

A LARVA OF THE ATLANTIC FLASHLIGHT FISH,
KRYPTOPHANARON ALFREDI
(BERYCIFORMES: ANOMALOPIDAE), WITH A
COMPARISON OF BERYCIFORM AND
STEPHANOBERYCIFORM LARVAE

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ABSTRACT

The first wildcaught larva of a flashlight fish is described from a single specimen of *Kryptophanaron alfredi*, 6.2 mm NL, collected with a midwater trawl in the Tongue of the Ocean, Bahamas. The larva lacks light organs, but an antrorse projection on each side of the snout represents at least the stalk of an incipient light organ. Other distinguishing features of larval *Kryptophanaron* include an elongate, heavily pigmented pelvic fin; a patch of pigment on and between the anteriormost dorsal-fin spines; numerous melanophores covering the head and trunk (but conspicuously absent on the caudal peduncle); prominent head spines and spiny scales. The distribution of head spines among larvae of major acanthomorph lineages is confusing phylogenetically, and larval specializations do not help resolve current controversy about "beryciform" monophyly. Larval morphology provides some support for a close relationship between the Berycidae and other berycoid families and corroborates hypotheses based on adult characters that: Anoplogastridae, Diretmidae, Anomalopidae, Trachichthyidae, and Monocentridae form a natural assemblage; anoplogastrids and diretmids are sister taxa; and trachichthyoids (anomalopids, trachichthyids, and monocentrids) are monophyletic. Larval features highlight a need to reassess relationships among trachichthyoids.

Kryptophanaron alfredi Silvester and Fowler is the only known Atlantic representative of the flashlight fish family Anomalopidae. It has been collected off Jamaica, Puerto Rico, Grand Cayman Island, Curacao, and the Bahamas (Colin et al., 1979; Johnson and Rosenblatt, 1988). A second species of *Kryptophanaron*, the eastern Pacific *K. harveyi* Rosenblatt and Montgomery, 1976, was made the type of a distinct genus, *Phthanophaneron*, by Johnson and Rosenblatt (1988). Adult anomalopids are characterized by the presence of a subocular light organ, which contains symbiotic luminescent bacteria (Harvey, 1921, 1922, 1925; Hameda and Tsuji, 1971; Leisman et al., 1980; Haygood et al., 1984) and can be occluded by downward rotation, erection of a ventral "shutter" of elastic skin, or by some combination of the two methods (Johnson and Rosenblatt, 1988). Reared yolk sac larvae (3.3–3.8 mm NL) of the Pacific anomalopid *Anomalops katoptron* were described and illustrated by Colin (1989). Larger larvae are undescribed, and thus the ontogeny of the luminous organ is unclear.

Two recent studies of beryciform phylogeny (Johnson and Patterson, 1993; Moore, 1993) have proposed different classifications. We follow Johnson and Patterson (1993) in recognizing two orders: Beryciformes (Anomalopidae, Anoplogastridae, Berycidae, Diretmidae, Holocentridae, Monocentridae, and Trachichthyidae) and Stephanoberyciformes (Barbourisiidae, Cetomimidae, Gibberichthyidae, Hispidoberycidae, Megalomyceteridae, Melamphaidae, Rondeletiidae, and Stephanoberycidae). *Sorosichthys*, previously considered to constitute a monotypic family, was relegated to the Trachichthyidae by Kotlyar (1992), and *Paradiretmus*, formerly the sole member of the Paradiretmidae, was synonymized with the pomacanthid genus *Centropyge* (Allen et al., 1976).

In their review of beryciform ontogeny, Keene and Tighe (1984) noted that

larvae or "pre-juveniles/juveniles" are known for representatives of six families:

Anoplogastridae, Diretmidae, Gibberichthyidae, Holocentridae, Melamphaidae, and Trachichthyidae. More recently, representative larvae have been (or are being) described for larvae of six additional beryciform or stephanoberyciform families: Monocentridae (Okiyama, 1988—see also Uchida, 1932, and Yamada et al., 1979, publications not listed by Keene and Tighe, 1984), Anomalopidae (Colin, 1989), Stephanoberycidae (Kotlyar and Evseyenko, 1989), Berycidae (Okiyama, 1988; Mundy, 1990), Barbourisiidae, and Rondeletidae (Paxton and Johnson, in prep.). In contrast to other beryciform larvae, those of anomalopids are known only from reared preflexion specimens (*Anomalops katoptron*—Colin, 1989; *Kryptophanaron alfredi*—Colin, pers. comm.). Herein, we describe the first wildcaught larva of a flashlight fish, a 6.2-mm NL specimen of the Atlantic anomalopid, *K. alfredi*. This specimen is important because it shows early development of structures associated with the incipient light organ and because it represents an unusual capture (see "Life History and Ecology" section below).

Many descriptions of larval beryciforms and stephanoberyciforms lack details concerning location and configuration of head spines, making comparisons among larvae difficult. Following our description of larval *K. alfredi*, we compare details of head spination and squamation among larval beryciforms and stephanoberyciforms. The purposes of this paper are to describe the new flashlight fish larva, to comment on one possible life-history strategy for flashlight fishes, and to examine information from a comparison of the morphology of all known beryciform and stephanoberyciform larvae in light of current hypotheses of beryciform relationships.

MATERIALS AND METHODS

The description of larval *K. alfredi* that follows is based on a single specimen (SIO 88-200), 6.2 mm NL, collected off Andros Island, Bahamas (25°21.7'N, 78°00.2'W) in January 1987. Identification of the specimen as *K. alfredi* is based on comparisons of fin-ray counts of the larva with those of adults of Atlantic beryciforms (Woods and Sonoda, 1973; Colin et al., 1979; Johnson and Rosenblatt, 1988) and presence in the larva of two projections on the snout that we believe represent at least the stalks of the incipient light organs (Johnson and Rosenblatt, 1988). After illustrating the preserved larva and describing its pigmentation, squamation and morphometry, the snout projection on the right side was removed and sent to Scripps Institution of Oceanography to be examined histologically for evidence of development of the light organ and morphological features associated with its support and occlusion (see Johnson and Rosenblatt, 1988). The larva was then cleared and stained to facilitate the examination of superficial head spines and scales. Categories of shape (e.g., large, deep) follow those of Leis and Trnski (1989).

Comparative larval and juvenile material examined in this study is listed below. Institutional acronyms follow Leviton et al. (1985). "CS" indicates a cleared and stained specimen; "SL" indicates standard length; "NL" indicates notochord length. Anomalopidae.—*Phithanophaneron harveyi*, USNM 319830 (1 specimen; 20 mm SL). Anoplogastridae.—*Anoplogaster cornuta*, MCZ RHB 3121 (1: 8.8 SL, CS); USNM 323335 (1: 4.5 NL); 215640 (1: 7.0 SL, CS); ZMUC P412186 (1: 10.5 SL). Berycidae.—*Beryx decadactylus*, MCZ 64866 (1: 11.5 SL); *Beryx* sp., MCZ 59033 (1: 16.0 SL, CS); USNM 314041 (1: 7.8 SL). Diretmidae.—*Diretmoides pauciradiatus*, MCZ 83504 (7: 9.5–13.0 SL); MCZ, RHB 2296 (2: 14.0, 17.5 SL, CS). *Diretmus argenteus*, MCZ 64777 (1: 12.5 SL, CS). Gibberichthyidae.—*Gibberichthys pumilus*, ANSP 102061 (1: 21.2 SL, holotype); ANSP 102062 (1: 15.7 SL, Paratype). Holocentridae.—Holocentrinae, MCZ JEC 7701 (2: 5.0 NL, 19.0 SL, CS); MCZ 85215 (2: 6.2, 10.0 SL, CS); MCZ 85252 (10: 4.3–10.0 SL); Myripristinae, MCZ 85248 (2: 6.5, 7.1 SL); MCZ 85249 (1: 6.0 SL). Melamphaidae.—*Poromitra capito*, ZMUC P412187 (1: 6.0 SL, CS); *Poromitra* sp., AMS I.27175-030 (1: 8.0 SL). Monocentridae.—*Monocentris japonica*, ORIT 1982-8-4 (1: 13.0 SL); 1975-11-10 (1: 12.0 SL); 1975-11-18/19 (1: 5.0 NL); 1977-10-20/21 (1: 5.0 NL); 1979-7-11 (1: 3.4 NL). Polymixiidae.—*Polymixia* sp., MCZ 95714 (1: 27.0 SL, CS); MCZ 64773 (1: 11.5 SL, CS). Trachichthyidae.—*Aulotrachichthys* sp., ZMUC P40134 (1: 5.3 SL); P40135 (1: 11.6 SL); P40136 (1: 11.6 SL); P40137 (2: 11.5 SL, 11.7 SL); P40138 (1: 21.0 SL). *Gephyroberyx darwini*, ZMUC P40139 (2: 6.4, 9.3 SL); P40140 (1: 12.0 SL); P40141 (1: 15.2 SL); MCZ MOC 10-132.0 (1: 8.7 SL, CS); *Hoplostethus* sp., SIO 68-534 (1: 21.5 SL); YPM 2839 (1: 18.0 SL, holotype of *Korsogaster nanus*); ZMUC P40142 (1: 6.0 SL); P40143 (2: 12.9, CS, 15.0 SL); P40144 (1: 13.0 SL);

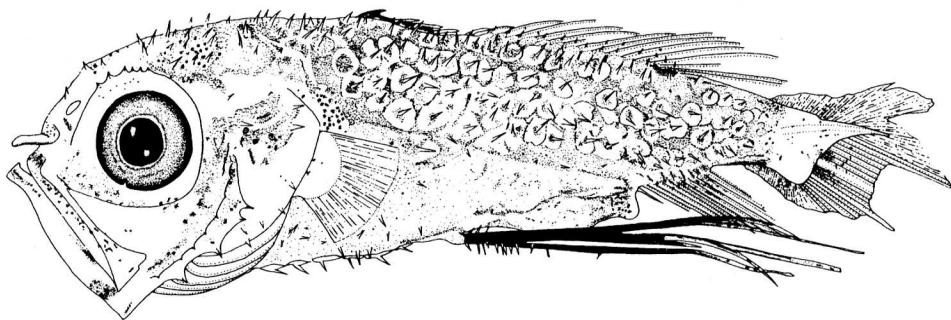


Figure 1. Larva of *Kryptophanaron alfredi*, SIO 88-200, 6.2 mm NL.

sogaster nanus); ZMUC P40142 (1: 6.0 SL); P40143 (2: 12.9 CS, 15.0 SL); P40144 (1: 13.0 SL); P40145 (1: 16.0 SL); P40146 (1: 18.5 SL); P40147 (1: 12.0 SL); P40148 (2: 7.0–9.2 SL); P40149 (1: 17.0 SL).

