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

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ABSTRACT

The larval and transformation stages of the unusual myctophid, *Scopelopsis multipunctatus* Brauer, are described. A character that the larvae of *Scopelopsis* share with a number of other genera in the Lampanyctinae is the sequential development of three or more pairs of early forming photophores. The sequence of development of early forming photophores is shown to be an especially useful character in revealing phylogenetic affinities when used in conjunction with other larval characters, such as body shape and pigment pattern. From our study of the development of *Scopelopsis*, a possible mechanism for the evolution of photophore patterns within the family Myctophidae is presented.

Brauer (1906), in his elegant report on the fishes collected during the German Deep-Sea Expedition of 1898-99, described for the first time a remarkable lanternfish, for which he established the genus *Scopelopsis*. His single specimen, a newly transformed juvenile, was unique in having the head and body studded with minute light organs, all of approximately the same size. All other lanternfish known to him were characterized by a specific pattern of photophores on the head and on the ventral and lateral regions of the body. These he grouped into the single genus *Myctophum*, under which he recognized four subgenera: *Myctophum, Diaphus, Lampanyctus*, and *Lampadena*. These two genera, along with *Neoscopelus*, a genus with an undifferentiated pattern of ventral photophores, and five other genera were included in the family Scopelidae.

Regan (1911) modified drastically this taxonomic arrangement by distributing Brauer's eight genera of scopelids into a scheme of three suborders. He placed the family Myctophidae within one of these suborders and included within it seven genera: *Scopelopsis, Neoscopelus, Scopelengys* (a genus related to *Neoscopelus* but lacking photophores), and the four subgenera of Brauer raised to generic rank. Parr (1928) further differentiated the family Myctophidae to include three subfamilies: Scopelengini for *Scopelengys*, Neoscopelini for *Neoscopelus*, and *Scopelopsis*, and Myctophini for *Myctophum, Lampanyctus, Diaphus*, and *Lampadena*.

Tåning (1932) noted that in a number of well-preserved specimens of *Scopelopsis*, certain photophores were larger and better developed than others, and that the scales covering these organs were equipped with the same lens-like modification typical of other members of Parr's Myctophini. He observed further that these larger photophores formed a pattern that corresponded with the kinds of photophore patterns found in the Myctophini and concluded, accordingly, that *Scopelopsis* belonged with *Myctophum, Lampanyctus*, and relatives in the subfamily Myctophini.

Fraser-Brunner (1949) reduced the number of subfamilies in the Myctophidae to two: The Neoscopelinae, to include *Neoscopelus, Scopelengys*, and *Solivomer*, and the Myctophinae, to in-

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clude *Scopelopsis* and 20 other genera. He provided the first substantial description of the photophore pattern of *Scopelopsis* and, in his illustration, differentiated the more conspicuous "primary" photophores from the minute "secondary" organs. Further, he recognized two major evolutionary lineages among these 21 genera and placed *Scopelopsis* among the group which included *Lampanyctus* and its relatives.

Authors since Smith (1949) have afforded full family status to the neoscopelines, separating the three genera from the Myctophidae. Recently, Paxton (1968) reviewed the osteology of the Myctophidae and constructed a higher classification to reflect generic relationships within the family. His views have been stimulative and complementary to our studies of larval myctophids (Moser and Ahlstrom, 1970). Our recent discovery of the larvae of *Scopelopsis* has served to crystallize our views of relationships within that part of the family which contains *Lampanyctus* and its allies. These ideas, based chiefly on larval morphology and sequence of photophore development, are set forth herein, following the description of *Scopelopsis* larvae.

MATERIALS AND METHODS

The developmental series of *Scopelopsis* used in this study was obtained chiefly from the R.R.S. *Discovery* plankton collections, housed at the British Museum (Natural History). A total of 29 specimens was taken off South Africa at stations 412, 413, 416, 418, 419, and 438 in August-September 1930. An additional five larvae were found on station 2352, occupied off South Africa in July 1938. A single transforming specimen came from station 2280 of the U.S. Antarctic Project ship *Eltanin*. Although adult specimens of *Scopelopsis* were obtained on EASTROPAC surveys, larvae were not taken.

A series of 25 specimens, from smallest larva to juveniles, was measured according to the method described in Moser and Ahlstrom (1970), to produce the table of morphometrics essential for description of the changes in body proportions. These specimens also were used for describing the development of the melanophore pattern and of photophores. A second series of 11 larvae was cleared with KOH and stained with Alizarin Red-S; a table of meristics was constructed from counts made on these specimens.

For purposes of discussion we have included information and illustrations of nine genera related to *Scopelopsis*. These specimens and data, accumulated over an extended period of time, have come largely from the plankton collections of the California Cooperative Oceanic Fisheries Investigations, the NORPAC Expedition, the EASTROPAC Expedition, and the Danish Oceanographic Expedition, in addition to the two sources mentioned above. Where specimens from these and other sources are illustrated, appropriate station data are included in the caption accompanying the figure.

DESCRIPTION OF DEVELOPMENT OF *SCOPELOPSIS MULTIPUNCTATUS*

(Figures 1-3)

LITERATURE

Regan (1916) described the species *Lampanyctus longipinnis* from a 15-mm larval specimen. Judging from the fin counts given in the description and from the somewhat illegible drawing, the specimen was a larva of *Scopelopsis multipunctatus*.

MORPHOLOGY

Larvae of *Scopelopsis* are moderately slender. Body depth at the pectoral fin base is 18-19% of the body length in larvae undergoing notochord flexion and is 20-24% (mean of 22%) in later larval stages and transforming specimens (Table 1). The gut is of moderate length in specimens undergoing notochord flexion; snout-anus length is 44-45% of body length. The gut is conical in these specimens and gradually arches posteriad to the short terminal section. Snout-anus distance increases slightly in later larval and transforming specimens, which have a snout-anus length of 50-54% (mean of 52%) of body length. In these, the gut is covered by trunk musculature.

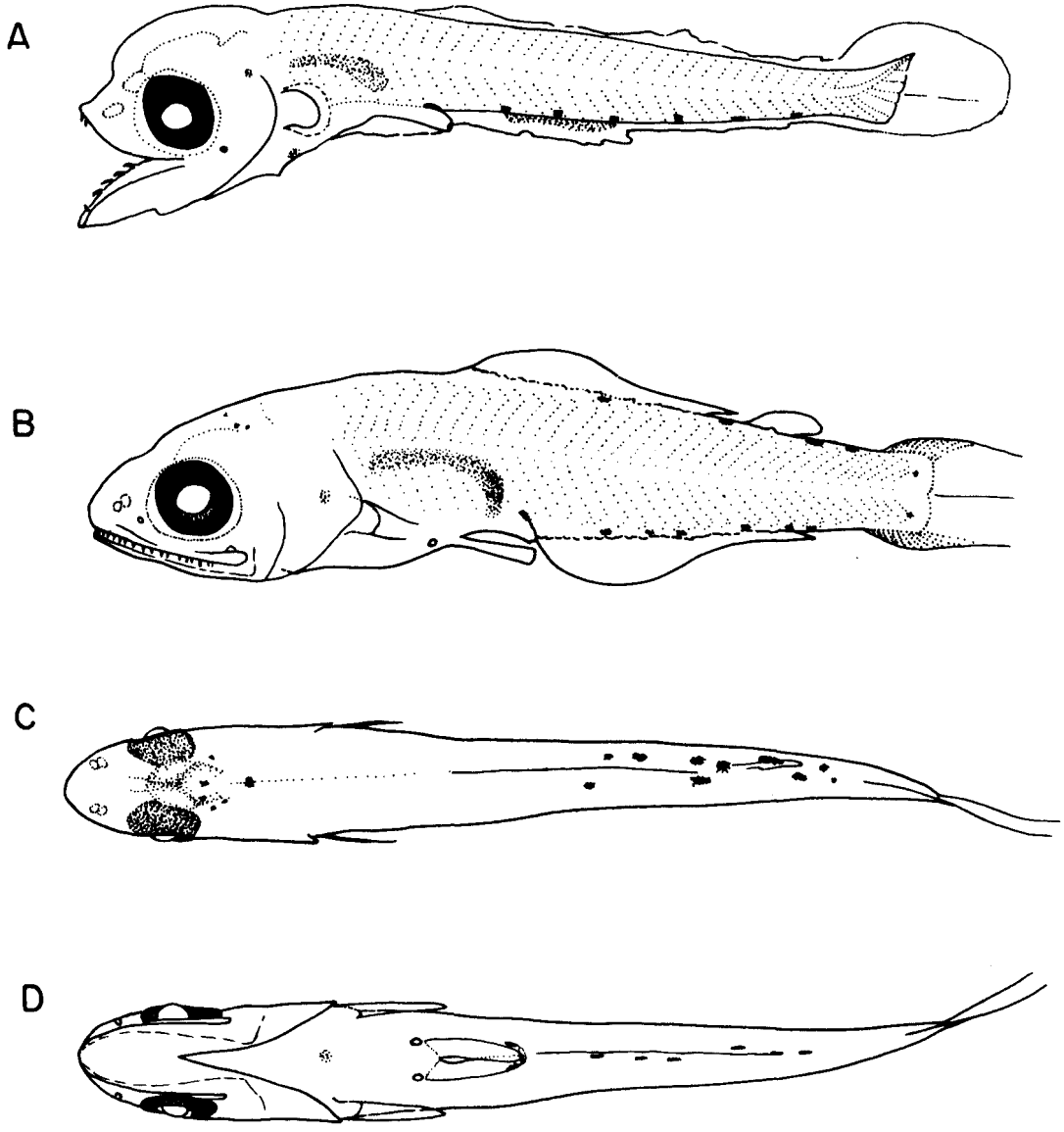

FIGURE 1.—Developmental stages of *Scopelopsis multipunctatus* Brauer.—A, 5.4-mm larva, R.R.S. *Discovery* Station 2352; B, 11.3-mm larva, R.R.S. *Discovery* Station 2352; C, 11.3-mm larva, dorsal view; D, 11.3-mm larva, ventral view.

