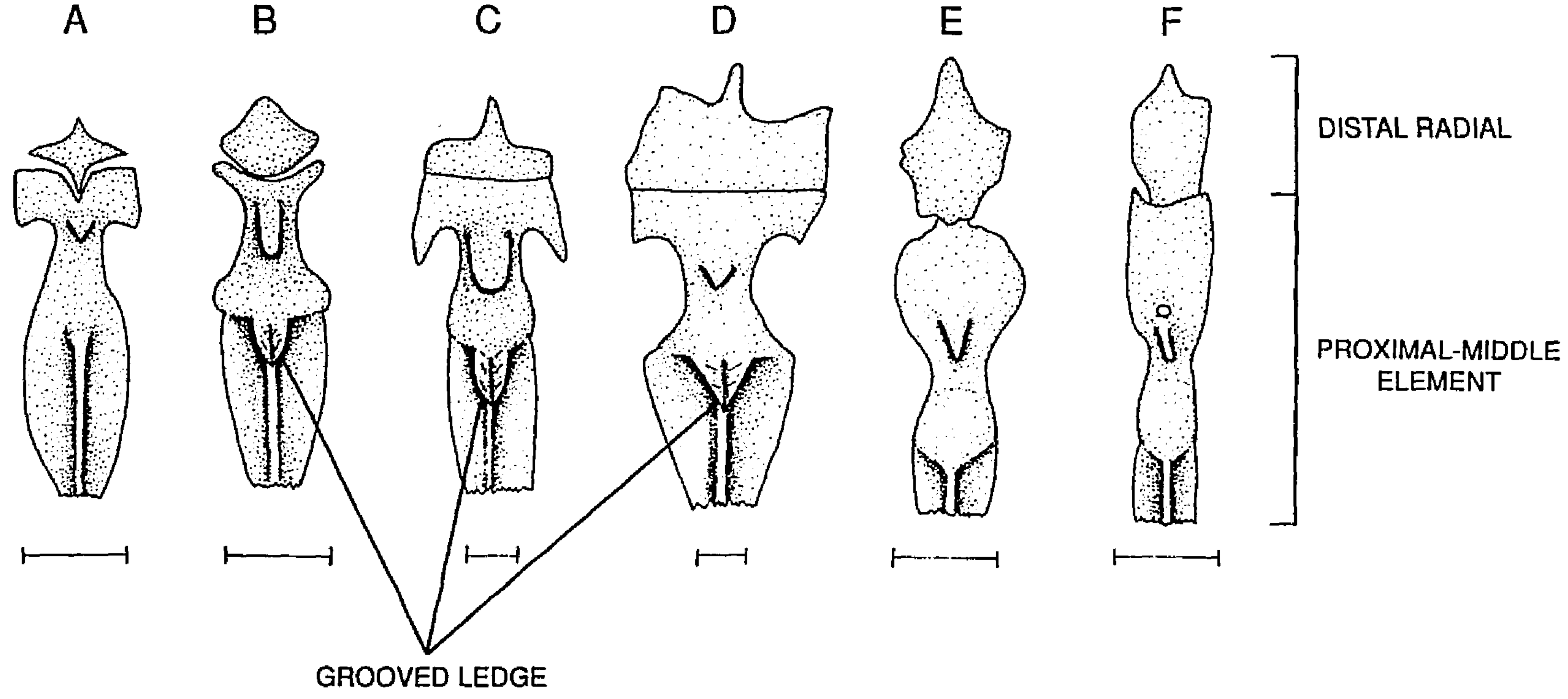

A
DORSAL-FIN SPINE
SUPRANEURALS
NEURAL SPINE
B
C
PROXIMAL-MIDDLE ELEMENT
D
E
DISTAL RADIAL
F

Figure 14. 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.


A
B
C
D
E
F
DISTAL RADIAL
PROXIMAL-MIDDLE ELEMENT
GROOVED LEDGE

proximal-middle pterygiophore (Figs. 13,14).-- 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. 13A,E). The distal radial is loosely connected to its serially associated (i.e., anterior) proximal-middle element, often resting in a groove (Fig. 14A) or on a ledge (Fig. 14E) of this element (although posteriorly, serially associated proximal-middle and distal elements are often widely separated, as in *Liopropoma* and *Aporops*, see character 21, Fig. 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. 13C,D; 14B,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. 13C,D; 14B,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. 13B, 14D).

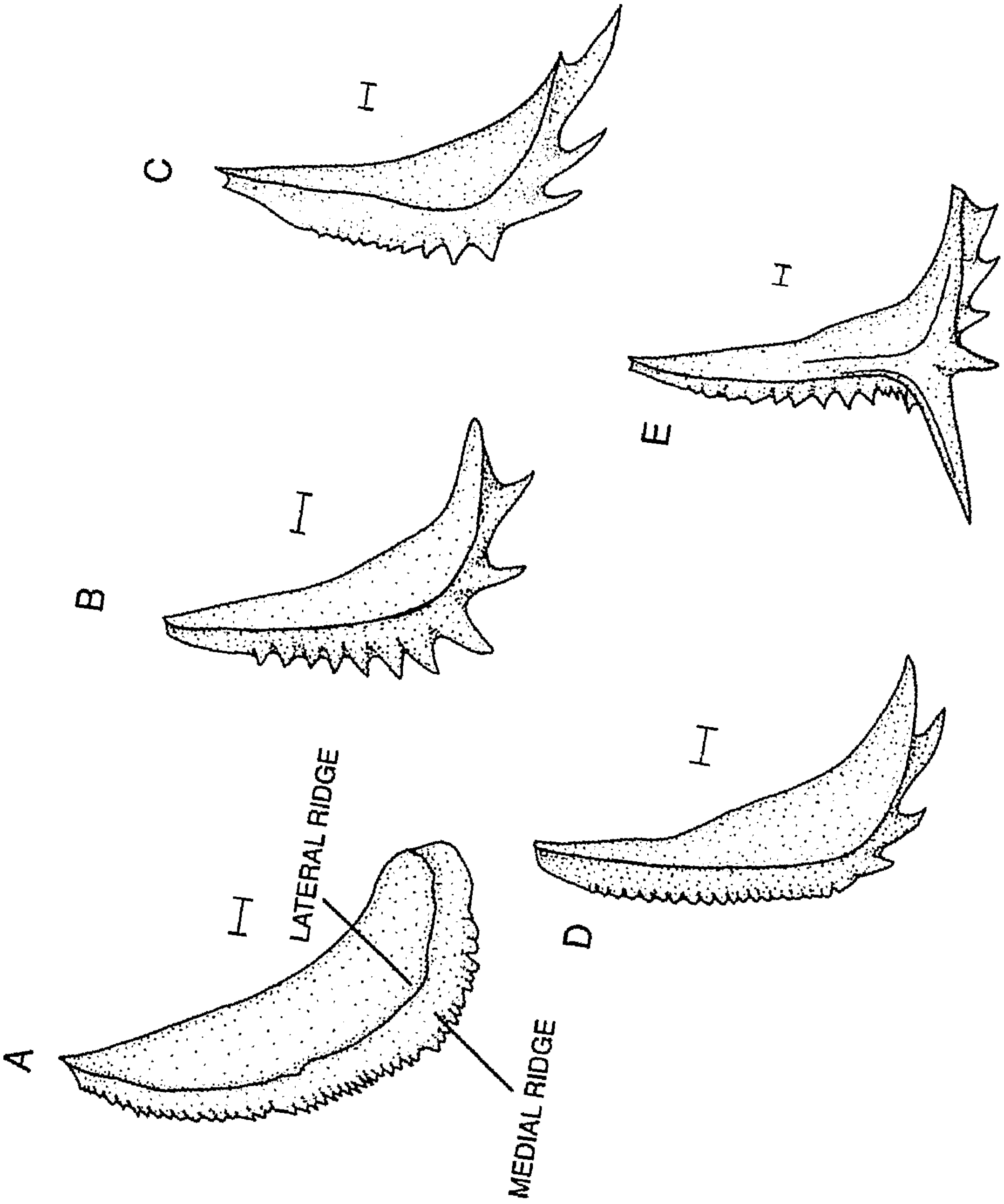
Meisler (1987) interpreted the condition observed in *Acanthistius* and anthiines as derived within the Serranidae, particularly because he observed no other percoid in which the distal radial rests posteriorly in a groove in the next proximal-middle element. I have seen a similar condition among percoids 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 percoids I examined, the distal radial is tightly bound to both its serially- and secondarily-associated proximal-middle elements (e.g., as in *Morone saxatilis*, Fig. 13F, 14F).

Even if one assumes 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. (One species of *Acanthistius*, *A. sebastoides*, usually has 12 -- W. D. Anderson, Jr., pers. comm.) Numbers of dorsal-fin spines vary widely among percoids, and in the absence of a sister-group hypothesis for the Serranidae, I am 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. 15).-- 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. 15E) and some epinephelins (e.g., *Plectropomus*, *Alphestes*), as well as the basal anthiines *Acanthistius* (Fig. 15B), *Trachypoma* (Fig. 15C), *Epinephelides*, *Hypoplectrodes* (Fig. 15D), *Othos* and some *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 my designation of genera as "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.

Figure 15. 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.


A
LATERAL RIDGE
MEDIAL RIDGE
B
C
D
E

Unlike the others, *Niphon* (Fig. 15E) has an elongate spine at the angle of the preopercle that I believe is autapomorphic. This spine (and the one immediately anterior to it) are lateral to the antrorse spines and appear to be extensions of the lateral preopercular ridge, whereas the antrorse spines of *Niphon* (Fig. 15E), *Plectropomus* and primitive anthiines (Fig. 15B-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 Serranidae is the polarity of this character equivocal. Lacking evidence to support that relationship, I tentatively 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.-- I am 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 I am 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 my 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.

My 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. 13A,C,D,F). In all epinephelines, the first dorsal-fin pterygiophore lacks a separate distal radial (Fig. 13B,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 supernumerary 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 I am unable to determine if the conditions in the two subfamilies should be considered homologous. 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 Anthiinae. 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 with the Epinephelinae, and accorded it tribal status on the basis of several characters, treated cladistically below, that I 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. 13A; *Acanthistius serratus*, 0/0/0+2/1+1/, Fig. 13C; *Pronotogrammus martinicensis*, 0/0/2/1+1/, Fig. 13D; and *Diploprion bifasciatus*, 0/0/1/1+1/, Fig. 13E). *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. 13B). 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 most species of *Acanthistius*, a genus usually considered a serranine but relegated to the Anthiinae by Heemstra and Randall (1986). Pending a resolution of relationships among serranid subfamilies, I 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 14-18 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, I 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. 15E) 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. 13A-D), whereas in all other epinephelines there is never more than one (Fig. 13E, also see Fig. 21).

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. 13A-D). In other epinephelines, the supraneurals are substantially shorter, and neither is typically expanded (Fig. 13E, also see Fig. 21).