Kryptophanaron alfredi

Figures 1, 2

General Morphology.—The 6.2-mm NL larva lacks a subocular light organ. It is laterally compressed, heavily pigmented, covered with spiny scales, and in an

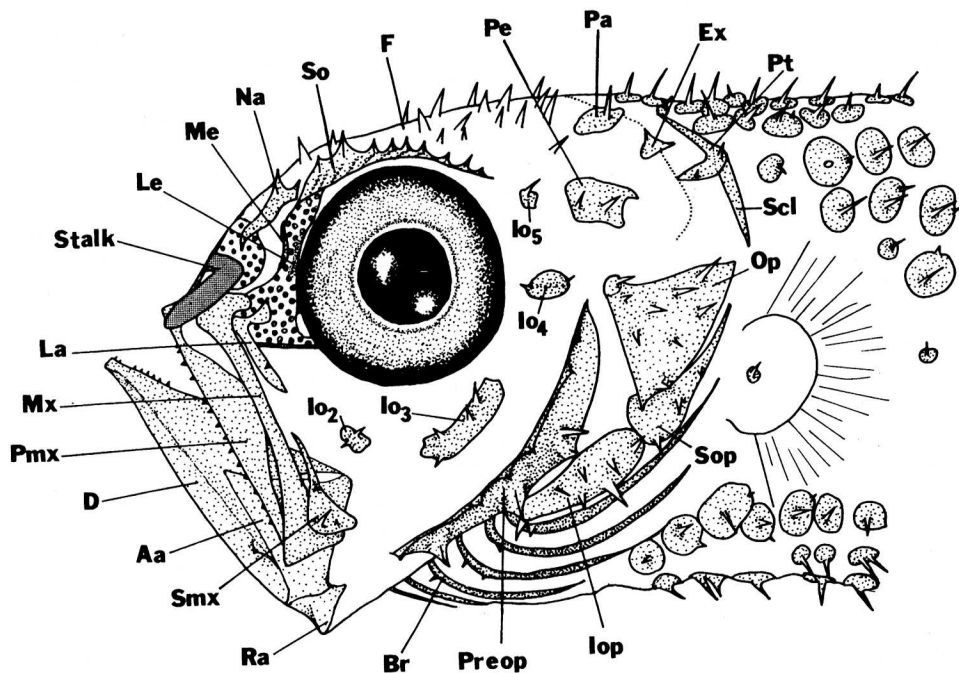


Figure 2. Head spination in larval *Kryptophanaron alfredi*, SIO 88-200, 6.2 mm NL. F—frontal, So—supraorbital ridge of frontal, Na—nasal, Me—mesethmoid, Le—lateral ethmoid, stalk—see Johnson and Rosenblatt (1988), La—lacrimal, Mx—maxilla, Pmx—premaxilla, D—dentary, Aa—anguloarticular, Smx—supramaxilla, Ra—retroarticular, lo_n—nth infraorbital, Br—branchiostegal, Preop—preopercle, lop—interopercle, Sop—subopercle, Op—opercle, Scl—Supracleithrum, Pt—posttemporal, Ex—extrascapular, Pa—parietal, Pe—pteryotic.

advanced state of notochordal flexion. The larva is moderately deep (body depth 25.8% NL at pectoral-fin base), has a round eye of moderate diameter (32.9% head length), a large head (33.9% NL), blunt snout (6.7% NL), and oblique mouth that reaches a vertical through the anterior orbit. The straight gut terminates posteriorly immediately in front of the anal fin (preanal length 71.0% NL), and body depth at the anus (16.1%) is less than at the base of the pectoral fin. The dorsal fin originates over the pectoral fin (predorsal length 38.7% NL). A striking morphometric feature is the long pelvic fin; the longest ray (fourth soft ray) is circa 45.2% NL and nearly reaches a vertical through the terminus of the notochord, but the tips of all pelvic-fin rays appear to be broken. The pelvic fin originates much further posteriorly, relative to the pectoral fin, than it does in adults. Lacking additional larval and juvenile specimens, we cannot describe the ontogenetic processes involved in the anterior migration.

The most unusual feature of the larva is the presence of an anteriorly directed, rod-like projection on each side of the snout. The projections are about 4.8% NL, highly pigmented ventromedially and bend towards one another proximally to connect across the snout. The projections are not tubes, and thus are not elaborate nostrils. Although adult *Kryptophanaron* lacks anteriorly directed projections on the snout, it possesses bilaterally paired, laterally pigmented, fibrocartilaginous "stalks" that are continuous anteriorly across the front of the snout and extend posterolaterally to articulate with the fibrocartilaginous "cup" that supports the light organ (Johnson and Rosenblatt, 1988). When the snout projection of the larva is bent backward to what is probably its normal position beneath the eye, its posterior extent suggests that it may represent the anlage of the cup and light organ, as well as the stalk. Although we can detect no evidence of differentiation within the structure in the cleared and stained specimen, examination of sections of the projection with light and electron microscopy reveals invaginations reminiscent of those characterizing the light organ of adults (M. Haygood, Scripps Institution of Oceanography, pers. comm., March 1993), suggesting that the projection does indeed include the incipient light organ. Symbiotic bacteria were not observed (M. Haygood, pers. comm.).

Pigmentation.—The head is heavily pigmented, unpigmented areas occurring only on the ventral portion of the opercle, the subopercle, interopercle, branchiostegals, otic region, cheek, portions of the upper and lower jaws, and snout. The remainder of the head, including the inside of the mouth at the dentary symphysis and the orbital region occupied by the light organ in adults, is covered with numerous tiny, somewhat diffuse melanophores. Larger, more distinct spots (=melanophores) occur on the frontals.

Most of the trunk is covered with small melanophores that are most numerous between and at the perimeter of scales. A patch of larger spots is present just above the base of the pectoral fin and another is on the gut proximal to the conspicuously naked tip of the anus. Trunk pigment diminishes abruptly posteriorly, leaving a largely unpigmented band around the caudal peduncle to the tip of the notochord.

All rays of the pelvic fin are heavily pigmented proximally, but pigment is less dense distally. The anal fin bears a patch of pigment on the proximal portions of approximately the seventh through tenth soft rays: this patch is confluent with the trunk pigment. Pigment is present on the ventralmost three rays of the upper caudal-fin lobe and dorsalmost four rays of the lower caudal-fin lobe; melanophores are present on approximately the basal third of those rays. Several scattered spots are present externally over the hypurals, urostyle, and on anlagen of the

procurrent caudal rays. The spinous dorsal fin has pigment on the membrane between the anteriormost four spines and at the proximal bases of the posterior-most dorsal soft rays. Incipient pectoral-fin rays lack pigment, but three melanophores are present in the center of the pectoral-fin base near its anterior margin.

Fins and Vertebral Column.—Adult complements of dorsal-fin rays (IV-I,15), anal-fin rays (I,11), pelvic-fin rays (I,6), and principal caudal-fin rays of the ventral lobe (9) are present. Some of those fin elements (particularly posteriormost anal and ventralmost caudal) are difficult to distinguish from adjacent rays, indicating recent differentiation. The larva is in an advanced state of notochord flexion, evidencing that flexion is accompanied by completion of some fins. The dorsal lobe of the caudal fin has about eight of the adult complement of 10 principal caudal-fin rays; the dorsalmost rays adjacent to the urostyle are poorly differentiated. Procurrent caudal rays also are incomplete, there being only one ventrally and none dorsally (the adult complement is 8 + 8). The pectoral fin lacks fully formed rays. Only six of the adult complement of eight branchiostegal rays were visible in the intact larva, but two more, the anteriormost, smallest branchiostegals, can be seen after clearing and staining.

Woods and Sonoda (1973) listed 30 vertebrae (16 + 14) for *K. alfredi*. All 16 precaudal, but only the first nine caudal vertebrae, are fully ossified in the larva. A tenth caudal vertebra has dorsal and ventral saddle-shaped ossifications. Posterior to that vertebra, there is evidence of four incipient centra: the first (PU₃) with ossified neural and hemal spines; the second (PU₂) with ossified neural crest and hemal spine; and third and fourth (PU₁ + U₁ and U₂) with small saddle-shaped ossifications ventrally.

