ROLE OF LARVAL STAGES IN SYSTEMATIC INVESTIGATIONS OF MARINE TELEOSTS: THE MYCTOPHIDAE, A CASE STUDY[1]

H. GEOFFREY MOSER AND ELBERT H. AHLSTROM[2]

ABSTRACT

The lanternfish family Myctophidae is the most speciose and widespread family of mid-water fishes in the world ocean. As presently recognized it contains about 30 genera and 300 nominal species. Their larvae are highly prominent in the plankton and make up about 50% of all larvae taken in open-ocean plankton tows.

Our studies of myctophid larvae, on a worldwide basis, have demonstrated that characters of the larval stages of lanternfishes are of great utility in systematic analysis. The genera and species can be recognized on the basis of eye and body shape, the shape and length of the gut, and pigment pattern and by the sequence of photophore development. In this paper the larvae of 55 species representing 24 genera are illustrated and used to demonstrate the usefulness of larvae in understanding the relationships of species within genera.

Characters of the larvae provide insight into generic affinities of lanternfish, allowing us to construct an evolutionary scheme of tribes and subfamilies that differs in some aspects from those proposed on the basis of adult characters. The concept of using larval characters in combination with adult characters to delineate phylogenetic lines in myctophids is discussed, as is our view of evolutionary strategy in the family.

A major facet of comprehensive systematic investigations is the search for functionally unrelated characters. Whether the independence of these characters is actual or merely apparent, they constitute useful elements in the analysis of systematic relationships. Ample evidence of this is the higher classification of teleosts (Greenwood et al., 1966) generated by the synthesis of a diverse array of classical taxonomic characters. The recent surge of serological and biochemical studies on fish has placed a fresh group of characters in the hands of systematic ichthyologists (De Ligny, 1969). Likewise, recent advances in fish cytogenetics (e.g., Ohno, 1970; Benirschke and Hsu, 1971; Ebeling, Atkin, and Setzer, 1971) are providing another group of taxonomic characters. It is likely that behavioral science will be still another source of taxonomic characters, as exemplified by the growing body of information on the acoustic behavior of fishes (Fish and Mowbray, 1970).

One group of well known taxonomic characters, those of the embryonic and larval stages, has received scant attention from all but a few systematic ichthyologists. Characters of the larvae have played a large role in the taxonomy of anguilliform fishes (Castle, 1969) partly because of the conspicuousness of eel leptocephali and partly because of the unavailability of adults of many of the families. Bertelsen's (1951) treatment of the ceratioid fishes is a superb example of the value of utilizing larval stages in a systematic revision of a large group of teleosts. Apart from these two groups, it is the larvae of myctophiform fishes which have received the most attention from taxonomists. Ege (1953, 1957) relied heavily on larval stages in his extensive works on the Paralepididae. Johnson (1971) employed larval characters in defining species and genera of Scopelarchidae. Bertelsen, Marshall, and Krefft (pers. commun.) have used larval stages extensively in their revision of the Scopelosauridae. Our studies on the family Myctophidae itself (Moser and Ahlstrom, 1970, 1972) indicated that larval characters can aid significantly in differentiating taxa and defining evolutionary lineages within this family.

The lanternfish family Myctophidae is the most speciose and widespread family of mid-water fishes in the world ocean. As presently recognized it contains about 30 genera and 300 nominal species. Their larvae are highly prominent in the plankton and make up about 50% of all larvae taken in open-ocean plankton tows.

[1]This paper was presented at the International Symposium on the Early Life History of Fish (sponsored by IABO, FAO, ICES, ICNAF, and SCOR) held at Oban, Scotland, 17-23 May 1973.

[2]Southwest Fisheries Center, National Marine Fisheries Service, NOAA, La Jolla, CA 92037.

Manuscript accepted Agust 1973.
FISHERY BULLETIN: VOL. 72, NO. 2, 1974.

Our studies of the larvae of this family have included material from all oceans. We have been able to identify larvae from all recognized genera except *Hintonia* and *Dorsadena*. Larval evidence supports giving generic status to *Metelectrona* and *Parvilux*. Including these, we have developmental series for 29 myctophid genera and for many genera we have series for all known species. This has afforded a more comprehensive view of the range and variability of larval characters, and we are increasingly impressed with the functional independence of the larval and adult characters. It is apparent that the world of the larvae and the world of the adults are two quite separate evolutionary theaters. Our studies of larval lanternfishes have disclosed a full range of characters, from generalized to specialized and from conservative to labile, equal in scope to those of the adults. These characters fall into several categories. An important group is the shape of various structures such as the eye, head, trunk, guts, and fins, especially the pectoral fins. Another group is the sequence of appearance and the position of fins, photophores, and bony elements. Another is the size of the larvae when fins and other features appear and the size of the larvae when they transform into juveniles. Pigmentation provides an important group of characters based on the position, number, and shape of melanophores. Finally, there are the highly specialized larval characters such as voluminous fin folds, elongated and modified fin rays, chin barbels, preopercular spines, etc. It is our purpose here to point out some of these characters and demonstrate how they can be of advantage in defining taxa and establishing phylogenetic lineages.

THE SUBFAMILY MYCTOPHINAE

The most trenchant character of larval myctophids is eye shape. Our studies show that lanternfish larvae fall naturally into two groups on the basis of eye shape—those with narrow elliptical eyes and those with round or nearly round eyes (Moser and Ahlstrom, 1970). The species composition of these two groups agrees closely with that of the two subfamilies, Myctophinae and Lampanyctinae, established by Paxton (1972) on the basis of osteological and photophore characters of adults. Larvae of the Myctophinae have elliptical eyes; some species have ventral prolongations of choroid tissue and some have the eyes on stalks. Paxton recognized 11 genera in the subfamily Myctophinae and distributed them into two tribes, the Myctophini and the Gonichthyini. Larvae of the species in each of these genera generally conform to a particular morph based on form, pigment, and developmental pattern and, although these morphs are remarkably diverse, we can find no character or set of characters that would divide the genera into tribes. Within each genus of the subfamily, however, the larval characters are indispensible in delineating groups of related species or subgenera. This is best illustrated by examining the important genera of the Myctophinae.

Protomyctophum larvae have a slender shape (Figure 1). For all species except *P. anderssoni*, the gut is short during most of the larval period and characteristically there is a marked interspace between the anus and the origin of the anal fin (Figure 1A-D). The gut elongates dramatically in late larvae, to fill the interspace. Gut development is completely dissimilar in *P. anderssoni*, where the gut is long at all larval sizes, in fact longer than in most other lanternfish larvae (Figure 1E). Series of ventral tail melanophores are formed in some species of both recognized subgenera (*Heirops* and *Protomyctophum* sensu stricto), for example in *P. Protomyctophum normani* (Figure 1A) and *P. Heirops thompsoni* (Moser and Ahlstrom, 1970). Larvae of the subgenera can be separated, however, on the basis of eye shape, the eyes of *Heirops* (Figure 1C, D) being characteristically narrower than those of *Protomyctophum* sensu stricto (Figure 1A, B). Choroid tissue is absent from the ventral surface of the eye in all species of the genus except *P. anderssoni*, which has a well-developed "teardrop" (Figure 1E). Larvae of *P. anderssoni* are so markedly different from those of all other species of *Protomyctophum*, which otherwise form a rather cohesive group, that this species should be placed in a separate subgenus or perhaps even in a distinct genus. This suggestion is supported by the unique placement of certain photophores and by the structure of the supracaudal luminous tissue in adults of this species.

Larvae of the genus *Electrona* are a less homogeneous group but are united by a commonality of body shape and especially gut shape (Figure 2). A marked interspace is present between the end of the gut and the origin of the anal fin. This space is closed only at the termination of the

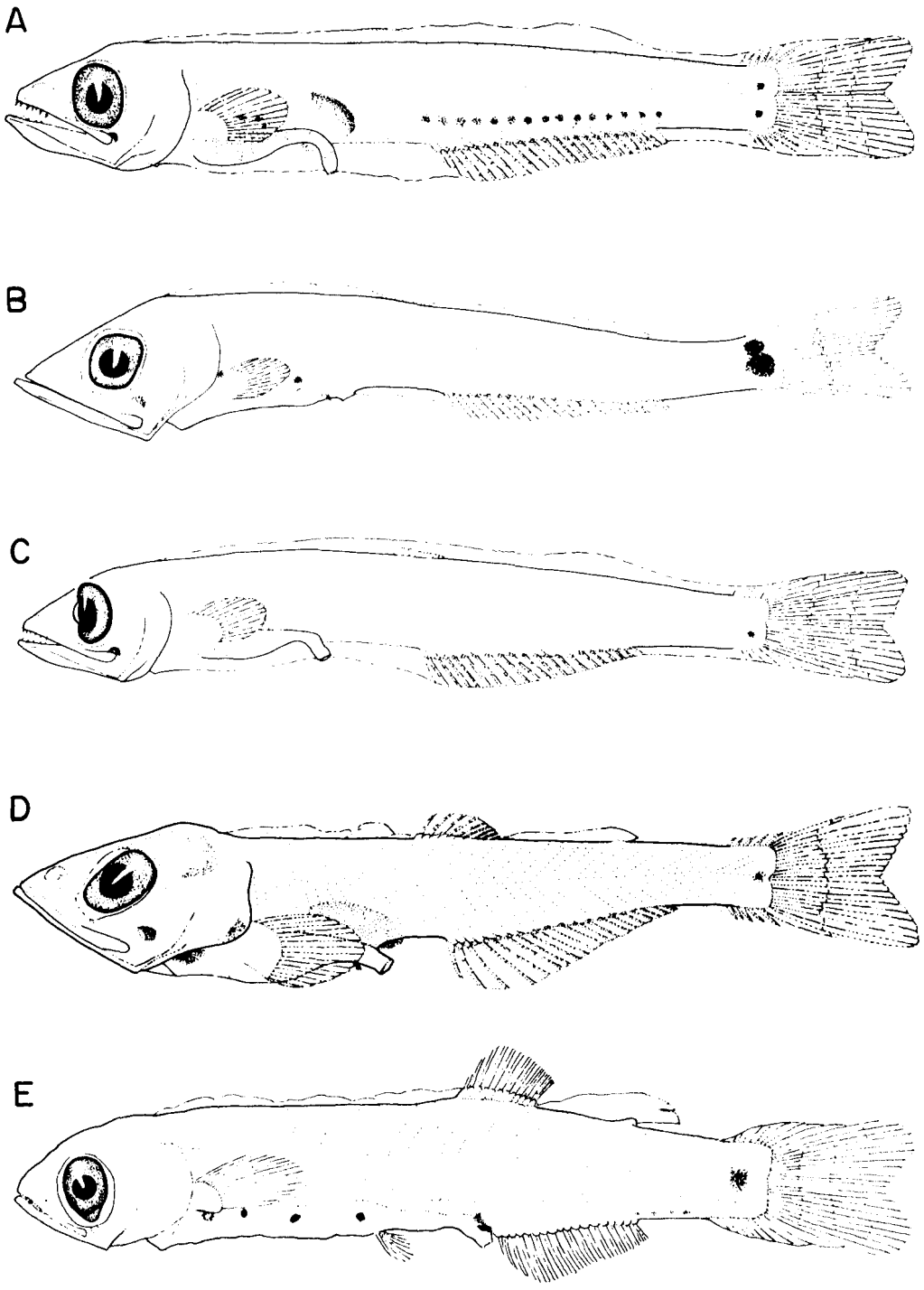

FIGURE 1.—Larvae of *Protomyctophum*. A. *P. Protomyctophum normani*, 15.2 mm; B. *P. Protomyctophum tenisoni*, 14.5 mm; C. *P. Hierops subparallelum*, 15.2 mm; D. *P. Hierops chilensis*, 11.0 mm; E. *P. anderssoni*, 15.7 mm.

