

DEVELOPMENT AND DISTRIBUTION OF LARVAE AND EARLY JUVENILES
OF THE COMMERCIAL LANTERNFISH, *LAMPANYCTODES HECTORIS*
(GÜNTHER), OFF THE WEST COAST OF SOUTHERN AFRICA
WITH A DISCUSSION OF PHYLOGENETIC
RELATIONSHIPS OF THE GENUS

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ABSTRACT: *Lampanyctodes hectoris* is a species of lanternfish which is becoming an important part of the pelagic fishery off South Africa. The Southwest Africa Pelagic Egg and Larval Survey has provided an abundance of larval specimens of this species. The larvae, transitional and early juvenile stages are described and illustrated for the first time and information on their distribution and relative abundance is provided. Larval characters are used in combination with selected adult characters to elucidate the phylogenetic affinities of this genus.

Lanternfishes of the family Myctophidae are the most ubiquitous and speciose (approximately 250 species in 30 genera) of all fishes in the oceanic mid-waters. Although their total biomass is unknown, the fact that lanternfishes, on the average, make up approximately one-half of all fish larvae taken in any oceanic plankton tow gives some impression of its immensity. Although they are small fishes, usually less than 100 mm in length, they may have the greatest biomass of any vertebrate family. Knowledge of their ecological role in the world ocean is poor, but initial studies suggest that these fishes are a major element in the oceanic food web. Among the commercially important organisms known to prey on lanternfishes are salmon (Shimada, 1948; Manzer, 1968), tunas (Alverson, 1963; Pinkas et al., 1971), rockfish (Pereyra et al., 1969), fur seals (Mead and Taylor, 1953) and cetaceans (Fitch and Brownell, 1968). Recent studies (Paxton, 1967; Holton, 1969; Legand and Rivaton, 1969; Collard, 1970; Baird et al., 1975) indicate that lanternfishes are important grazers on herbivorous zooplankton.

Historically, lanternfishes have not been commercially exploited because of their small size and relatively diffuse distribution in the water column. A growing body of observations indicates that some species of lanternfishes aggregate in large numbers at certain times during their life cycles and, at such times, may be available to a fishery. There have been several well-documented observations of lanternfish swarming at the surface in dense "balls." *Benthoosema panamense* exhibits this behavior during daylight in the eastern Pacific and tuna boat skippers report that yellowfin and skipjack tuna feed exclusively on these swarms

when they are observed (Alverson, 1961). Similar swarms of *Diaphus garmani* were reported at night in the central Pacific (Nakamura, 1970). Lanternfishes also aggregate in extensive shoals. Observations from submarines indicate that some species of lanternfishes, such as *Ceratoscopelus maderensis* (Backus et al., 1968) and *Benthoosema panamense* (Barham, 1971), form extensive aggregations in slope waters. G. Krefft (Institut für Seefischerei, Hamburg, pers. comm.) has achieved catch rates of 1¼ metric tons/hour of *Diaphus dumerili* with a commercial herring trawl off Buenos Aires. It is well known that myctophids are often a major element in deep scattering layers of the ocean (Barham, 1966; Pearcy and Mesecar, 1971). Additional knowledge of these phenomena may lead to the commercial harvesting of lanternfishes.

Recently a fortuitous fishery for the lanternfish *Lampanyctodes hectoris* has developed incidental to the anchovy/pilchard fishery off the western coast of South Africa (Centurier-Harris, 1974). Annual landings of lanternfishes (mostly *L. hectoris*) were 1,134 metric tons or 0.3 percent of the pelagic fishery catch in this region in 1969 and increased to 42,560 metric tons or 10.45 percent of the catch in 1973. The location of the fishery is shown in figure 1. This species is particularly desirable because of its high content (20 percent by weight) of fine quality oil.

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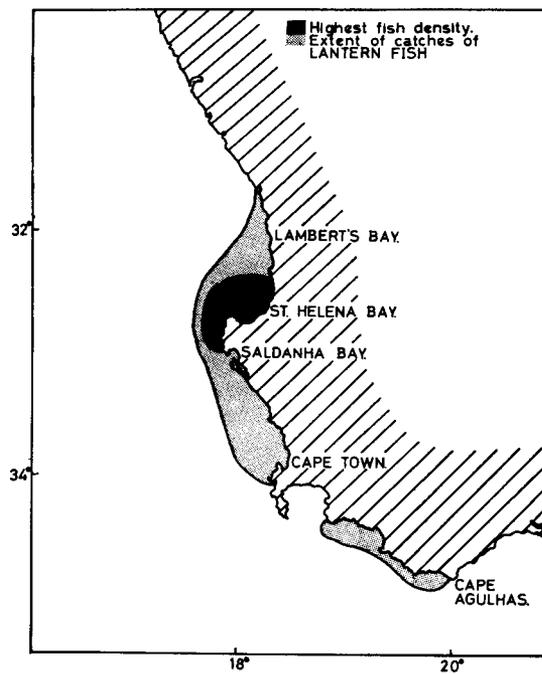