Spination (Fig. 2).—The trunk is covered with large, tack-like scales, most of which have a single spine projecting outward from near the center of a circular scale plate. There are about 25 scales in a linear series from the posttemporal to the caudal peduncle, significantly fewer than the adult complement of about 150 (Woods and Sonoda, 1973). A 20-mm SL juvenile of *Phthanophaneron harveyi* (see "Morphological Comparisons of Beryciform and Stephanoberyciform Larvae" below), which exhibits characters of both larvae and adults, has about 30 of the adult 110 scales in a lengthwise series, suggesting that scales are added ontogenetically.

In the whole specimen, it was difficult to determine whether the numerous spines on the head are cranial spines (ornamentation) or spiny scales, but in the cleared and stained larva it is evident that there are no scales on the head. There are nine small spines on the supraorbital ridge of the frontal, and small spines are present on all bones of the opercular series, including both the lateral and medial ridges of the preopercle. Not all spines associated with the opercular series are marginal; rather, one to several spines are present on the lateral aspect of the preopercle, interopercle, subopercle, and opercle. There are numerous cranial spines, including two small spines on the pterotic, one on the parietal, circa 17 on the frontal, and one on the nasal. The extrascapular bears a single tiny spine, and two small spines are present on the posttemporal. A single serration is present near the posteroventral end of the dentary, two minute spines are present on the supramaxilla, a single tiny spine is present on the lacrimal, and several very small spines are present in the region of the ventrally displaced infraorbitals (see Johnson and Rosenblatt, 1988). Each of the five dorsalmost branchiostegals bears one or two small spines on its ventral margin near the proximal end (about where the element bends dorsally to meet the hyoid arch). All fins, except the pectoral, which is incomplete, have rays adorned proximally with spicule-like spines ("spi-

nules"—Fig. 1). Approximately six small scutes, each bearing a spine and being only slightly larger and stouter than the scales, are present on the ventral midline between the gular region and the pelvic fin. Minute teeth are present in both jaws.

Development of Light Organs.—A developmental series of flashlight fishes encompassing the ontogeny of the light organs is lacking. The snout projections in larval *Kryptophanaron* represent at least the fibrocartilaginous stalks associated with the light organs of adults. If the light organ and supporting fibrocartilaginous cup develop separately from the stalk, then the posterior portion of the stalk must somehow attach itself to the cup. Because there is no apparent anlage below the eye from which the light organ and supporting fibrocartilaginous cup could develop separately, we believe it is likely that these structures differentiate within the distal end of the stalk anlage as it grows. Corroborating this hypothesis is the microstructure of the projection, which, like the light organ of adults, is characterized by invaginations of epidermal tissue (M. Haygood, pers. comm.). Additional material and observations are needed to explain fully the ontogeny of the light organ and its acquisition of symbiotic bacteria.

Life History and Ecology.—Little information about the habits of early life history stages of flashlight fishes can be gathered from the specimen of *Kryptophanaron* described herein. The larva was captured in a midwater trawl (IKMT) at a maximum of 400 m (presumably from surface to 400 m in an oblique tow—H. J. Walker, pers. comm.). Depth of the bottom was not included in the collection data, but the coordinates (25°21.7'N, 78°00.2'W) establish the depth at approximately 1,690 m (minimally ca. 1,200 m in surrounding waters, maximally ca. 2,400 m—1991 NOAA Bathymetric Chart of the Straits of Florida). The larva was thus captured in the water column, somewhere between the surface and 400 m. J. M. Leis (Australian Museum, pers. comm., February 1993) collected a preflexion specimen of *Anomalops* in an oblique bongo-net tow from the surface to about 100 m in water >1,500 m in depth in the Coral Sea. He noted that the *Anomalops* larva was taken in one of only two samples made outside of but close to Osprey Reef at night. Numerous tows taken in the same location during the day yielded no flashlight fish larvae, suggesting that the larvae may migrate upward at night.

We find it surprising that despite extensive ichthyoplankton sampling in areas where adult anomalopids are common (e.g., the DANA expeditions included numerous plankton collections throughout Indonesia where *Anomalops* is common—Johnson and Rosenblatt, 1988), only two wild-caught larvae have been identified. This raises the possibility that larval flashlight fishes are not normally pelagic, and that the single specimens of larval *Kryptophanaron* and *Anomalops* taken in the water column were “strays.” Colin (1989) noted that eggs of *A. katoptron* and *Photoblepharon palpebratus* were positively buoyant in one rearing attempt but negatively buoyant in two others. Citing Meyer-Rochow (1976) and “unpublished observations,” he speculated that the eggs are probably naturally positively buoyant. Meyer-Rochow (1976) examined spawning and fecundity in *P. palpebratus* and noted that, in the laboratory, females produced up to 1,000 sticky, spherical buoyant eggs; however, eggs remained in the water column for only 5 to 10 h and then continued developing while adhered to a substrate (rocks or artificial grass). If flashlight fish eggs are spawned within the typical (daytime) adult habitat of caves, large crevices, etc., their adhesive nature could prevent dispersal into the water column. Possibly, inoculation of the light organs with bacteria requires close proximity to the adults early in ontogeny and, thus, precludes the planktonic larval life that characterizes other beryciforms and most

marine shore fishes. Unfortunately, the distribution in the water column of the bacteria harbored in the light organ of adults is unknown; the bacteria have not been identified because all attempts to culture them have been unsuccessful (Harvey, 1921, 1922; Leisman et al., 1980; Wolfe and Haygood, 1991; Haygood and Distel, 1993). A recent study (Haygood and Distel, 1993) suggested that the bacteria of flashlight fishes are not species of *Photobacterium*, the genus occurring in most other fish light-organ symbioses (including monocentrids). Rather, the bacteria of anomalopids (as well as ceratioids) appear to represent new taxa that are most closely related to the common, free-living luminescent bacteria of the genus *Vibrio* (Haygood and Distel, 1993).

Alternative early life history strategies can explain the paucity of anomalopid larvae in plankton collections (e.g., the larvae only occur very close to reefs where relatively few samples have been taken—Leis, pers. comm.). Further investigation is needed.

MORPHOLOGICAL COMPARISONS OF BERYCIFORM AND STEPHANOBERYCIFORM LARVAE

Details of head spination and squamation in known larvae of beryciforms, stephanoberyciforms, and *Polymixia* are summarized in Table 1. The most striking aspect of the data presented in Table 1 is the abundance of head spines in larval beryciforms and the paucity of ornamentation in larval stephanoberyciforms. Below, we briefly characterize and compare larval features of beryciforms, stephanoberyciforms, and *Polymixia*.

Anoplogastridae (Fig. 3A).—Larvae of *Anoplogaster cornuta* were illustrated and described by Keene and Tighe (1984) and Okiyama (1988). Distinctive features include a large parietal spine, large peak-like supraorbital spine, and large posteroventrally directed preopercular spine. Based on our observations of 4.5- to 10.5-mm SL specimens, we also note the presence of spines or serrations on the supramaxilla, anguloarticular, dentary, lacrimal, nasal, pterotic, extrascapular, posttemporal, and lateral preopercle. The frontal and base of the parietal spine are rugose, tack-like larval scales are present only on the ventral midline between the pelvic-fin girdle and cleithral symphysis, and rays of the dorsal and anal fins bear spinules laterally.

Diretmidae (Fig. 3B, C).—Development of *Diretmus* and *Diretmoides* was described and illustrated by Post (1976) and Post and Quero (1981). Larvae of *Diretmichthys* Kotlyar 1990, are unknown. Like anoplogastrids, larvae of diretmids have a large posterodorsally directed parietal spine (referred to as an epiotic spine by Post and Quero, 1981), a short peak-like supraorbital spine, and a large preopercular spine, which projects posteroventrally in *Diretmus* and anteroventrally in *Diretmoides* (Post and Quero, 1981). Detailed examination of ornamentation in 9.5–17.0 mm SL larvae reveals spines or serrations on the supramaxilla, anguloarticular, dentary, lacrimal, nasal, frontal, pterotic, extrascapular, posttemporal, and lateral preopercle. As in anoplogastrids, the frontal and the base of the parietal spine are rugose, and tack-like larval scales are restricted to the ventral midline on the anterior trunk. In specimens larger than about 15 mm SL, the dorsal- and anal-fin rays are adorned laterally with projections that are similar to, but broader than, the spinules of anoplogastrids.

Anomalopidae (Figs. 1, 2).—Rared preflexion larvae of *K. alfredi* less than circa 5.0 mm NL closely resemble reared preflexion larvae of *Anomalops katoptron* in that they are elongate (head length > body depth at pectoral-fin base), heavily

Table 1. Spination in larvae of beryciforms and stephanoberyciforms (sensu Johnson and Patterson, 1993) and *Polymixia*. + or - indicates presence or absence of ornamentation. R = rugosity; Sp = spine(s); Sr = serrate ridge(s); Nsr = non serrate ridge(s); preop = preopercle; D = dorsal fin; A = anal fin; P₁ = pectoral fin; P₂ = pelvic fin; C = caudal fin. Information for *Optivus* and *Paratrachichthys* is from Jordan and Bruce (1993); Barbouriidae and Rondeletidae—Paxton and Johnson (MS.); Melamphaidae—Ebeling and Weed (1973) and Keene and Tighe (1984); and Stephanoberycidae—Kotlyar and Evseyenko (1989).