The head is moderately large, its length being 24-28% (mean of 27%) of the body length for the larval series. The dorsal profile of the snout is concave in our smallest specimen (5.4 mm), but is straight in a 6.2-mm larva, and becomes distinctively bulbous in later larvae and in transforming specimens. The eyes are large in *Scopelopsis* larvae, but undergo a slight diminution, relative to head size, with progressive larval development. Eye length measured vertically is 38% of the head length in the smallest larva, but decreases to 35% in a 6.2-mm larva. This dimension averages 30% of the head length in larvae which have completed notochord flexion,

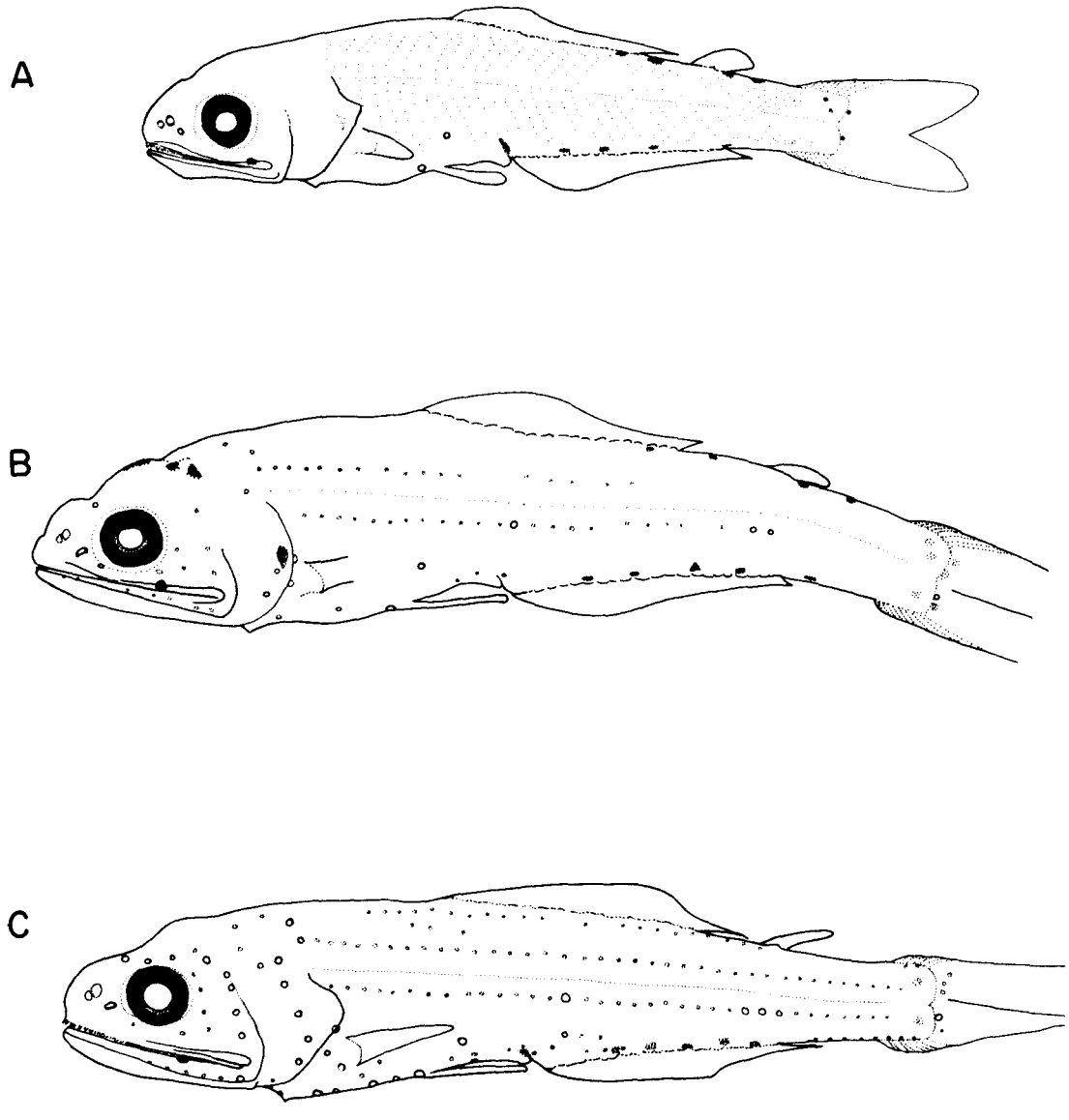

FIGURE 2.—Developmental stages of *Scopelopsis multipunctatus* Brauer.—A, 13.4-mm larva, R.R.S. *Discovery* Station 412; B, 17.6-mm transformation stage, R.R.S. *Discovery* Station 2280; C, 16.7-mm transformation stage, R.R.S. *Discovery* Station, 419.

but this is reduced to an average of 25% in transforming specimens and to 22% in a newly transformed juvenile. The eyes are round or nearly so in *Scopelopsis*; eye width, measured horizontally, averages 92% of eye length for the larval series. In the 17.4-mm juvenile, the horizontal measurement is slightly greater than the vertical. Choroid tissue is absent from the ventral surface of the eye. The initial lateral teeth of the lower jaw are characteristically curved anteriad. Later, the more typical dentary teeth form anterior to the curved teeth; the latter occupy the posterior half of each dentary in larger larvae.

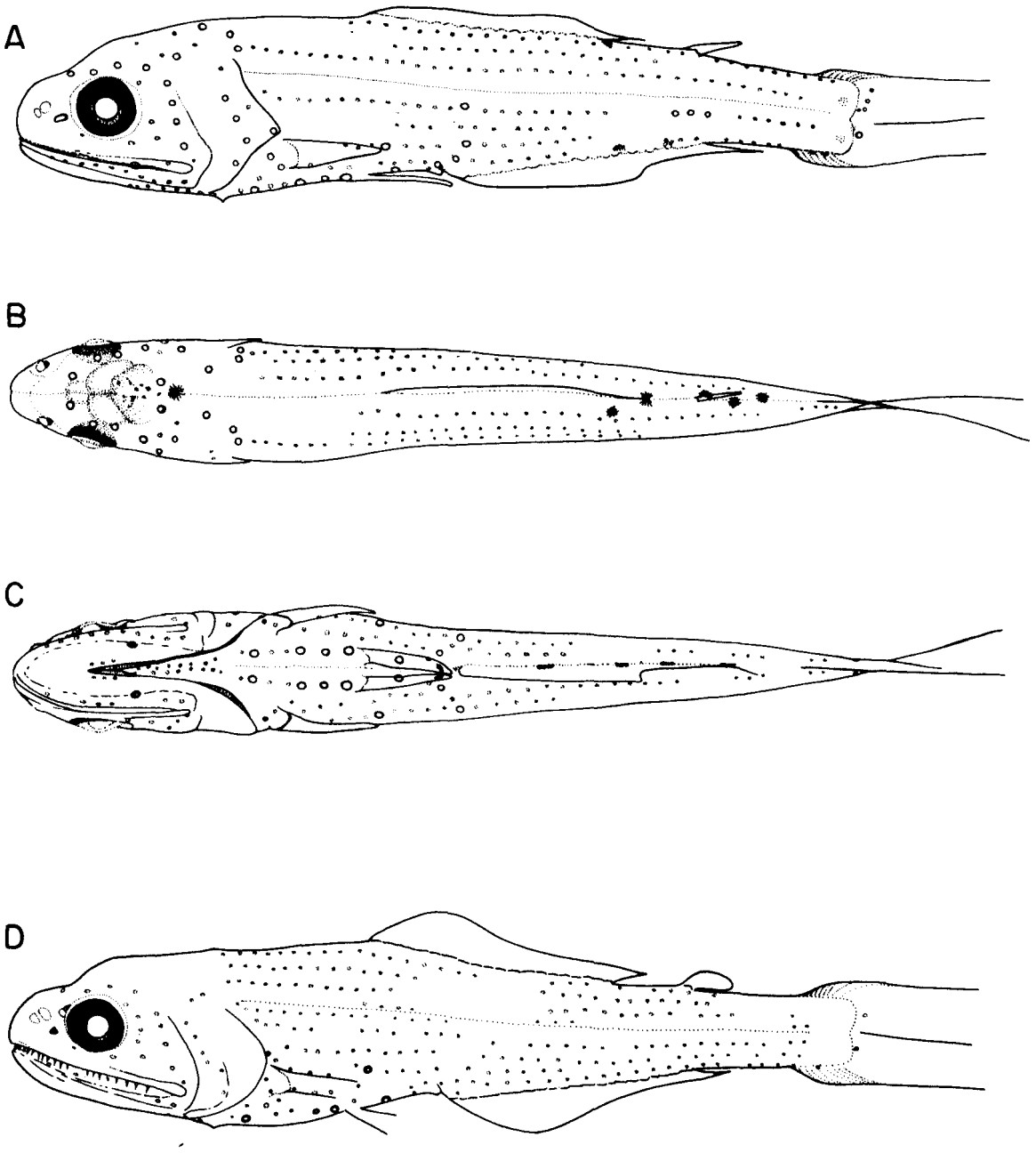

FIGURE 3.—Developmental stages of *Scopelopsis multipunctatus* Brauer.—A, 17.5-mm transformation stage, R.R.S. *Discovery* Station 419; B, 17.5-mm transformation stage, dorsal view; C, 17.5-mm transformation stage, ventral view; D, 17.4-mm juvenile, R.R.S. *Discovery* Station 412.

TABLE 1.—Measurements (mm) of larvae of *Scopelopsis multipunctatus*. (Specimens below dashed line have completed notochord flexion.)

Body length	Snout to anus	Head length	Head width	Inter-orbital width	Body depth at base of pectoral fin	Eye length	Eye width	Snout to origin of anal fin	Snout to origin of dorsal fin	Snout to origin of pelvic fin
5.4	2.4	1.3	0.76	0.46	1.0	0.50	0.43	2.8	--	--
6.2	2.8	1.7	0.87	0.58	1.1	0.59	0.52	3.1	2.8	2.4
10.8	5.4	2.8	1.4	1.2	2.2	0.87	0.81	5.4	4.6	4.1
11.3	5.8	3.2	1.5	1.3	2.5	1.0	0.95	5.8	5.0	4.6
12.2	6.4	3.2	1.6	1.3	2.7	1.0	0.90	6.4	5.2	4.8
12.3	6.3	3.2	1.6	1.3	2.6	0.94	0.86	6.3	5.2	4.8
12.4	6.5	3.3	1.7	1.4	2.6	1.0	1.0	6.5	5.4	5.0
12.8	7.1	3.3	1.8	1.4	3.0	1.1	1.0	7.1	5.6	5.4
13.0	6.8	3.4	1.7	1.4	2.8	1.0	0.95	6.8	5.7	5.2
13.1	7.1	3.4	1.8	1.5	3.1	1.0	0.91	7.1	5.8	5.3
13.2	6.7	3.2	1.8	1.5	2.8	0.97	0.83	6.8	5.5	5.2
13.4	7.0	3.6	2.1	1.5	3.1	1.0	0.87	7.0	5.8	5.3
13.5	6.9	3.5	1.8	1.4	2.8	1.1	0.91	6.9	5.8	5.2
13.8	7.4	3.7	1.8	1.4	2.8	1.1	1.0	7.4	6.1	5.5
13.9	6.9	3.5	1.8	1.5	2.9	1.0	0.92	6.9	5.9	5.3
14.2	7.4	3.8	2.0	1.5	3.2	1.0	0.95	7.4	6.2	5.7
14.3	7.4	3.7	1.8	1.4	3.1	1.0	0.95	7.4	6.2	5.5
14.6	7.4	3.8	1.8	1.7	3.2	1.1	1.0	7.4	6.2	5.4
14.9	7.8	4.2	2.0	1.7	3.2	--	--	7.8	--	6.1
15.2	8.2	4.2	1.9	1.7	3.3	--	--	8.2	7.0	6.2
15.5	8.2	4.4	2.0	1.7	3.4	--	--	8.2	7.0	6.2
[1]16.7	8.8	4.6	2.3	1.9	3.8	1.2	1.1	8.8	7.0	6.7
[1]17.5	8.8	4.8	2.5	1.8	3.6	1.2	1.2	8.8	7.2	6.9
[1]17.7	8.8	4.8	--	--	3.8	1.2	1.2	--	7.4	6.7
[2]17.4	9.0	4.9	2.4	1.9	3.7	1.1	1.2	9.0	7.2	6.9

[1] Transformation stage.
[2] Juvenile.

FIN DEVELOPMENT

Our smallest specimen (5.4 mm) is undergoing flexion of the tip of the notochord and already has the adult complement of 10 superior and 9 inferior principal caudal rays (Table 2). In the next smallest larva (6.2 mm), also undergoing notochord flexion, a single procurrent ray is forming in the superior and inferior series. The adult complement of 10-11 superior and 10-12 inferior procurrent rays is present in larvae 13.0 mm and larger.