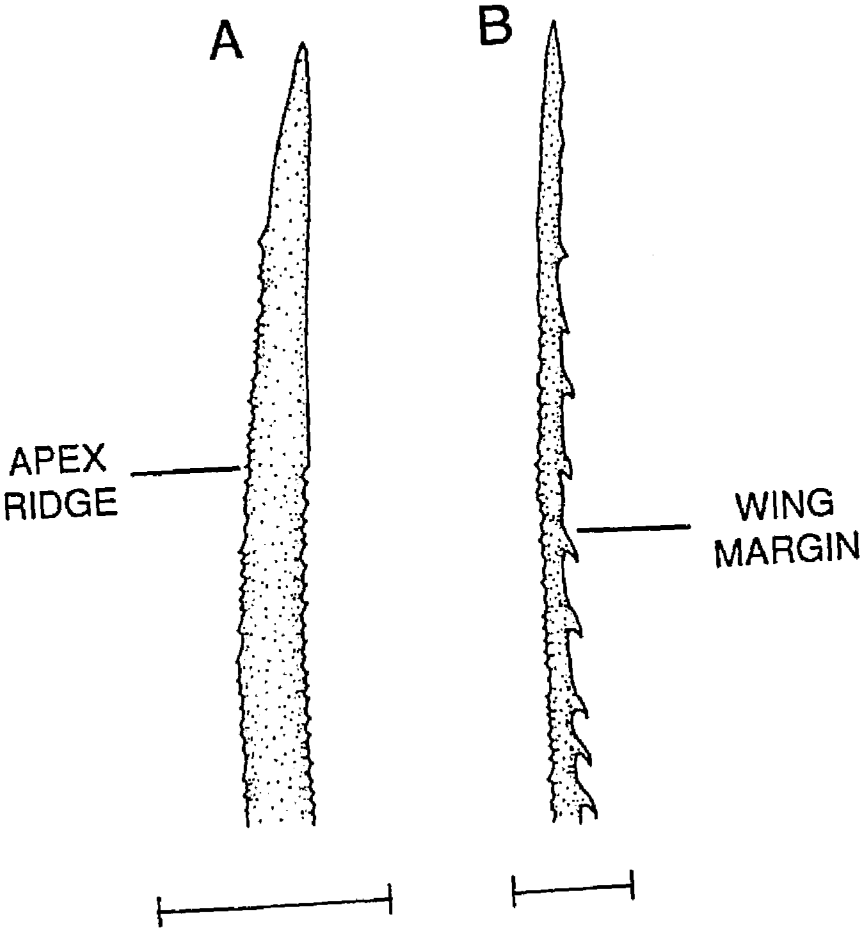
10. The spine serially associated with the first dorsal-fin pterygiophore is extremely elongate in larvae and encased in a fleshy sheath.-- In larvae of most other serranids, the spine serially associated with the first pterygiophore, though sometimes produced relative to other dorsal spines, is usually 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. 16).-- Serrate

Figure 16. 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.


A
B
APEX
RIDGE
WING
MARGIN

fin spines are lacking in larvae of serranines, most anthiines and all epinephelines except the Epinephelini. Baldwin (1990) 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 illustrated patterns of serrations on fin spines of American grouper larvae. 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. 16B). 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. 16A). 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. Differences 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 tribe 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 (see Leis, 1986). Leis (1986) noted that this migration does not occur in larvae of four species of *Plectropomus* examined by him, and I 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

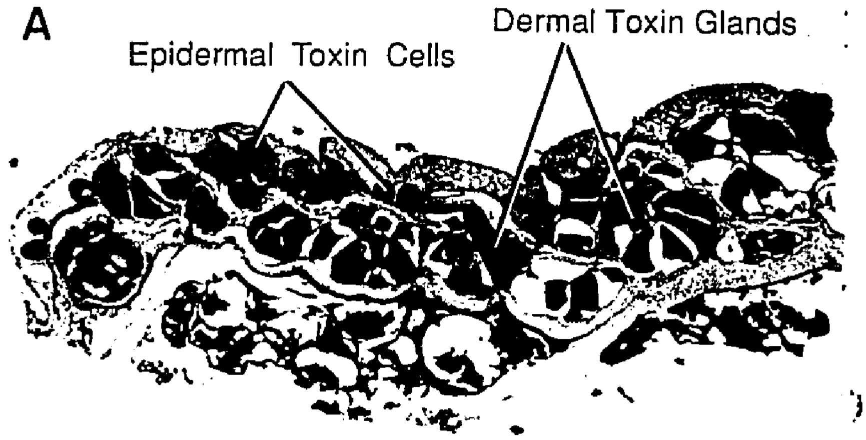
14. The elongate dorsal-fin spine(s) in larvae are filamentous.-- When present, elongate dorsal-fin spines in larvae of epinephelins, *Niphon* and anthiines are robust. In larval diploprionins, liopropomins and grammistins, elongate dorsal-fin spines are thin, flexible and sometimes encased in elaborately 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.

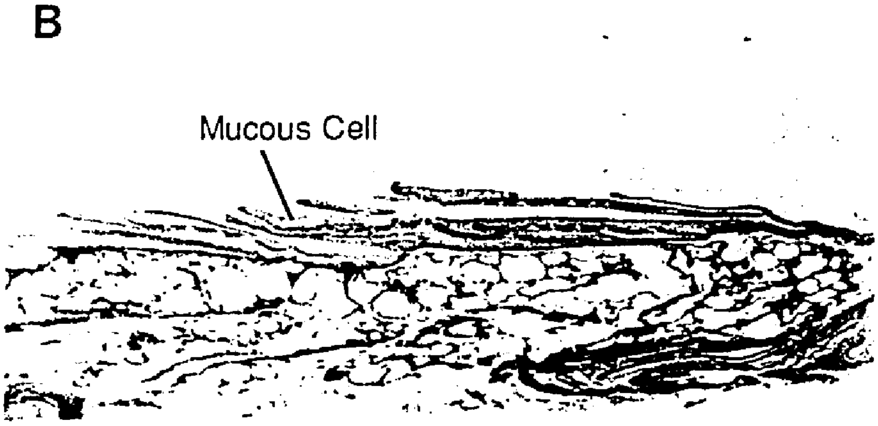
15. Larvae lack elongate spine at angle of preopercle.-- Serranines have poorly developed preopercular spination, but epinephelins, *Niphon* and anthiines have an elongate (often serrate) spine at the angle of the preopercle. Although preopercular spines in larval diploprionins, liopropomins and grammistins 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

Figure 17. 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*.


A
Epidermal Toxin Cells
Dermal Toxin Glands


B
Mucous Cell

Bean and *Diploprion* Cuvier to his tribe Diploprionini; those genera share the following derived features:

16. Epidermis with mucous cells that contain the skin toxin grammistin (Fig. 17).-- 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. 17A). This toxin is a hemolysin that is positive to Dragendorff reagent, negative to biuret and ninhydrin reagents, produces a positive (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. I 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. 17B). The presence of grammistin in the epidermis is a derived feature within the Epinephelinae; it is lacking in other 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 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. 17A). 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 me 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. I am 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. 18).-- 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. 18) have numerous small, semicircular, round or oblong concavities that impart a texture of rugosity.

18. Bases of dorsal and anal fins covered with ridges of tissue (Fig. 19).-- 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. 19).

19. First circulus of scales forms a bar that projects posteriorly along the midline and, in regenerated scales, functions as the first ctenus (Fig. 20).-- 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. My 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

Figure 18. 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 = 1mm.

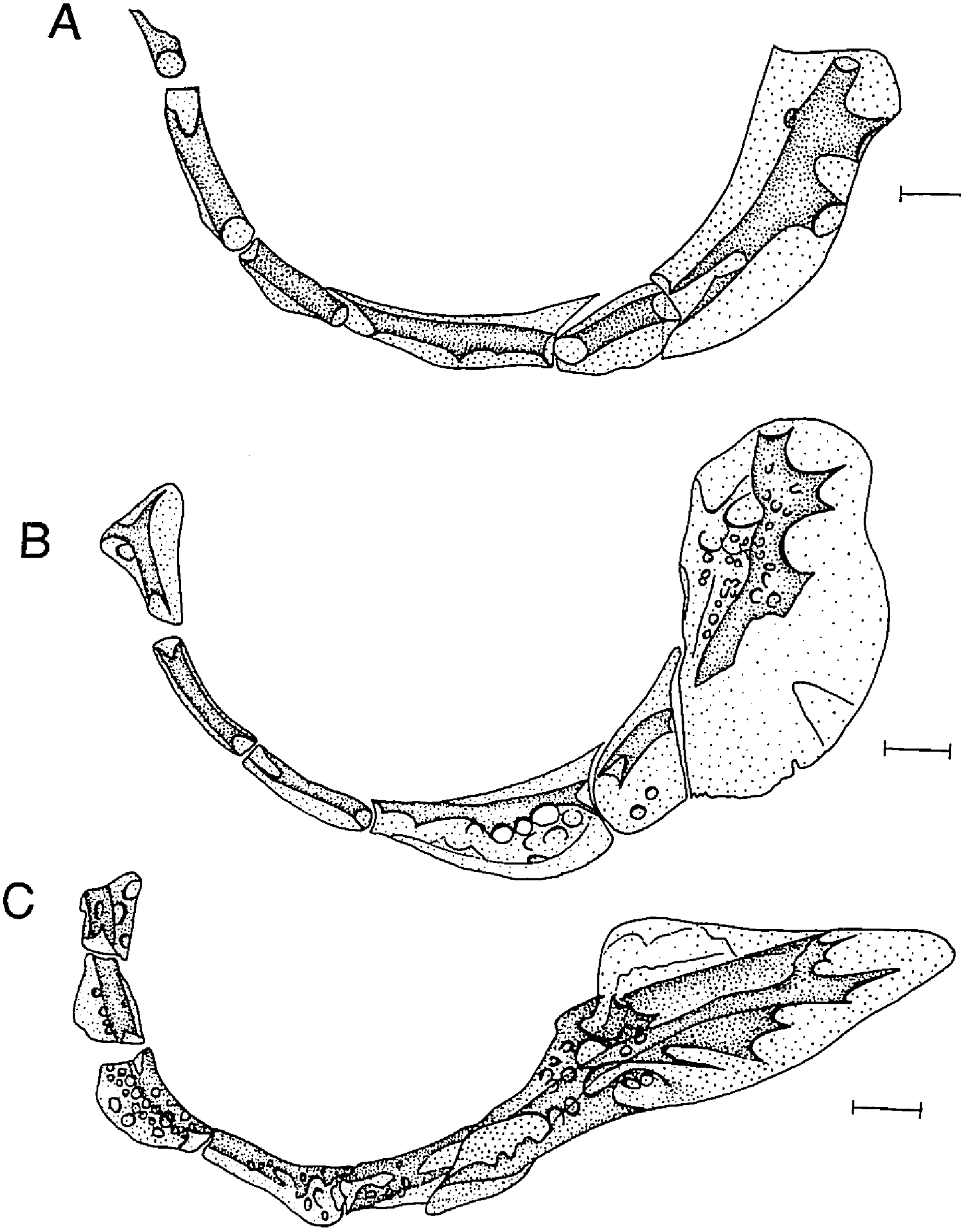
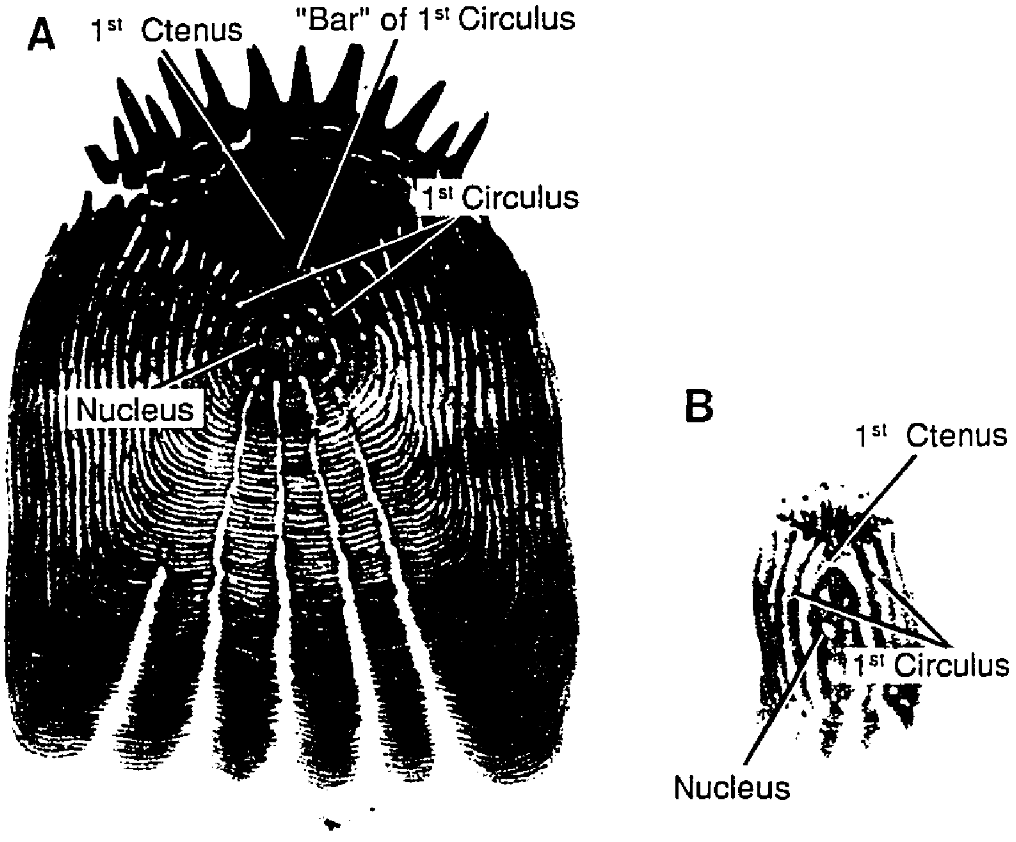

A
B
C

Figure 19. Skin at base of spinous dorsal fin in *Diploprion bifasciatus*, USNM 183096, 209 mm SL.