	Maxilla	Supra-maxilla	Retro-articular	Angulo-articular	Dentary	Infra-orbitals	Nasal	Frontal	Supra-orbital	Parietal	Pterotic	Branchio-stegals	Extra-scapula
BERYCIFORMS													
Anoplogastridae													
<i>Anoplogaster</i>	-	+	-	+	+	+	+	R	+	large Sp, R	Sr	-	Sr
Diretmidae													
<i>Diretmoides</i>	-	+	-	+	+	+	+	R, Sr	+	large Sp, R	Sr	-	Sr
<i>Diretmus</i>	-	+	-	+	+	+	+	R, Sr	+	large Sp, R	Sr	-	Sr
Anomalopidae*													
<i>Kryptophanaron</i>	-	+	-	-	+	+	+	Sp	+	Sp	Sp	+	Sp
Trachichthyidae													
<i>Aulotrachichthys</i>	-	+	-	+	+	+	+	Sr	+	Sr	Sr	+	Sr
<i>Gephyroberyx</i>	-	+	-	+	+	+	+	Sr	+	Sr/Sp	Sr	+	Sr
<i>Hoplostethus</i> sp.	-	+	-	+	+	+	+	Sr	+	Sr	Sr	+	Sr
<i>H. mediterraneus</i>	-	+	-	+	+	+	+	Sr	+	Sr	Sr	-	Sr
<i>Optivus</i>	-	+	-	+	+	+	+	Sr	+	Sr	Sr	-	Sr
<i>Paratrachichthys</i>	-	-	-	+	-	-	-	Nsr	+	Nsr	Nsr	-	Nsr
Monocentridae													
<i>Monocentrus</i>	-	+	+	+	+	+	+	+	+	Sr/Sp	Sr	-	Sr
Berycidae													
<i>Beryx</i>	+	+	+ ^b	+	+	+	+	R, Sp	+	-	Sr	-	Sr
Holocentridae													
<i>Holocentrus</i>	-	-	-	+	+	+	large spine	Sr	+	Sr	Nsr	-	Sr
<i>Myripristis</i>	-	-	-	+	+	+	large spine	Sr	+	Sr	Sr	-	Sr

Table 1. Continued

	Maxilla	Supra-maxilla	Retro-articular	Angulo-articular	Dentary	Infra-orbitals	Nasal	Frontal	Supra-orbital	Parietal	Pterotic	Branchio-stegals	Extra-scapula
STEPHANOBERYCIFORMS													
Barbourisiidae	-	-	-	-	-	+	+	Sr	+	-	-	-	Sr
Rondeletiiidae ^c	-	-	-	-	-	-	-	-	-	-	-	-	-
Gibberichthyidae	-	-	-	-	-	-	-	-	-	-	-	-	-
Melamphaidae	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Poromitra capito</i>	-	-	-	-	-	-	-	Sp	-	-	-	-	Sr
<i>Poromitra</i> sp. (AMS)	-	-	-	-	-	-	-	Sr	+	-	-	-	Sr
Other <i>Poromitra</i>	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Scopelogadus</i>	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Melamphaes</i>	-	-	-	-	-	-	-	-	-	-	-	-	-
Stephanoberycidae	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Acanthochaenus</i>	-	-	-	-	-	-	-	-	-	-	+ ^d	-	-
<i>Polymixia</i>	-	-	-	+	-	+	-	Sr/Nsr	+	Sr	Sr	-	Sr

Table 1. Extended

	Supra- occipital	Post- temporal	Supra- cleithrum	Lateral preop.	Medial preop.	Sub- opercle	Inter- opercle	Opercle	Tack- like scales	Ventral scutes	Fin spinules
BERYCIFORMS											
Anoplogastridae											
<i>Anoplogaster</i>	-	+	-	+	large Sp ^e	-	-	Nsr	+ ^s	-	D, A
Diretmidae											
<i>Diretmoides</i>	-	+	-	+	large Sp ^e	-	-	Nsr	+ ^s	+	D, A
<i>Diretmus</i>	-	+	-	+	large Sp ^e	-	-	Nsr	+ ^s	+	D, A
Anomalopidae											
<i>Kryptophanaron</i>	-	+	-	+	+	+	+	Sp	+	+	D, A, P ₂ , C
Trachichthyidae											
<i>Aulotrachichthys</i>	-	+	+	+	+	+	+	Sr	+	+	D, A, P ₁ , P ₂ , C
<i>Gephyroberyx</i>	-	+	+	+	+	+	+	Sr	+	+	D, A, P ₁ , C
<i>Hoplostethus</i> sp.	-	+	+	+	+	+	+	Sr	+	-	D, A, P ₁ , P ₂ , C
<i>H. mediterraneus</i>	-	+	-	+	+	+	+	Sr	+	-	-
<i>Opivus</i>	-	+	-	+	+	-	-	Sr	+	+	-?
<i>Paratrachichthys</i>	-	Nsr	-	+	-?	-	-	+	-	-	-
Monocentridae											
<i>Monocentris</i>	small Sp	+	-	+	+	-	+	Sr	+ ^h	+	-
Berycidae											
<i>Beryx</i>	-	+	-	+	+	+	+	-	- ⁱ	-	-
Holocentridae											
<i>Holocentrus</i>	large Sp	+	-	+	large Sp ^f	+	+	large Sp	- ⁱ	-	-
<i>Myripristis</i>	large Sp	+	-	+	large Sp ^f	-	-	large Sp	- ⁱ	-	-

Table 1. Extended Continued

	Supra-occipital	Post-temporal	Supra-cleithrum	Lateral preop.	Medial preop.	Sub-opercle	Inter-opercle	Opercle	Tack-like scales	Ventral scutes	Fin spinules
STEPHANOBERYCIFORMS											
Barbouriidae	-	-	-	+	-	-	+	-	+j	-	-
Rondeletidae	-	-	-	-	-	-	-	-/+	-	-	-
Gibberichthyidae	-	-	-	-	-	-	-	-	-	-	-
Melamphaidae											
<i>Poromitra capito</i>	-	+	-	+	+	-	-	-	-	-	-
<i>Poromitra</i> sp. (AMS)	-	+	+	+	+	-	-	-	-	-	-
Other <i>Poromitra</i>	-	-	-	+	+	-	-	-	-	-	-
<i>Scopelogadus</i>	-	-	-	-	-/+k	-	-	-	-	-	-
<i>Melamphaes</i>	-	-	-	-	-/+l	-	-	-/+l	-	-	-
Stephanoberycidae											
<i>Acanthochoaenus</i>	-	-	-	-	-	-	-	-	-m	-	-
<i>Polymixia</i>	-	+	+	+	+	+	+	-	-i	-	-

^a *Anomalops* is not included because spination is lacking in the preflexion (3.8 mm and smaller) larvae described by Colin (1989).

^b Retroocular spines were noted by Handy (1990) but are not visible in the poorly stained material.

^c Paxton and Johnson (ms.) noted few head spines but early development of the adult condition of spongy bone on the frontal, sphenotic, parietal, supraoccipital, epiotic and pterotic.

^d According to Kotlyar and Eysencko (1989), "behind the eye at the level of the upper edge of the orbit there is one spine...".

^e Laterally directed spine.

^f Posteriorly directed spine.

^g Scales present only as patch on ventral midline between pelvic-fin girdle and cleithral symphysis (not present until ca. 18 mm SL in directrids).

^h A 5.5-mm NL specimen with tiny spines emerging from epidermis that resemble the spines of the tack-like scales of other beryciforms and are the precursors of the large spines that project from each scale in larger specimens.

ⁱ Scales present at ca. 8-12 mm SL but without spines (*Beryx*) or with adult-like spines posteriorly (holocentrids, *Polymixia*).

^j This is also an adult condition.

^k Ebeling and Weed (1973) depicted small preopercular spines in larval *S. mizolepis mizolepis* but not in *S. beanti*.

^l Ebeling and Weed (1973) depicted preopercular and opercular spines in larval *M. cyclops* but not in other *Melamphaes*.

^m Adult condition of circular scales with a short spine projecting from a star-shaped base at the center of the plate present at ca. 17.0 mm SL.