The pectoral fins are represented by their inconspicuous bases in the 5.4- and 6.2-mm specimens; the fins themselves are membranous, with no ossified rays. Description of the gradual acquisition of ossified rays described for pectoral fins of other species (Moser and Ahlstrom, 1970) is precluded by the gap in our series of *Scopelopsis*. Larvae 10.8 mm and larger have the adult complement of 10-11 rays in each fin.

The bases of the dorsal and anal fins are beginning to form on the 5.4- and 6.2-mm larvae, but no rays are ossifying. Larvae 10.8 mm and larger have the adult complement of 21-23 dorsal and 23-25 anal rays.

The pelvic fin buds are present in the 6.2-mm larva, and larvae 10.8 mm and larger have the adult number of 8 rays in each fin. The adipose fin is beginning to develop at 6.2 mm and is well formed by 10.8 mm.

Gill rakers and vertebrae develop later than do the fins. Gill rakers are first apparent in the 10.8-mm larva and are added gradually. On the first arch, the full complement of 7-9 epibranchial rakers is achieved at 13.5 mm while, on the lower limb of the arch, the full complement of 15-17 rakers is present at 15.2 mm. A 10.8-mm larva already has 34 vertebral centra forming; the adult number of 37-40 vertebrae is present in larvae 12.2 mm and larger.

TABLE 2.—Meristic characters of cleared and stained larvae of *Scopelopsis multipunctatus*.

Length (mm)	Primary caudal fin rays		Secondary caudal fin rays		Branchiostegal rays		Pectoral fin rays		Hypural elements		Gill rakers (right arch)		Anal fin rays	Dorsal fin rays	Pelvic fin rays		Vertebrae
	Superior	Inferior	Superior	Inferior	Left	Right	Left	Right	Superior	Inferior	Upper left limb	Lower right limb			Left	Right	
5.4	10	9	--	--	--	--	--	--	--	--	--	--	--	--	--	--	--
6.2	10	9	1	1	--	--	--	--	--	1	--	--	--	--	--	--	--
10.8	10	9	9	10	8	8	11	11	4	3	4	12	24	23	8	8	34
12.2	10	9	9	10	9	9	10	10	4	3	6	12	24	22	8	8	39
13.0	10	9	10	11	10	10	10	11	4	3	6	14	23	21	8	8	38
13.5	10	9	11	12	9	9	10	10	4	3	7	14	24	22	8	8	39
13.9	10	9	10	12	9	9	11	11	4	3	7	14	25	23	8	8	39
14.3	10	9	11	12	9	10	11	11	4	3	7	14	24	22	8	8	38
15.2	10	9	11	11	10	10	11	12	4	3	8	16	24	22	8	8	39
15.7	10	9	9	11	10	10	11	10	4	3	8	15	23	22	8	8	39
17.6	10	9	10	12	10	10	10	11	4	3	8	16	24	23	8	8	39

PIGMENTATION

Scopelopsis larvae develop a distinct pattern of melanophores. The smallest larva in our series (5.4 mm) has a prominent median melanophore at the nape and a smaller melanophore embedded in the otic region at each side of the head. Another large melanophore is embedded at the ventral midline, just below the bases of the pectoral fins. An equally prominent melanophore lies above the gut, at the point where the free terminal section diverges from the body. An elliptical shield of melanophores lies above the developing gas bladder but is partially masked by the body wall musculature. A series of six evenly spaced melanophores is embedded along the ventral midline of the tail. All the melanophores that constitute this initial pattern remain throughout the larval period. The series at the ventral midline of the tail usually contains five or six melanophores in older larvae; specimens with fewer than three or more than eight were not found.

Another major area of pigmentation is visible in a 6.2-mm larva, which has two melanophores in the dorsal midline posterior to the adipose fin. In larger larvae this series extends anterior to the dorsal fin, with the usual condition being a series of three, four, or five melanophores on, or on either side of, the midline. An 11.3-mm larva has the maximum number of 10 melanophores in this series, with several of the melanophores positioned along the base of the dorsal fin.

Final additions to the melanophore pattern are in the head and caudal fin. In specimens 10.8 mm and larger, a melanophore is embedded anterior to the base of each pectoral fin, and specimens 11.3 mm and larger have one to several melanophores above the posterior region of the brain. Larvae 10.8 mm and larger have one to several melanophores embedded in the hypural region of the tail; these melanophores may lie over the superior hypurals, the inferior elements, or both. Similarly, in specimens 12.3 mm and larger, one to several melanophores may be found at the base of the caudal rays, either at the superior group, the inferior group, or both. Some specimens lack these caudal ray melanophores. A few larvae have an additional median melanophore at the junction of the hypural elements and the rays.

PHOTOPHORE DEVELOPMENT

A number of photophores develop in larvae of *Scopelopsis* in a prescribed sequence.[2] As in most other myctophids the Br_2 are the first to form. They are just visible in our smallest specimen (5.4 mm) and are well formed in a 10.8-mm specimen. The next to appear is the posteriormost PO pair which is just visible in the 10.8-mm larva but is well formed, although small, in

[2] For clarity, a diagram of the characteristic photophore groups of adult myctophids is shown in Figure 4.

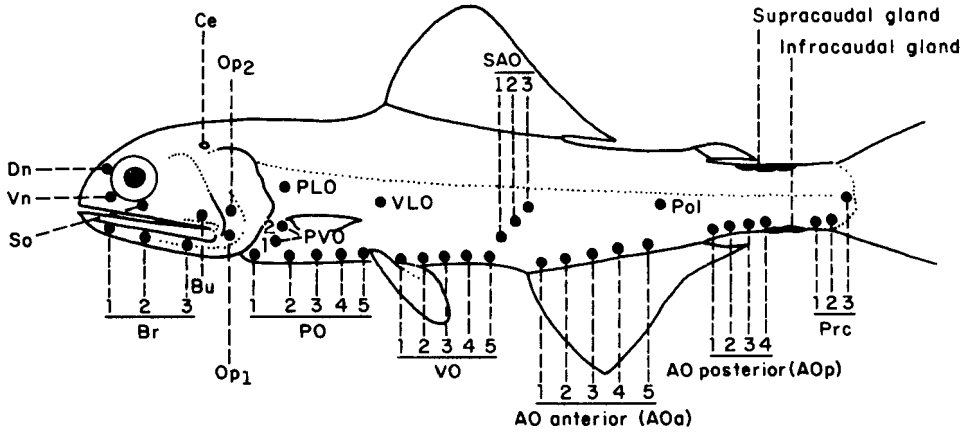

FIGURE 4.—Diagram of characteristic photophore groups of adult myctophids (modified from Nafpaktitis and Nafpaktitis, 1969 and Fraser-Brunner, 1949).

larger specimens in the series. The next to develop are the Vn; they appear anteroventral to the eye in the 11.3-mm larvae and become progressively cup-shaped as development proceeds. At the end of the larval period they are the largest photophores present. During transformation they begin to be overlain with tissue and bone so that they are difficult to see in juveniles and adults; this is doubtless why they have been overlooked by recent authors (Fraser-Brunner, 1949; Nafpaktitis and Nafpaktitis, 1969). The fourth pair of photophores to develop are the VLO; they first appear slightly posterior to, but well above, the bases of the pelvic fins in a 13.4-mm larva.

The four pairs of photophores described above are the only ones to develop until the larvae reach about 15-mm length. In a series of five larvae 14.9-15.7 mm long, a number of other photophores are beginning to appear. In the jaw region one is visible just below the terminus of each maxillary, and another is forming above and slightly anterior to the end of the maxillary. One or two others are developing in a line extending dorso-anteriad from the latter cheek organ. Dorsally on the head, a photophore is developing above the lateral margin of each olfactory lobe. In the PO series two pairs are evident, one slightly posterior to the juncture of the cleithra and another pair equidistant between this pair and the most posterior pair, described above. A VO pair is developing midway between the bases of the pelvic fins and the anus. Farther posterior on the body, the SAO_3 are developing as are the posteriormost Prc pair.

The photophore pattern is augmented further in the three remarkable transforming specimens illustrated in Figures 2 and 3, in which the adult pattern of photophores is clearly emerging. The three represent a developmental series of which the 17.6-mm specimen is the least advanced, followed by the progressively more advanced 16.7- and 17.5-mm specimens. In the 17.6-mm specimen the previously described photophore pattern on the head is augmented by several organs below and to the rear of the eye, by a line of organs along the lower jaw, and by several on the opercle. On the body a PLO and one PVO is present at the pectoral fin base, several organs are forming above the vent, and two POL are arranged horizontally above the end of the anal fin. In addition, two horizontal lines of photophores are beginning to appear, one above and one below the lateral line. The adult photophore arrangement of *Scopelopsis* is clearly manifest in the 16.7- and 17.5-mm specimens. Photophores are beginning to cover the head in a definite pattern; some of these are considerably larger and more defined than others. On the body the many regular rows of secondary organs are emerging, al-

though the following larger and more distinct primary photophores stand out on the 17.5-mm specimen: PO_{1-4}, $PVO_{1 \text{ and } 2}$, VLO, VO, SAO_{1-3}, POL_{1-3}, Prc.

In the 17.4-mm juvenile it is evident that the photophores on the body are on the posterior margin of each scale pocket, thus explaining their regular arrangement into horizontal rows. The specimen is partially skinned, but one can see that some body photophores remain decidedly larger than others (notably two of the PO, the VLO, and VO), while generally the distinction between primary and secondary organs is less marked. On the head, certain of the cheek photophores remain large and distinct and, additionally, the two-part Dn is now present as are the small anterior and posterior Br.

Opinion has been divided on whether or not the dichotomy of primary and secondary photophores, described above, is present in adult *Scopelopsis*. In his original description Brauer (1906) did not distinguish between primary and secondary organs. Tåning (1932) stated that some of the organs were larger than others and, moreover, made the important observation that the scales over these larger organs were equipped with a special lenslike modification typical of other myctophids. He noted that among the prominent photophores were a PLO, two PVO, a VLO, three SAO in a rather steep line, and two POL in a horizontal line. His statement, " . . . in fact we find all the different groups of organs which we have in all other species of the subfamily Myctophini, small, but larger than the very small organs scattered all over the body . . ." was unaccompanied by an illustration. Fraser-Brunner (1949) recognized that certain photophores were more highly developed than others and termed these primary organs in contrast to the less highly developed secondary organs. He gave the following formula: "PLO above, both PVO below base of pectoral. Five PO. Five VO. Three SAO in an oblique series. AO in two series. Two POL in horizontal series. Five or more Prc." His accompanying illustration shows the basic photophore pattern but is somewhat illegible, especially in the caudal region. Nafpaktitis and Nafpaktitis (1969) could not differentiate primary and secondary photophores in their material. Wisner (in press) employed a large series of excellently preserved specimens in his description of *Scopelopsis* and showed that the ability to differentiate primary from secondary photophores is dependent on the condition of the specimen. In specimens which had retained most of their scales he identified primary photophores as those with a lenslike modification of the overlying scale. His photophore formula and clear illustration corroborate the observations of Tåning (1932) and Fraser-Brunner (1949); further refinements include his observation of 7-10 anterior AO, 5-6 posterior AO, 4-6 Prc, 2 or 3 POL, and 3 prominent cheek photophores in a diagonal line anterior to the preopercle. Additionally he shows definitively the two-part Dn and the embedded Vn. The observations of Tåning (1932), Fraser-Brunner (1949), and Wisner (in press) along with the evidence presented herein demonstrate that certain of the multitudinous light organs of *Scopelopsis* are more highly developed than others and that these "primary organs" are arranged in a pattern that corresponds to the general pattern of other members of the family. Our observations on ontogenetic series largely confirm the arrangement of primary photophores postulated by these authors, but some of our findings suggest discrepancies that may only be clarified by further examination of undamaged adults. For example, we find only four well-developed PO and a single large VO in transforming specimens and in juveniles and adults available to us. This as well as the exact frequencies of AO and Prc series await elucidation by workers with large series of intact adults.