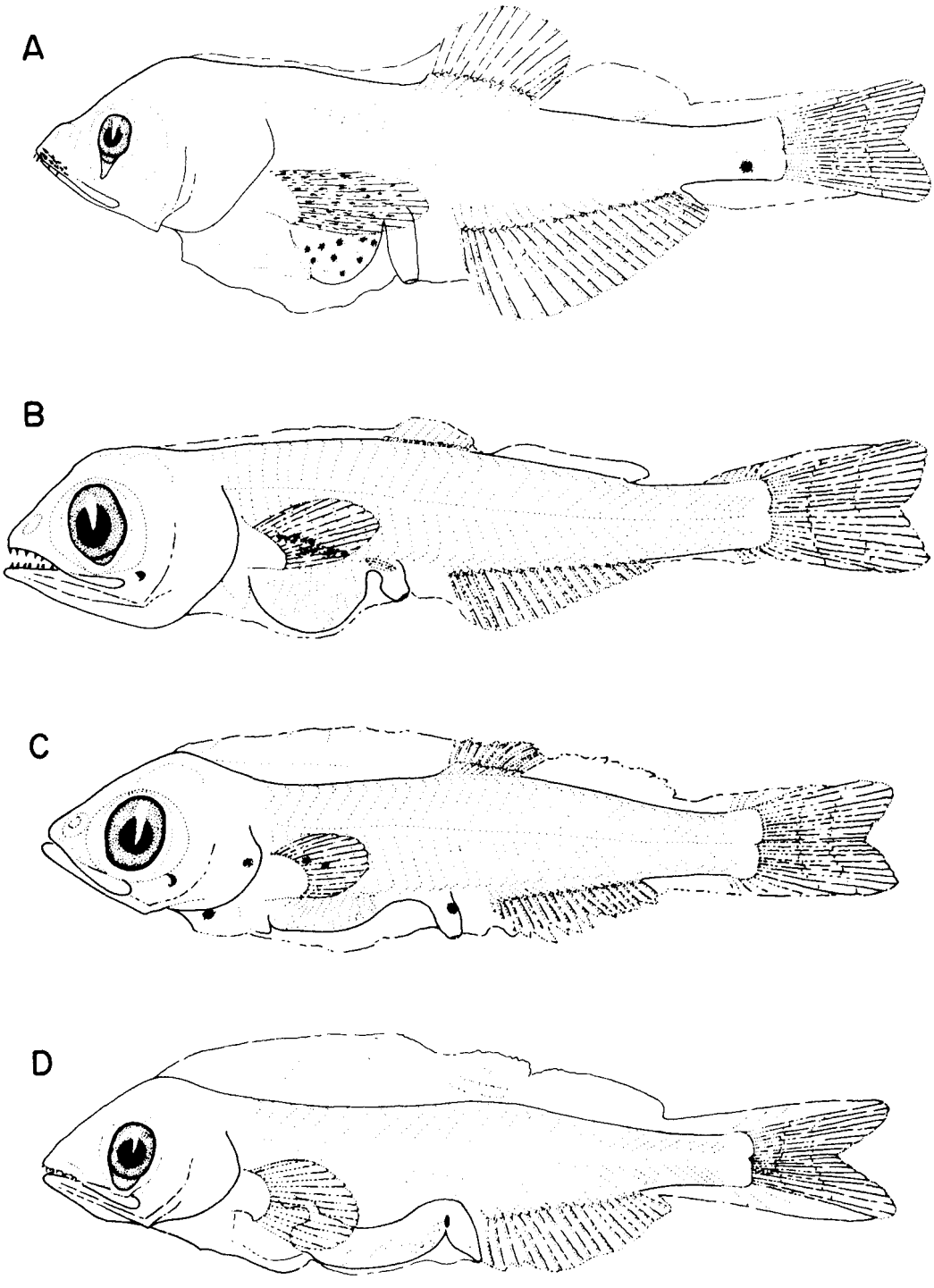

FIGURE 2.—Larvae of *Electrona* and *Metelectrona*. A. *E. antarctica*, 12.7 mm; B. *E. carlsbergi*, 11.1 mm; C. *E. subaspera*, 10.5 mm; D. *M. ahlstromi*, 10.3 mm.

larval period. None of the species forms photophores during the larval period other than the Br_2 pair.

The characters that most clearly separate the three developmental lines in *Electrona* are eye shape and the amount of choroid tissue developed under the eye. *Electrona antarctica* has an elongate choroid mass uniquely divided into two narrow eyes (Figure 2A). Also, *E. antarctica* larvae attain a large size (20 mm), are the deepest-bodied of all *Electrona* larvae, and have the heaviest pigmentation. The two species in the second developmental line transform at a small size (ca. 10 mm in *E. rissoi* and 12-13 mm in *E. carlsbergi*), have a small choroid mass under a moderately narrow eye, and develop scant pigment (Figure 2B). In the third line, consisting of *E. subaspera* and *E. paucirastra*, the eye is the least narrow, has no choroid tissue, and the larvae attain a large size (20 mm) (Figure 2C).

The larva of the species described as *Metelectrona ahlstromi* (Wisner, 1963) is illustrated in Figure 2D. It is more laterally compressed than any species of *Electrona* and has no interspace between the anus and origin of the anal fin. In some features it resembles the larvae of *Hygophum*; it has a late-forming dorsal fin and the gut is shaped very similarly to that in *H. taaningi* and *H. macrochir*. Its pigment is unique and the eye is distinct, with the ventral edge of the scleral envelope characteristically squared off. Also, in late-stage larvae, in addition to the Br_2, a second pair of photophores (PO_5) develops, a feature found in neither *Hygophum* nor *Electrona*. Paxton (1972) synonymized *Metelectrona* with *Electrona* and suggested that *M. ahlstromi* and *E. ventralis* are synonyms, however, the uniqueness of the larva strongly suggests the resurrection of *Metelectrona* as a valid genus.

The genus *Benthosema* is the least cohesive of any genus in the subfamily Myctophinae, from the viewpoint of larval structure (Figure 3). We can find only four types of larvae in the world ocean, although Nafpaktitis (1973) recognizes five species on adult characters. We cannot distinguish larvae of *B. pterota* and *B. panamense* although Nafpaktitis has listed a number of convincing characters that distinguish the adults of the two species. We find two highly divergent species pairs. One is composed of *B. glaciale* and *B. suborbitale* with a narrow eye subtended by a lunate choroid mass and with a pronounced interspace between the anus and the anal fin origin, reminiscent of *Protomyctophum* and *Electrona* (Figure 3A-C). In the other pair, consisting of *B. panamense-pterota* and *B. fibulatum*, the eye is wider, is subtended by a mere sliver of choroid tissue and the gut, of moderate length, lacks a postanal interspace (Figure 3D, E).

The one feature held in common by the four species is the development of some photophores in addition to the Br_2 during the larval period. The only other myctophine genera that develop photophores in addition to the ubiquitous Br_2 during the larval period are *Diogenichthys*, *Myctophum*, and *Metelectrona*. This feature is much more prevalent among genera of the Lampanyctinae and is helpful in defining groups of related genera there (Moser and Ahlstrom, 1972).

In *B. panamense-pterota* and *B. fibulatum* the Dn pair is formed soon after the Br_2 at about 5.0-6.0 mm. The PO_5 pair is the third to appear in

TABLE 1.—Sequence of photophore formation in larvae of three species of *Benthosema*.

Species	Size larva (mm)	Photophores	No. of photophore pairs	Smallest juvenile (mm)
B. fibulatum	ca. 4.0	Br_2	1	13.2
	5.4	Br_2 Dn	2	
	6.0	Br_2 Dn PO_5	3	
	6.4	Br_2 Dn PO_5 PO_1	4	
	7.3	Br_2 Dn PO_5 PO_1 AOa_1	5	
	7.7-8.7	Br_2 Dn PO_5 PO_1 AOa_1 PO_2	6	
	ca. 10.0	Br_2 Dn PO_5 PO_1 AOa_1 PO_2 Op_2 VLO	8	
B. pterota (panamense)	4.0	Br_2	1	11.8
	5.0	Br_2 Dn	2	
	6.0	Br_2 Dn PO_5	3	
	ca. 7.0	Br_2 Dn PO_5 PVO_1	4	
	7.1	Br_2 Dn PO_5 PVO_1 Op_2	5	
	7.5	Br_2 Dn PO_5 PVO_1 Op_2 VO_1 PVO_2	7	
	8.0	Br_2 Dn PO_5 PVO_1 Op_2 VO_1 PVO_2 PO_1 AOa_1	9	
B. suborbitale	4.1	Br_2	1	10.7
	8.3-9.2	Br_2 PO_1 PO_2	3	
	9.4	Br_2 PO_1 PO_2 Br_1 Br_3 Op_2	6	
	11.5	Br_2 PO_1 PO_2 Br_1 Br_3 Op_2 PO_3 PO_4 PO_5 AOa_1 AOa_2	11	

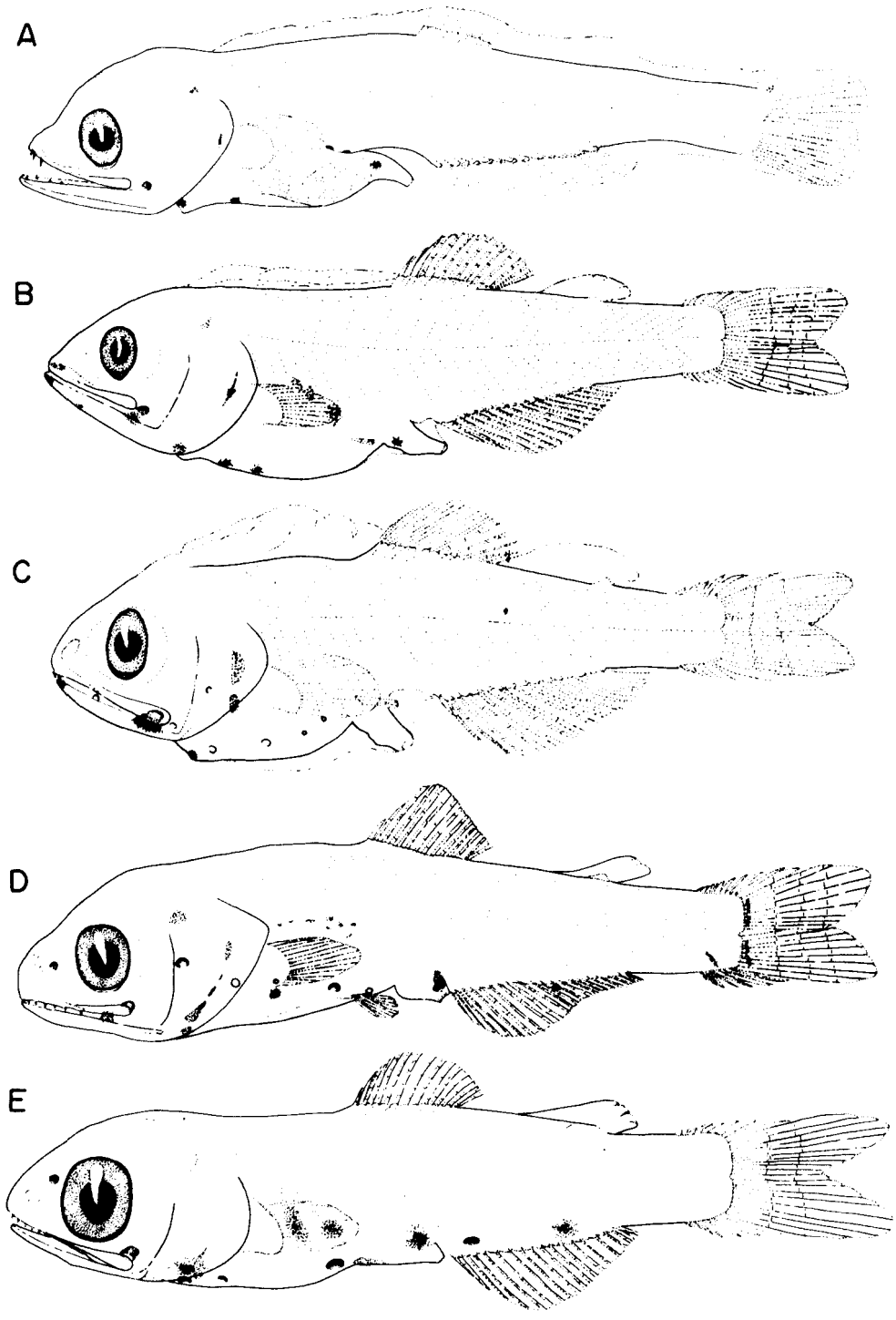

FIGURE 3.—Larvae of *Benthosema*. A. *B. glaciale*, 7.2 mm; B. *B. glaciale*, 10.5 mm; C. *B. suborbitale*, 9.2 mm; D. *B. pterota*, 8.5 mm; E. *B. fibulatum*, 8.7 mm.

larvae about 6.0 mm long. Thereafter the pattern diverges as shown in Table 1, but both species gradually add about a dozen pairs during the larval period. Specimens of *B. pterota* from the Persian Gulf off India, formed photophores at somewhat larger sizes than larvae of *B. panamense*, but in the same sequence. Transformation occurs at a small size, 10-12 mm in *B. panamense-pterota* and 11-13 mm in *B. fibulatum*.