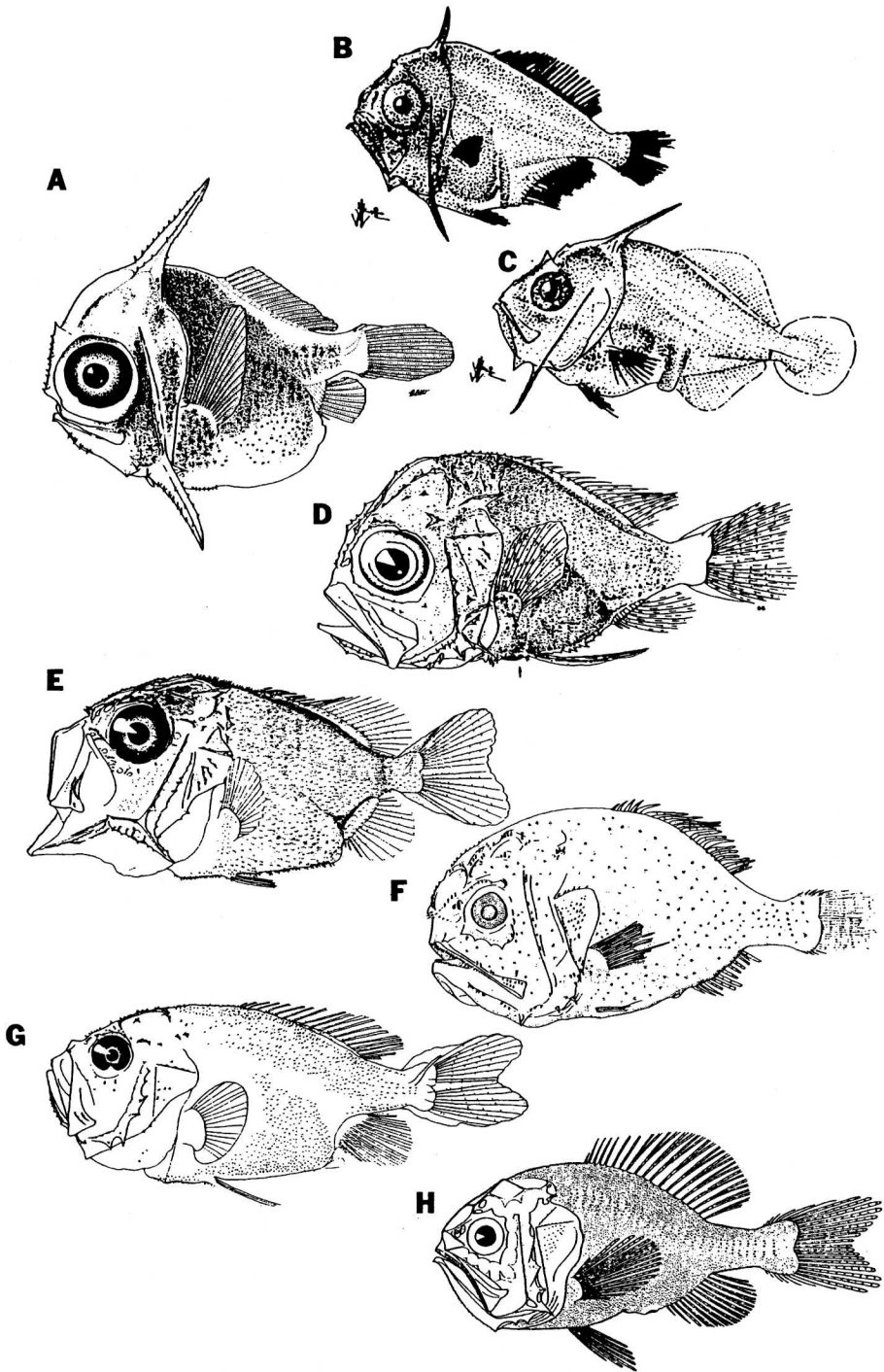
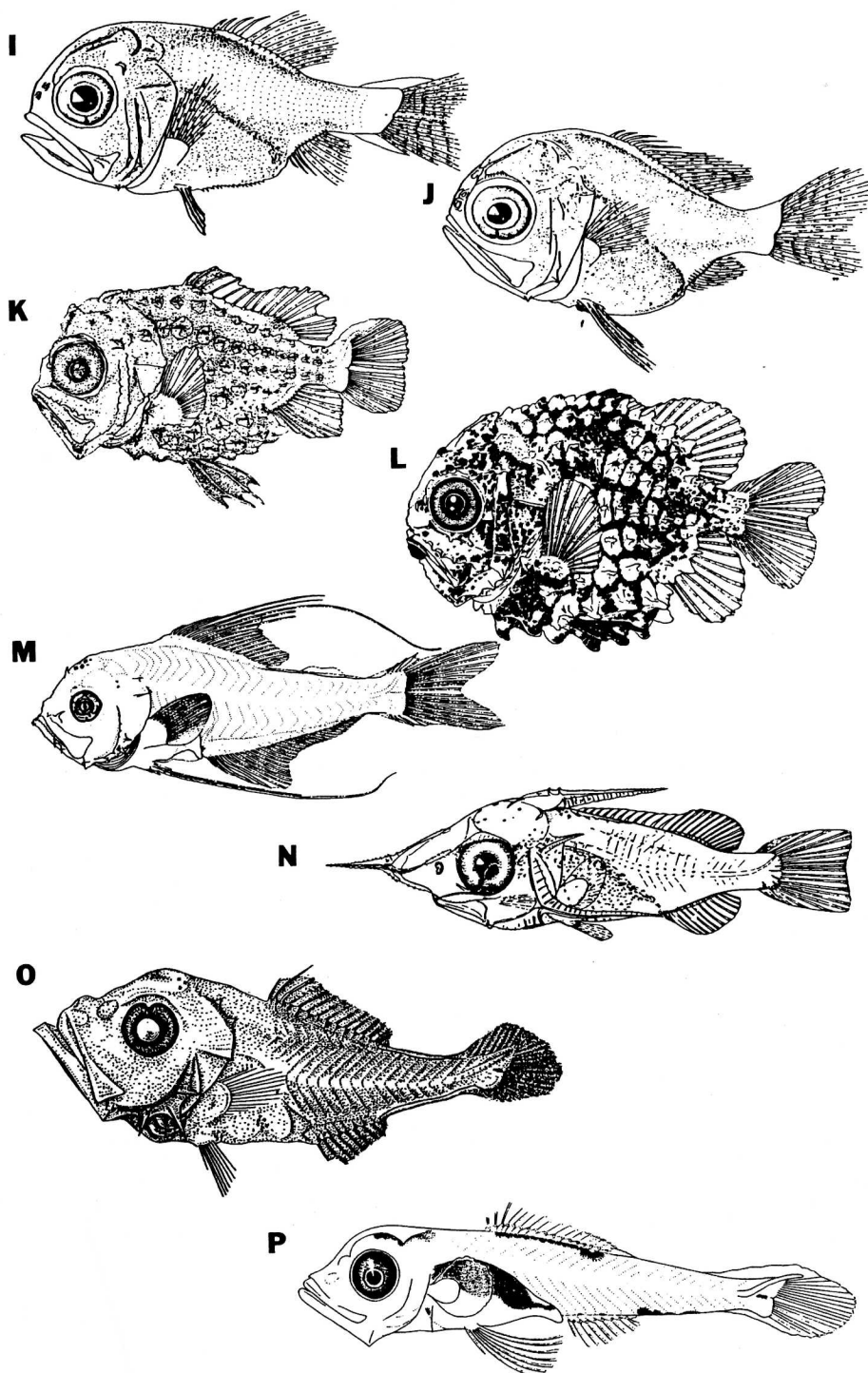


Figure 3. Selected larvae of Beryciformes. A) *Anoplogaster cornuta*, 6.0 mm SL (from Keene and Tighe, 1984); B) *Diretmus argenteus*, ca. 8.0 mm SL, and C) *Diretmoides pauciradiatus*, ca. 9.0 mm SL (from Post and Quero, 1981); D) *Aulotrachichthys* sp., 7.9 mm SL (from Jordan and Bruce, 1993); E) *Gephyroberyx japonicus*, 11.0 mm SL (from Okiyama, 1988); F) *Hoplostethus* sp., 21.5 mm SL (from Johnson, 1970, as *Korsogaster nanus*); G) *Hoplostethus* sp., 10.7 mm SL (from Okiyama, 1988); H) *Hoplostethus*



sp., 18.0 mm SL (from Parr, 1933, as *Korsogaster nanus*); I) *Optivus* sp., 7.2 mm SL (from Jordan and Bruce, 1993); J) *Paratrachichthys* sp., 7.6 mm SL (from Jordan and Bruce, 1993); K) *Monocentris japonica*, 6.5 mm SL, and L) *M. japonica*, 13.0 mm SL (from Okiyama, 1988); M) *Beryx splendens*, 7.5 mm SL (from Mundy, 1990); N) *Holocentris vexillarius*, 8.5 mm SL (from McKenney, 1959); O) *Poromitra capito*, 13.2 mm SL, and P) *Melanphaes lugubris*, 6.2 mm SL (from Keene and Tighe, 1984).

pigmented, and have large, precocious, fan-like pelvic fins (P. L. Colin, pers. comm.; Colin, 1989). The specimen of larval *Kryptophanaron alfredi* described here is the largest known anomalopid larva. It differs from other beryciform larvae primarily in having superficial cranial bones embellished with simple spines rather than serrate ridges or elaborate spines (Fig. 2).

A juvenile specimen of *Phthanophaneron harveyi* (USNM 319830, 20 mm SL), collected between 30 and 33 m in the Gulf of California by G. R. Allen and D. R. Robertson, has fully developed light organs. It does not have adult pigmentation (most of trunk and fins dark in adults), and shares with the *K. alfredi* larva a similar pattern of pigmentation on the fins, including a heavily pigmented pelvic fin, pigment on and between the four anteriormost dorsal spines, a patch of pigment at the bases of the middle rays of the anal fin, two patches of pigment on the principal caudal-fin rays (one on the upper lobe and one on the lower lobe), and pigmented areas on the procurrent caudal-fin rays. The juvenile *P. harveyi* has, in addition, a patch of pigment on the soft dorsal fin at the bases of several rays between the middle and posterior end of the fin (the flexion-stage larva of *K. alfredi* has a patch of pigment at the bases of the posteriormost dorsal soft rays). Head spination in juvenile *P. harveyi* resembles that of adult anomalopids in that finely serrate ridges (vs. prominent solitary spines in the larval *K. alfredi*) cover the cranium. Juvenile *P. harveyi* differs from flexion-stage larval *Kryptophanaron* and all adult anomalopids in being covered with scales bearing relatively longer, narrower spines. All of those spines, as well as the spinules adorning the bases of most fin rays, are covered with skin. Parr (1933), describing a similar condition of slender spines encased in "dermal papillae" in the circa 18.0-mm SL holotype of the trachichthyid *Korsogaster nanus*, noted that it gives the specimen a furry appearance.