SYSTEMATIC RELATIONSHIPS

The efficacy of using the larval and transformation stages of lanternfishes to elucidate specific and supraspecific relationships has been clearly demonstrated (Pertseva-Ostroumova, 1964; Moser and Ahlstrom, 1970). We (Moser and Ahlstrom, 1970) showed that the genera of Myctophidae can be divided into two groups on the basis of larval eye shape—those with narrow elliptical eyes and those with round or nearly

round eyes. That these are phylogenetically natural groups is supported by Paxton (1968, 1972) who, on the basis of adult osteology and photophore arrangement, formally established the same two groups of genera as subfamilies. He grouped the 11 genera with narrow-eyed larvae into the subfamily Myctophinae and the 17 genera with round-eyed larvae into the subfamily Lampanyctinae. Further, in our paper we described the evolutionary lineages within the Myctophinae as evidenced by the structure of the larvae. Many of our conclusions agreed with those of Paxton (1968), derived from adult characters, but we differed ultimately with his distribution of the 11 myctophine genera into two tribes and with his derivation of the subfamily Lampanyctinae from an already highly evolved lineage of the subfamily Myctophinae. The larvae of the subfamily Lampanyctinae, although morphologically conservative compared with those of the Myctophinae, are useful, nonetheless, in revealing evolutionary lineages within the subfamily. The diversity of eye shape, so spectacular in the Myctophinae, is absent in the Lampanyctinae, but the eyes of many genera are distinctive because of their size, subtle but characteristic deviation from the basic rounded outline, or presence of a ventral crescent of choroid tissue. Likewise each genus of Lampanyctinae has a characteristic body shape, although the subfamily lacks the diversity of body form, so dramatic in the Myctophinae. The peculiar modifications of the paired fins, common among the larvae of Myctophinae, are generally absent in the Lampanyctinae; only in the lampanyctine genera *Lampanyctus* and *Lobianchia* do the pectoral fins attain some degree of specialization.

Three characters that are shared by the larvae of many lampanyctine genera are: 1) the sequential development of three or more pairs of early-forming photophores, 2) the development of a series of melanophores at the dorsal and at the ventral margins of the body, particularly in the tail region, and 3) the development of one or more melanophores above the brain. The sequence of development of early-forming photophores is an especially useful character that may provide a key to the elucidation of phylogenetic lineages within the Lampanyctinae. Eleven of the 17 genera of Lampanyctinae develop such early-forming photophores and can be grouped as follows:

Group A—Br_2, PO_5, and Vn form in that sequence; fourth pair, either PLO or VLO, form later in larval period.
- *Scopelopsis* - VLO fourth pair to form.
- *Notoscopelus* - PLO fourth pair to form.
- *Lampichthys* - PLO fourth pair to form.

Group B—Br_2, Vn, PLO, and PO_5 form sequentially; photophores very small.
- *Ceratoscopelus* - all four pairs formed early in larval period.
- *Bolinichthys* - some species develop larval photophores, as above, and others develop only the Br_2 as larvae.
- *Lepidophanes* - Vn, PLO, and PO_5 form almost simultaneously after the Br_2; OP_1, and OP_2 form just before transformation.

Group C—Br_2, PLO, and PO_5 early-forming.
- *Lampadena* - Br_2, PLO, and PO_5 appear sequentially; later in larval period, PO_1 and Vn form sequentially.
- *Lampanyctodes* - Br_2, PLO, and PO_5 formed on 9.2-mm larva; smaller larvae and, consequently, information on sequence of appearance, not available.

Group D—Br_2, PO_5, and PO_1 early-forming.
- *Gymnoscopelus* - Br_2, PO_5, and PO_1 form sequentially, early in the larval period; much later, the VO_1 and then PO_2 appear.
- *Diaphus* - two species groups; *D. theta* and relatives form Br_2, PO_5, PO_1, VO_1, PO_2, OP_2, VO_5, PO_3, PO_4, VLO sequentially; *D. pacificus* and relatives form Br_2, PO_5, PO_1, PO_2, PVO_1, PO_3, VO_1, sequentially; photophores added gradually in *Diaphus* larvae with transformation at small size.
- *Lobianchia* - Br_2, PO_1, PO_5, PVO_1, PVO_2 form sequentially.

The above groupings suggest phylogenetic affinities which, in most cases, are supported by other characters of the larvae and adults. The sequential development of the Br_2, PO_5, and Vn photophores is unique to the genera of Group A (*Scopelopsis, Lampichthys, Notoscopelus*). The arrangement of primary photophores, so conspicuous in the transforming specimens of *Scopelopsis*, affirms the close relationship of this genus

with *Notoscopelus* and *Lampichthys*, since the three genera are the only myctophids with horizontal POL photophores on the posterior lateral surface of the body. *Scopelopsis* and *Notoscopelus* have either two or three such photophores in a horizontal line below the lateral line, while in *Lampichthys* the two horizontal photophores form a right angle with a third POL that is placed midway between the two upper POL's and the ventral series. Other characters of the larvae substantiate the close relationship of these three genera. The larvae are similar in shape of the eye, head, and body. *Scopelopsis* and *Lampichthys* have extremely similar pigment patterns and differ only in the number and size of the melanophores in each area (Figures 1-3, 5). *Notoscopelus* differs only slightly from the other two, in its lack of a melanophore in the ventral midline below the pectoral fin and in having a prominent series of melanophores along the lateral line (Figure 6).

Characters of the adults affirm the close relationship of the three genera. *Scopelopsis* and the several species of *Notoscopelus* have the highest numbers of dorsal fin rays, 21-23 and 22-27 respectively, in the family. The Dn light organ at the anterodorsal margin of the orbit is composed of two contiguous structures in *Scopelopsis* and *Notoscopelus*; it consists of a small photophore, with a margin of black pigment, dorsal to a larger opaque mass of tissue that lacks marginal pigment. In *Lampichthys* a mass of black tissue lies below the opaque luminous tissue, which extends posteriad over the entire dorsal surface of the orbit. *Scopelopsis* is covered entirely by small secondary photophores, as is the body of *Lampichthys*. Such photophores are absent from the head of *Lampichthys;* however, the four or five prominent cheek photophores of *Lampichthys* are comparable to those of *Scopelopsis*. A single opaque patch of luminous tissue lies below each pectoral fin base in *Scopelopsis*. In *Lampichthys*, a luminous patch is present in exactly the same position; however, several additional patches are present on the lateral surfaces of the body. In *Notoscopelus*, luminous patches are much more extensive, although the prominent patch below the base of each pectoral fin is present in all species of the genus.

The sequential development of the Br_2, Vn, PLO, and PO_5 is unique to the genera in group B (*Ceratoscopelus, Lepidophanes, Bolinichthys*); this, along with the small size of the photophores, and their early appearance, points to close relationship of the three genera. The larvae of some species of *Bolinichthys* are an exception, since they develop only the Br_2. Other characters of the larvae, such as a similarity in body shape and a general paucity of pigment, also suggest the close relationship of the three genera (Figures 7, 8, 9). Paxton (1972) has pointed out a number of osteological characters of the adults that link the three genera, and the similarity in the arrangement of luminous patches among species of the three genera is well established in the literature.

The larvae of *Lampadena* and *Lampanyctodes* (group C above) develop the Br_2, PLO, and PO_5. The PLO photophores become conspicuously developed on small larvae of *Lampadena* soon after the formation of the Br_2 pair; the PO_5 pair appear shortly thereafter (Figure 10). The Vn pair is later-forming and may be preceded by the PO_1 pair, or the two pairs may form simultaneously. The sequence of development of early-forming photophores on *Lampanyctodes hectoris* has not been fully established. The Br_2, PLO, and PO_5 pairs were well developed on the smallest larva (9.2 mm) available for study (Figure 11). A 14.5-mm transforming specimen of *Lampanyctodes* had 13 pairs of photophores developed, including the Vn and PO pairs. Even so, the only genera with this combination of three early-forming photophores are *Lampadena* and *Lampanyctodes*. Also, the larvae of the two genera are similar in body shape and in pigmentation.

The larvae of *Gymnoscopelus* (group D above) form the Br_2, PO_5, and PO_1 early (Figure 12). Later in the protracted larval period, the VO_1 and then PO_2 appear. In some species (e.g., *G. aphya*) the larvae reach a length of 28 mm and are the largest of all myctophid larvae. *Diaphus* and *Lobianchia* also develop the Br_2, PO_5, and PO_1 early in the larval period and are included in group D. This, however, is virtually the only larval character that the two genera share with *Gymnoscopelus*. They develop photophores grad-

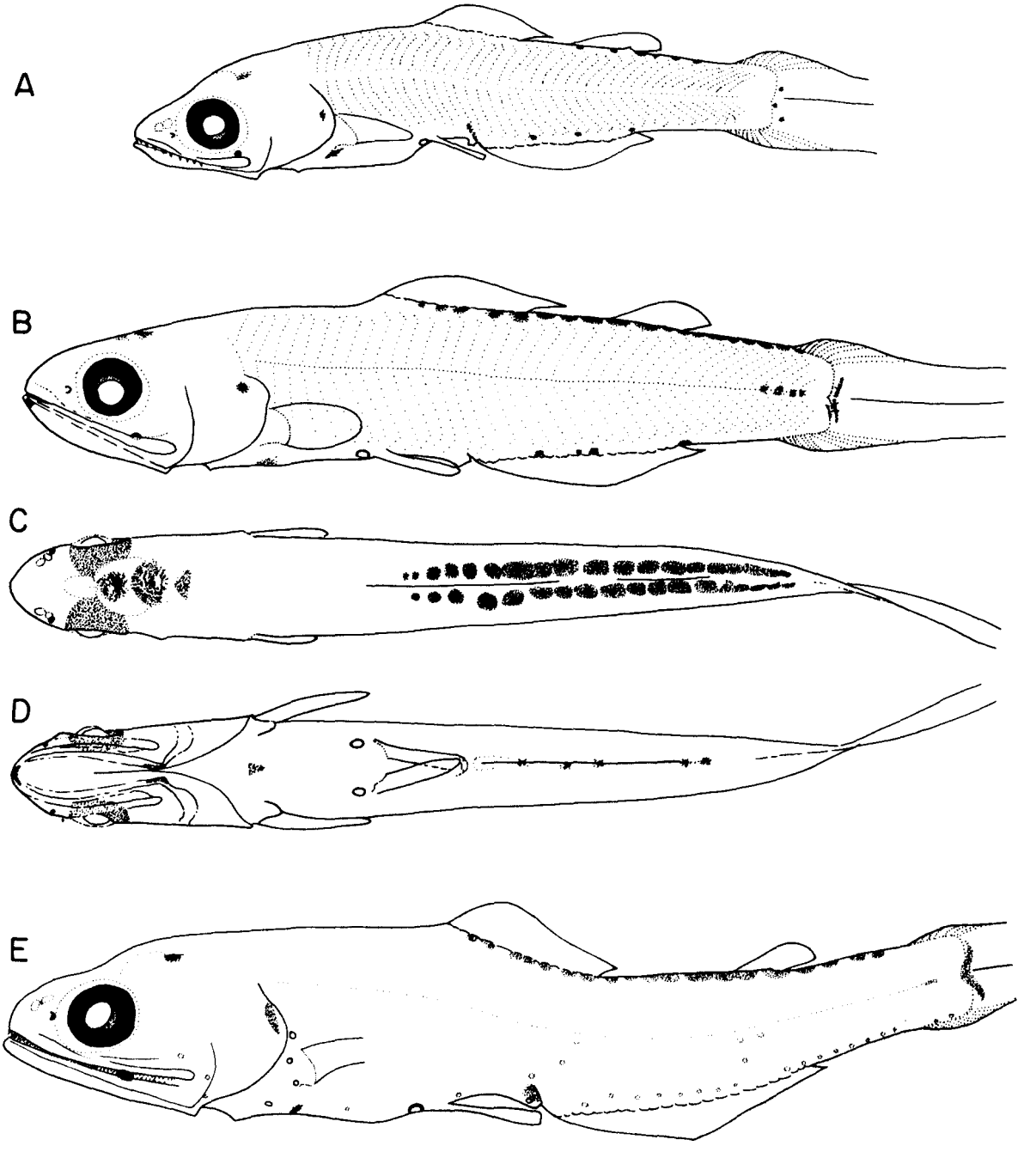

FIGURE 5.—Developmental stages of *Lampichthys procerus* (Brauer).—A, 11.4-mm larva, U.S. NS *Eltanin* Station 314; B, 14.5-mm larva, R.R.S. *Discovery* Station 100c; C, 14.5-mm larva dorsal view; D, 14.5-mm larva, ventral view; E, 20.3-mm transformation stage, U.S. NS *Eltanin* Station 306.