RIDGE OF
MODIFIED TISSUE

Figure 20. Photomicrographs of scales. A) *Belonoperca chabanaudi*, USNM 217813, 67.5 mm SL; B) *Acanthistius serratus*, AMS I. 19602004, 67.0 mm SL.


A
1st Ctenus
"Bar" of 1st Circulus
1st Circulus
Nucleus
B
1st Ctenus
1st Circulus
Nucleus

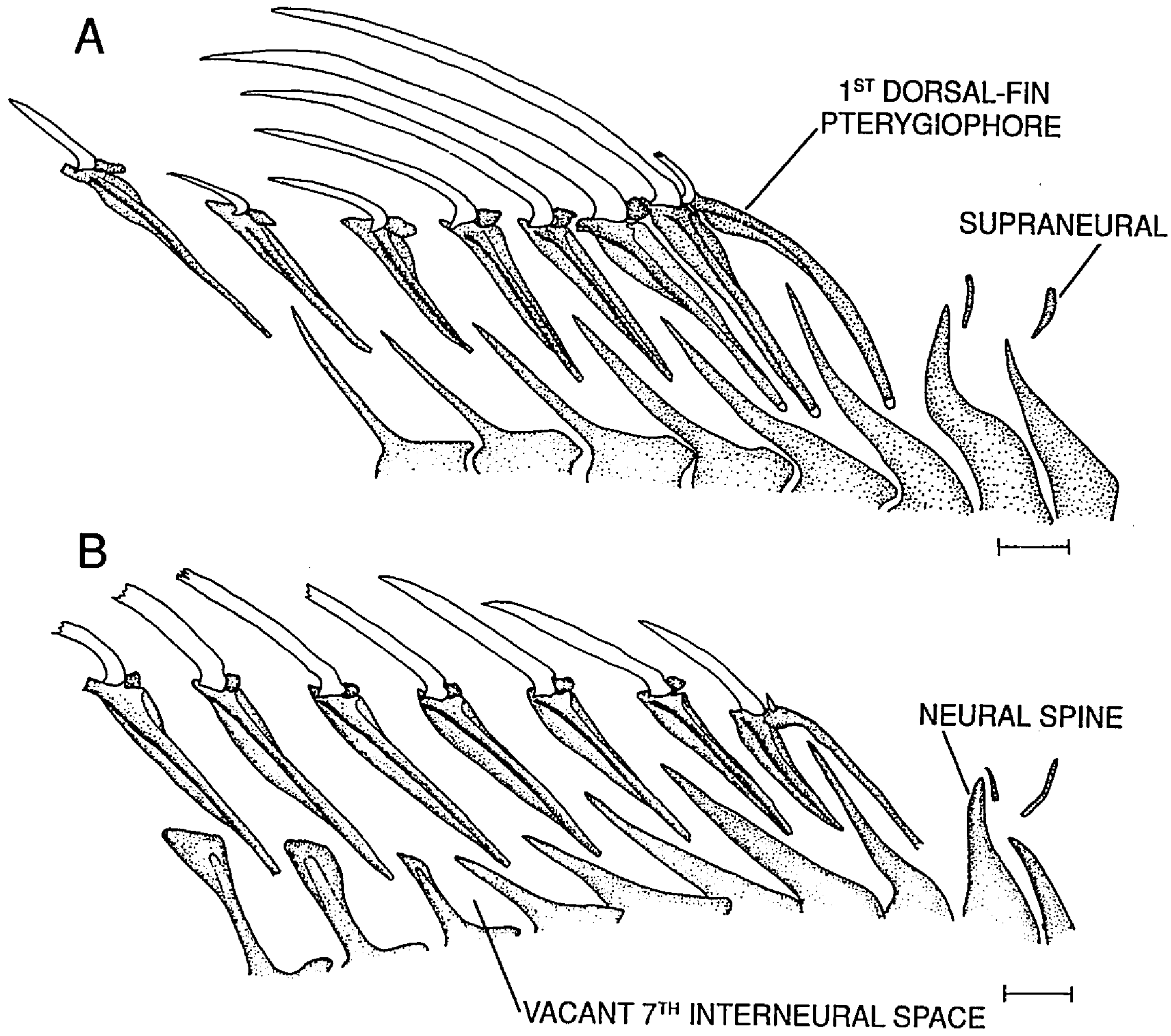
unique morphology of the first circulus described by McCully (Fig. 20A), but that *Acanthistius* does not. In most serranids, the first circulus either is closed posteriorly and has no bar originating from it (see Fig. 20A,B), or it is open posteriorly such that the two free ends abut the posterior edge of the scale plate (Fig. 20B; also see Figs. 24, 30C-E). I have not examined scales of all species of *Acanthistius*, but those of *A. cinctus* and *A. serratus* (Fig. 20B) 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, I agree that the presence of a bar projecting from the first circulus (and functioning as the first ctenus, or "scalelet" of McCully, 1961, in regenerated scales) is a derived feature within the Serranidae, but believe it diagnoses a tribe that includes *Aulacocephalus*, *Belonoperca* and *Diploprion* and excludes *Acanthistius*.

Liopropomini + Grammistini

Despite the apparent absence of the ichthyotoxin 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. <u>First dorsal-fin pterygiophore thin and curved</u> (Fig. 21).-- In other epinephelines and the outgroups, the first dorsal-fin pterygiophore has well-developed laminar flanges along its length (see Fig. 13). 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. 13). In *Liopropoma* (Fig. 21A), *Rainfordia* and the grammistins (e.g., *Aporops*, Fig. 21B), 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.

Figure 21. 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.


A
1ST DORSAL-FIN PTERYGIOPHORE
SUPRANEURAL
B
NEURAL SPINE
VACANT 7TH INTERNEURAL SPACE

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. 21).-- The serially associated proximal-middle and distal elements of the anteriormost dorsal-fin pterygiophores in most serranids are very closely associated (Figs. 13, 21A). 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. 21A) and grammistins (e.g., *Aporops*, Fig. 21B), however, the distal radials of at least the third through last pterygiophore become widely separated from their serially associated proximal-middle element. 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 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.

My 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 I note the possibility that *P. mexicana* Schultz, 1958 is a junior synonym of *B. roseus* Günther, 1880. For purposes of this paper, I 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 mm SL, and noted that it greatly resembles *Liopropoma*. Johnson (1983) included *Jeboehlkia* in his

Liopropomini, but did not examine the holotype. My examinations of the holotype of *J. gladifer* (USNM 201422), a cleared and stained adult specimen and the single known larval specimen (see 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. 22).-- In most other epinephelines, serranids and percoids, the posteroventral portion of the maxilla lacks projections, although some anthiines and epinephelins have a maxillary projection. *Jeboehlkia* and *Pseudogramma* have a very small, almost ventrally directed maxillary process (Fig. 22B) that bears little resemblance to the large, anteriorly directed, hook-like process of *Liopropoma* (Fig. 22A) and *Rainfordia* (Fig. 22C). 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. 22D). 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. 23).-- In most percoids, the subocular shelf is a thin flange of bone that extends medially from the third infraorbital (Fig. 23A). This shelf may extend anteriorly and posteriorly over the second and fourth infraorbitals, but those bones do not bear separate 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. 23B). *Rainfordia* has separate shelves extending from each of the second through sixth infraorbitals (Fig. 23C). Meisler (1987) noted the presence 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. I am aware of no other features indicative of a close relationship between those serranines and liopropomins and consider the states in the two

Figure 22. 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.

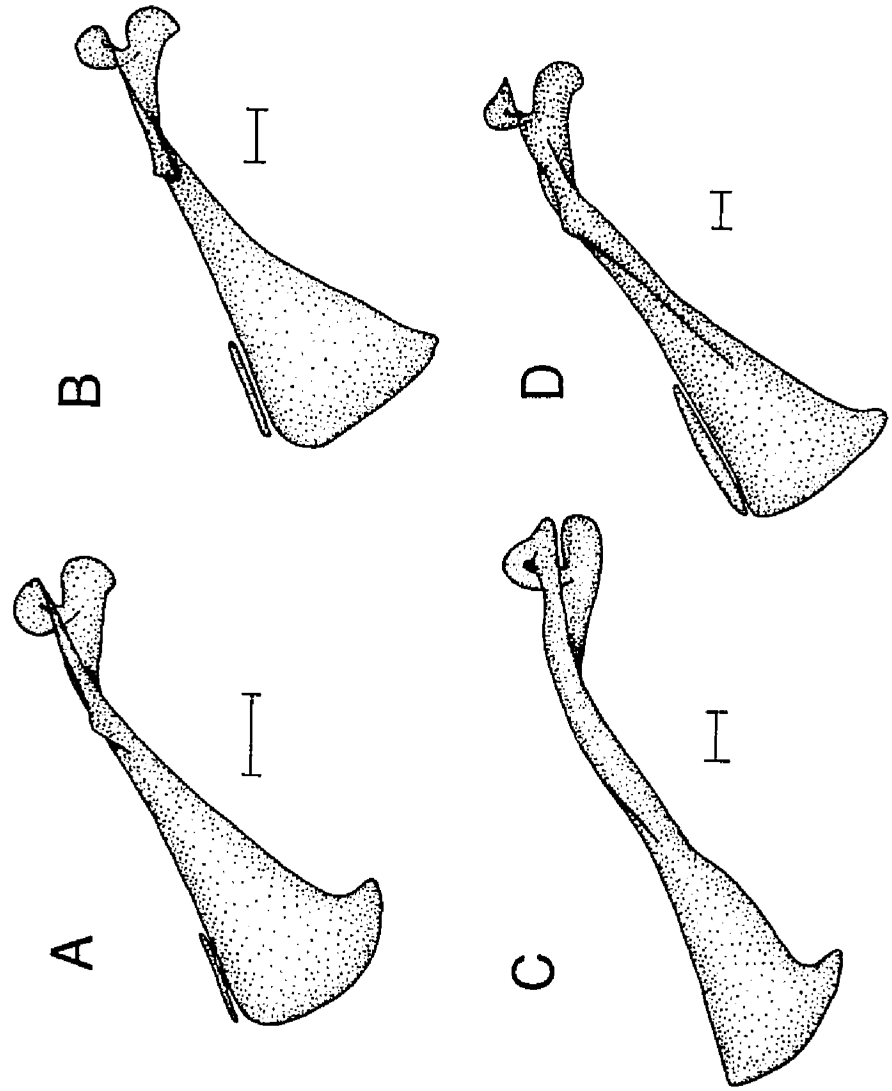
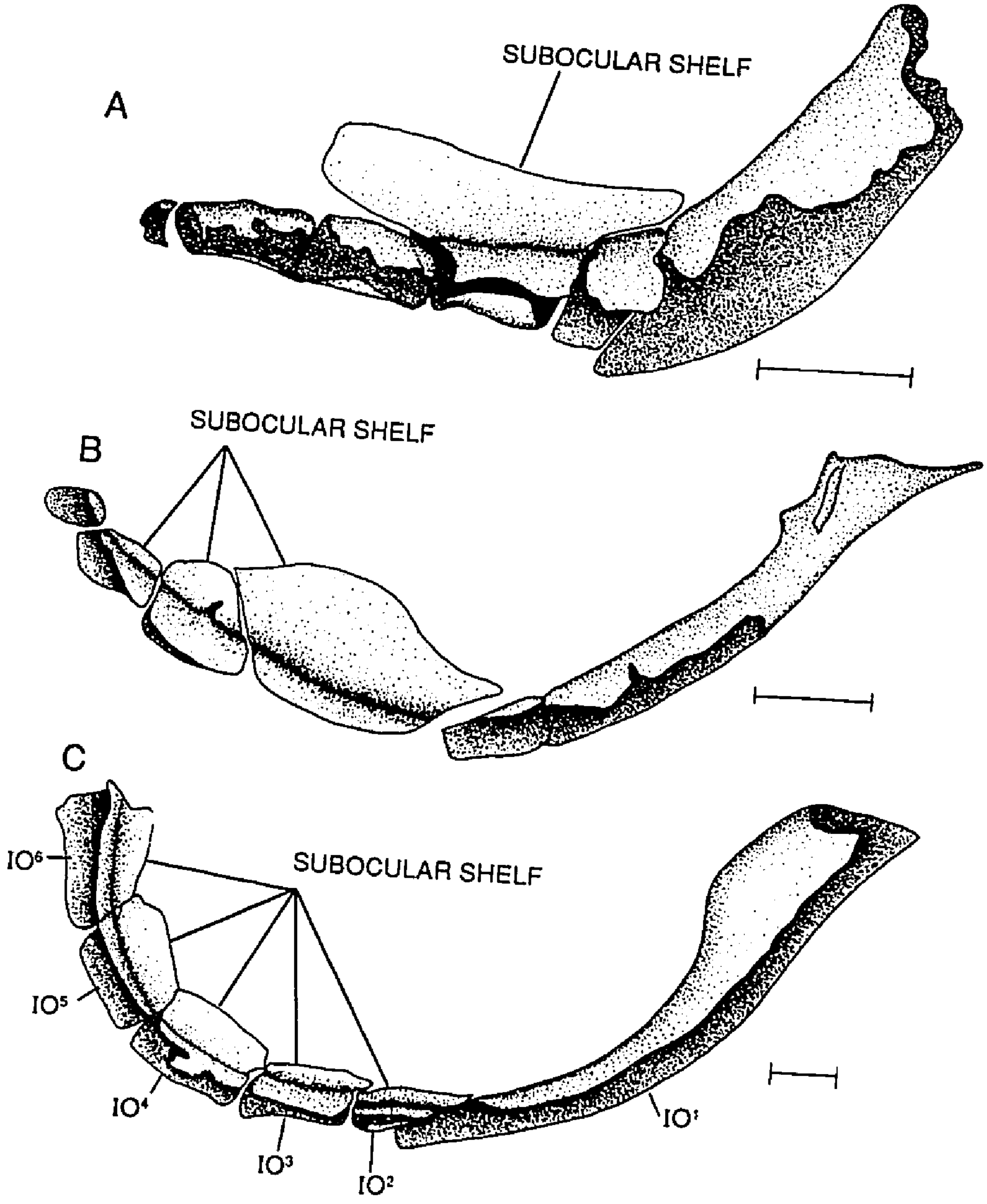