Trachichthyidae (Fig. 3D–J).—Larvae of *Aulotrachichthys*, *Gephyroberyx*, *Hoplostethus*, *Optivus*, and *Paratrachichthys* have been described and illustrated (Crossland, 1981; Kotlyar, 1984b; Okiyama, 1988; Jordan and Bruce, 1993). Keene and Tighe (1984) noted that early-stage larvae of *Trachichthys mento* are known from the unpublished notes of E. H. Ahlstrom; however, *T. mento* is a species of *Hoplostethus* (see Paxton et al., 1989). Larvae of the most recently described trachichthyid genus, *Parinoberyx* Kotlyar 1984, are unknown.

Larvae of many trachichthyids are highly ornamented, having spines on nearly all exposed bones of the head except the maxilla, retroarticular, and supraoccipital (e.g., *Gephyroberyx* and *Aulotrachichthys*, Table 1). Other trachichthyids, most notably larval *Paratrachichthys*, are considerably less ornate. For example, larval *Paratrachichthys* lacks the tack-like scales that characterize other known trachichthyid larvae, as well as ornamentation on the supramaxilla, dentary, lacrimal, and nasal (Jordan and Bruce, 1993). The largest larva of *Paratrachichthys* examined by Jordan and Bruce (1993) is 10.0 mm SL and possibly the complete complement of ornamentation has not yet developed. Variation in spination among larval trachichthyids may be useful in a study of their interrelationships.

In their review of beryciform larvae, Keene and Tighe (1984) included Parr's (1933) illustration of the holotype of *Korsogaster nanus* (Fig. 3H herein), an 18.0-mm SL specimen collected in the Atlantic Ocean near the Bahamas, and Johnson's (1970) illustration of the second known specimen of *K. nanus* (Fig. 3F herein), a 21.5-mm SL specimen (SIO 68-534) from the equatorial Pacific. The two illustrations do not appear to depict the same species (compare head spination and the shape of the larvae, especially the snout). Parr (1933) and Johnson (1970) listed different anal- and pectoral-fin ray counts for their specimens (II,11 and 17,

respectively, for the holotype; III,8 and 19, for the other), but our examination indicates a total of 12 anal-fin elements in both specimens.

Woods and Sonoda (1973) relegated *K. nanus* to the synonymy of *Hoplostethus mediterraneus*, saying only that "Reexamination of the type of *Korsogaster nanus* Parr and comparison with specimens of similar size of *Hoplostethus mediterraneus* shows that the former is nothing more than a post-larval specimen in which the scales have not yet developed." Although counts of dorsal- and anal-fin rays of the holotype (19 and 12 total elements, respectively, are typical of both *H. mediterraneus* and *H. occidentalis*, the presence of 17 pectoral-fin rays is not typical of any known western Atlantic species of *Hoplostethus* (*H. mediterraneus* and *H. occidentalis* usually have 15—Woods and Sonoda, 1973). It is thus unlikely that *K. nanus* is a specimen of *H. mediterraneus*, and Parr (1933) may correctly have recognized it as a new species. Woods and Sonoda (1973) were probably correct in considering it a species of *Hoplostethus* which, although not delineated cladistically, is the only genus of Atlantic trachichthyoid having representatives with both 19 dorsal-fin elements and the anus in the normal position immediately anterior to the anal fin (Woods and Sonoda, 1973).

Based on the collection locality (central equatorial Pacific), Johnson's (1970) specimen of *Korsogaster* also appears to represent a species of *Hoplostethus*, which is the only trachichthyoid genus known from that area (Kotlyar, 1980: fig. 1). Johnson's specimen is probably not *H. mediterraneus* because it has more pectoral-fin rays (19 vs. usually 15), and because *H. mediterraneus* is known from the Pacific only around Australia and New Zealand (Paxton et al., 1989; Kotlyar and Pakhorukov, 1993).

A more complete investigation of trachichthyid taxonomy, including the compilation of frequency distributions of counts of adults and their geographical distributions, is needed to determine the proper placement of both specimens previously relegated to *Korsogaster nanus*.

Monocentridae (Fig. 3K, L).—Okiyama (1988) described larvae of *Monocentris japonica* and illustrated four specimens, 3.4 mm NL–13.0 mm SL. The information presented below and in Table 1 is based on our examination of several of those specimens and Okiyama's (1988) illustrations. Postflexion larvae (ca. 6.5 mm SL and greater) have ornamentation on the supraoccipital, parietal, frontal, supraorbital ridge of frontal, nasal, lacrimal, supramaxilla, dentary, anguloarticular, preopercle, pterotic, posttemporal, and extrascapular. Larval *Monocentris* are unusual in having ornamentation on the supraoccipital (present among other beryciforms examined only in holocentrids, but possibly this is an artifact of the limited size series of most larvae that were available). Scales are present in a 5.0-mm NL specimen as minute spines (scale plates not visible), and in Okiyama's illustration of a 5.8-mm specimen, scales are round plates each bearing a large, pyramidal spine. The scales are large (only ca. 11 in a linear series) as they are in *Kryptophanaron*, but the number of scales does not increase ontogenetically. The light organs on the lower jaw are present but only partially pigmented in an 11.5-mm SL specimen; they are completely black by 13.0 mm SL. *Monocentris* shares with larval *Kryptophanaron* and juvenile *Phthanophaneron* highly pigmented pelvic fins (pelvic fin small but also with pigment in larval *Aulotrachichthys*) and pigment on and between the anteriormost dorsal-fin spines. A 13.0-mm SL specimen of *Monocentris* has the most dense trunk pigment between and at the perimeter of the scales as does our 6.2-mm NL larva of *Kryptophanaron*.

Berycidae (Fig. 3M).—Larvae of *Beryx* have been described and illustrated by Okiyama (1988) and Mundy (1990). They are the only known beryciform or stephanoberyciform larvae with elongate, filamentous dorsal-fin spines. Larval

Beryx are also unusual in having sparse pigmentation on the trunk and in lacking ornamentation on the pterotic and parietal (Table 1). Larval *Beryx* and larval *Kryptophanaron* share elongate pelvic-fin rays, but at least some of the rays are filamentous in the former, and the fin is more highly pigmented in the latter.

Early stage larvae (5.0 mm SL and smaller) of *Centroberyx affinis* have recently been discovered (A. G. Miskiewicz, Water Board, Sydney, Australia, pers. comm., June 1993). A 5.0-mm SL specimen has sparse trunk pigment, few head spines, an elongate second dorsal-fin spine, and several elongate pelvic-fin rays (Miskiewicz, pers. comm.). Larger larvae are needed to determine if additional specializations develop.

Holocentridae (Fig. 3N).—Larval holocentrids have been described by McKenney (1959), Jones and Kumaran (1962), Aboussouan (1966), and Leis and Rennis (1983). Holocentrids differ from all other beryciform and stephanoberyciform larvae in having large rostral, supraoccipital, and posteriorly directed preopercular spines. There are also smaller spines or serrations on the anguloarticular, dentary, lacrimal, frontal, supraorbital, parietal, pterotic, extrascapular, posttemporal, and opercle (Table 1). Johnson (1984) noted that the large rostral projection of holocentrid larvae is formed by a modification of the supraethmoid, but his subsequent examination of this structure reveals that it represents a transient fusion of the nasal bones (Tyler et al., 1993). In myripristine holocentrids, the large nasal projection is bifurcate distally, whereas in holocentrines, the two sides of the projection are fused along their entire length (Jones and Kumaran, 1962; Leis and Rennis, 1983).

Stephanoberyciformes (Fig. 3O, P).—Head spination is not extensive in any stephanoberyciform larvae. Larval barbourisiids have ornamentation on the lacrimal, nasal, frontal, supraorbital, extrascapular, preopercle, and interopercle, but none of the spines is prominent (Paxton and Johnson, in prep.). Larvae of *Barbourisia* also have minute thumbtack-like scales which, unlike larval scales found in beryciforms, resemble scales of adults. Head spines in larvae of *Rondeletia* are lacking, except for two minute spines on the opercle (Paxton and Johnson, in prep.); larvae of the stephanoberycid *Acanthochaenus luetkeni* have only one spine, presumably on the pterotic (Kotlyar and Evseyenko, 1989; Table 1), and a stephanoberycid larva, tentatively identified as *Malacosarcus macrostoma*, lacks spination (Boehlert and Mundy, 1992). Late larvae and juveniles of *Gibberichthys* also are devoid of spination, but have the pelvic fins greatly modified into a long, trailing, ornate structure in the "kasidoron" stage (Robins and de Sylva, 1965).

A variety of patterns of head spination exists among larval melamphaid (Table 1), ranging from no ornamentation (e.g., *Melamphaes typhlops*, Ebeling and Weed, 1973: fig. 34) to prominent spines on the frontal, supraorbital, extrascapular, posttemporal, supracleithrum, and preopercle (e.g., *Poromitra* sp., AMS I.27175-030, see Table 1). *Poromitra capito* also has several prominent head spines, as does a larval type, tentatively identified as *Poromitra oscitans* (Bruce Mundy, NMFS-Hawaii, pers. comm., December 1992), from Hawaii. Head spination in other larval *Poromitra*, *Melamphaes*, and *Scopelogadus*, when present, is confined to small spines on the margins of the preopercle and opercle (Ebeling and Weed, 1973).