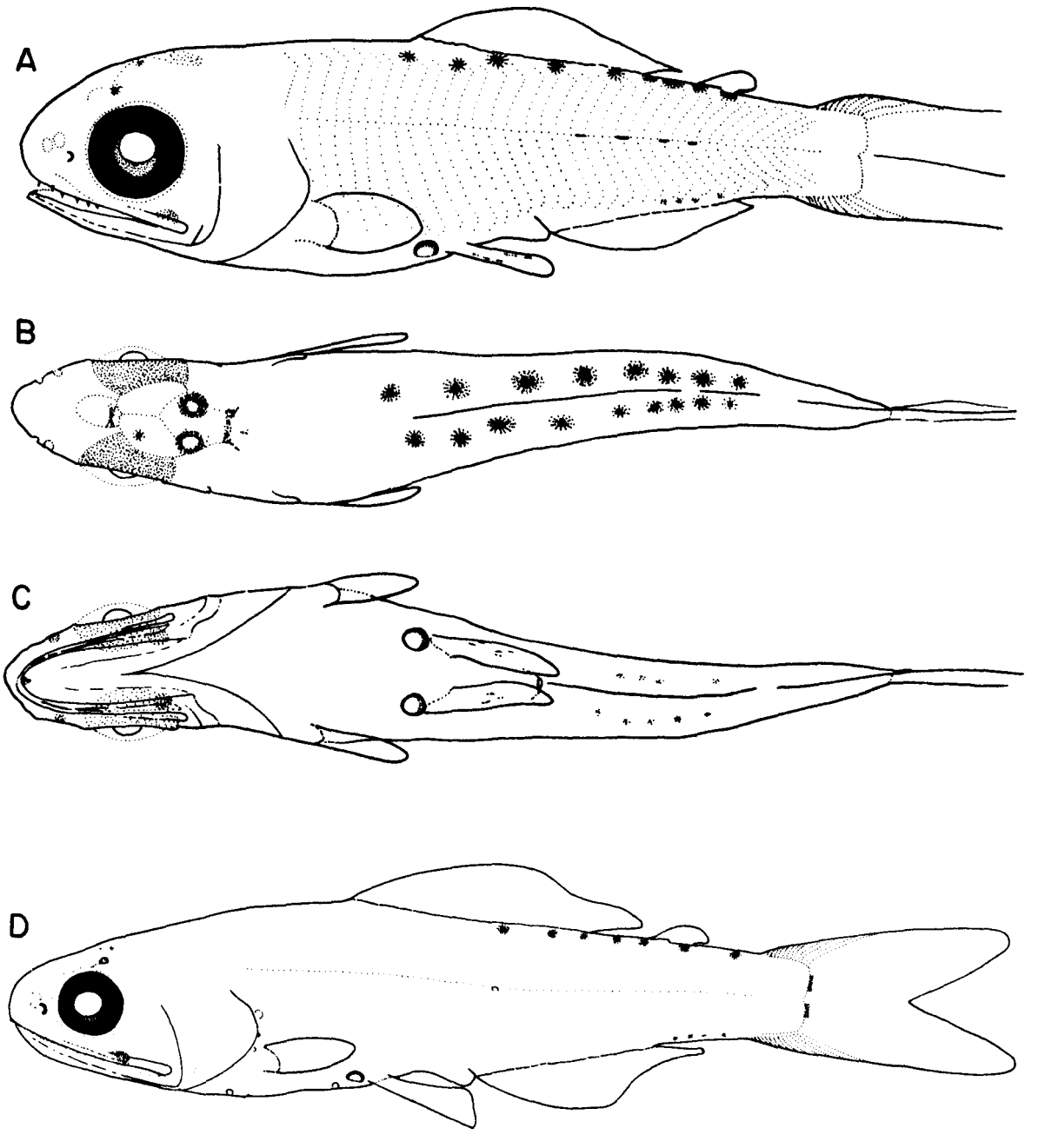

FIGURE 6.—Developmental stages of *Notoscopelus resplendens* (Richardson).—A, 11.2-mm larva, CalCOFI 6310-97.90; B, 11.2-mm larva, dorsal view; C, 11.2-mm larva, ventral view; D, 21.0-mm transformation stage, CalCOFI 6207-90.110.

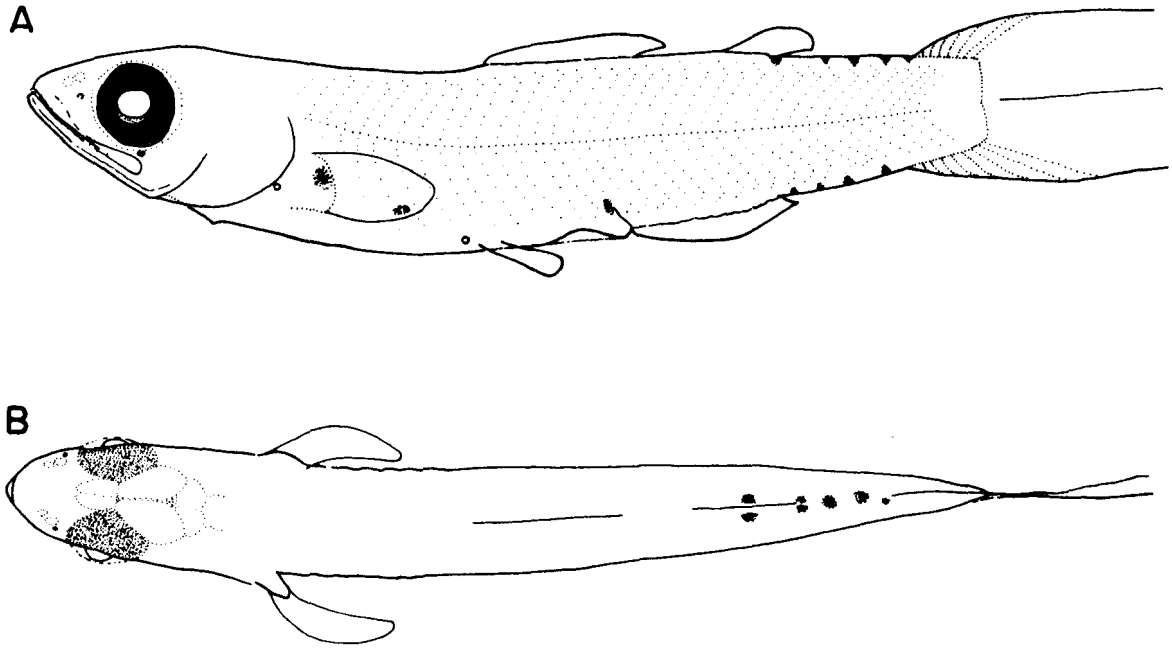

FIGURE 7.—Developmental stage of *Ceratoscopelus maderensis* (Lowe).—A, 13.4-mm larva, RV *Meteor* Station 72-39; B, 13.4-mm larva, dorsal view.

ually during the larval period, which appears to be rather short; most species transform within the size range of 10-15 mm. Also, the characteristic shape and basic pigment pattern of larval *Diaphus* and *Lobianchia* are distinctively different from those of *Gymnoscopelus*. In shape and pigmentation, the larvae of *Gymnoscopelus* resemble most closely those of group A (*Scopelopsis, Lampichthys, Notoscopelus*).

Of the remaining six genera of the subfamily Lampanyctinae, *Notolychnus* develops no photophores during the larval period, and *Lampanyctus, Triphoturus,* and *Stenobrachius* develop only the Br_2 as larvae. Our developmental series of *Taaningichthys* is incomplete; however, larvae up to 18 mm long have no photophores. In our largest larva (19.3 mm), the PO_5 are just beginning to develop. The larvae of this genus are apparently neustonic, and this may have an important influence on photophore development. They are most similar to larvae of *Lampadena* in pigment pattern but are much more slender. The small larvae of *Taaningichthys minimus* are unusual in having a conspicuous series of embedded melanophores above the vertebral column (Figure 13). The larvae of *Hintonia* are as yet unknown.

From our studies of the larvae of the subfamily Lampanyctinae, the genera *Scopelopsis, Lampichthys, Notoscopelus, Gymnoscopelus, Ceratoscopelus, Bolinichthys, Lepidophanes, Lampanyctodes, Lampadena,* and *Taaningichthys* emerge as a natural assemblage based on sequence of photophore development, morphology, and pigmentation. The grouping of these genera as a phylogenetic unit conflicts with the phylogenetic scheme proposed by Paxton (1968, 1972). His arrangement of the 17 genera of the subfamily Lampanyctinae into four tribes, based on a combination of adult osteology and photophore pattern, is shown in Figure 14. We agree that *Notolychnus valdiviae* has an ample array of unique adult and larval characters to warrant its placement in the monotypic tribe Notolychnini. Likewise we concur with the establishment of a separate tribe Diaphini for *Diaphus* and *Lobianchia,* two genera with a dis-