Photophores appear relatively late in larvae of *B. suborbitale* and *B. glaciale*, however, the Br_1, Br_2, Op_2, and PO series appear in late larvae of both species (Table 1). Transformation occurs at about 9-11 mm in both species. The larvae of *B. panamense-pterota* and *B. fibulatum* are close to the larvae of *Diogenichthys* in several characters including body shape, gut shape, and early appearance of photophores.

As in *Benthosema*, the larval characters of *Hygophum* suggest some divergence within the genus, although all species have a highly characteristic series of isthmal melanophores, form the dorsal fin late in the larval period, and develop no photophores other than the Br_2, as larvae (Figure 4). The genus contains three divergent types of larvae. The most unusual of these are the extremely elongate larvae of *H. reinhardti* and *H. atratum*, which have very narrow eyes that are underlain by prominent choroid tissue and are borne on short stalks (Figure 4A). The amount of pigmentation along the gut and tail and on the myosepta and fin fold increases throughout the larval period.

A second larval type is represented by the largest number of species, *H. proximum*, *H. hygomi*, and *H. brunni*, all illustrated (Figure 4B-D), as well as *H. benoiti*, *H. hanseni*, and an undescribed form in our collection. These larvae are only moderately slender and have unstalked eyes of moderate width, subtended by prominent choroid tissue. Melanophores are located chiefly on the head and gut, however some species have pigment on the myosepta and fin fold. The trend in this group of species is for the early larval stages to have the heaviest pigment and for melanophores to be lost as development proceeds.

A third type of larva is exhibited by *H. macrochir*, *H. taaningi*, and an undescribed form in our collection (Figure 4E, F). These are relatively deep-bodied, have large, relatively wide eyes with little or no choroid tissue, and lack tail pigment. Also, the gut has a highly distinctive form; the anterior half has a very small diameter and opens dorsally into a prominent enlarged posterior section. In *H. macrochir* this enlarged section is covered with large melanophores. Larvae of this group occur only in the Atlantic.

The genus *Hygophum* affords an excellent example of the taxonomic utility of larval stages. The juveniles and adults of some species are notoriously difficult to identify. In contrast, the larvae of these species are highly distinct and can be readily identified. We have 11 such distinct larval types, whereas only 9 species are currently known for the adults. Search for adults of the two remaining larval types has led to the discovery of two undescribed species. In addition, characters of the adults of this genus reveal little about the relationships of the member species (Becker, 1965). A study of the larvae, however, shows that there are three highly distinct subgeneric groups, each containing from two to six closely related species. Such an independent view of the complete species complement of a genus is an invaluable tool in the formal revision of that genus.

Larvae of the species of *Symbolophorus* are perhaps the most cohesive of all myctophine genera (Figure 5A). In all species known to us the pectoral fin is large and is supported by an elongate aliform base. Also, the pelvic fins are large and develop earlier than in any other lanternfish genus. The narrow eyes have choroid tissue and are borne on short stalks. The amount of pigmentation decreases towards the end of the larval period. Most species attain a large size—up to 24 mm. The species differ principally in the size at which various larval structures appear.

The closely related genus, *Myctophum*, has a diversity of larval form unmatched in the family (Figures 5, 6, 7). Before taking up the bulk of the species in this genus we must first examine the most aberrant of all lanternfish larvae, that of *M. aurolaternatum* (Figure 5B). In this remarkable larva the eyes are borne on long stalks and the free trailing section of the gut is almost as long as the fish itself. The dorsal fin forms at the margin of the fin fold. These characters are so bizarre that it would seem preposterous to identify it as a lanternfish larva, much less that of *M. aurolaternatum*. Nonetheless, Å. Vedel Tåning first suggested the true identity of this larva (E. Bertelsen, pers. commun.) which we can now confirm since recently receiving the critical transforming specimens through the courtesy of Warren Freihofer (California Academy of Science). The uniqueness of this larva would certainly suggest

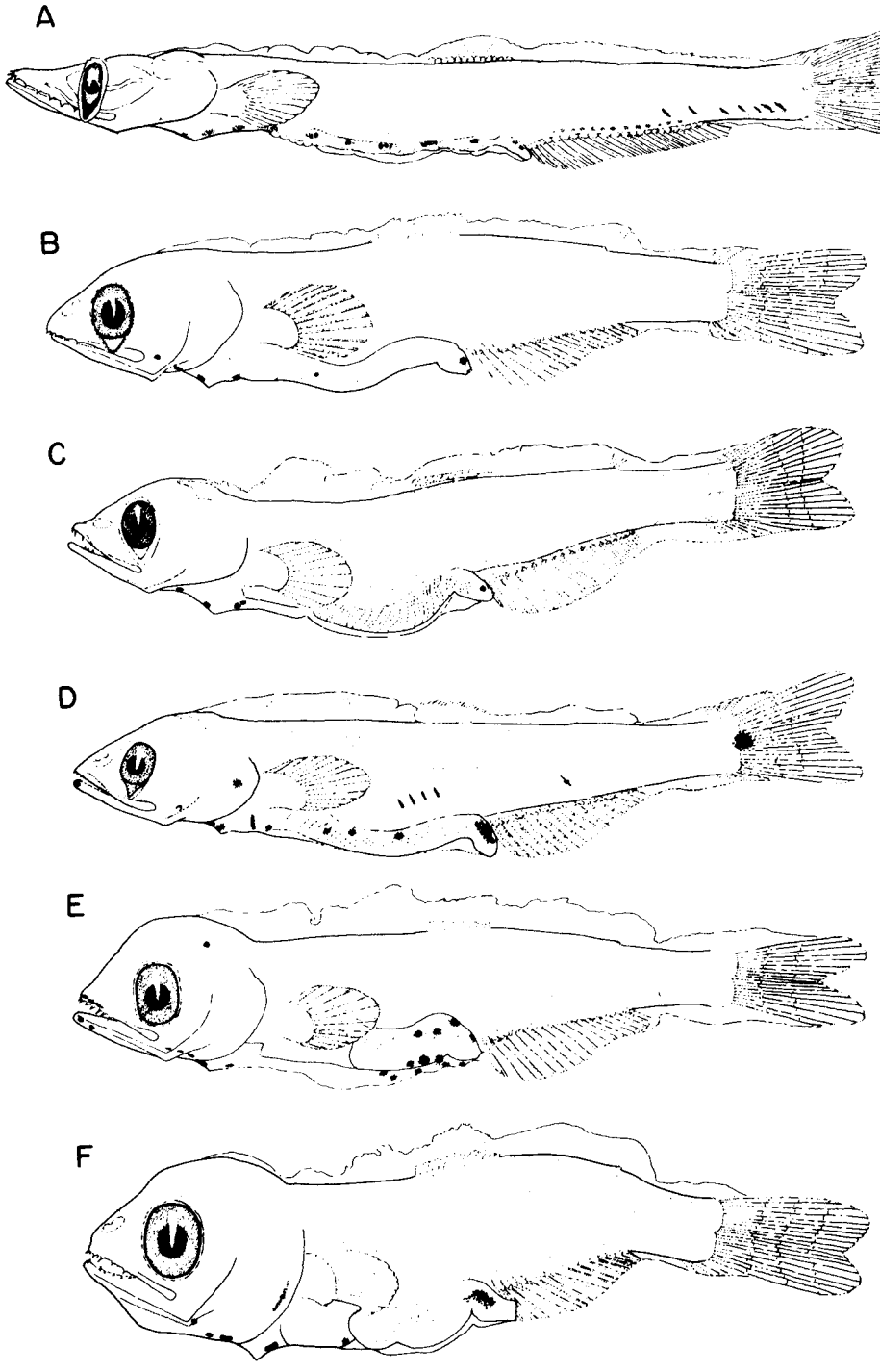

FIGURE 4.—Larvae of *Hygophum*. A. *H. reinhardti*, 12.8 mm; B. *H. proximum*, 8.9 mm; C. *H. hygomi*, 8.1 mm; D. *H. brunni*, 9.7 mm; E. *H. macrochir*, 7.3 mm; F. *H. taaningi*, 6.8 mm.