A
B
C
D

Figure 23. 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.


A
SUBOCULAR SHELF
B
SUBOCULAR SHELF
C
IO^6
SUBOCULAR SHELF
IO^5
IO^4
IO^3
IO^2
IO^1

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. 24).-- 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 (also see 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. 24). My attempts to document this fusion developmentally were unsuccessful, however, because cteni already are "fused" to circuli in the smallest larvae (15-17 mm SL) on which I could find scales.

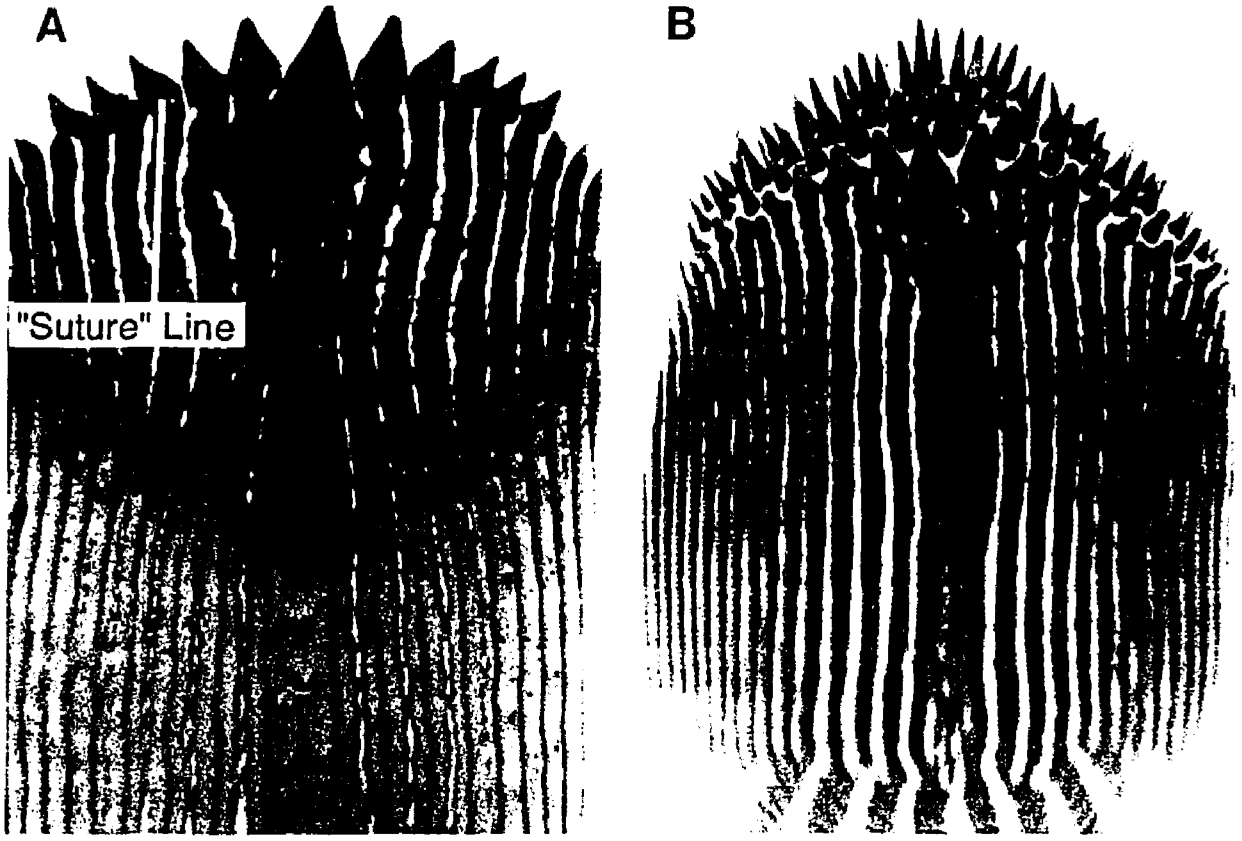
Despite the differences that exist among liopropomins in morphology of scales (those of *Rainfordia* bear only a single row of cteni, Fig. 24A; those of *Liopropoma* (Fig. 24B), *Pikea mexicana* and *P. cubensis* have more than one row but differ from one another substantially in size) the presence of cteni that are continuous with ends of circuli is a unique feature that infers 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

Figure 24. Photomicrograph of liopropomin scales. A) *Rainfordia opercularis*, USNM 203247, 98.0 mm SL; B) *Liopropoma carmabi*, USNM 198283, 43.5 mm SL.


A
"Suture" Line
B

(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 ichthyotoxin grammistin.-- Randall et al. (1971) described large, dermal toxin-secreting glands in *Grammistes*, *Grammistops* (see Fig. 17A), *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.

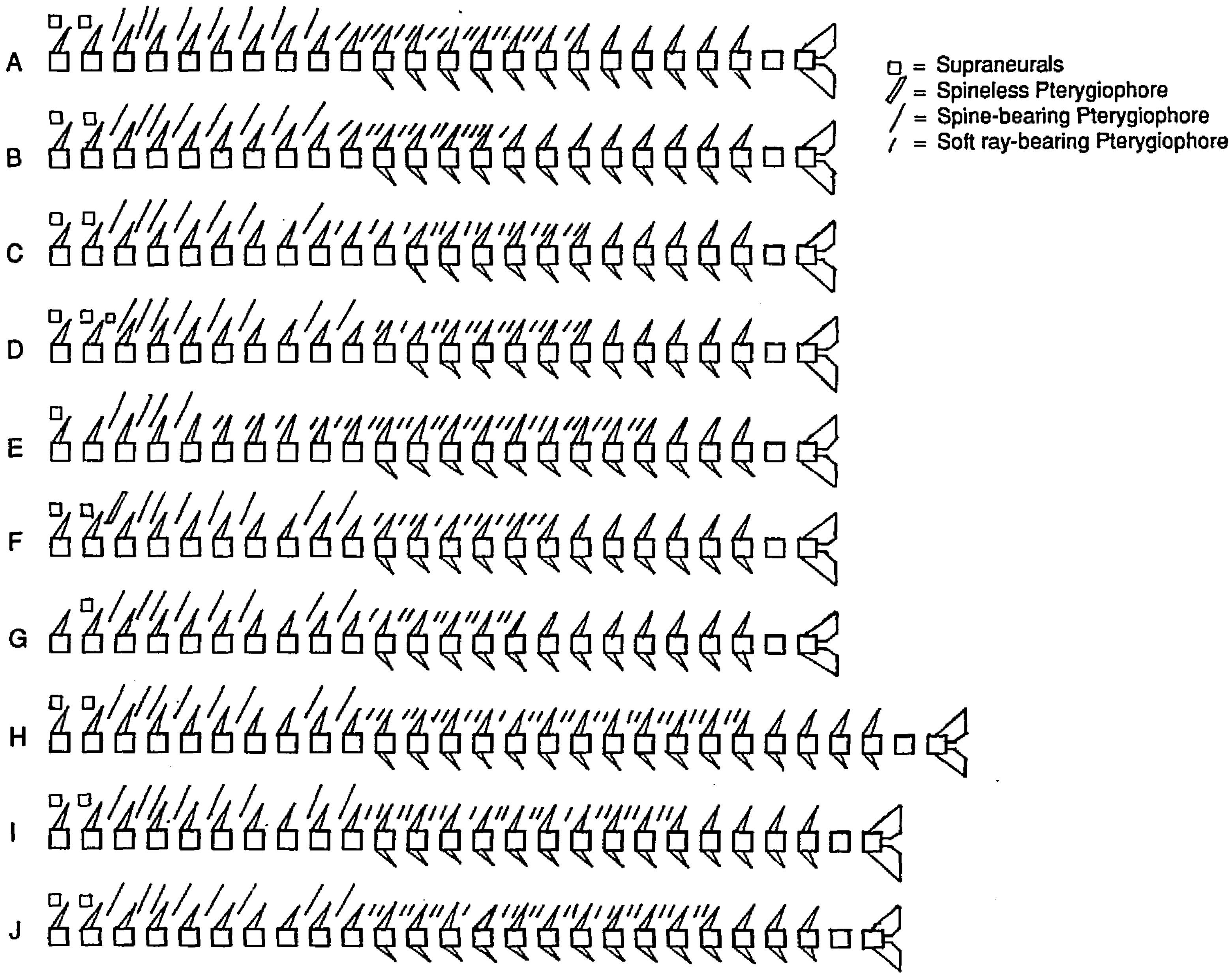
27. Procurrent caudal-fin rays fewer than 10.-- Serranines, anthiines and other epinephelines have 10 or more (most have 13-28) total procurrent caudal-fin rays, whereas grammistins have six to nine.

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 many 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 bifasciatus*). 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*). I consider the high number of dorsal trisegmental pterygiophores in grammistins to be a derived condition within the Epinephelinae.

29. Seventh interneural space vacant (Figs. 21, 25).-- In other epinephelines, serranines and anthiines, a pterygiophore supernumerarily supporting a dorsal-fin spine inserts into the seventh interneural space (as in *Liopropoma*, Fig. 21A). In grammistins (e.g., *Aporops*, Fig. 21B) 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 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), I 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. 25A,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. 25C-J). Although loss of the seventh pterygiophore (and spine) in *Diploprion* and *Liopropoma* (Fig. 25A,B) yields the condition observed in *Grammistes* (seven dorsal-fin spines, none supported by pterygiophores in the seventh and ninth interneural spaces, Fig. 25C), this hypothesis requires that a new pterygiophore (and spine) form in the ninth interneural space in other grammistins. Insertion

Figure 25. 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*.