Figure 1. Region of the fishery for *Lampanyctodes hectoris* off South Africa (from Centurier-Harris, 1974).

Little is known about the life history of this important species of lanternfish. However, an extensive plankton survey, the Southwest African Pelagic Egg and Larval Survey (SWAPELS), was initiated by the Sea Fisheries Branch in 1972 (O'Toole, 1974). Although the data from this survey are not completely analyzed, some information on the distribution and relative abundance of *L. hectoris* larvae will be presented in this paper, the principal purpose of which is to describe the larval, transitional, and early juvenile stages of *L. hectoris*. Previously, Moser and Ahlstrom (1972) illustrated a 9.2 mm larva of *L. hectoris* and gave a partial description of the sequence of photophore formation based on the few specimens available. Examination of the abundant larval specimens from SWAPELS has shown that Moser and Ahlstrom (1972) were in error and that their 9.2 mm larva was *Lampadena* sp. The larvae of *Lampanyctodes hectoris* have a unique generic morph, a concept discussed extensively by Moser and Ahlstrom (1970, 1972, 1974). A number of larval characters give insight into the relationships of this genus with other myctophid genera and these will be treated in the discussion section of this paper.

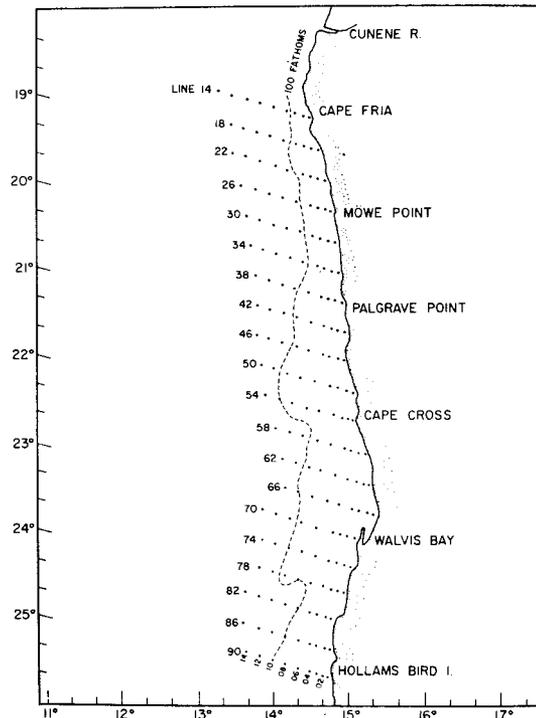


Figure 2. Station plan for Southwest African Pelagic Egg and Larval Survey (SWAPELS).

METHODS

Specimens for the developmental part of this study were obtained from two plankton surveys of SWAPELS (Fig. 2). Survey 1 was carried out from August 1972 to March 1973 and Survey 2 from August 1973 to April 1974. The net used on both surveys was a 57 cm bongo net; 0.940 mm and 0.940 mm mesh were paired on Survey 1 and 0.940 mm was used on the left unit and 0.500 mm on the right on Survey 2. Oblique tows were made to a depth of 50 m at all stations except where the bottom was shallower than 50 m.

Techniques used for describing the development of *L. hectoris* are outlined in Moser and Ahlstrom (1970).

Lampanyctodes hectoris (Günther)

Figures 3 and 4

Literature.—The illustration of the 9.2 mm larva of *Lampanyctodes hectoris* and the remarks on photophore formation in that species in Moser and Ahlstrom (1972) are in error and refer to a larva of *Lampadena* sp. There are no illustrations or descriptions of *L. hectoris* larvae in the literature.