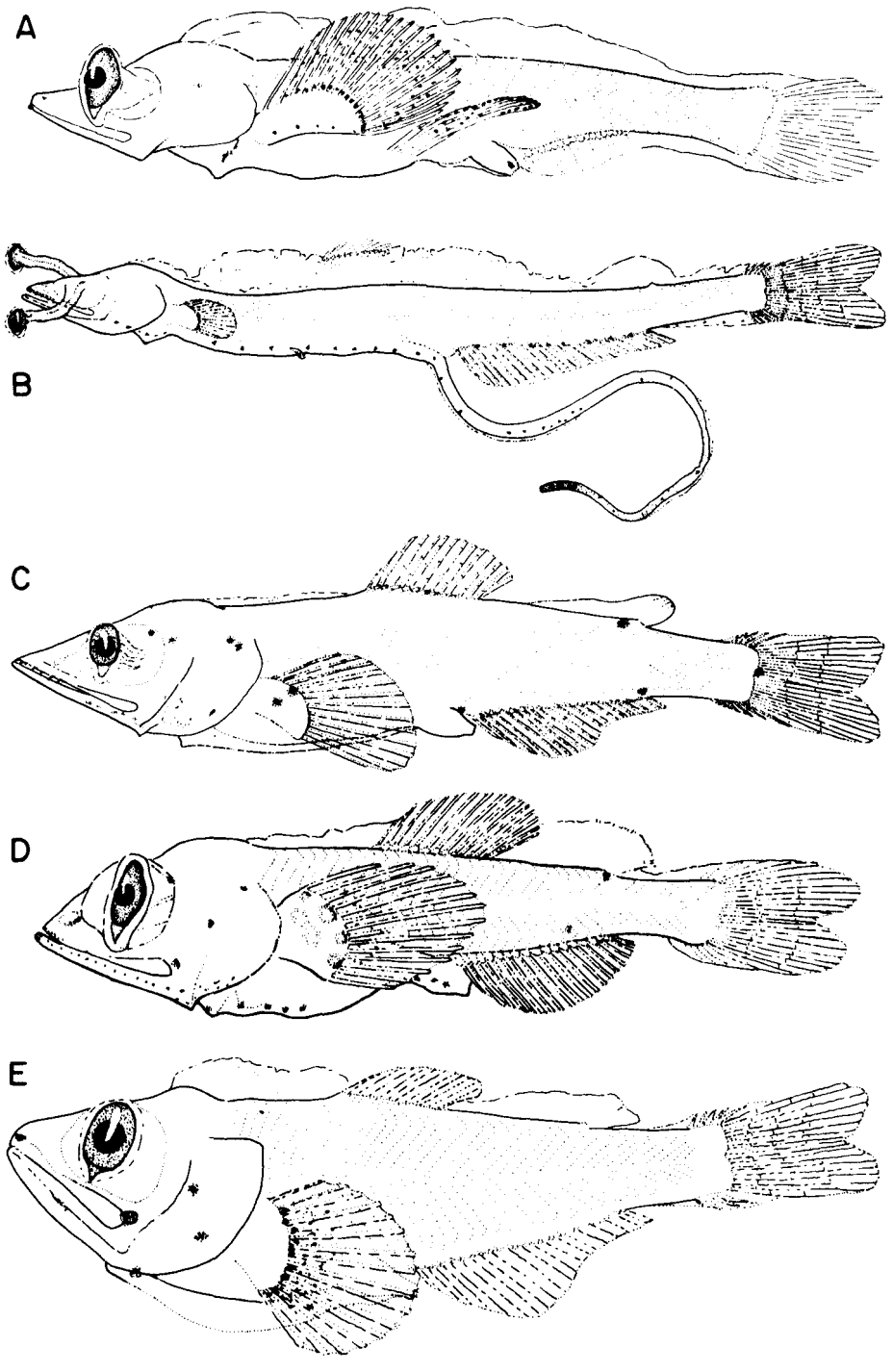

FIGURE 5.—Larvae of *Symbolophorus* and *Myctophum*. A. *S. californiense*, 9.6 mm; B. *M. aurolaternatum*, 26.0 mm; C. *M. punctatum*, 13.6 mm; D. *M. nitidulum*, 8.2 mm; E. *M. phengodes*, 9.8 mm.

the creation of a distinct genus for *M. aurolaternatum* and it is highly probable that corroborative characters will appear after careful reexamination of the adults.

With the removal of *M. aurolaternatum*, the remaining larvae of *Myctophum* form a diverse, yet recognizable, group. All have large broad pectoral fins supported on a highly characteristic fan-shaped base. The species may be divided into two groups, those which form only the Br_2 photophores and those which develop additional photophores during the larval period. In the first group the elongate larva of *M. punctatum* (Figure 5C) has stalked eyes and a slightly aliform pectoral fin base, reminiscent of *Symbolophorus* larvae, and may be the closest relative of that genus among the species of *Myctophum*. A closely related species, *M. nitidulum*, is also stalk-eyed, but is deeper-bodied, more heavily pigmented, and has a more fan-shaped pectoral fin base (Figure 5D). It is obvious from our studies that *M. nitidulum* is one member of a complex, that includes *M. affine* (not illustrated) and several other species. The lightly pigmented larva of *M. phengodes* has only a suggestion of stalked eyes but is similar in body shape to *M. nitidulum* (Figure 5E). The larval characters substantiate Paxton's (1972) decision to abolish the genus *Ctenoscopelus*, established for this species by Fraser-Brunner (1949).

The other major group of *Myctophum* is characterized by the appearance of the Dn photophore anterior to the eye, usually early in the larval period. These species fall into three rather distinct species groups on the basis of body and eye shape. The first is a group of four rotund broad-headed species, which have large unstalked eyes subtended by a short mass of choroid tissue. Of these, the larvae of *M. asperum* are the most heavily pigmented, particularly on the body (Figure 6A). Pigment is confined to the head in *M. obtusirostre*, is heavy under the posterior part of the gut in *Myctophum* sp. (possibly *brachygnathum*) and is developed on the jaws, branchistegal membrane and lower part of the pectoral fin base in *Myctophum* sp. (possibly *fissunovi*) as seen in Figure 6B-D. The latter three species form the PLO photophores on the pectoral fin base soon after the appearance of the Dn organs (Table 2).

Nafpaktitis (1973) has listed a number of characters for distinguishing adult *M. obtusirostre* from *M. brachygnathum*. He showed that *M. pristilepis* is a synonym of *M. brachygnathum*. The status of *M. imperceptum* Bekker and Borodulina has yet to be determined.

A second larval type is represented by *M. selenops* (Figure 7A) and a closely related species restricted to the Indian Ocean and Persian Gulf for which we can find no adult (Figure 7B). In these rotund species, the head is relatively longer and narrower than in the previous group and the slightly stalked eyes are narrower and bear more elongate choroid tissue. The two species differ in that the eyes of the unnamed larva are more definitely stalked than in *M. selenops*. Also the pigment pattern is markedly different, as is the size at which photophores appear. We have carefully examined larvae of *M. selenops* from the Atlantic, Indian, and Pacific Oceans, find them to be identical in all three oceans, and seriously question Wisner's (1971) allocation of the Hawaiian population as a distinct species, based on slight differences in relative eye size and SAO photophore orientation.

The third type of larvae that develop the Dn photophores is represented by *M. spinosum* (Figure 7C) and *M. lychnobium* (Figure 7D). These are elongate fusiform larvae with moderately narrow unstalked eyes, underlain by a pronounced choroid mass. *M. spinosum* is the more slender of the two and is extremely heavily pigmented, especially in older larvae. Pigmentation in *M. lychnobium* is confined to that in the illustrated

TABLE 2.—Sequence of photophore formation in species of *Myctophum* that form two or more pairs during the larval stage.

Species	Size range (mm)	Size at first formation (mm)				Size at transformation (mm)
		Br_2	Dn	PLO	PO_1	
M. asperum	ca. 3.0-9.8	4.2	4.6	9.8	—	Early transf. 11.4
M. obtusirostre	ca. 3.0-8.9	3.8	4.0	ca. 7.1	8.9	Late transf. 12.5
M. sp. (possibly *fissunovi*)	ca. 3.0-7.1	4.1	4.1	7.1	—	—
M. sp. (possibly *brachygnathum*)	6.0-11.4	6.0	6.0	ca. 9.0	ca. 9.0	Late transf. 13.8
M. lychnobium	3.5-12.1	ca. 6.0	6.3	12.1	—	Late transf. 14.2
M. spinosum	3.5-13.7	ca. 5.5	7.2	13.7	—	Late transf. 14.5
M. selenops	3.5-7.5	5.1	5.1	6.2	7.5	Late transf. 11.4
M. sp.	4.0-9.1	ca. 7.0	9.1	—	—	—

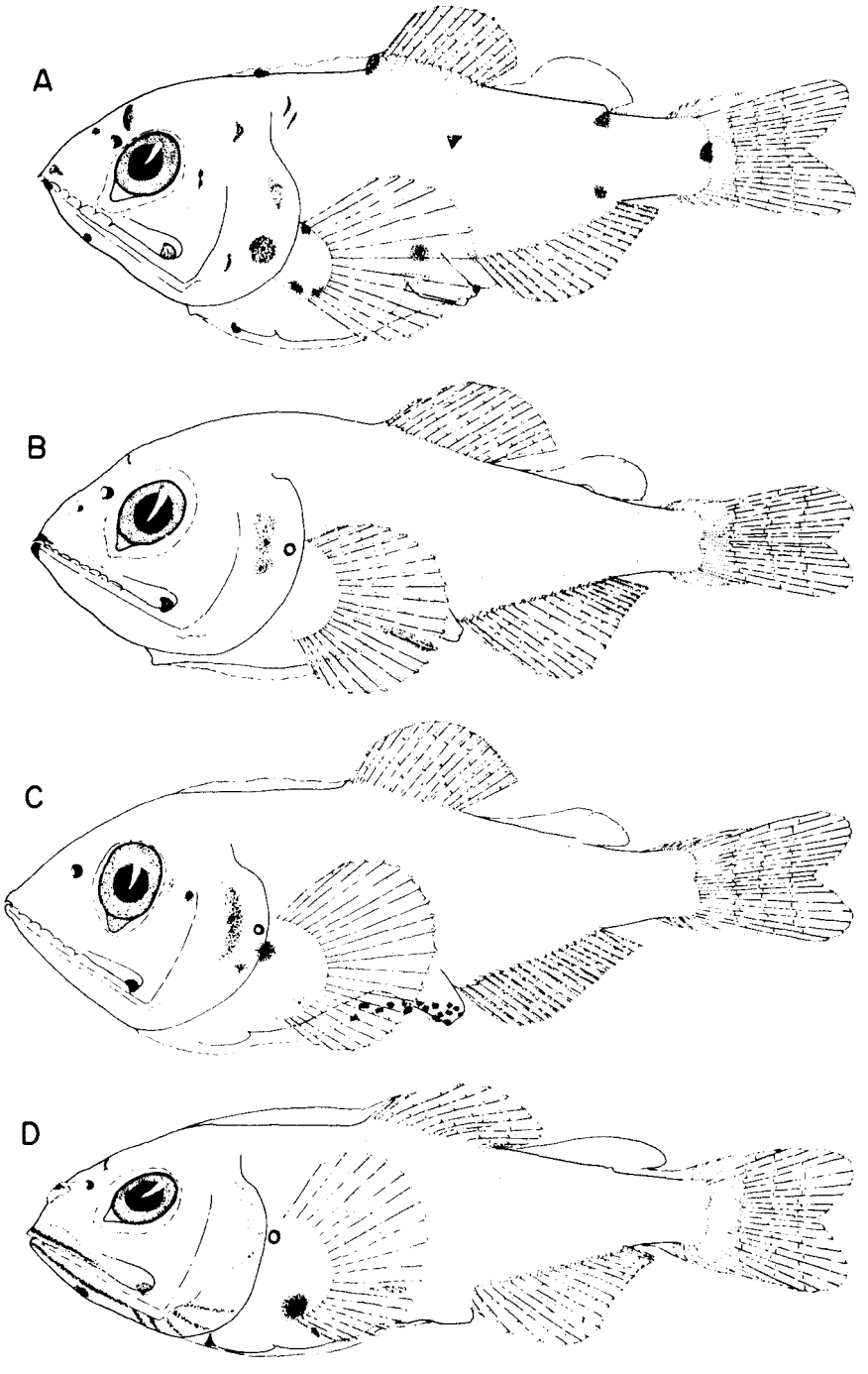

FIGURE 6.—Larvae of *Myctophum*. A. *M. asperum*, 6.8 mm; B. *M. obtusirostre*, 7.6 mm; C. *M.* sp. (possibly *brachygnathum*), 7.5 mm; D. *M.* sp. (possibly *fissunovi*), 7.4 mm.