A
B
C
D
E
F
G
H
I
J
□ = Supraneurals
= Spineless Pterygiophore
= Spine-bearing Pterygiophore
= Soft ray-bearing Pterygiophore

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. 25D). None of the scenarios described above can explain the condition in *Rypticus* (Fig. 25E), wherein there are only three or four spines.

In grammistins, but not other epinephelines, the sixth and seventh neural spines are greatly inclined posteriorly (Fig. 21B). 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. 26).-- 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. 26A). 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. My 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. 26B).

31. Second anal-fin pterygiophore straight, not bending posteriorly (Fig. 27).-- In other serranids, the proximal-middle radial of the second anal-fin pterygiophore is straight proximally and bends posteriorly near the distal extremity (Fig. 27A,B). In the Grammistini, the second anal-fin pterygiophore is straight throughout its entire length (Fig. 27C-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. 28).-- Adults of other epinephelines and the outgroups

Figure 26. Nasal organ (overlying tissues removed). A) *Epinephelus guttatus*, VIMS/CBL 3692, 65.0 mm SL; B) *Grammistops ocellatus*, USNM 260562, 73.0 mm SL. Scale bar = 1mm.

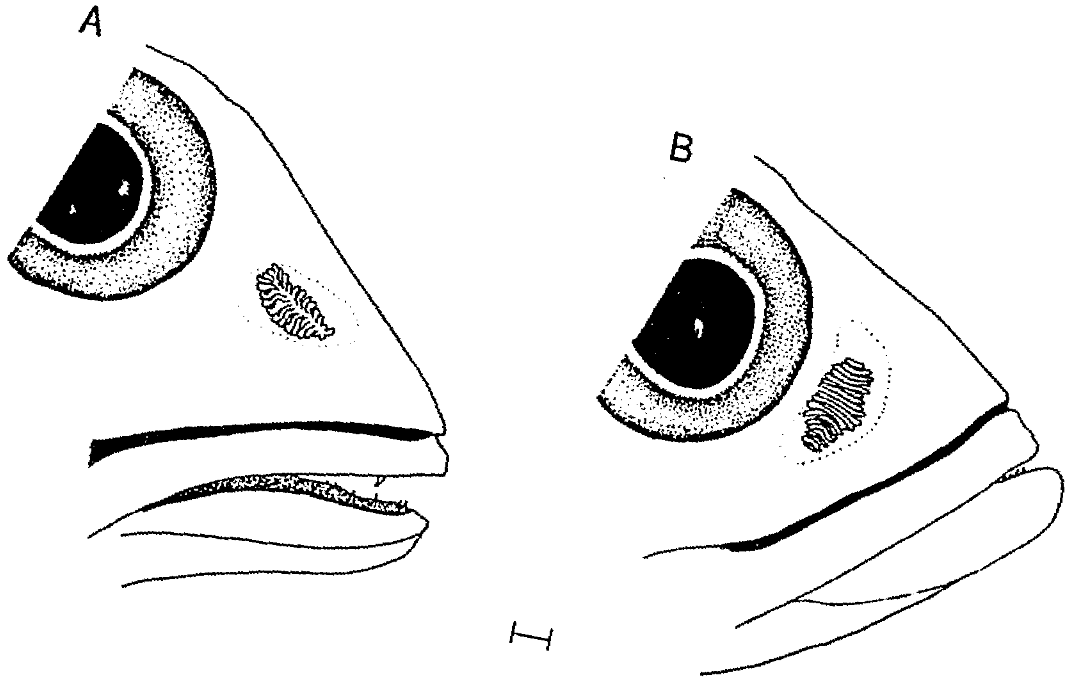

A
B

Figure 27. 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.

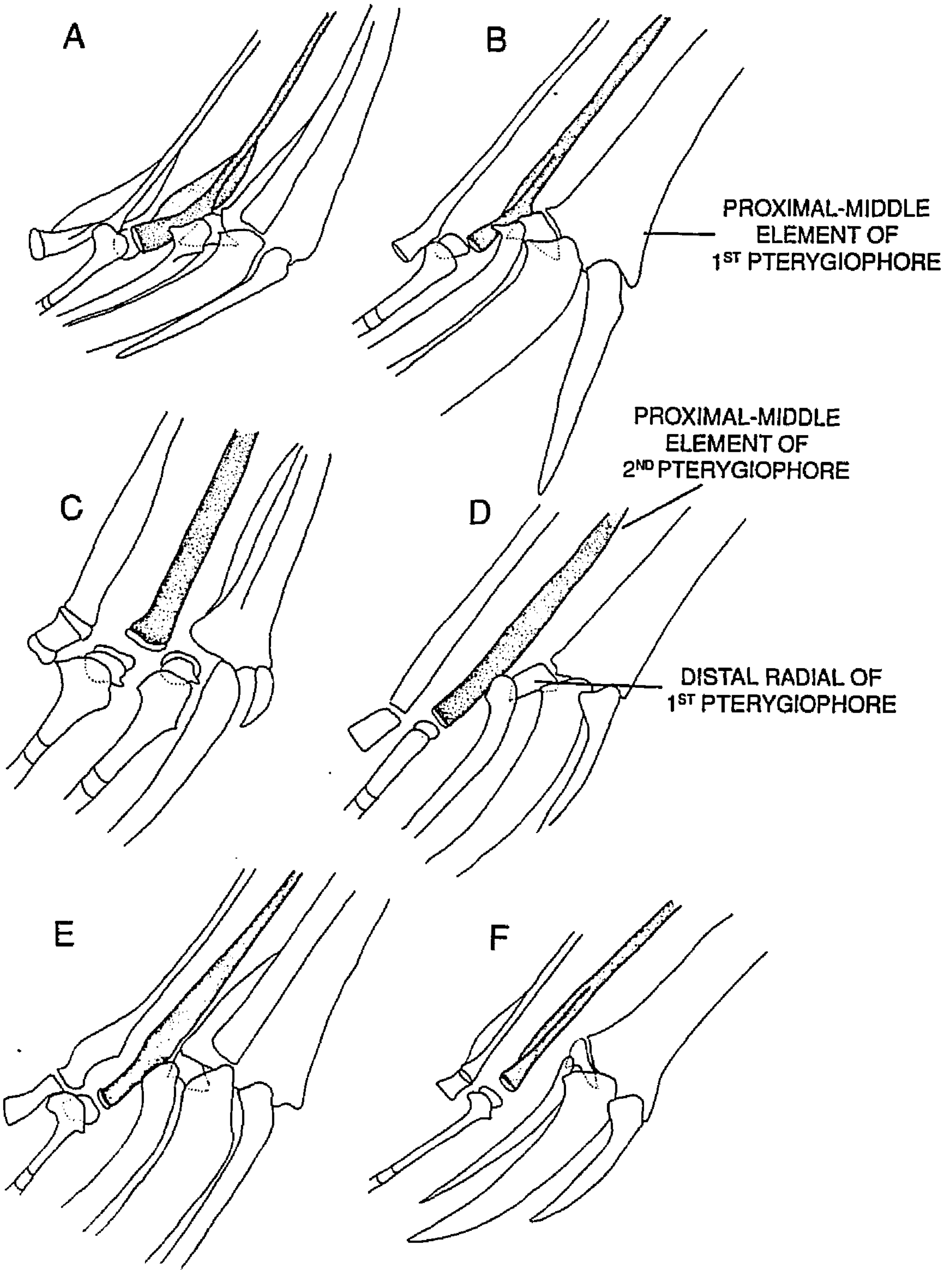
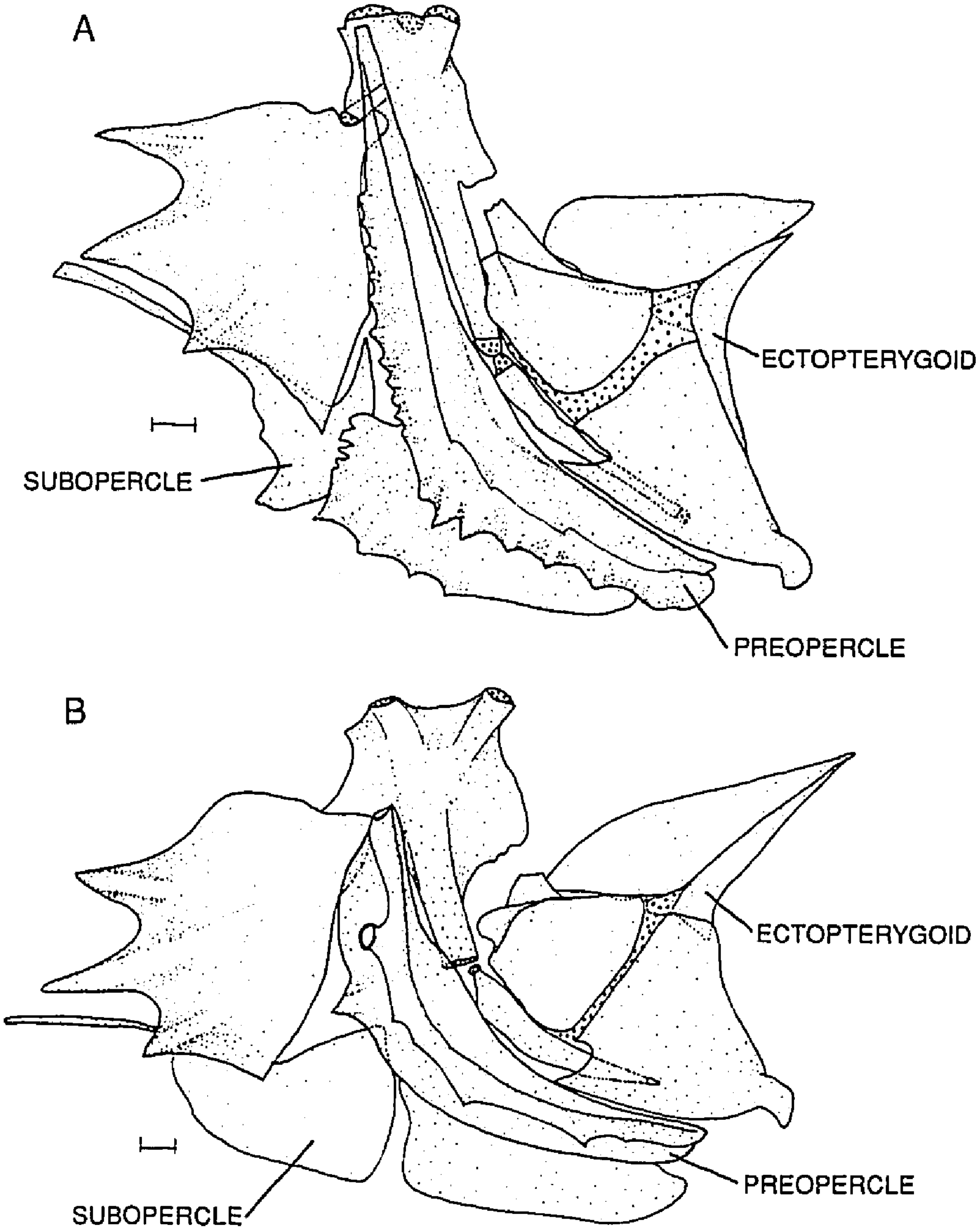

A
B
PROXIMAL-MIDDLE ELEMENT OF 1ST PTERYGIOPHORE
C
PROXIMAL-MIDDLE ELEMENT OF 2ND PTERYGIOPHORE
D
DISTAL RADIAL OF 1ST PTERYGIOPHORE
E
F

Figure 28. 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.