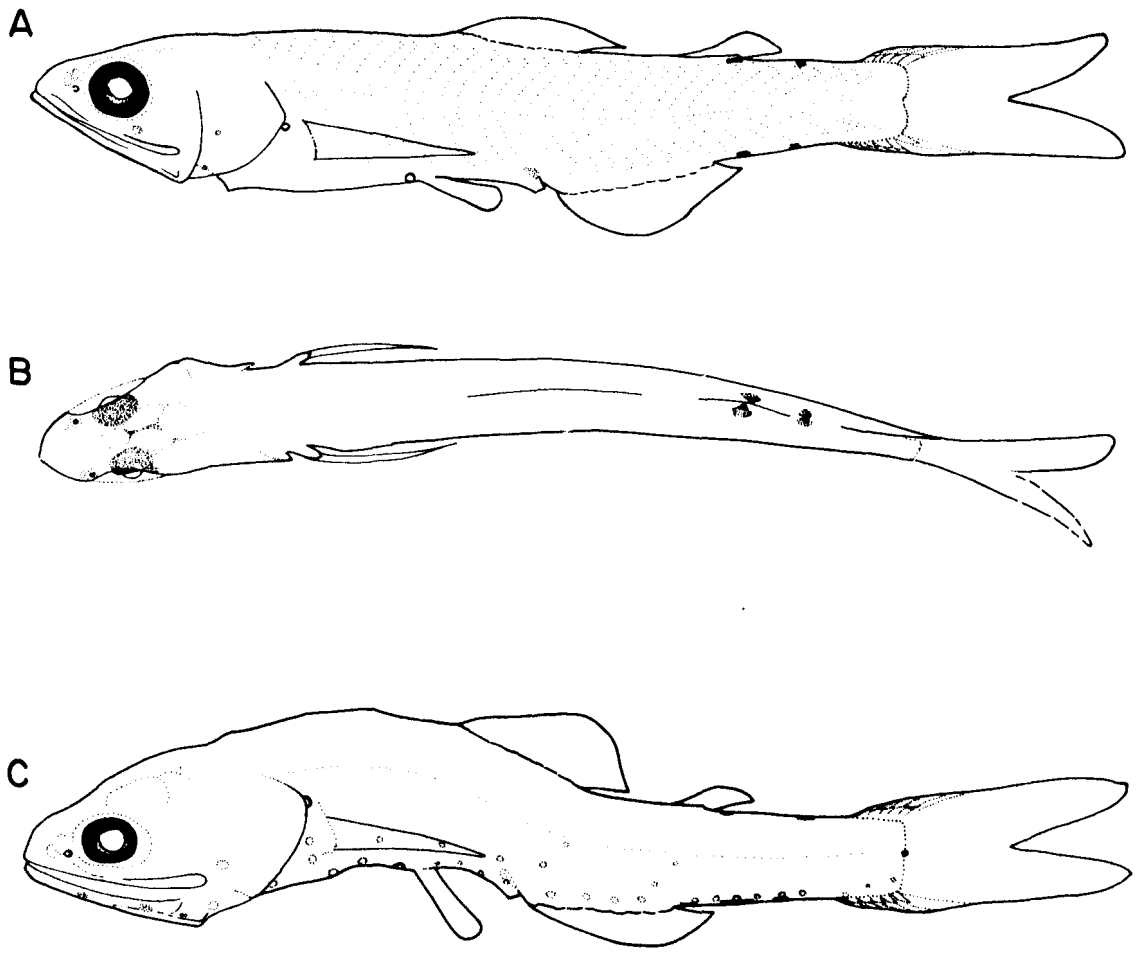

FIGURE 8.—Developmental stages of *Lepidophanes guentheri* (Goode and Bean).—A, 13.5-mm larva, R.S. *Dana* Station 3998X; B, 13.5-mm larva, dorsal view; C, 12.7-mm transformation stage, R.S. *Dana* Station 3998X.

tinct facies of adult and larval characters. Paxton placed the remaining 14 genera into two tribes, the Lampanyctini and Gymnoscopelini. On the basis of larval characters, we cannot concur with his distribution of genera among the two tribes. He included eight genera (*Lampanyctus, Stenobrachius, Triphoturus, Ceratoscopelus, Lepidophanes, Bolinichthys, Taaningichthys,* and *Lampadena*) in the tribe Lampanyctini and restricted the tribe Gymnoscopelini to six genera (*Gymnoscopelus, Lampanyctodes, Notoscopelus, Lampichthys, Scopelopsis,* and *Hintonia*). Paxton found no single character that would differentiate any of the four tribes from all others in the subfamily and relied on a combination of osteological and photophore characters to define the tribes. His most trenchant characters separating the Gymnoscopelini from the Lampanyctini were the presence of a supramaxillary bone in the Gymnoscopelini and its absence in the Lampanyctini and the presence of a Dn photophore in the former and its absence in the latter.

Our findings in the larvae suggest a different distribution of genera for the two tribes. On the basis of larval characters described earlier

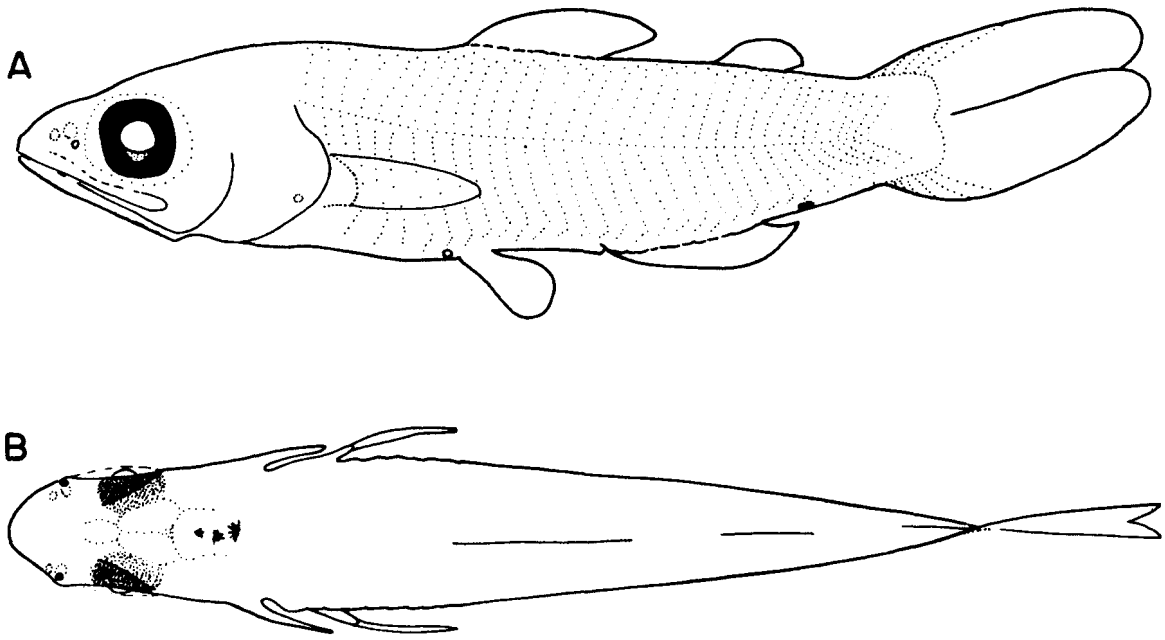

FIGURE 9.—Developmental stage of *Bolinichthys* sp.—A, 10.6-mm larva, R.R.S. *Discovery* Station 702; B, 10.6-mm larva, dorsal view.

we would enlarge the tribe Gymnoscopelini to include *Ceratoscopelus, Lepidophanes, Bolinichthys, Lampadena,* and *Taaningichthys* as well as the six genera assigned to the tribe by Paxton. We would restrict the tribe Lampanyctini to *Lampanyctus, Stenobrachius,* and *Triphoturus,* three genera with distinctive larvae that develop only the Br_2 photophores, and are characterized by an abrupt transformation from larva to juvenile. Our suggested modification of Paxton's scheme is shown in Figure 15.

Even though we propose a different distribution of genera in the tribes Gymnoscopelini and Lampanyctini, there is a striking concordance between our groupings of related genera and Paxton's, derived from quite different criteria. For example, both methods suggest a close relationship for *Scopelopsis, Lampichthys,* and *Notoscopelus* as well as for *Ceratoscopelus, Lepidophanes,* and *Bolinichthys.*

It should be noted that the heaviest development of accessory luminous tissue occurs in the genera we place in the tribe Gymnoscopelini and that such luminous tissue is best developed on *Ceratoscopelus, Bolinichthys, Lepidophanes, Lampichthys,* and *Hintonia.* On *Ceratoscopelus townsendi* and various species of *Bolinichthys,* conspicuous patches of luminous tissue form on the head between the orbits, especially in adult males. In these genera there may be a direct relation between the absence of the Dn photophores and the presence of accessory luminous tissue on the head.

A PROPOSED THEORY FOR THE EVOLUTION OF PHOTOPHORE PATTERN IN MYCTOPHIDAE

Perhaps the most intriguing result of our studies of larvae of the tribe Gymnoscopelini is a theory for the evolution of photophore pattern in lanternfishes. The only previous theory was proposed by Bolin (1939) and fully developed by Fraser-Brunner (1949). Fraser-Brunner (1949) postulated an hypothetical ancestral myctophid with a pair of continuous photophore rows on the ventral margin, beginning with the

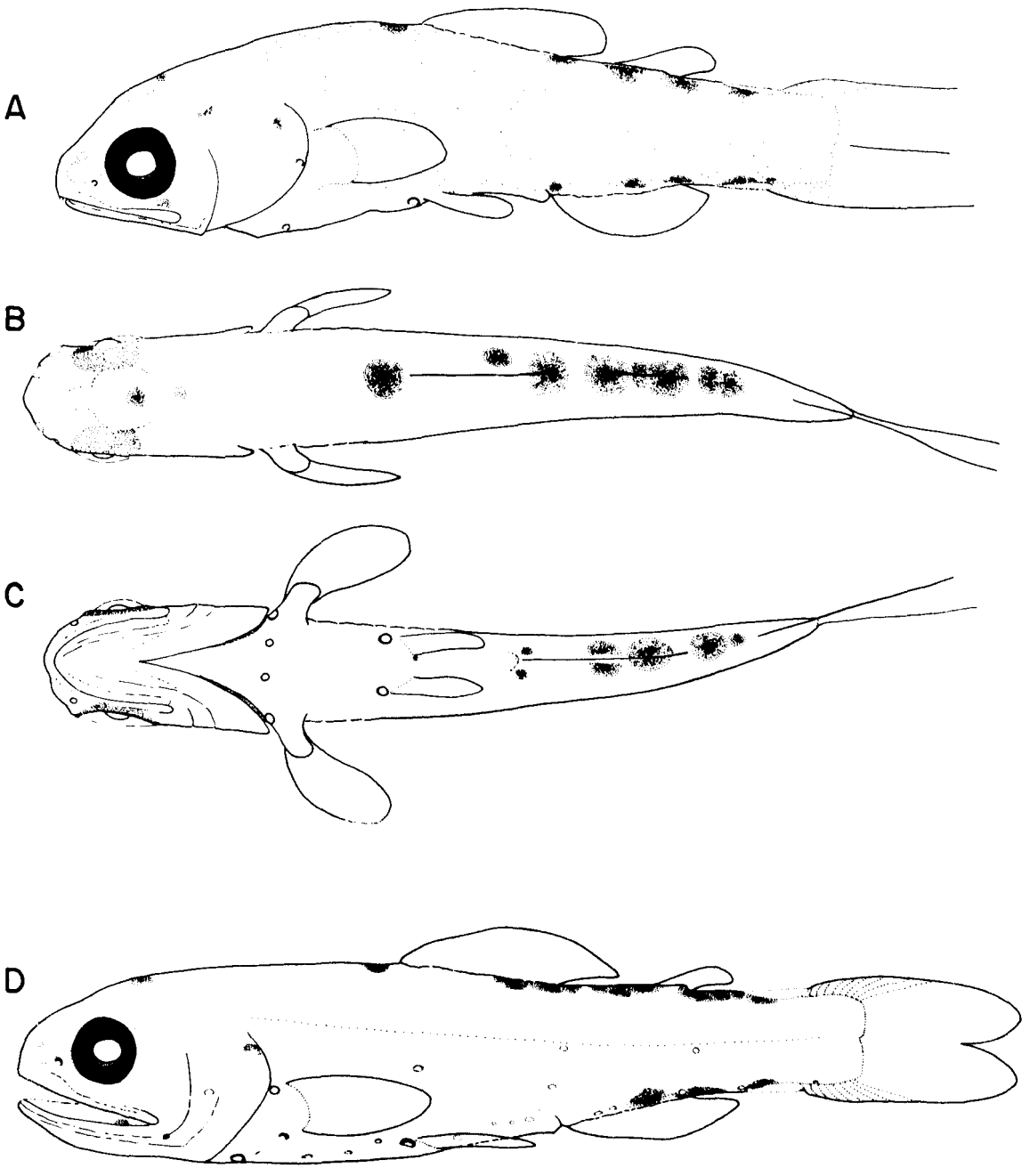

FIGURE 10.—Developmental stages of *Lampadena urophaos* Paxton.—A, 13.4-mm larva, CalCOFI 5011- S-T3; B, 13.4-mm larva, dorsal view; C, 13.4-mm larva, ventral view; D, 19.6-mm transformation stage, CalCOFI 6210-117.90.