Polymixia.—Although no longer considered to be closely related to beryciforms or stephanoberyciforms (Zehren, 1979; Rosen, 1985; Stiassny, 1986; Johnson and Patterson, 1993), *Polymixia* is included in our comparison because considerably more head spination is present in larval *Polymixia* than in most stephanoberyci-

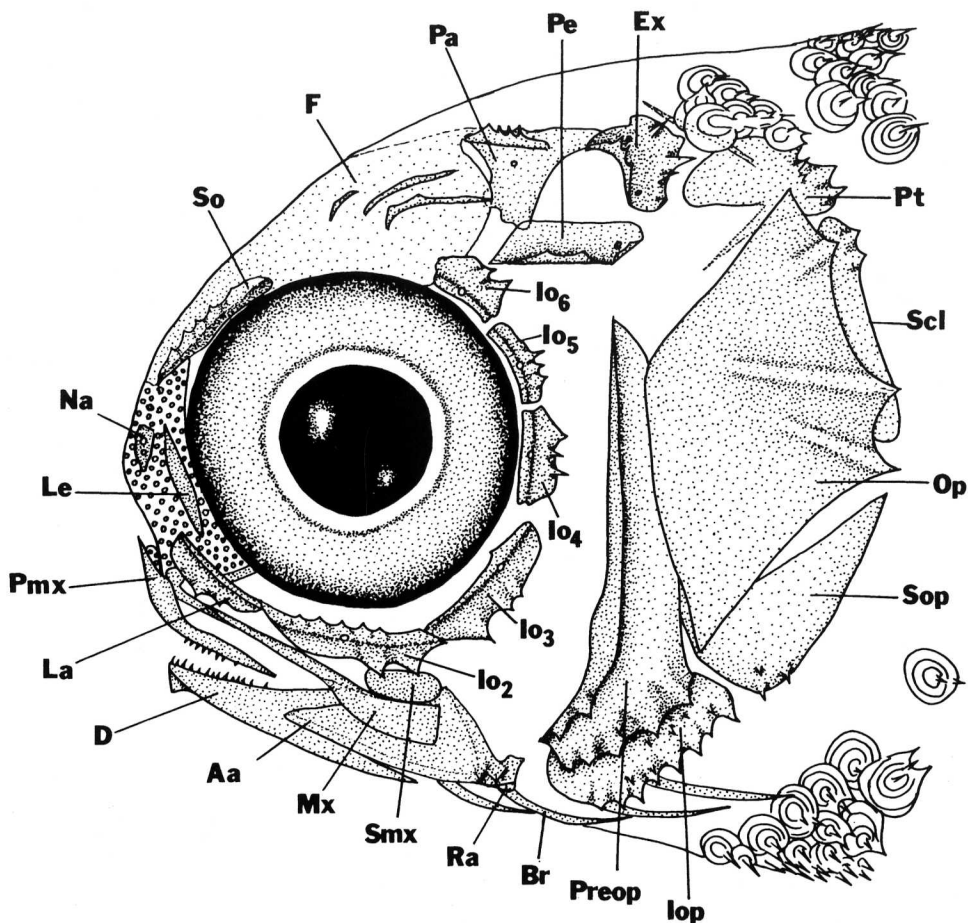


Figure 4. Head spination in larval *Polymixia*, MCZ 64773, 11.5 mm SL. F—frontal, So—supra-orbital ridge of frontal, Na—nasal, Le—lateral ethmoid, Pmx—premaxilla, La—lacrimal, D—dentary, Aa—anguloarticular, Mx—maxilla, lo_n — n^{th} infraorbital, Smx—supramaxilla (anterior supramaxilla not visible), Ra—retroarticular, Br—branchiostegal, Preop—preopercle, lop—interopercle, Sop—subopercle, Op—opercle, Scl—supracleithrum, Pt—posttemporal, Ex—extrascapular, Pe—pterotic, Pa—parietal.

forms, making it the most primitive acanthomorph taxon with extensive spiny ornamentation in the larvae. Larval *Polymixia* have not been described or illustrated, but we have examined an 11.5-mm SL cleared and stained specimen (MCZ 64773). That specimen has spines or serrations on the anguloarticular, lacrimal, frontal, supraorbital, parietal, pterotic, extrascapular, posttemporal, supracleithrum, preopercle, interopercle, and subopercle (Fig. 4).

PHYLOGENETIC SIGNIFICANCE OF ORNAMENTATION IN LARVAL BERYCIFORMS

Composition of the Beryciformes and their affinities with other acanthomorph fishes are controversial. Stiassny and Moore (1992) and Moore (1993) proposed that the Holocentridae are more closely related to perciform fishes than to other

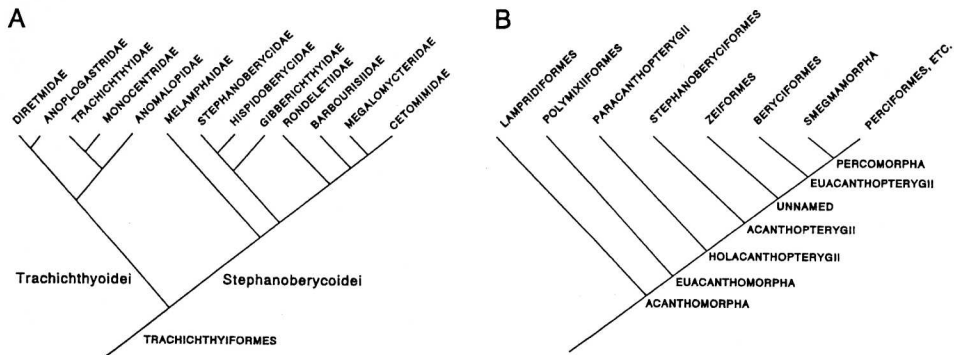


Figure 5. Two recent hypotheses of "beryciform" relationships. A) Moore (1993); B) Johnson and Patterson (1993). Johnson and Patterson's (1993) Stephanoberyciformes = Moore's (1993) Stephanoberycoidae; their Beryciformes = Moore's Trachichthyoidei plus the Holocentridae and Berycidae. Holocentrids and berycids are not included in Moore's (1993) Trachichthyiformes.

beryciforms, and included all stephanoberycoid and berycoid families except Holocentridae and Berycidae in an order Trachichthyiformes. Within that order, the berycoid families (Anomalopidae, Anoplogastridae, Diretridae, Monocentridae, and Trachichthyidae—i.e., Moore's "trachichthyoids") are the sister group of a natural assemblage comprising the stephanoberycoid families (Fig. 5A). Johnson and Patterson (1993) argued for a monophyletic order Beryciformes that includes holocentrids and berycids but excludes stephanoberycoids, which they considered a separate clade (Stephanoberyciformes) that diverged prior to the Beryciformes. They proposed the following phyletic sequence among basal acanthomorph lineages: [Lampridiformes [Polymixiiformes [Paracanthopterygii [Stephanoberyciformes [Zeiformes [Beryciformes [Percomorpha]]]]]] (Fig. 5B).

Interrelationships of Acanthomorphs.—Johnson and Patterson (1993) noted that the propensity for larvae of their Beryciformes and many percomorphs to develop extensive spination on superficial cranial bones is congruent with their hypothesis that the two are sister groups (their Euacanthopterygii), because such ephemeral head spination is lacking in more primitive acanthomorphs. Our discovery of numerous small head spines in a single larval specimen (11.5 mm SL) of *Polymixia* (Fig. 4) requires that we reassess this character.

The scheme of Johnson and Patterson (1993) places *Polymixia* three clades removed from the Beryciformes, but it is now apparent that its larva has head spination similar to that of larval beryciforms that is lacking in at least two of the intervening clades, paracanthopterygians and stephanoberyciforms (Fig. 5B), including the uncommon presence of ornamentation on the parietal. Johnson and Patterson (1993) noted that in adult *Polymixia*, beryciforms, and some zeiforms, the extrascapular contacts the parietal, conducting a branch of the occipital commissural sensory canal from the extrascapular onto the parietal. The bony housing for the canal on the parietal in larval *Polymixia* and beryciforms includes a small or large spine or serrate ridge. Among acanthomorphs, parietal spines in larvae are known elsewhere only in scorpaeniforms, which have a sensory canal that passes through a foramen in each parietal (Johnson, 1993). This condition is fundamentally different from that of *Polymixia* and beryciforms, where the sensory canal is on but does not penetrate the parietal.

Although a close relationship between *Polymixia* and beryciforms is inferred

by the parietal (and other?) ornamentation shared by their larvae, such a relationship is strongly refuted by other character evidence. *Polymixia* lacks the characters that define Johnson and Patterson's (1993) Holacanthopterygii, Acanthopterygii and Euacanthopterygii (Fig. 5B), and thus parietal ornamentation either evolved independently in larval *Polymixia* and beryciforms or it is a primitive acanthomorph condition that has been lost several times. Stephanoberyciforms lack parietal ornamentation, but in that group, the enlarged extrascapular usually completely covers the parietal (Johnson and Patterson, 1993), and it is unclear whether the absence of parietal ornamentation is due to morphological constraints or ancestry.

The data are confusing, and ornamentation in larvae may be of little value in assessing higher level relationships among acanthomorphs. As suggested by Johnson (1993), larval specializations are generally most informative about relationships at the family level and below.

One aspect of spination of acanthomorph larvae that has been insufficiently investigated is comparative development, i.e., heterochrony. Adults of many cladistically primitive acanthomorphs (*Polymixia*, stephanoberyciforms, beryciforms) as well as some percomorphs (e.g., scorpaeniforms) have numerous head spines, all or most of which first appear in the larval stage. This scenario is different from the most common condition in marine perciforms wherein most head spination of larvae is not present in adults. Some beryciforms and scorpaeniforms display conditions intermediate between that of stephanoberyciforms (few head spines in larvae but those present persist in adults) and perciforms (many head spines in larvae but few if any of those are present in adults). For example, the huge parietal and preopercular spines of *Anoplogaster* and diretmids are lost in adults, as are the rostral and supraoccipital spines of holocentrids. A more detailed survey of the ontogenetic trajectories of head spines in acanthomorphs is needed to determine what role heterochrony has played in the acquisition of ornamentation in adults or larvae, the latter generally being considered a "de novo" adaptation to an ephemeral period in the plankton.