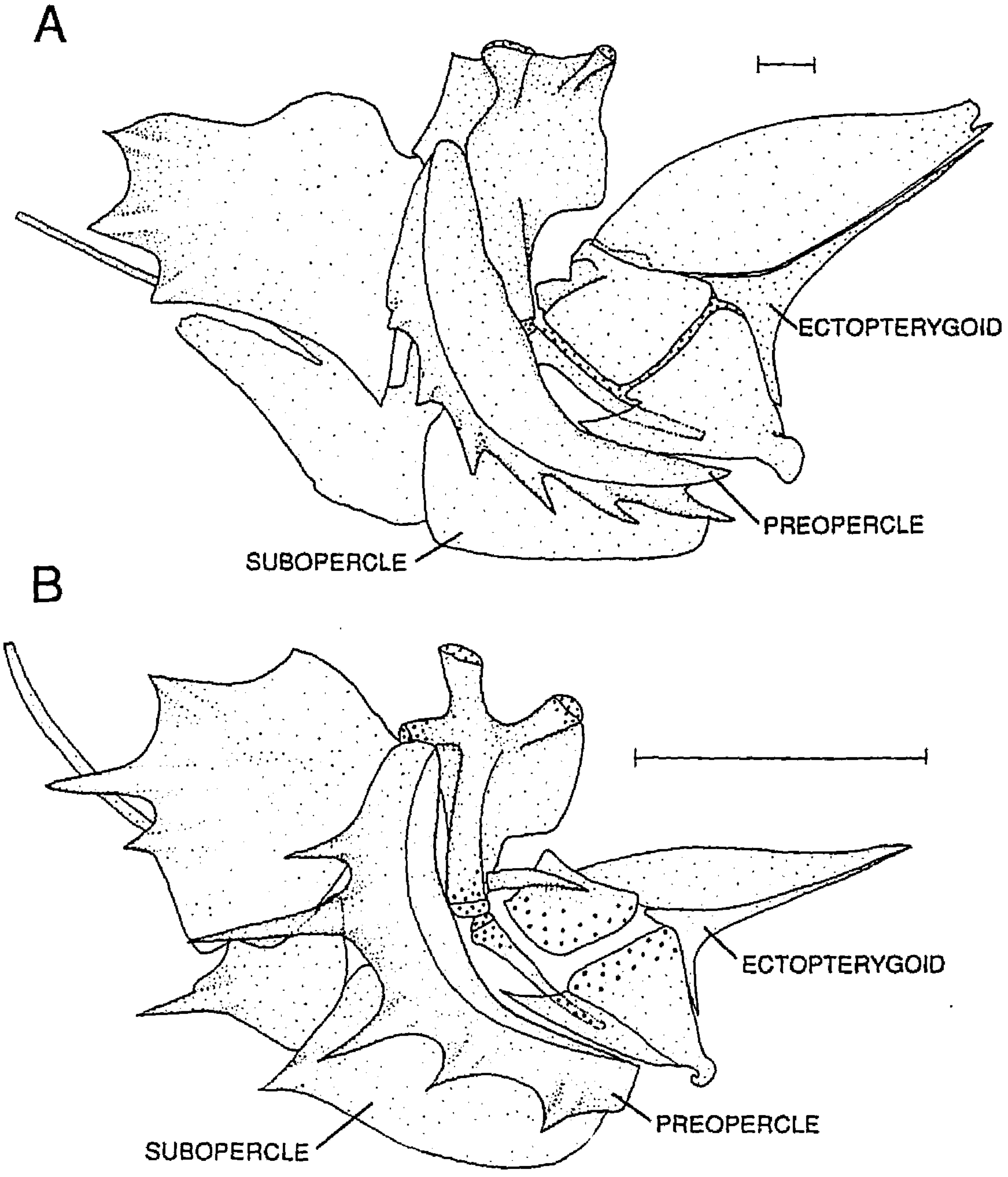

A
ECTOPTERYGOID
SUBOPERCLE
PREOPERCLE
B
ECTOPTERYGOID
PREOPERCLE
SUBOPERCLE

typically have numerous spines or serrations on the posterior margin of the preopercle (Figs. 4, 28A). Among grammistins, fewer spines (two or three in *Grammistes*, *Pogonoperca* and *Rypticus*, one in *Grammistops* and *Pseudogramma* and its relatives -- Fig. 28B, also see Fig. 34) 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. 29A). Considering the distribution of other characters, it 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 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. My 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. 29B). 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. 28B). In *Jeboehlkia*, however, larval spines apparently are never resorbed. A complete ontogenetic sequence is

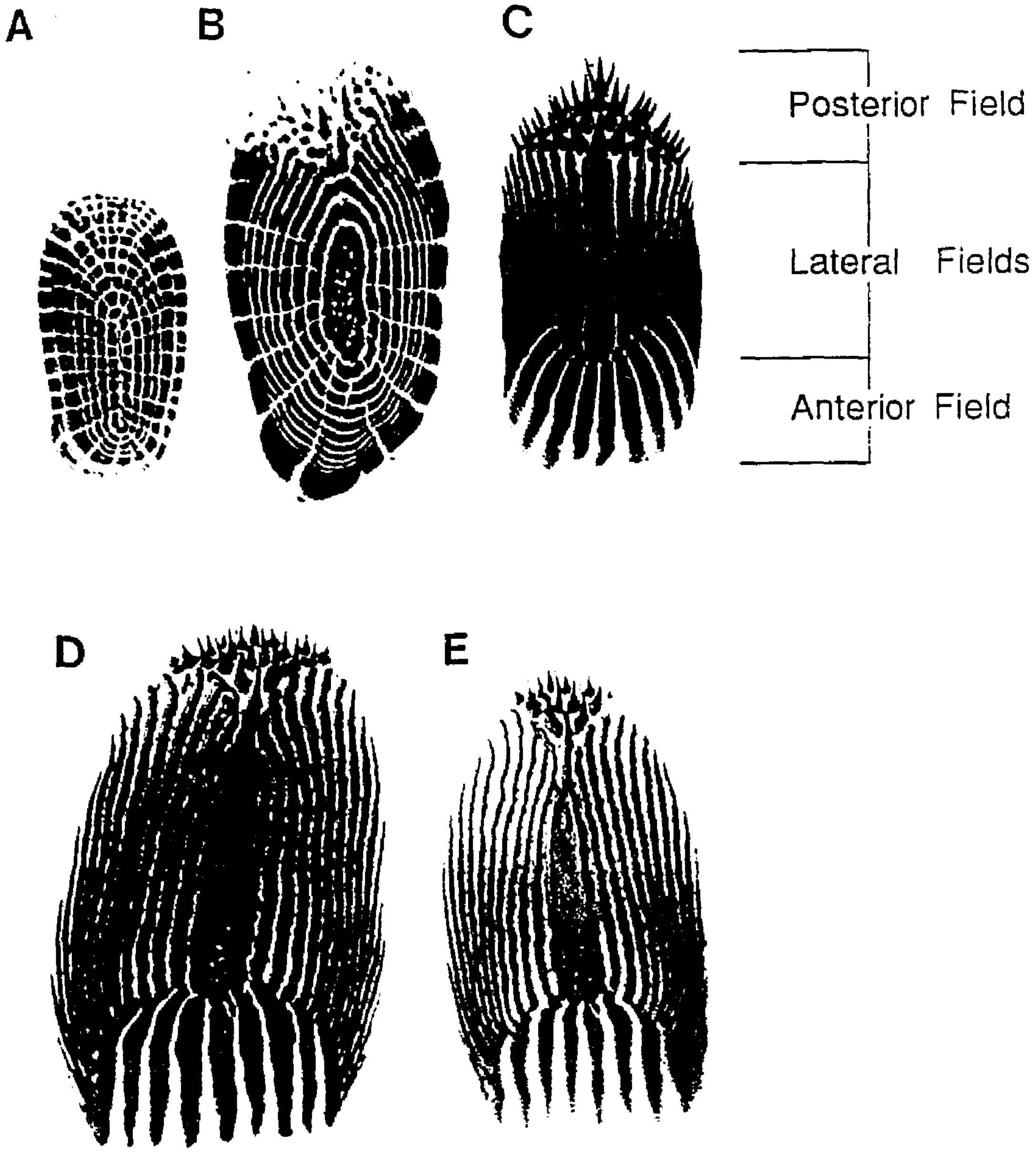
Figure 29. Suspensorium, right side. A) *Jeboehlkia gladifer*, Indian River Coastal Zone Museum 107:7433, 55.0 mm SL; B) *Pseudogramma gregoryi*, MCZ 79302, 10.8 mm SL.


A
ECTOPTERYGOID
PREOPERCLE
SUBOPERCLE
B
ECTOPTERYGOID
PREOPERCLE
SUBOPERCLE

needed to confirm this, but the preopercular spines in adult *Jeboehlkia* (Fig. 29A) 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 I suspect that a high number of preopercular spines in adult *Jeboehlkia* is due to paedomorphosis, I do not know what the adult complement of spines would be if truncation were not involved; accordingly, in the character matrix (Table 5), character 32 for *Jeboehlkia* is coded as missing. This reduces the length of the tree by one step (removes a reversal) 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. 28A).

33. Scales without cteni and with radii in all fields (Fig. 30).-- Scales of most serranids are ctenoid and have radii only in the anterior field (see Fig. 20). *Grammistes* (Fig. 30A), *Pogonoperca* and *Rypticus* have cycloid scales with radii in all fields. The scales of *Grammistops* (Fig. 30B) 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

Figure 30. 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.


A
B
C
Posterior Field
Lateral Fields
Anterior Field
D
E

intermediate between the cycloid scales of *Grammistes, Pogonoperca* and *Rypticus* (Fig. 30A) and scales of *Jeboehlkia, Aporops, Pseudogramma* and *Suttonia* (Fig. 30C-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 5) becomes the ctenoid scale of *Pseudogramma* and relatives ("1" in Table 5) by adding 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 ontogenetically 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 (see Baldwin, 1990: 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 5. Polarity for the Grammistini was established using liopropomins and diploprionins as the first and second outgroups, respectively.

Grammistes + *Pogonoperca*

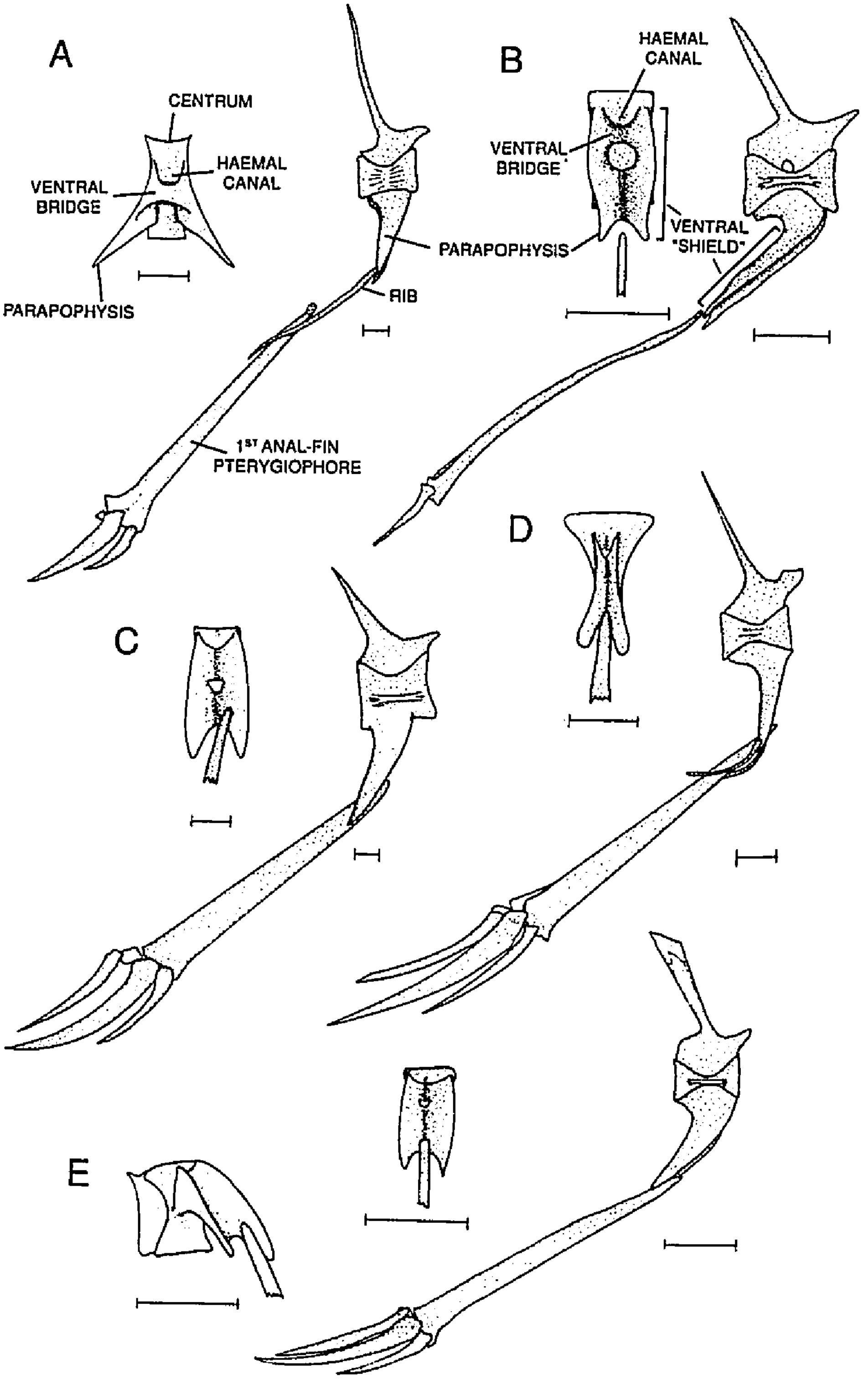
36. Precaudal vertebrae 11.-- The number of caudal vertebrae varies considerably among serranids, but the presence of 10 precaudal vertebrae is a conservative feature within the family. *Grammistes* and *Pogonoperca* share the derived condition of 11 precaudal vertebrae, found elsewhere among serranids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

Figure 31. 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 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.