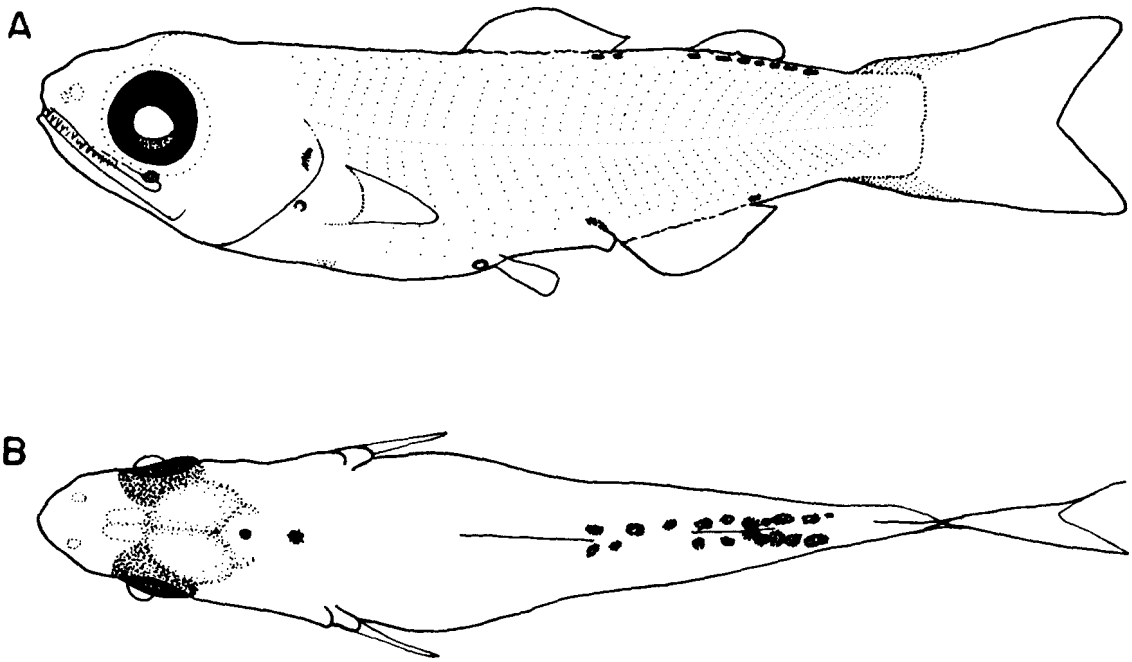

FIGURE 11.—Developmental stage of *Lampanyctodes hectoris* (Günther).—A, 9.2-mm larva, R.R.S. *Discovery* Station 1374; B, 9.2-mm larva, dorsal view.

most ventral jaw photophore (Br_3) and extending posteriad to the tail. Above these ventral rows on each side was a lateral row that extended from the middle jaw photophore (Br_2) posteriad to the anus. A third row began with the upper jaw photophore (Br_1) and ended with the upper opercular photophore. Fraser-Brunner proposed that the photophore patterns of all extant lanternfish species were derived by upward migration of certain photophores on the ventral and lateral rows of the ancestral form. His chief evidence for such upward migration was that, in present-day myctophids, certain lateral photophores, such as the posterior two SAO and the POL, lie above gaps in the ventral series. These gaps were presumably produced by the upward migration of photophores to the lateral position they now occupy. He found other indirect evidence in the presence of small modified scales which overlie certain of the lateral photophores in some species. Since these scales were out of the meristic lines of the larger scales, Fraser-Brunner concluded that they were scales that had been "taken with" the photophores during their upward migration.

Fraser-Brunner's (1949) hypothesis has remained unchallenged or at least tacitly accepted by workers up to the present; however, we believe that it contains a number of deficiencies which warrant an alternative theory for the evolution of the photophore pattern in lanternfishes. Firstly, we believe that the presence of certain lateral photophores above gaps in the ventral row is tenuous indirect evidence of migration, since there are many examples of lateral photophores lying directly above photophores in the ventral series, and there are equally numerous examples of gaps in the ventral series with no overlying photophores whatsoever. Further, we find the presence of small specialized scales over certain of the lateral photophores to be inconclusive evidence of upward migration from the ventral series, since some lateral photophores are overlain by normal-sized scales that are aligned with the other scales in their row. Also, if a photophore had carried its scale with it dur-

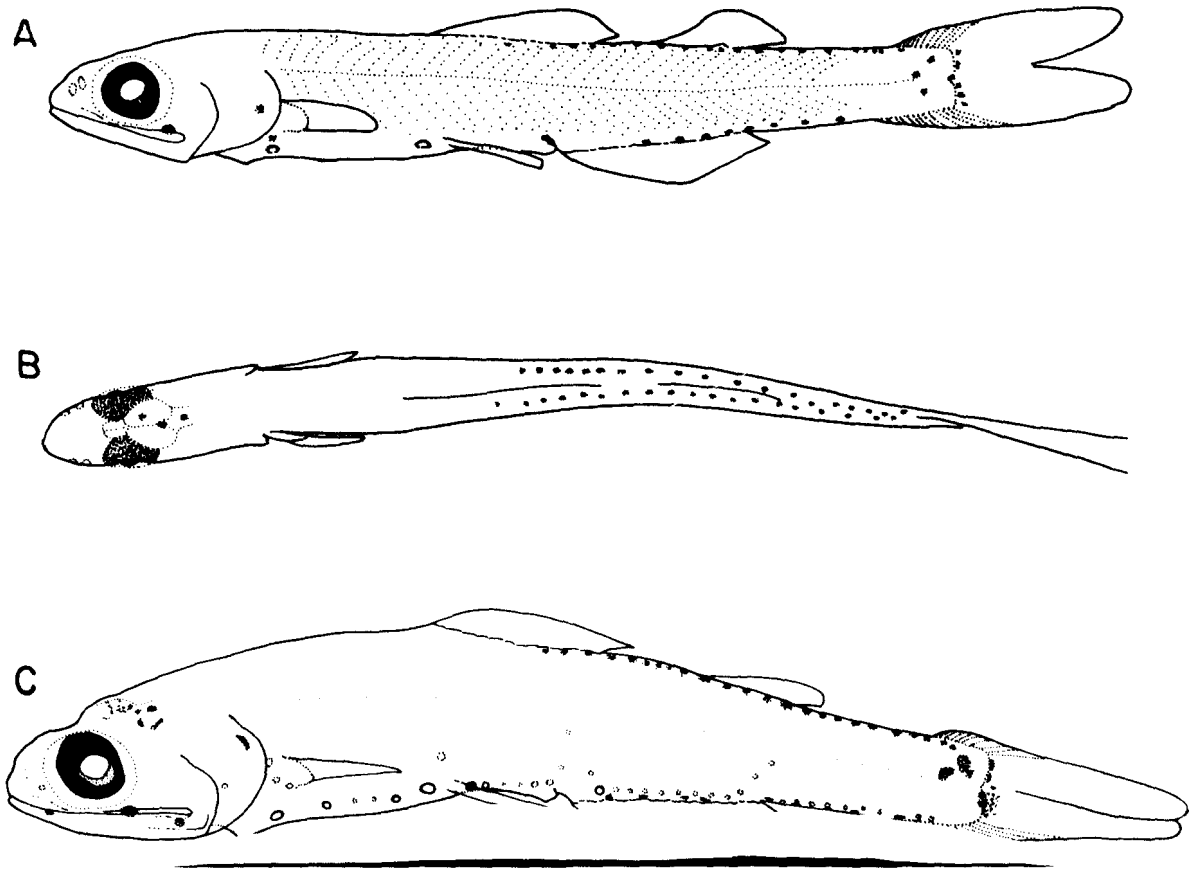

FIGURE 12.—Developmental stages of *Gymnoscopelus aphya* Günther.—A, 23.5-mm larva, U.S. NS *Eltanin* Station 319; B, 23.5-mm larva, dorsal view; C, 27.7-mm transformation stage, U.S. NS *Eltanin* Station 1341.

ing its upward migration, one might expect a comparable deletion or modification at its origin in the ventral scale row. There is none. Another major deficiency in the theory is its inability to explain the photophore pattern of a species such as *Notolychnus valdiviae* which has four pairs of photophores near the dorsal midline. If derived from the ventral series, the dorsal photophores would be supplied by peripheral nerves of the ventral or medial spinal rami that would have to extend dorsad across the horizontal septum; such an arrangement seemed so unlikely for species with photophores above the lateral line that we traced the nerve supply to such photophores in *Triphoturus mexicanus*, *Bolinichthys* sp., and *Notolynchnus valdiviae*. In *T. mexicanus* the VLO, SAO_3, POL_2, and Prc_3 lie above the lateral line, and in *Bolinichthys* the latter three photophores lie above the line. These light organs are supplied by a branch of the lateral vagus nerve, the superficial lateral-line nerve. In *Notolychnus* the VLO, SAO_3, POL_2 and Prc_2 lie extremely high on the body near the dorsal midline. The VLO and SAO_3 are supplied by the dorsal ramus of the lateral vagus nerve. The nerve supply to the POL_2 was difficult to determine but appeared also to be the dorsal ramus of the lateral vagus nerve. The Prc_2 is innervated by the superficial lateral-line nerve.