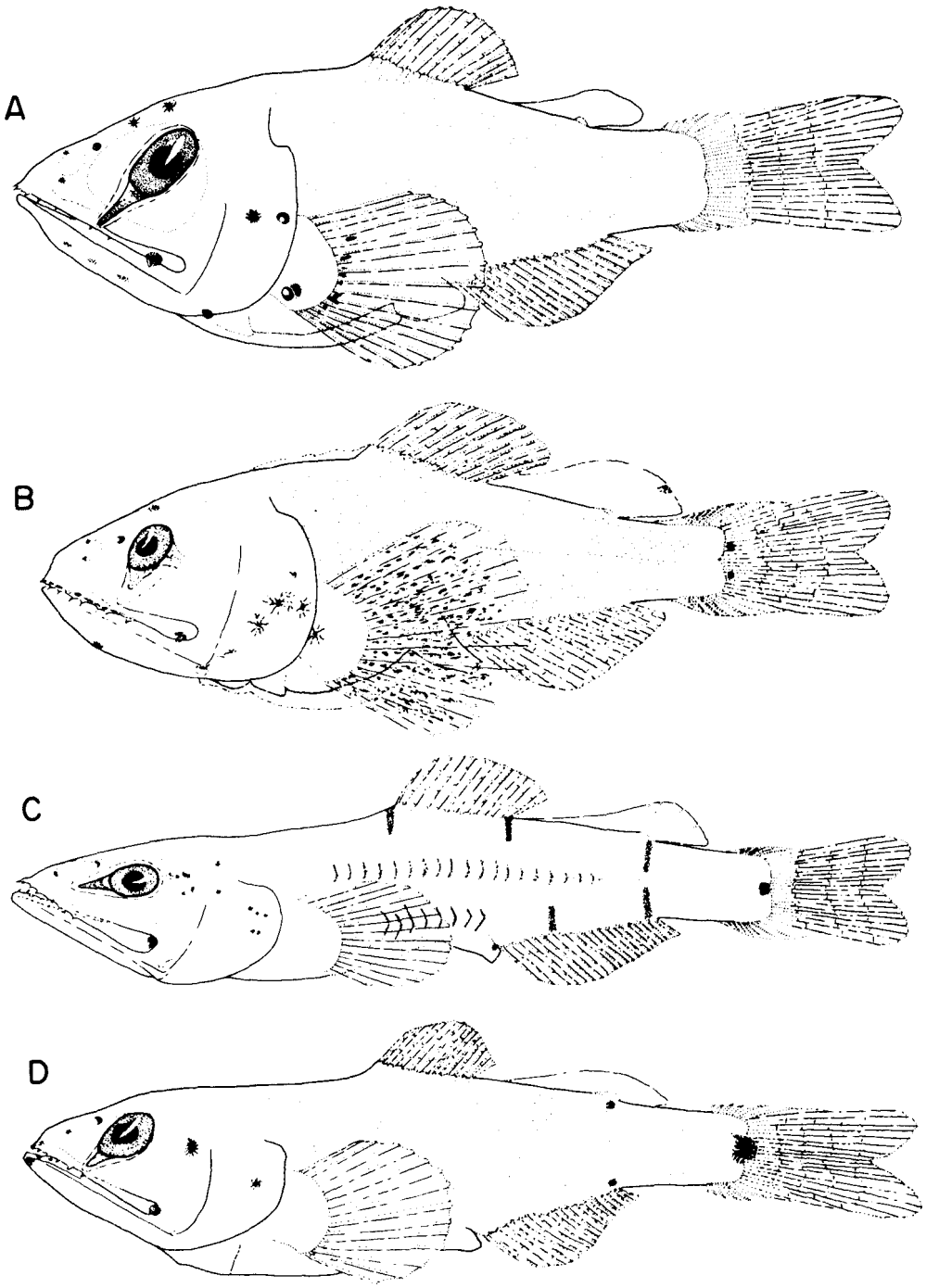

FIGURE 7.—Larvae of *Myctophum*. A. *M. selenops*, 7.8 mm; B. *M.* sp., 9.1 mm; C. *M. spinosum*, 9.0 mm; D. *M. lychnobium*, 9.5 mm.

specimen. Only larvae of *M. lychnobium* have been taken in the eastern Pacific, whereas both species have been taken in the central and western Pacific and in the Indian Ocean. Taxonomists dealing with adult characters only, have placed *M. lychnobium* in synonymy with *M. spinosum* but the distinctiveness of the larvae suggests that the adult characters should be reexamined.

The larvae of *M. spinosum* and *M. lychnobium*, although clearly developing the Dn pair of photophores, resemble the larvae of *M. punctatum* in body shape and pigmentation, a species which does not develop the Dn as larvae. Actually, there are some common characters of pigmentation and eye structure which appear in all of the groups of *Myctophum* species described above. What we appear to be dealing with is a mosaic of larval characters in a highly complex genus. The taxonomy of *Myctophum* presently is confused; our work on the larvae should help define the number of species in the genus and, perhaps, adult characters will emerge that can be combined with larval characters to define the phyletic lines within the genus.

Larvae of the four genera known collectively as the slendertailed myctophids are shown in Figure 8. Quite obviously there are two highly divergent generic pairs. *Loweina* and *Tarletonbeania* are characterized by large oval eyes, posterior placement of median fins to accommodate the immense fin fold, and elongated lower pectoral rays bearing spatulate processes. *Gonichthys* and *Centrobranchus* are characterized by a deep but markedly compressed head and body and small narrow eyes with extremely elongate choroid tissue. As stated earlier, the larval characters suggest strongly that the two generic pairs are not closely related and should not be grouped into a tribe. The *Gonichthys-Centrobranchus* pair is similar in eye shape and gut shape to some species of *Myctophum*, however no species of *Myctophum* even approaches this pair in body shape. The characters of the other pair are so divergent as to give no clue of their affinities within the subfamily Myctophinae.

THE SUBFAMILY LAMPANYCTINAE

The subfamily Lampanyctinae is considerably larger than the Myctophinae; it contains about 19 genera and 200-250 species compared with 12 genera and about 75 species in the Myctophinae. Paxton (1972) divided the genera into four tribes on the basis of a combination of osteological features and characters of the photophores. In a previous paper (Moser and Ahlstrom, 1972) we discussed Paxton's placement of genera in these tribes and indicated that the larval characters suggested a somewhat different distribution of genera among the four tribes. For the purposes of this discussion the tribes referred to here are those suggested by the larval characters.

In general, the larvae of the Lampanyctinae are much less diverse in larval characters and specializations than are the larvae of the Myctophinae, although exceptions to this may be found in two of the lampanyctine tribes, the Diaphini and the Lampanyctini.

The tribe Diaphini is made up of two genera —*Diaphus* contains about 50 species and *Lobianchia* has 3 species. Both genera develop photophores, in addition to the Br_2, during the larval period; in fact more are developed in *Diaphus* than in any other lanternfish genus.

There are two basic larval types in *Diaphus* (Figure 9A, B). One has a slender body, small head, and a series of persistent melanophores on the ventral midline of the tail. The other type has a deeper body, bulbous head, and a single persistent ventral tail melanophore, or none. It is exceptional for larvae of either type to develop pigment on the head and it never occurs between the eyes, as is common in *Lampanyctus*. Both types do form embedded melanophores at the base of the caudal fin rays.

The slender type is restricted to the species that develop a suborbital photophore as adults (*Diaphus* sensu stricto of Fraser-Brunner, 1949) and is represented in Figure 9A by *D. theta*. The stubby type is represented by *D. pacificus* (Figure 9B). The specimens illustrated for the two species are rather early larval stages which have not yet formed their larval photophores, other than the Br_2. The first additional pair to form in both types is the PO_5 and then the PO_1 (Table 3). The large genus *Diaphus*, except for the Atlantic species ably reviewed by Nafpaktitis (1968), is in a state of taxonomic confusion. Various workers (Fraser-Brunner, 1949; Bolin, 1959) have attempted to split the genus into smaller, more cohesive groups; the larval evidence would suggest that at least two divergent groups are present.

The larvae of the three species of *Lobianchia* are

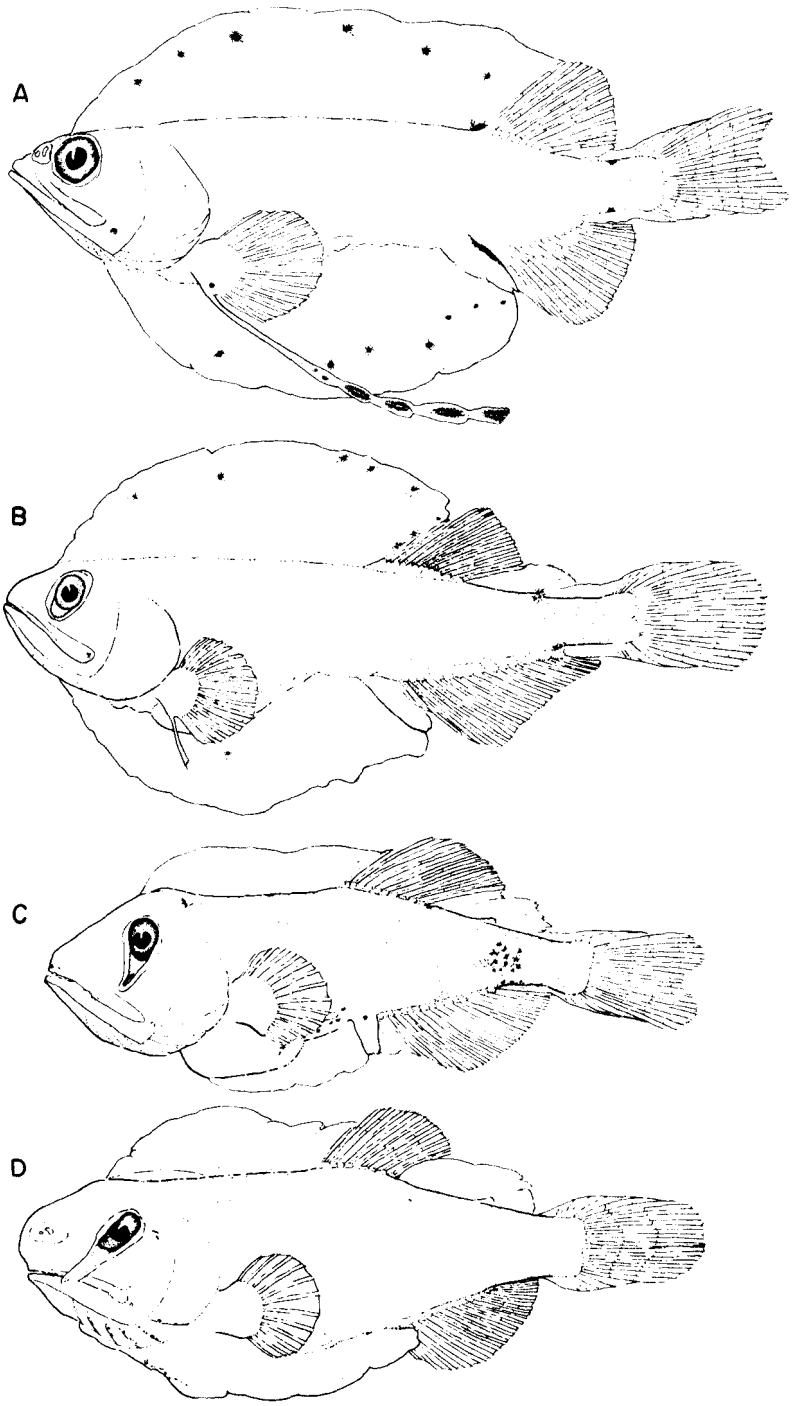

FIGURE 8.—Larvae of Gonichthyini. A. *Loweina rara*, 17.6 mm; B. *Tarletonbeania crenularis*, 18.9 mm; C. *Gonichthys tenuiculus*, 7.7 mm; D. *Centrobranchus choerocephalus*, 7.3 mm.