A
CENTRUM
HAEMAL CANAL
VENTRAL BRIDGE
PARAPOPHYSIS
RIB
1ST ANAL-FIN PTERYGIOPHORE
B
HAEMAL CANAL
VENTRAL BRIDGE
PARAPOPHYSIS
VENTRAL "SHIELD"
C
D
E

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. 21.

39. Parapophyses of last precaudal vertebra fuse posteriorly and then bifurcate ventrally (Fig. 31)- 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. 31A). 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. 31B-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 cteni (Fig. 30).-- 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 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. 31).-- 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 bifasciatus*, Fig. 31A). 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. 31C-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. 28B). 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 I 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. 28).-- 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. 28A). Additionally, the ectopterygoid usually bends ventrally to run along the anterior margin of the quadrate (Fig. 28A). 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. 28B). 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.

Larvae of *Grammistops* are unknown, but in larval *Pseudogramma* (Fig. 29B), 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. 29A).

A similar scenario could explain the presence of a well-developed dorsal subopercular limb in adult *Jeboehlkia* (Fig. 29A), 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. 28B).

Although I suspect that paedomorphosis may be responsible for long ectopterygoid and subopercular limbs in adult *Jeboehlkia*, I do not code those characters (40, 41) for *Jeboehlkia* as "missing," as I did in the case of the preopercular spines (character 32). This is because I 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 my 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 me 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. 21A). In *Jeboehlkia* and the pseudogrammid genera (e.g., *Aporops*, Fig. 21B), 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. 30).-- 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. 30C-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. 30).-- A single row of cteni on the posterior margin of the scale occurs in some anthiines and in the liopropomin, *Rainfordia* (see Fig. 24A). 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. 20) 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. 30C-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 26-28 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. 21A). In *Aporops*, *Pseudogramma* and *Suttonia*, the eighth through tenth neural spines are expanded distally such that each resembles an upright oar (see Fig. 21B).

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. 32).-- Epaxial musculature terminates anteriorly in most serranids on the supraoccipital crest, well posterior to the interorbital region (Fig. 32A). In the "pseudogrammid" genera, the epaxial musculature covers the supraoccipital dorsally and extends anteriorly to the interorbital region of the frontals (Fig. 32B).

49. Uppermost pectoral-fin ray reduced to an articular base (Fig. 33).-- 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. 33A). In the "pseudogrammids," all that remains of the uppermost pectoral-fin ray is a modified base, which articulates with the scapula anteriorly, and rests posteriorly in the branched base of the next pectoral-fin ray (Fig. 33B). 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. 33C), a small first pectoral-fin ray is nested within the lateral and medial hemitrichs of the base of the second pectoral 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

Figure 32. 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.

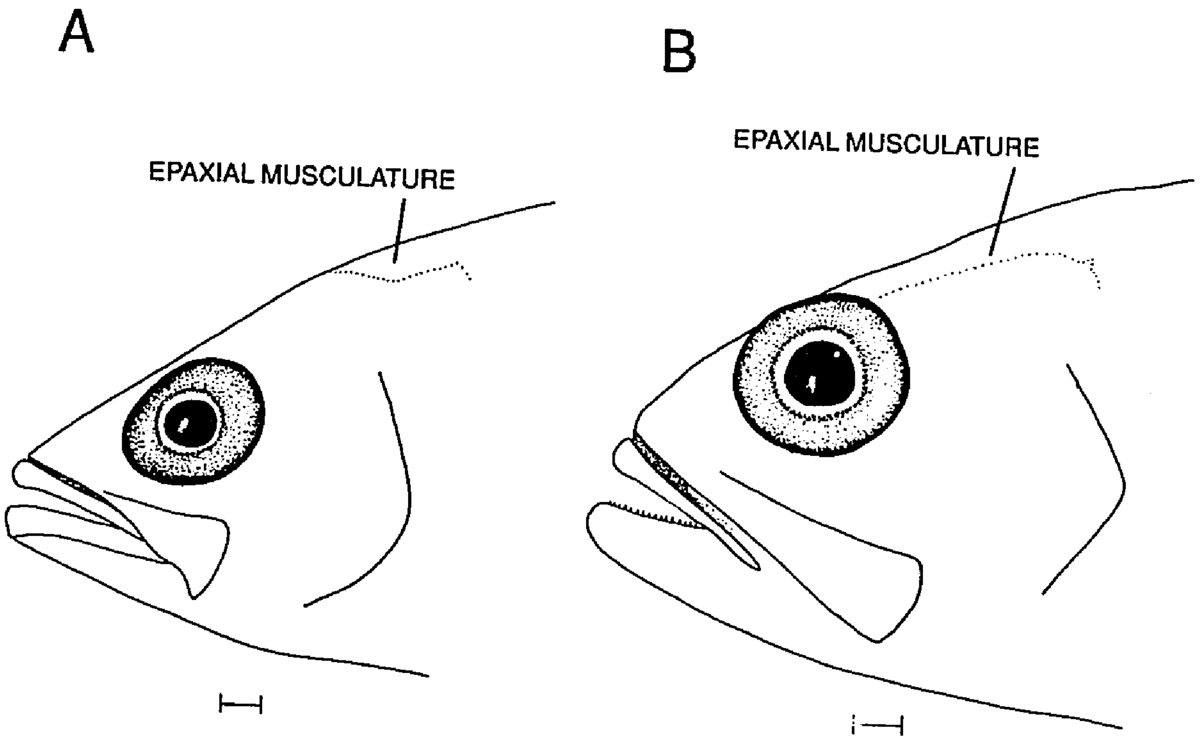

A
EPAXIAL MUSCULATURE
B
EPAXIAL MUSCULATURE

Figure 33. Dorsal portion of pectoral-fin skeleton, right side. First pectoral-fin ray heavily stippled, cartilage lightly stippled. A) *Diploprion bifasciatus*, USNM 218889, 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.

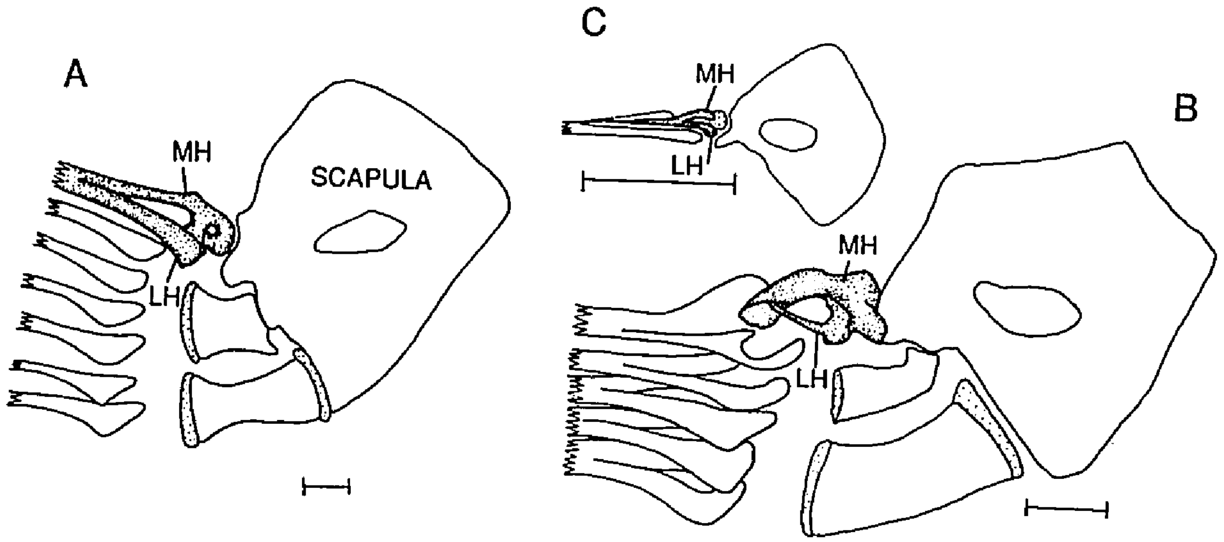
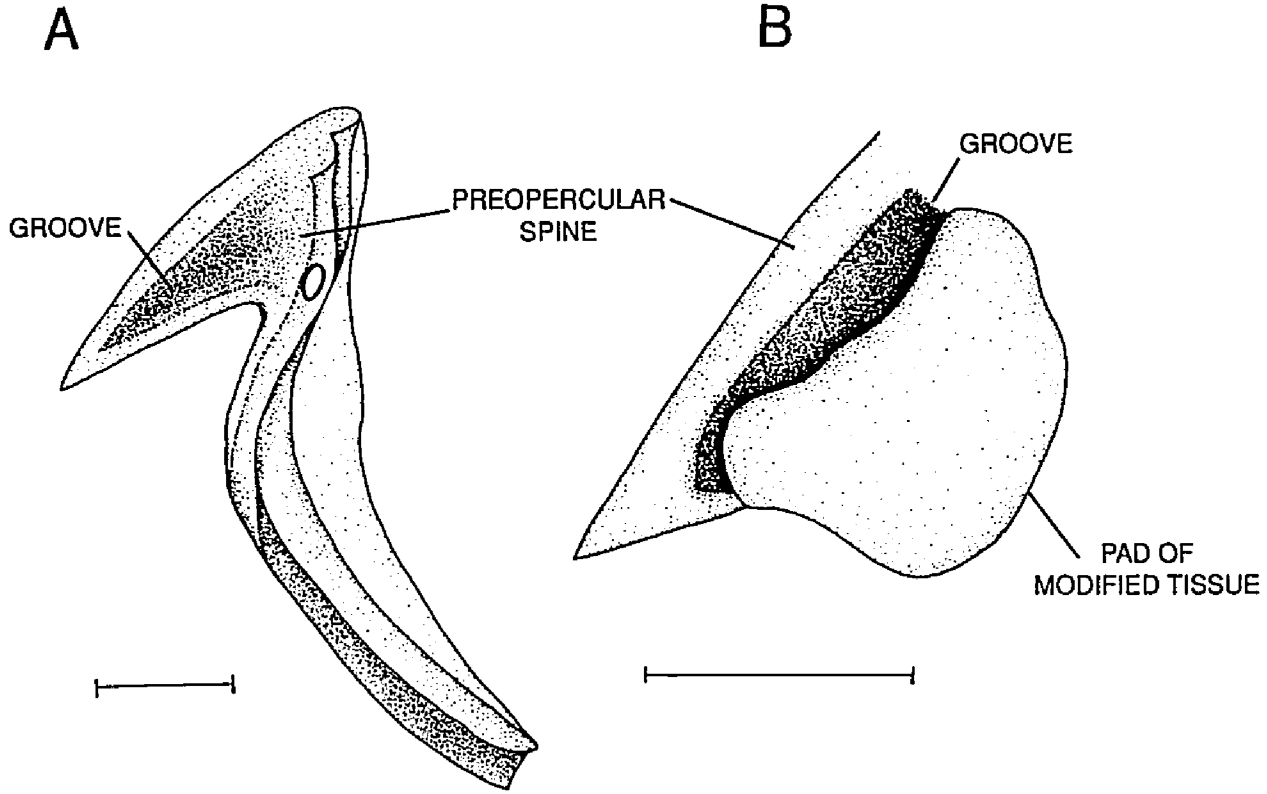

A
MH
SCAPULA
LH
C
MH
LH
B
MH
LH

Figure 34. 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.