Ray (1950), in her detailed study of the peripheral nervous system of *Stenobrachius leucopsarus*, showed that all body photophores, except three pairs, are supplied by ventral rami of spinal nerves. The exceptions, SAO_3, POL, and Prc_4,

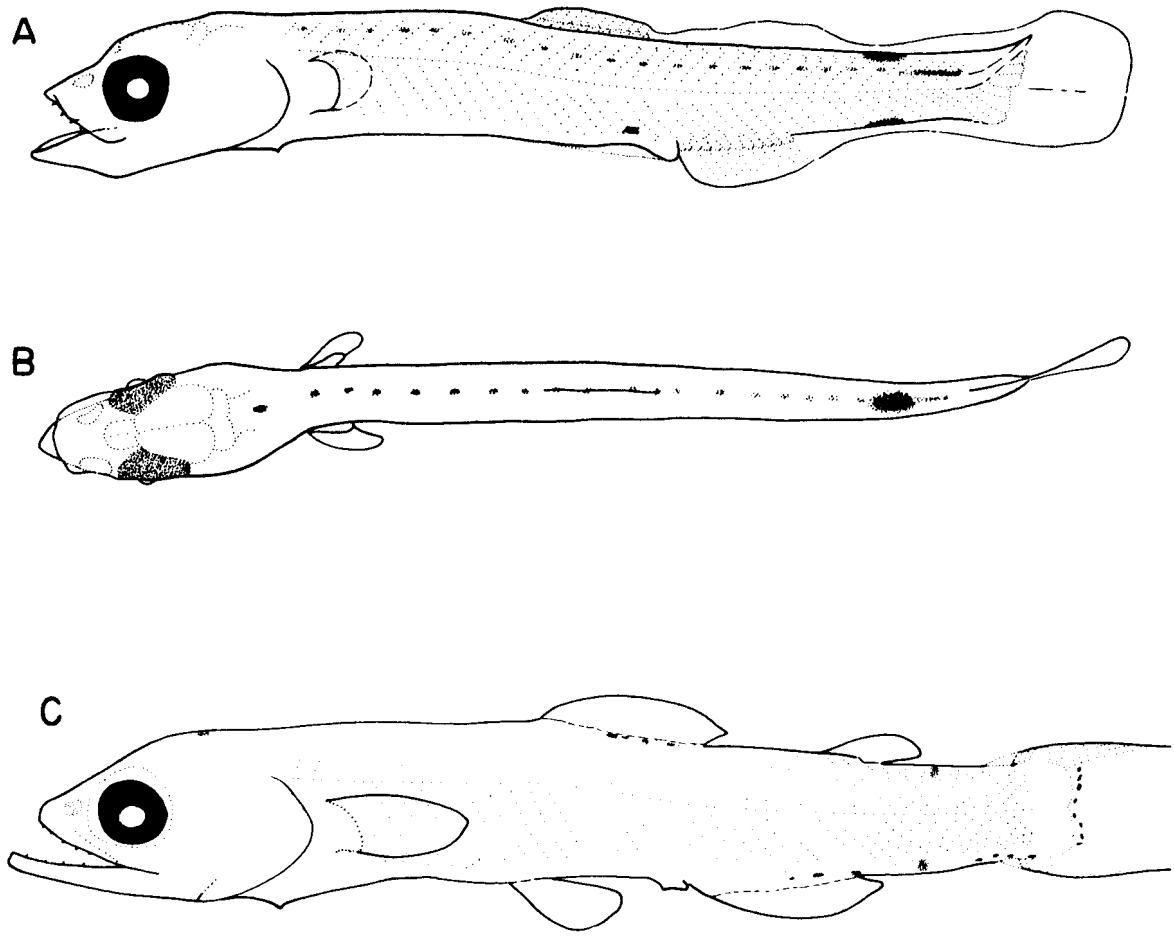

FIGURE 13.—Developmental stage of *Taaningichthys minimus* Tåning.—A, 7.3-mm larva, Hawaii Institute of Marine Biology, China Hat Series 3; B, 7.3-mm larva, dorsal view; C, 14.4-mm larva, SIO-FCRG Cruise 71-2.

are innervated by medial rami of spinal nerves; however, the first two of these each receive a small ramulus from a ventral spinal ramus. Ray believed that the innervation of lateral body photophores by ventral components of spinal nerves supported Bolin's (1939, p. 131-132) suggestion that lateral body photophores were derived by upward displacement of certain photophores from a single pair of ventral photophore rows. In lanternfish, such as *T. mexicanus*, *Bolinichthys*, and *Notolychnus*, the photophores which lie above the lateral line have always been considered homologous to their counterparts that lie below the line in other genera. Our finding of a cranial nerve supply for photophores above the lateral line in *T. mexicanus*, *Bolinichthys* sp., and *Notolychnus* casts considerable doubt on the theory that these photophores could have arisen from upward displacement, "from a primitively ventral and strictly linear series" (Bolin, 1939, p. 131-132) or even from "two ventrally located, parallel series of photophores, such as we find in *Vinciguerria*" (Bolin, 1939, p. 97).

An alternative hypothesis for the evolution of photophore patterns became apparent to us when studying the transforming stages of *Scopelopsis* (Figures 2, 3). It is obvious that in these specimens, the so-called primary photophores

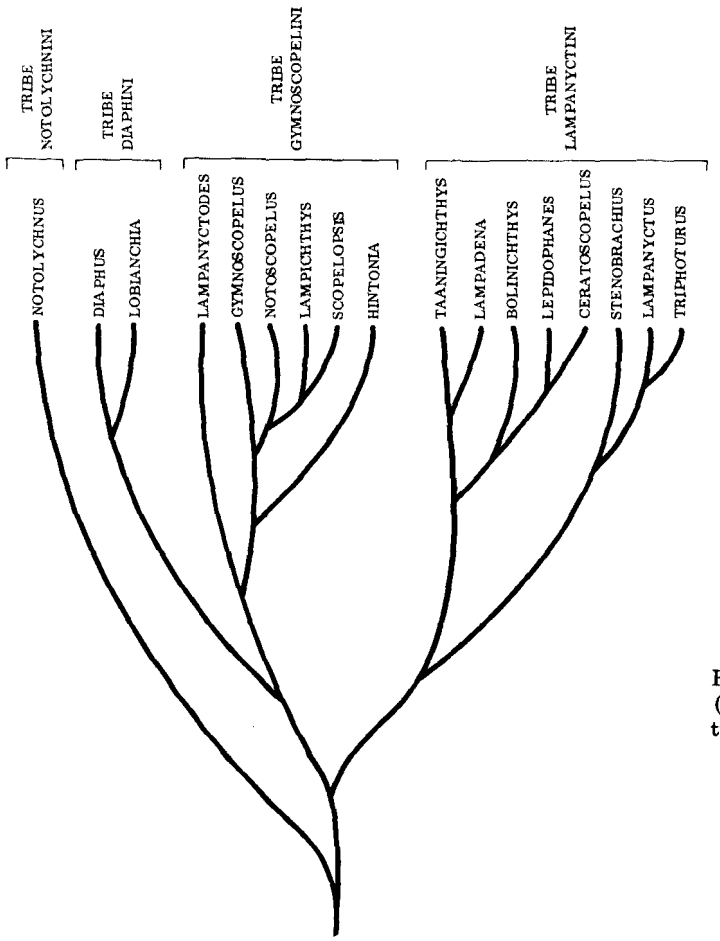

FIGURE 14.—Dendrogram of Paxton's (1968, 1972) arrangement of genera and tribes in the subfamily Lampanyctinae.

take their places very properly in the horizontal lines of smaller secondary photophores that cover the body. In these remarkable specimens, the primary photophores appear merely as enlarged members in the meristic series of light organs. Accordingly, it is tempting to speculate that this reflects a possible ancestral stage in the evolution of myctophid photophore patterns. We postulate that the archetypal pattern of light organs in lanternfishes was a generalized arrangement consisting of a single unspecialized photophore at the posterior margin of each scale pocket and a series of similar photophores distributed over the head. The progressive enlargement and specialization of certain photophores of the generalized pattern and concurrent diminution or loss of the "secondary" photophores would seem a propitious mechanism for adaptation and subsequent species diversification. The enlargement of photophores in the ventral midline to form a pair of longitudinal rows was universal in the family. Clarke (1963) suggested that these downward oriented photophores emit a continuous light of ambient wavelength which conceals the fish by breaking up its silhouette, that would otherwise be easily detected by predators hunting from below. This and other theories for the universality of the ventral photophore rows are discussed by McAllister (1967). The placement of the ventral and lateral photophores in a pattern unique to each species is an obvious mechanism for species recognition and reproductive isolation (Harvey, 1952, 1957; Marshall, 1954; Bolin, 1961).

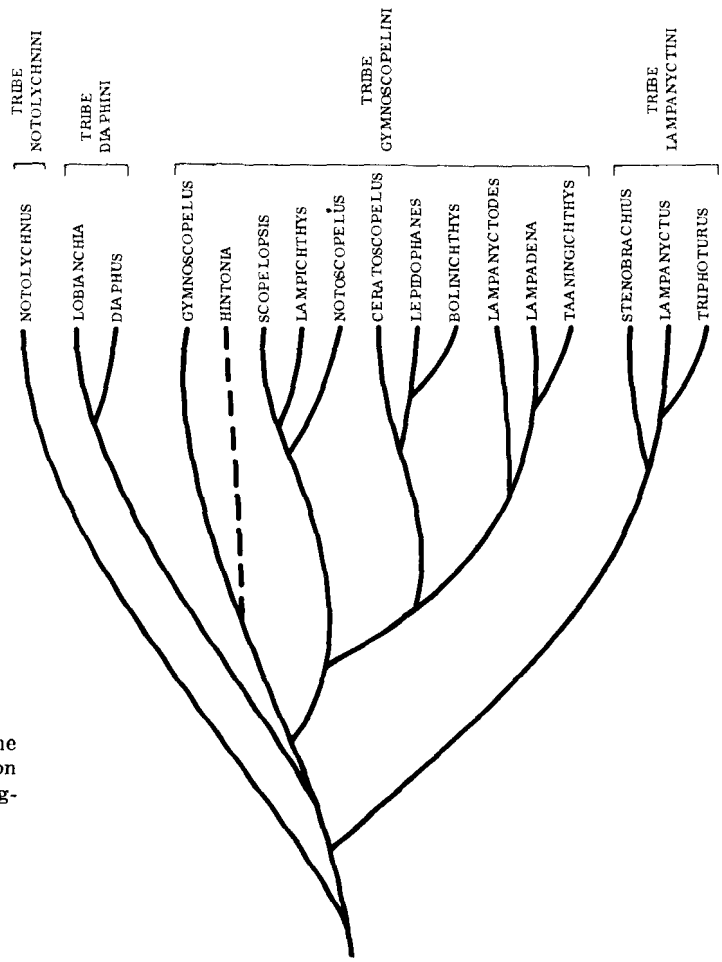

FIGURE 15.—Dendrogram showing the generic relationships and tribal division of the subfamily Lampanyctinae as suggested by larval characters.

Whatever were the adaptive forces that marshalled the light organs of myctophids into specific patterns, we believe that the ancestral myctophids had unspecialized photophores distributed over the head and body (one at the margin of each scale pocket) and that the specific patterns were derived by enhancement of some photophores and the concomitant deletion of others. Among the 28 known genera of myctophids are six (*Scopelopsis, Hintonia, Lampichthys, Bolinichthys, Lepidophanes,* and *Lampanyctus*) in which at least some species have minute photophores on the body, in addition to the typical pattern of primary photophores. The minute photophores may occur at every scale pocket (e.g., *Scopelopsis*) or may be restricted to a certain region of the body (e.g., *Hintonia*). Typically, those species with such minute photophores also have one or more head photophores that are lacking in most other myctophids. Previous workers have considered the minute photophores of these genera to be secondary structures, which have evolved after the primary organs; however, we believe that they reflect an ancestral stage in the evolution of photophore pattern. We believe that *Scopelopsis* most closely approximates the photophore pattern of ancestral myctophids since the distinction between "primary" and "secondary" organs is less apparent than in the other genera retaining secondary photophores. Moreover, every photophore position described for lanternfishes has its counterpart in *Scopelopsis*, and we find that every known myctophid photophore pattern can be generated

by enhancement of selected photophores of this species. Such a mechanism for the evolution of photophore pattern seems much less cumbersome than the theory of upward migration of photophores from the ventral series. The minor upward displacement of some ventral photophores may be a plausible explanation for the slightly arched AO and VO rows found in some myctophids but, for reasons outlined above, we find it improbable that such a mechanism could be responsible for the profoundly diverse photophore patterns of contemporary lanternfishes.

ACKNOWLEDGMENTS

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