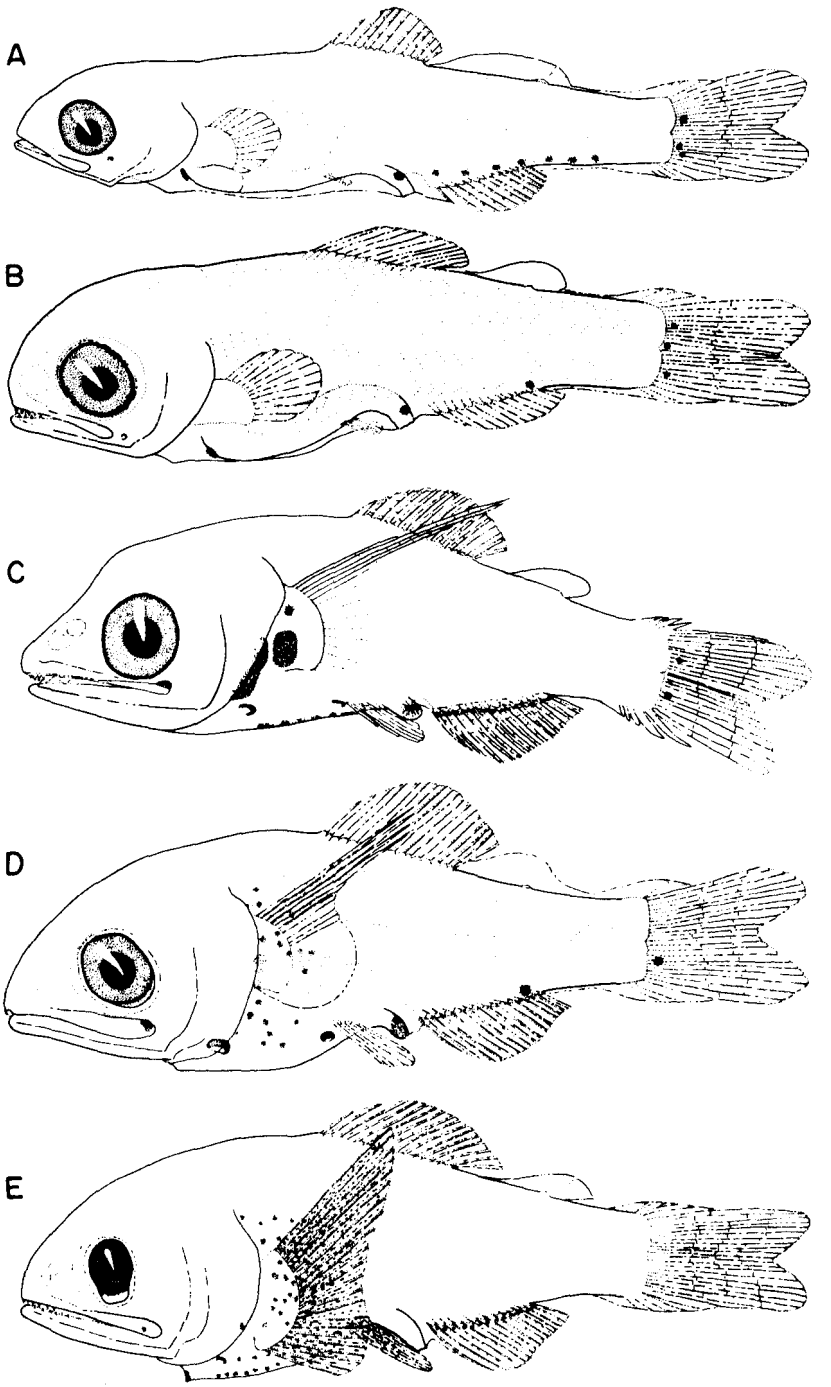

FIGURE 9.—Larvae of *Diaphus* and *Lobianchia*. A. *D. theta*, 6.9 mm; B. *D. pacificus*, 5.2 mm; C. *L. urolampus*, 7.2 mm; D. *L. gemellari*, 6.7 mm; E. *L. dofleini*, 8.2 mm.

TABLE 3.—Sequence of photophore formation in larvae of two species of *Diaphus*.

Species	Size larva (mm)	Photophores	No. of photophore pairs	Smallest juvenile (mm)
D. theta	6.2	Br_2 PO_5	2	ca. 12.0
	7.6	Br_2 PO_5 PO_1	3	
	8.2	Br_2 PO_5 PO_1 VO_1	4	
	8.6	Br_2 PO_5 PO_1 VO_1 PO_2 Op_2	6	
	9.0	Br_2 PO_5 PO_1 VO_1 VO_1 PO_2 Op_2 PO_3 PO_4 VO_5	9	
	9.2	Br_2 PO_5 PO_1 VO_1 PO_2 Op_2 PO_3 PO_4 VO_5 VLO	10	
D. pacificus	5.7	Br_2 PO_5 PO_1	3	9.8
	6.2	Br_2 PO_5 PO_1 PO_2 PVO_1	5	
	6.5	Br_2 PO_5 PO_1 PO_2 PVO_1 PO_3	6	
	7.5	Br_2 PO_5 PO_1 PO_2 PVO_1 PO_3 VO_1	7	

deep-bodied, have large broad heads, and are easily identified by their unique wing-shaped pectoral fins (Figure 9C-E). The larvae of all three species are heavily pigmented and develop the Br_2, PO_1, and PO_5 photophores sequentially. In *L. urolampus* (Figure 9C) and *L. gemellari* (Figure 9D) the eyes are large and nearly round and the lower pectoral rays are delayed in developing. In *L. dofleini* the lower pectoral rays develop along with the produced upper rays and the eye is completely different (Figure 9E). With its narrow elliptical shape and unique squarish mass of choroid tissue, it is the single obvious exception to the rule of narrow eyes in the subfamily Myctophinae and rounded eyes in the Lampanyctinae. All other larval characters identify this species as a *Lobianchia,* and we conclude that the narrowing of the eye in this species occurred independently as a secondary adaptation.

In our view the tribe Lampanyctini contains the genera *Lampanyctus, Triphoturus, Stenobrachius,* and *Parvilux.* As recently as Fraser-Brunner's (1949) review of the family Myctophidae, *Lampanyctus* was still a catchall genus with a number of disparate subgenera. Since then the subgenera *Stenobrachius, Triphoturus,* and *Lepidophanes* have been removed from *Lampanyctus* and afforded generic status. *Lepidophanes* has been further split into the genera *Lepidophanes* and *Bolinichthys.* All of the separated genera have distinctive larval morphs. With their removal, the species of *Lampanyctus* form a more coherent assemblage of 40-50 species, and despite the diversity of larval specializations encountered in the genus, there is a central morph and pattern of larval development.

Lampanyctus larvae are deep-bodied and bigheaded. In older larvae characteristic pigment can develop at a variety of locations such as the tip of the lower jaw, between the eyes, the back of the head, the side of the head, the adipose fin, the pectoral fin, internally in the region of the cleithra, and along the myosepta. The pigment patterns are of prime importance in identifying the larvae to species.

There are several rather distinct larval types in *Lampanyctus.* One of these consists of a group of species whose adults are characterized by having the pectoral fins much reduced or even absent, and has been separated recently as a distinct genus *Paralampanyctus* by Kotthaus (1972) with *P. niger* as type. Previously, Günther (1887) had proposed the generic name *Nannobrachium* for this species and this has priority over *Paralampanyctus* (John Paxton, pers. commun.). There is a remarkable trend of jaw specialization in the larvae of this group (Figure 10). The larva of *L. ritteri* has jaws of moderate length and the other species shown have progressively longer jaws with more prominent teeth, particularly anteriorly. This trend culminates in the larva of *Lampanyctus* sp. (possibly *achirus*) which somewhat resembles a larval billfish. This species will lack the pectoral fin in juveniles and adults, even though it is well developed in the larvae. The pectoral fins are also large in *L. regalis* and *L. niger* larvae, but will be small and weakly developed in adults. This disparity is even more apparent in another eastern Pacific species, which lacks pectoral fins as an adult, but whose larvae have the largest pectoral fins with the highest number of rays that we have encountered among *Lampanyctus* larvae. Other less spectacular specializations appear in the other subgroups of *Lampanyctus,* but it appears that the larval characters will be helpful in defining the species composition of the several subgenera.

Representatives of other genera of Lampanyctini, *Triphoturus, Stenobrachius,* and *Parvilux* are illustrated in Figure 11A-C. Small larvae of *Triphoturus* and *Stenobrachius* have a row of melanophores along the ventral margin of the tail

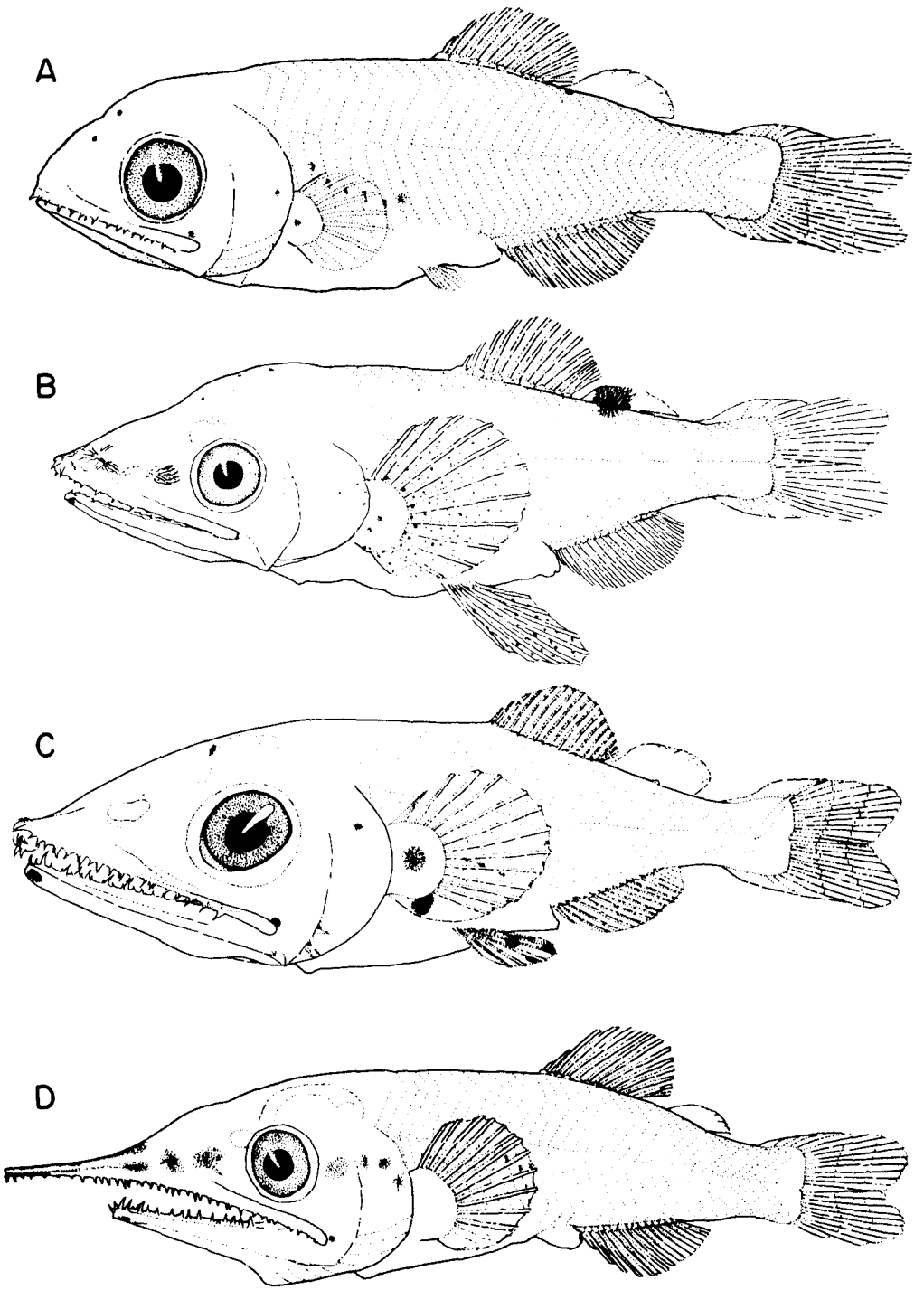

FIGURE 10.—Larvae of *Lampanyctus*. A. *L. ritteri*, 10.1 mm; B. *L. regalis*, 9.1 mm; C. *L. niger*, 8.7 mm; D. *L.* sp. (possibly *achirus*), 13.4 mm.