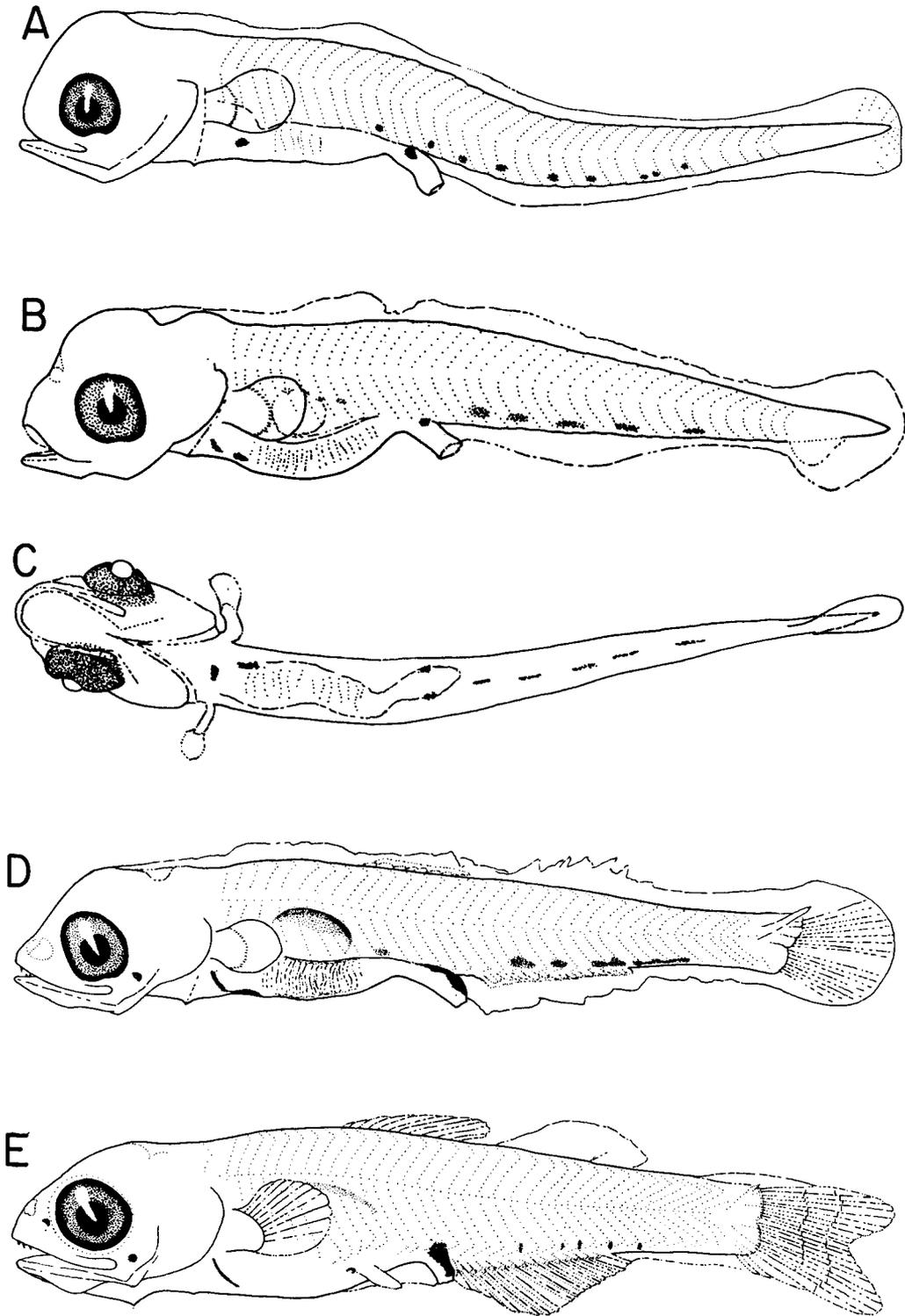


Figure 3. Larvae of *Lampanyctodes hectoris*. A. 3.8 mm; B. 5.0 mm; C. 5.0 mm, ventral view; D. 6.8 mm; E. 8.7 mm.