Relationships of the Holocentridae and Berycidae.—Based on anatomy of the pelvic-fin skeleton, Stiassny and Moore (1992) and Moore (1993) suggested that holocentrids are more closely related to perciforms and relatives than to other beryciforms, and Moore (1993) excluded berycids and holocentrids from his Trachichthyiformes (berycoids plus stephanoberycoids). Johnson and Patterson (1993) noted that the three characters supporting Moore's (1993) trachichthyiforms are common among acanthomorphs, and argued that the affinities of holocentrids and berycids are with other beryciforms, not perciforms or stephanoberycoids.

Larval characters of holocentrids do not offer convincing evidence for either hypothesis. One feature of larval holocentrids, a large serrate supraoccipital spine, occurs elsewhere only in perciforms. However, its presence in several apparently unrelated percoid families (e.g., cepolids, *Hapalogenys*, leiognathids, lobotids, lethrinids, pentacerotids, and priacanthids) suggests that it has evolved numerous times; other, less plastic characters are needed to support a holocentrid-perciform association. Another character, presence of ornamentation on the nasal, may provide evidence for Johnson and Patterson's (1993) Beryciformes because nasal ornamentation is lacking in *Polymixia*, paracanthopterygians, stephanoberyciforms, and most percomorphs (present in some scorpaeniforms, acanthuroids, and several percoids). However, the simple spines or serrate ridges on the nasal bones

of most beryciform larvae bear little resemblance to the enlarged nasal projection of larval holocentrids, and homology is questionable.

Moore (1993) noted that "no unequivocal features have been found to unite the Berycidae to the rest of the so called 'beryciforms'." Our examination of larval beryciforms indicates that larval *Beryx* shares with the berycoid families the presence of spines or serrations on the supramaxilla. Supramaxillary ornamentation is lacking in larvae of other lower acanthomorphs (*Polymixia*, paracanthopterygians, stephanoberyciforms, holocentrids—although it is present in adults of some stephanoberycids and some holocentrids) as well as most perciforms (where the supramaxilla is frequently absent). We tentatively interpret this character as providing corroborative evidence for part of (berycids plus berycoids) Johnson and Patterson's (1993) Beryciformes.

Interrelationships of Beryciforms.—Larval features provide corroborative evidence for several previously proposed hypotheses of beryciform interrelationships and possibly conflicting information for another. Based on osteological features of adults, Zehren (1979) and Moore (1993) suggested that the Anomalopidae, Anoplogastridae, Diretmidae, Monocentridae and Trachichthyidae (trachichthyoids of Moore, 1993) constitute a monophyletic assemblage. Larvae of those families share the presence of tack-like scales and ornamentation on the lateral face of the opercle. Scales of young trachichthyoids are true "larval scales," i.e., a transient condition in an ontogenetic sequence that produces an adult scale morphologically different from the larval one. Tack-like scales also characterize larval *Barbourisia*, but the presence of the same type of scale in adults of that taxon suggests a nonhomologous ontogenetic trajectory of retention of the larval condition. In *Kryptophanaron* and trachichthyids, larval scales cover most of the trunk, but in *Anoplogaster* and diretmid larvae examined, larval scales have an unusual distribution, occurring only on the ventral midline between the pelvic-fin girdle and cleithral symphysis. Outgroup comparison with *Polymixia* and paracanthopterygians indicates that tack-like larval scales are derived for acanthopterygians, but information that would order the two derived states is lacking. Spinous scales are present in larvae of several percoid groups (Johnson, 1984) and also may have evolved more than once within Beryciformes. We observed no structural differences in the tack-like larval scales among beryciforms, but acknowledge that a parsimony analysis is needed to corroborate their homology.

Spinination on the opercle in most larval acanthomorphs is confined to the posterior margin of the bone, appearing as small serrations or large spines. In the beryciform families Anoplogastridae, Anomalopidae, Diretmidae, Monocentridae, and Trachichthyidae, the lateral aspect of the opercle is adorned with spines (*Kryptophanaron*), serrate ridges (trachichthyids and monocentrids), or non-serrate ridges (anoplogastrids and diretmids).

Moore (1993) noted that the prominent parietal spines in larvae and configuration of the second gill arch are synapomorphies of *Anoplogaster* plus diretmids. From Table 1, we add the presence of a small peak-like supraorbital spine; a large, anteroventrally, ventrally, or posteroventrally directed preopercular spine; and, possibly, the restriction of larval scales to the belly anteriorly. A large preopercular spine also characterizes holocentrids and many percomorphs, but in those taxa, the spine is typically directed posteriorly, not ventrally.

Zehren (1979) and Moore (1993) cited two characters, absence of the fourth pharyngobranchial toothplate and presence of an autogenous neural arch on the second preural centrum, as evidence of the monophyly of anomalopids + monocentrids + trachichthyids (trachichthyoids of Johnson and Rosenblatt, 1988). A

more accurate description of the first character is, fourth toothplate fuses ontogenetically to third; our observations indicate that the fourth toothplate is present as a separate element in the smallest cleared and stained larval trachichthyoids examined, e.g., *Gephyroberyx* and *Kryptophanaron*. A single larval character, presence of early forming, heavily pigmented pelvic fins, may corroborate the monophyly of the trachichthyoids. It is present in larvae of *Kryptophanaron*, *Monocentris*, *Aulotrachichthys*, *Optivus*, *Paratrachichthys*, and at least some *Hoplostethus* (Jordan and Bruce, 1993; this study). Anoplogastrids, diretmids, and most other beryciform and stephanoberyciform larvae lack early forming, pigmented pelvic fins (present in larval *Beryx* and some melamphaid—Keene and Tighe, 1984; Mundy, 1990). Absence of early forming, pigmented pelvic fins in larvae of *Gephyroberyx* and some *Hoplostethus* we examined is problematic, and may indicate that the condition in larval trachichthyids evolved independently of that in anomalopids and monocentrids.

Zehren (1979) noted that monocentrids and trachichthyids share 26 of the 94 derived character states identified in his study of "beryciform" phylogeny but acknowledged that none is unique to those families. All but one of those states also characterize anomalopids, and that state also occurs in diretmids, berycids, holocentrids, and stephanoberyciforms. Zehren (1979) pointed out that monocentrids and trachichthyids have similar patterns of frontal crests and that they share the condition of the subocular shelf being developed along only a portion of the second infraorbital (third if the lacrimal is counted as the first). Moore (1993) also considered monocentrids and trachichthyids to be sister groups, but he provided no additional synapomorphies. He noted that the morphology of the subocular shelf is highly variable among trachichthyiforms, and he considered the pattern of frontal crests as a synapomorphy of his trachichthyoids, not of trachichthyids and monocentrids.

Larval morphology provides no evidence for a monocentrid-trachichthyid relationship. Larvae of some, but not all, trachichthyids share features with larval *Kryptophanaron*, suggesting that the Trachichthyidae may be paraphyletic as presently recognized. For example, the small spines or serrations on the branchiostegal rays and spinules on rays of the paired fins of larval *Kryptophanaron* (rare characters among acanthomorph larvae) are also present in larval *Aulotrachichthys*, *Gephyroberyx* and *Hoplostethus* spp. (both specimens previously relegated to *Korsogaster nanus*), but not in *Paratrachichthys* and larvae tentatively identified as *H. mediterraneus*. Possibly, those features are present in larger specimens of *Paratrachichthys* and thus only suggest a paraphyletic *Hoplostethus* or, more likely, reversal in *H. mediterraneus*.

Serrate branchiostegal rays and spinulose fin rays are not present in larval *Monocentris*, but two features shared by larval *Monocentris* and *Kryptophanaron* and juvenile *Phthanophaneron* may indicate a closer relationship between those taxa than previously suggested. They share the presence of large scales and pigment on and between the three to four anteriormost dorsal-fin spines which are lacking in most trachichthyids. We have not observed the pattern of anterior spinous dorsal-fin pigmentation typical of anomalopids and *Monocentris* in other beryciform or stephanoberyciform larvae, and we have seen it only infrequently in percomorph larvae; however, adult *Hoplostethus crassispinnus* Kotlyar, 1980, has this pigment pattern. Among percoids, patterns of pigmentation are often most variable at specific and generic levels (Leis, 1986; Baldwin, 1990); thus, the identification of other trachichthyoid larvae is needed to confirm the utility of pigmentation in beryciforms above the generic level.

In summary, larval *K. alfredi* shares some uncommon features with larval

monocentrids and it shares other unusual characters with certain trachichthyids; however, no larval features are uniquely shared by trachichthyids and monocentrids. More complete ontogenetic series of trachichthyoid larvae are needed to determine the distribution of the characters described above; only then can larval morphology contribute meaningfully to a study of trachichthyoid interrelationships.

ACKNOWLEDGMENTS

For material, information or other assistance we thank L. Daniel, K. Hartell, J. Leis, I. Kinoshita, M. Okiyama, J. Olney, T. Orrell, R. Rosenblatt, K. Sasaki and H. J. Walker. M. Haygood made and examined sections of the snout projection of larval *Kryptophanaron* with light and electron microscopy and shared with us the results. M. Haygood, J. Leis, J. Paxton, R. Rosenblatt, V. Springer, H. J. Walker and an anonymous reviewer made helpful comments on a draft of this manuscript.

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DATE ACCEPTED: July 23, 1993.

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