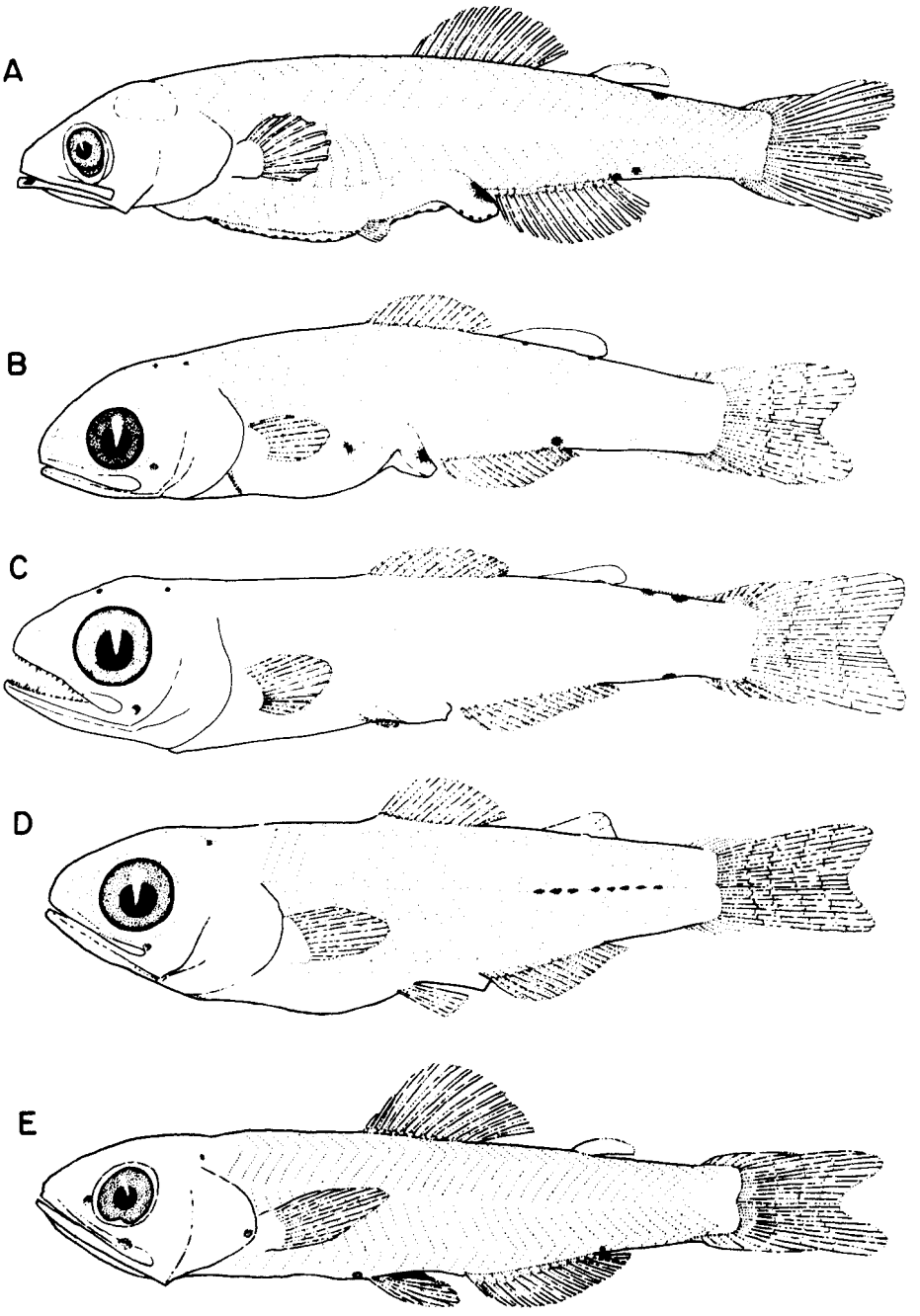

FIGURE 11.—Larvae of Lampanyctini and Gymnoscopelini. A. *Triphoturus mexicanus*, 10.5 mm; B. *Stenobrachius leucopsarus*, 10.4 mm; C. *Parvilux ingens*, 14.4 mm; D. *Bolinichthys supralateralis*, 9.4 mm; E. *Ceratoscopelus townsendi*, 16.6 mm.

but these coalesce into one or two spots in mid-stage larvae. *Triphoturus* larvae are characterized further by their distinctive head shape and by the series of melanophores along the ventral midline below the gut. *Stenobrachius* larvae add considerable pigment late in the larval period, particularly along the dorsum and on the myosepta of the trunk. The larvae of *Parvilux* are distinct in shape and pigmentation. Paxton (1972) placed this genus in *Lampanyctus* based on osteological characters. In certain photophore arrangements, however, particularly in the posterior placement of the VLO and the nonangulate arrangement of the SAO, the genus appears to us to be more closely related to *Stenobrachius* than to *Lampanyctus*. These characters in addition to the distinctness of the larvae would suggest that the validity of *Parvilux* should be reconsidered.

The tribe Gymnoscopelini judged from larval and/or adult characters contains a dozen genera (*Notoscopelus*, *Lampichthys*, *Scopelopsis*, *Ceratoscopelus*, *Lepidophanes*, *Bolinichthys*, *Lampadena*, *Taaningichthys*, *Dorsadena*, *Lampanyctodes*, *Gymnoscopelus*, and *Hintonia*). The larvae of these genera are united by a group of common characters, including a distinctive, usually slender, body outline, a series of melanophores on the dorsal and ventral midlines of the tail (in most genera), and the development of a group of photophores during the larval period, most notably the PO_5, PLO, and Vn. The larvae of this tribe were treated extensively in a previous paper with representative larvae illustrated for 10 of the 12 genera (Moser and Ahlstrom, 1972). Additional species of *Bolinichthys* (*B. supralateralis*, Figure 11D), *Ceratoscopelus* (*C. townsendi*, Figure 11E), *Lampadena* (*L. luminosa*, Figure 12B), *Lepidophanes* (*L. gaussi*, Figure 12C) are illustrated herein. Illustrations of *Notoscopelus resplendens* (Figure 12A) and *Scopelopsis multipunctatus* (Figure 12D) are included for comparative purposes. It need only be mentioned here that the clusters of closely related genera within this tribe are readily apparent from examining the larval characters, especially the sequence of photophore development, and these groupings agree closely with those established on the basis of adult characters.

The species *Notolychnus valdiviae* has so many unique adult characters that Paxton (1972) assigned it to the monotypic tribe *Notolychnini*. Likewise the larva has a number of unusual characters (Figure 12E). The shape of the eye is variable from specimen to specimen; it can be narrow and elliptical or nearly round, but most typically would be classified as irregular in shape. The shape of the head, body, and gut is unusual and distinctive. The larval characters are of little help in elucidating the affinities of this species within the Myctophidae and, when added to the list of unique adult characters, only magnify the problem. It would seem to make just as much sense to establish a separate subfamily for *Notolychnus* as to place it in a monotypic tribe in the subfamily Lampanyctinae.

The larvae illustrated in this paper comprise 55 species representing 24 genera. Illustrations are included for larvae of 11 of the 12 genera in the subfamily Myctophinae; not included are illustrations of *Diogenichthys* (see Moser and Ahlstrom, 1970 for *D. laternatus* and *D. atlanticus*). In the subfamily Lampanyctinae larvae are illustrated for 13 of the 19 genera. The omitted genera (*Lampichthys*, *Lampanyctodes*, *Gymnoscopelus*, and *Tanningichthys*), all from the tribe Gymnoscopelini, are illustrated in Moser and Ahlstrom (1972). Larvae of *Hintonia* and *Dorsadena* have not yet been identified.

SOME EVOLUTIONARY CONSIDERATIONS

With this brief review of lanternfish larvae completed, let us now turn to an interesting problem of myctophid evolution to which study of the larvae may contribute importantly—the evolution of photophore pattern. With a single exception, all adult myctophids have two conspicuous rows of photophores that extend the length of the body on each side of the ventral midline. The photophores are grouped and positioned in a definite and often diagnostic pattern. Also, lanternfishes have a specific pattern of photophores on the sides of the body, below the lateral line, and on the ventral aspect of the head. The exception is *Taaningichthys paurolychnus*, which appears to lack body photophores entirely. In addition to these photophores, some lanternfish genera have photophores positioned in a pattern above the lateral line and some have small "secondary" photophores distributed more generally over regions of the body and head. Another type of luminous structure present on most myctophids are discrete glands located at the caudal peduncle. Typically, these are sexually dimorphic in character and, doubtless, play some part in courtship

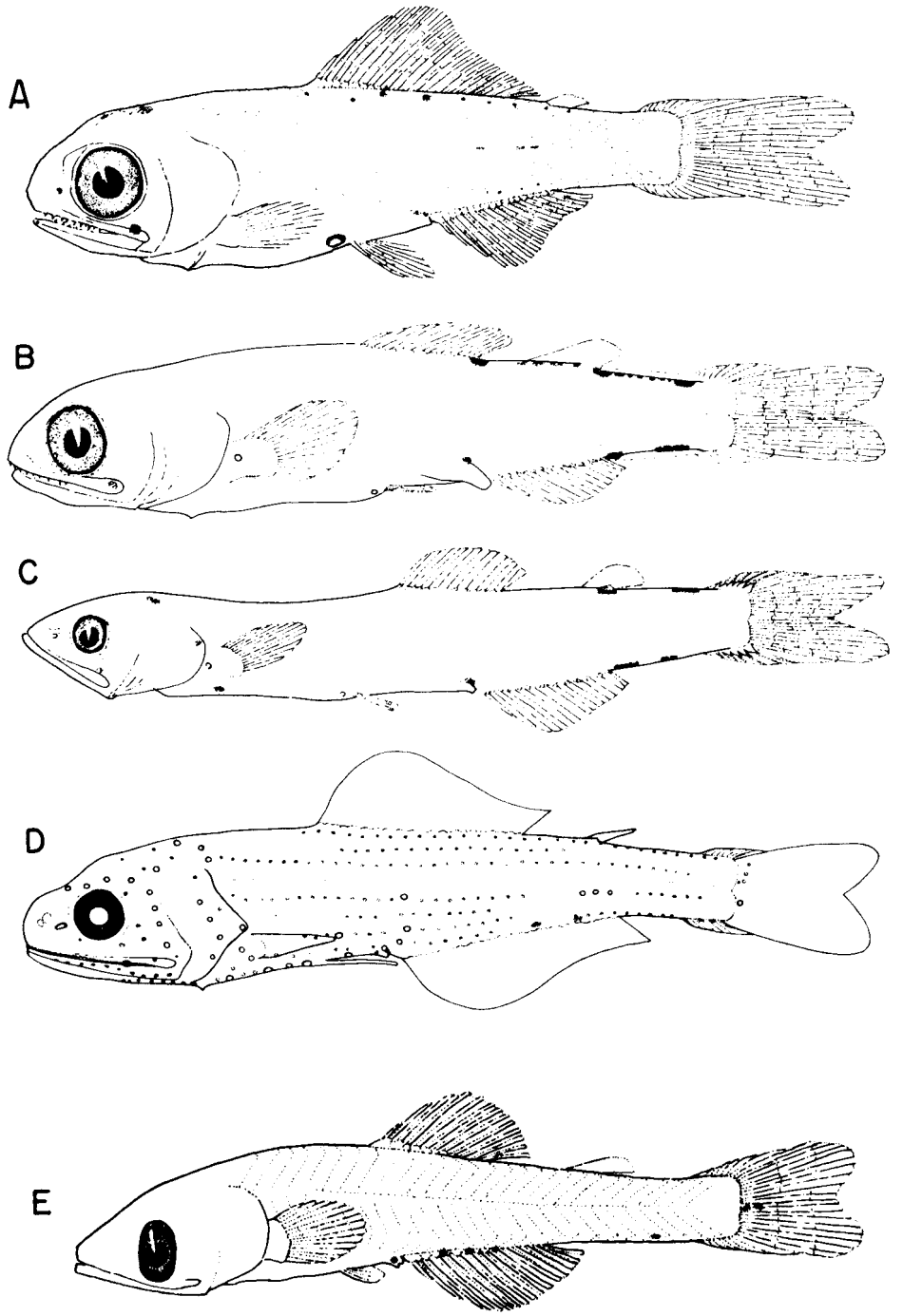

FIGURE 12.—Larvae of Gymnoscopelini and Notolychnini. A. *Notoscopelus resplendens*, 11.2 mm; B. *Lampadena luminosa*, 12.8 mm; C. *Lepidophanes gaussi*, 13.5 mm; D. *Scopelopsis multipunctatus*, 17.5 mm; E. *Notolychnus valdiviae*, 9.2 mm.

behavior. Finally, some myctophids have small patches of soft whitish, apparently luminous, tissue located at various regions of the body.