A
B
GROOVE
PREOPERCULAR SPINE
GROOVE
PAD OF MODIFIED TISSUE

the greatly expanded articular head of the medial hemitrich.

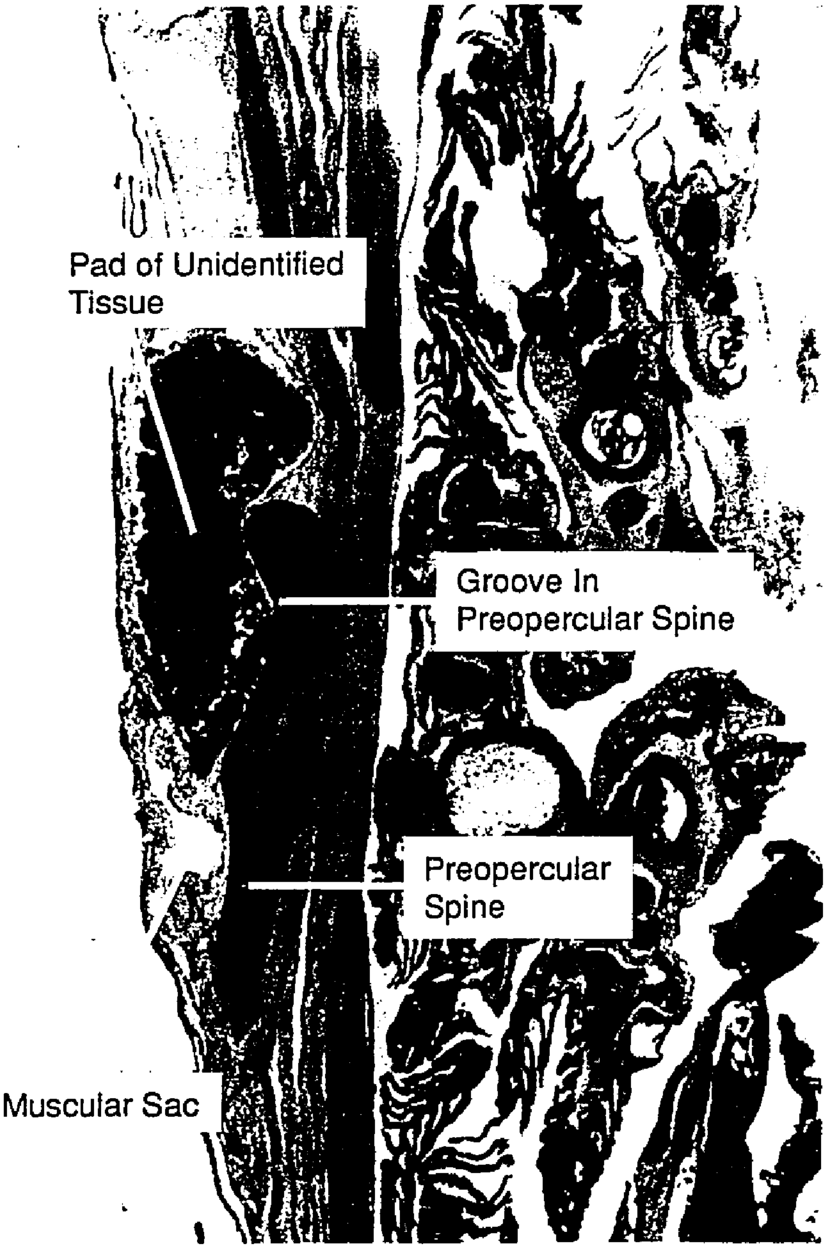
50. Base of preopercular spine covered with pad of modified tissue (Fig. 34).-- As noted previously, *Grammistops* and the "pseudogrammids" have a single preopercular spine (character 32'). Gosline (1960) noted that in "pseudogrammids," there is a pad of glandular-like tissue at the base of this spine (Fig. 34B), which in some species is curved downward, and has a groove that extends the length of the spine (Fig. 34A). Initially I 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 do not stain with Sudan Black B; lying beneath this pad of tissue is what appears to be a muscular sac (Fig. 35). 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. 27).-- In all other serranids with three anal-fin spines, the third spine is supported by both the proximal-middle element of the second anal-fin pterygiophore (supernumerary association) and the distal radial of the first pterygiophore (serial association - Fig. 27A-E). In the "pseudogrammids," the first distal radial becomes widely separated from the second pterygiophore, carrying with it the third anal-fin spine (Fig. 27F).

Pseudogramma + *Suttonia*

47'. Lateral line incomplete.-- 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*, or 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.

Figure 35. Photomicrograph of cross section (Sudan Black B histological preparation) through head of *Pseudogramma polyacantha*, USNM 295992, 44.5 mm SL.


Pad of Unidentified Tissue
Groove In Preopercular Spine
Preopercular Spine
Muscular Sac

Possibly, an incomplete lateral line in *Pseudogramma* and *Suttonia* is attributable to paedomorphosis (A. Gill, USNM, pers. comm.). If, as in some pseudochromoids, the lateral line of "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 I 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.

My 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, I 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 larval morphology provides the only evidence of a monophyletic Epinephelini and the clade comprising diploprionins, liopropomins and grammistins. This 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). I am aware that missing data can cause problems in cladistic analyses (see Platnick et al., 1991), and note that the only nodes on the cladogram (Fig. 12) 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 my 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*, I 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 my 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. I 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 12 merits further discussion. It emerges as the single most parsimonious tree only because of the way in which I treated multistate characters. Much has been written about analyzing multistate characters (e.g., 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, I attempted to analyze the 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 (see 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, I was left with the former method, treating multistate characters as "unordered" in the computer analysis, which, despite being criticized by Mickevich (1982) as "nihilistic," I 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 me 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), I note that analyzing the multistate characters used in this study in the order they appear in the character matrix (Table 5, 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 12, 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). I 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 12 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 positions of *Jeboehlkia* and *Grammistops* by providing an additional three synapomorphies of *Jeboehlkia*, *Pseudogramma* and its relatives.

SUMMARY

If classifications of fishes are to represent phylogeny, then cladistic studies are needed at all taxonomic levels, including generic and specific (assuming cladistic studies can provide accurate reconstructions of phylogeny). The existence of subfamilial phylogenies aids systematists in classifying new species, potentially checking classificatory errors that historically have led to nomenclaturial instability. In recent years, the concept of Serranidae has changed from a poorly defined group of generalized lower percoids to a cladistically defined apparently natural assemblage. This transformation has made possible studies of subfamilial relationships. Herein I provide the first cladistic hypothesis of relationships among genera of the subfamily Epinephelinae based on larval and adult morphology.

A complete understanding of serranid phylogeny, however, must await the identification of the serranid sister group. In fact, a significant obstacle in our efforts to understand the evolutionary history of the large and diverse Percoidei has been the general inability to recognize sister-group relationships among families. This is, in part, attributable to the difficulty in recognizing ancestral states in morphologically diverse families, such as the Serranidae, in the absence of a sister-group hypothesis. The problem is compounded and confounded in the Percoidei by the fact that similar morphological features appear to have evolved independently numerous times. Studies at the generic level are critical to improving our understanding of the phylogeny of percoids, because only by gaining a thorough knowledge of morphology (or genetics, physiology, behavior, etc.) within a family can characters shared with other families be recognized.

This study 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 I 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, I was forced to treat the multistate characters as unordered in my analysis. I acknowledge that the accuracy of my hypothesis of grammistin phylogeny depends, to a large extent, on the validity of this method.

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APPENDIX

Material Examined.-- Epinepheline larvae: *Diploprion bifasciatus* (reared material): USNM 290877, 290878 (29 eggs); 290879, 17 specimens, 1.5-2.0 mm NL; 290880, 13, 2.6-2.8 mm NL; 290881, 4, 2.4-2.8 mm NL; 290882, 18, 2.8-3.1 mm NL (1 specimen, 2.9 mm NL, cleared and stained, hereafter abbreviated "cs"); 290883, 8, 2.9-3.1 mm NL; 290884, 13, 3.0-3.3 mm NL (2 specimens, 3.0 and 3.1 mm NL, cs); 290885, 4, 3.3-3.4 mm NL; 290886, 9, 3.0-3.6 mm NL (1 specimen, 3.6 mm NL, cs); 290887, 1, 3.3 mm NL; 290888, 2, 4.0 and 4.3 mm NL; 290889, 5, 3.6-3.9 mm NL (1 specimen, 3.9 mm NL, cs); 290890, 5, 3.3-3.8 mm NL; 290891, 2, 4.6 and 4.7 mm NL (4.7-mm SL specimen cs); 290892, 3, 3.8-6.6 mm NL (1 specimen, 6.3 mm NL, cs); 290893, 1, 3.6 mm NL (cs); 290894, 1, 8.8 mm SL; 290895, 4, 9.8-15.5 mm SL; 290896, 2, 7.3 and 11.0 mm SL (cs); 290919, 1, 16.2 mm SL; (wild-caught specimens): CSIRO ASO6/82, stn. 1(1), 2, 5.7 and 7.1 mm NL; ASO6/82, stn. 1(2), 1, 5.8 mm NL; ASO5/83, stn. 6(3), 1, 10.4 mm SL; ASO3/83, stn. 2(1), 1, 10.9 mm SL; USNM 285416, 1, 13.3 mm SL; 174258, 1, 31.4 mm SL. *Belonoperca chabanaudi*: ZMUC P43671, 1, 6.9 mm SL; P43672, 1, 7.2 mm SL; P43673, 1, 8.8 mm SL; USNM 309607, 1, 11.8 mm SL. *Grammistes sexlineatus*: AMS I. 24997-002, 1, 5.5 mm SL; 24997-004, 1, 6.2 mm SL; 24997-003, 1, 9.7 mm SL; 24996-001, 1, 11.4 mm SL; ZMUC P43674, 1, 6.5 mm SL; P43675, 2, 6.6 and 7.3 mm SL; P43676, 3, 7.1-8.2 mm SL (1 specimen, 7.9 mm SL, cs). *Jeboehlkia gladifer*, MCZ 81740, 1, 10.2 mm SL; *Liopropoma*: MCZ 81674, 2, 11.5 and 14.0 mm SL; 85974, 1, 17.9 mm SL; 85971, 1, 22.5 mm SL; 85972, 1, 25.0 mm SL; ZMUC uncat., DANA Sta. 3868, 1, 5.9 mm SL. *Rypticus*: ARC 427341, 1, 11.7 mm SL (cs); MCZ 67224, 1, 5.9 mm SL; 85830, 1, 10.5 mm SL; 85829, 1, 12.9 mm SL; 85828, 1, 16.7 mm SL. *Pseudogramma*: MCZ 79310, 20, 5.8-14.5 mm SL; 64172, 1, 7.0 mm SL; 79036, 1, 12.0 mm SL; 79311, 1, 14.0 mm SL; 79318, 1, 14.2 mm SL; 79299, 1, 15.0 mm SL; VIMS 08274, 1, 3.6 mm NL; 08275, 1, 5.7 mm NL; 08276, 1, 11.4 mm SL, cs.

Adult (and juvenile) Epinephelinae: *Anyperodon leucogrammicus* USNM 218817, 1, cs; *Aporops bilinearis*, USNM 218920, 3, 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*, USNM 218889, 1, cs; USNM 183096, 3; *Epinephelus guttatus*, VIMS/CBL 3692, 16; *E. morio*, VIMS/CBL 3735, 1; *E. nebulosus*, VIMS 7533, 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 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.

Adult Anthiinae: *Acanthistius cinctus*, NMNZ P.19458, 1, cs; *A. serratus*, AMS I. 19602004, 1, cs. *Caesioperca lepidoptera*, NMNZ, P. 19913, 1, cs; *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 macculochi*, 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.

Adult Serraninae: *Centropristis philadelphica*, VIMS 7961, 1; *C. striatus*, VIMS/CBL 3810, 1. *Chelidoperca*, USNM 307787, 1, cs. *Diplectrum formosum*, VIMS 2478, 1; *D. bivittatum*, VIMS 03848, 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 Adult 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, 1. *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.

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