The most popular speculation as to the possible function of the patterns of photophores and luminous scales is that they function in species recognition (see McAllister, 1967). An explanation for the universality of the two ventral rows was postulated by Clarke (1963). His suggestion that these downward directed rows emit a continuous light of ambient wavelength, which conceals the fish from deeper-living predators by countershading, has much appeal.

We have long been interested in the mechanism by which such patterns of photophores could have evolved and believe we have gained some insight into this mechanism through our studies of the larval stages. Our proposal, as expressed in an earlier paper (Moser and Ahlstrom, 1972), is that ancestral myctophids had a generalized arrangement of unspecialized photophores, one at the posterior margin of each scale pocket, and a group of similar photophores on the head. We further proposed that the specific photophore patterns of contemporary myctophids evolved through progressive enlargement and specialization of certain photophores of the generalized pattern and concurrent diminution or loss of the unspecialized photophores. This idea came to us upon discovering the remarkable transforming specimens of *Scopelopsis multipunctatus*, the adults of which have a small photophore at each scale pocket and a group of photophores on the head. In the adults, the "primary" organs can be distinguished only by their modified lens-bearing scales, but in the transforming specimens (Figure 11D) the primary photophores stand out clearly as enlarged members of the meristic series of light organs. It struck us that a similar arrangement of photophores might have existed in the adults of an ancestral species, and led to the development of our ideas on the evolution of photophore pattern. Our theory was further strengthened by neurological findings and by what we feel are inherent weaknesses in Bolin's (1939) and Fraser-Brunner's (1949) theory that photophore patterns evolved by the upward migration of organs from ventral rows of photophores.

Viewed from the standpoint of our theory the subfamily Myctophinae would be considered highly specialized, since it is here that diminution of secondary photophores has reached its highest degree; they are totally lacking in the subfamily. The individual "primary" photophores are typically highly developed and concentrated ventrally on the body. The ventral location of photophores in Myctophinae is probably related to their habitat. That is, they are generally shallow-living active fishes that have well-developed gas bladders and it is plausible that concentration of photophores ventrally on the body evolved as an adaptation for countershading and protection from deeper-living predators. This view of the Myctophinae is completely contrary to those previously held for this subfamily. On the basis of the "upward migration" theory of photophore evolution, myctophines were thought to be primitive unspecialized forms. Formerly, we too subscribed to this view, and contrasting the then supposed primitive features such as low photophore position and short jaws of the adults with the highly specialized and diverse features of the larvae, we proposed that the evolutionary pace had differed in the larval and adult stages of the subfamily. Our altered opinion would view both larvae and adults of the Myctophinae as highly advanced and would interpret the low photophores, prominent gas bladders, short jaws, and often narrow caudal peduncles as specialized adaptations of active surface-dwelling fishes.

Our view of the Lampanyctinae must also be revamped. Formerly we considered the diverse and often dorsally oriented pattern of photophores and accessary luminous tissue to be highly specialized features. Possibly, the luminous scalelike patches and luminous glands are specialized adaptations, but we feel that the presence of small secondary photophores and the dorsal positioning of primary photophores in many of the genera, indicate a retention of the ancestral condition. The Lampanyctinae are generally deeper-living than the Myctophinae and many genera are lethargic fishes that rest vertically in the water column (Barham, 1970). In deeper-living fishes with such a behavior pattern there would be little evolutionary advantage in having ventrally concentrated photophores, and the fat-invested swim bladders and long jaws typical of many genera could have evolved in relation to habitat and activity pattern. It is interesting that the most obvious exception in the subfamily, the Diaphini, are active, often surface-dwelling fishes with relatively short jaws and ventrally concentrated photophores. It is obvious from the present paper that the larvae of Lampanyctinae exhibit much less diversity than the Myctophinae, but we

no longer view the adult myctophines as being more "primitive" than the adult lampanyctines. We feel that the adults of both subfamilies are equally specialized and that these specializations are basically related to their particular habitat.

In summary, thorough study of the larvae of a teleost family such as the Myctophidae can be most helpful in species validation, in analyzing affinities at all taxon levels, and in assessing phylogenetic lineages. Also, the above discussion would indicate that larval studies can provide interesting insights into the major directions of evolution within a family of fish.

ACKNOWLEDGMENTS

George Mattson executed 15 of the illustrations (Figures 1E, 4A, 5A and D, 8A-D, 10A, B, and D, 11A and E, and 12A and E) and we thank him for his efforts. The remaining illustrations were made by one of us (H. G. Moser). Larval specimens came from a variety of sources and we are especially indebted to the following persons for their generous provision of material: E. Bertelsen and J. Nielsen, Zoological Museum, Copenhagen; N. B. Marshall and A. Wheeler, British Museum; W. Nellen, Institute für meereskunde, Kiel, Germany; R. McGinnis and B. Nafpaktitis, University of Southern California (USC); R. J. Lavenberg, Los Angeles County Museum; R. Rosenblatt and R. Wisner, Scripps Institution of Oceanography (SIO); T. Clarke and J. Miller, University of Hawaii; W. Freihofer, California Academy of Sciences. We would like to thank B. Nafpaktitis and R. McGinnis, USC; R. Wisner, SIO; J. Paxton, Australian Museum, Sydney; and G. Krefft, Fisheries Institute, Hamburg, Germany, for sharing their vast knowledge of lanternfishes with us in numerous discussions. Discussions with N. B. Marshall, British Museum; B. Robison, Stanford University; and A. Kendall, Middle Atlantic Coastal Fisheries Center, National Marine Fisheries Service (NMFS); Sandy Hook, have been helpful in stimulating some of the ideas put forth herein. We appreciate the able technical assistance of Elaine Sandknop, Elizabeth Stevens, and Patricia Lowery, Southwest Fisheries Center La Jolla Laboratory, NMFS. Kenneth Raymond kindly lettered the illustrations.

LITERATURE CITED

BARHAM, E. G.
1970. Deep-sea fishes lethargy and vertical orientation. *In* G. B. Farquhar (editor), Proceedings of an international symposium on biological sound scattering in the ocean, p. 100-118. Maury Center for Ocean Science, Department of the Navy, Wash., D.C. MC Rep. 005.

BECKER, V. E.
1965. Lanternfishes of the genus *Hygophum* (Myctophidae, Pisces). Systematics and distribution. Tr. Inst. Okeanol. Akad. Nauk SSSR 80:62-103. (In Russ., Engl. Transl. No. 45, Natl. Mar. Fish. Serv., Syst. Lab., Wash., D.C.)

BENIRSCHKE, K., AND T. C. HSU (editors).
1971. An atlas of mammalian chromosomes, Vol. 5 and 6. Springer-Verlag, N.Y., 200 p.

BERTELSEN, E.
1951. The ceratioid fishes. Ontogeny, taxonomy, distribution and biology. Dana Rep., Carlsberg Found. 39, 276 p.

BOLIN, R. L.
1939. A review of the myctophid fishes of the Pacific coast of the United States and of Lower California. Stanford Ichthyol. Bull. 1:89-156.
1959. Iniomi Myctophidae. Rep. Sci. Results "Michael Sars" North Atl. Deep-Sea Exped. 1910. 4, 2(7):1-45.

CASTLE, P. H. J.
1969. An index and bibliography of eel larvae. J. L. B. Smith Inst. Ichthyol., Rhodes Univ., S. Afr. Spec. Publ. 7, 121 p.

CLARKE, W. D.
1963. Function of bioluminescence in mesopelagic organisms. Nature (Lond.) 198:1244-1246.

DE LIGNY, W.
1969. Serological and biochemical studies on fish populations. Oceanogr. Mar. Biol. Annu. Rev. 7:411-513.

EBELING, A. W., N. B. ATKIN, AND P. Y. SETZER.
1971. Genome sizes of teleostean fishes: increases in some deep-sea species. Am. Nat. 105:549-561.

EGE, V.
1953. Paralepididae I. (*Paralepis* and *Lestidium*). Taxonomy, ontogeny, phylogency and distribution. Dana Rep., Carlsberg Found. 40, 184 p.
1957. Paralepididae II. (*Macroparalepis*). Taxonomy, ontogeny, phylogeny and distribution. Dana Rep., Carlsberg Found. 43, 101 p.

FISH, M. P., AND W. H. MOWBRAY.
1970. Sounds of Western North Atlantic fishes. Johns Hopkins Press, Baltimore, 207 p.

FRASER-BRUNNER, A.
1949. A classification of the fishes of the family Myctophidae. Proc. Zool. Soc. Lond. 118:1019-1106.

GREENWOOD, P. H., D. E. ROSEN, S. H. WEITZMAN, AND G. S. MYERS.
1966. Phyletic studies of teleostean fishes, with a provisional classification of living forms. Bull. Am. Mus. Nat. Hist. 131:341-455.

GÜNTHER, A.
1887. Report on the deep-sea fishes collected by H.M.S. *Challenger* during the years 1873-76. Rep. Sci. Res. Voyage H.M.S. Challenger 22:335 p., 73 plates.

JOHNSON, R. K.
1971. A revision of the alepisauroid family Scopelarchidae (Pisces: Myctophiformes). Ph.D. Thesis, Scripps Inst. Oceanogr., La Jolla, 474 p.

KOTTHAUS, A.
1972. Die meso-und bathypelagischen Fische der Meteor-Rossbreiten-Expedition 1970 (2. und 3. Fahrtabschnitt). "Meteor" Forsch.-Ergeb. D11:1-28.

McALLISTER, D. E.
1967. The significance of ventral bioluminescence in fishes. J. Fish. Res. Board Can. 24:537-554.

MOSER, H. G., AND E. H. AHLSTROM.
1970. Development of lanternfishes (family Myctophidae) in the California Current. Part I. Species with narrow-eyed larvae. Bull. Los Ang. Cty. Mus. Nat. Hist. Sci. 7, 145 p.
1972. Development of the lanternfish, *Scopelopsis multipunctatus* Brauer 1906, with a discussion of its phylogenetic position in the family Myctophidae and its role in a proposed mechanism for the evolution of photophore patterns in lanternfishes. Fish. Bull., U.S. 70:541-564.

NAFPAKTITIS, B. G.
1968. Taxonomy and distribution of the lanternfishes, genera *Lobianchia* and *Diaphus*, in the North Atlantic. Dana Rep., Carlsberg Found. 73, 131 p.
1973. A review of the lanternfishes (family Myctophidae) described by Å. Vedel Tåning. Dana Rep., Carlsberg Found. 83, 46 p.

OHNO, S.
1970. The enormous diversity in genome sizes of fish as a reflection of nature's extensive experiments with gene duplication. Trans. Am. Fish. Soc. 99:120-130.

PAXTON, J. R.
1972. Osteology and relationships of the lanternfishes (Family Myctophidae). Bull. Los Ang. Cty. Mus. Nat. Hist. Sci. 13, 81 p.

WISNER, R. L.
1963. A new genus and species of myctophid fish from the South-Central Pacific Ocean, with notes on related genera and the designation of a new tribe, Electronini. Copeia 1963:24-28.
1971. Descriptions of eight new species of myctophid fishes from the eastern Pacific Ocean. Copeia 1971:39-54.