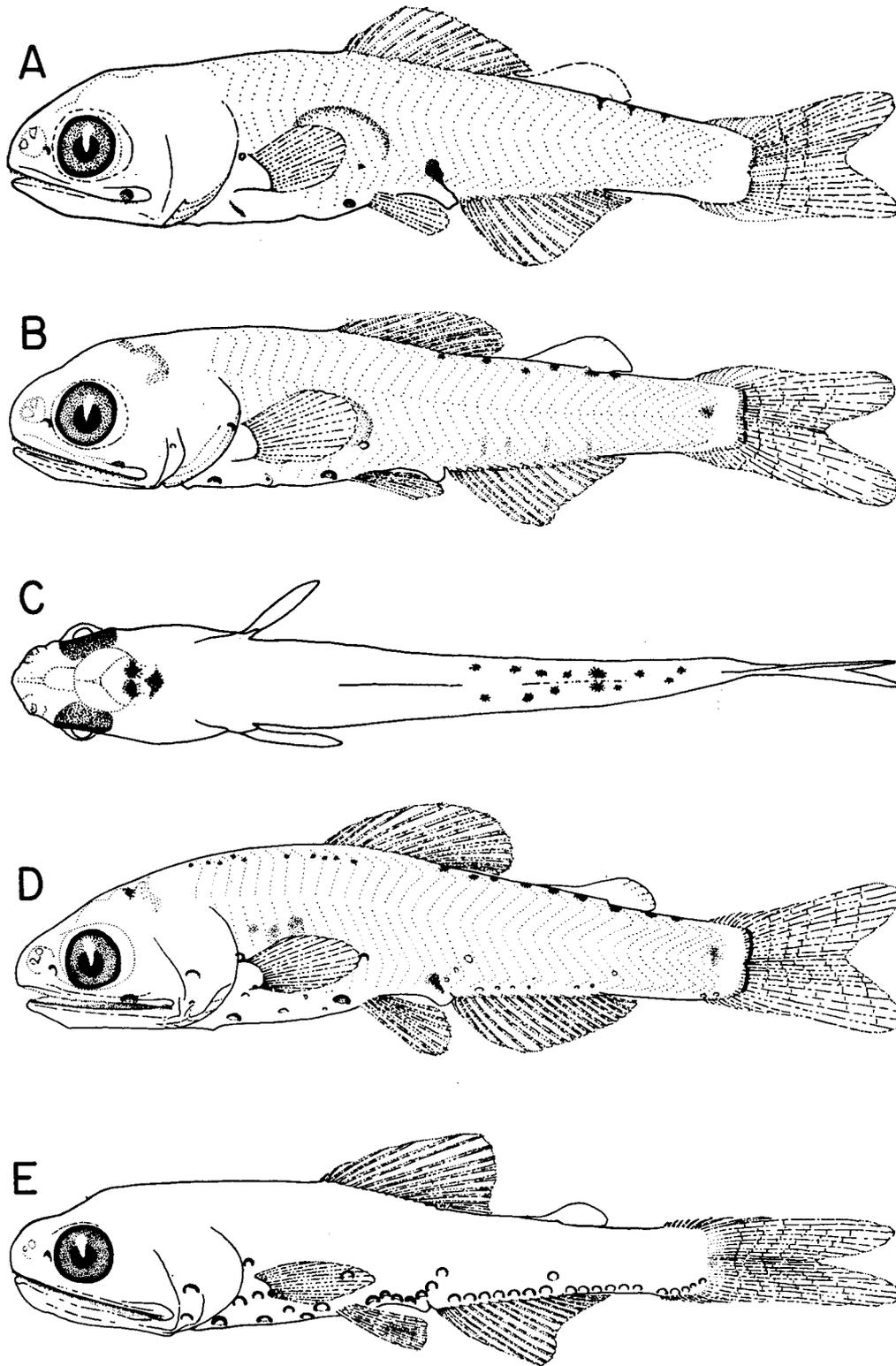


Figure 4. Developmental stages of *Lampanyctodes hectoris*. A. 11.7 mm larva; B. 13.0 mm larva; C. 13.0 mm larva, dorsal view; D. 14.9 mm transforming specimen; E. 14.2 mm juvenile.

TABLE 1. Measurements (mm) of larvae of *Lampanyctodes hectoris*. (Specimens between dashed lines are undergoing notochord flexion).

Body length	Snout to anus	Head length	Head width	Snout length	Eye width	Eye length	Length of ventral eye tissue	Body depth	Pectoral fin length	Snout to origin of pelvic fin	Snout to origin of anal fin	Snout to origin of dorsal fin
3.8	1.8	0.75	0.50	0.15	0.23	0.29	-	0.49	0.20	-	-	-
4.0	1.8	0.72	0.43	0.12	0.20	0.27	-	0.43	0.19	-	-	-
4.3	2.0	0.85	0.52	0.16	0.24	0.30	-	0.45	0.25	-	-	-
4.5	2.3	0.96	0.53	0.20	0.27	0.31	-	0.63	-	-	-	-
4.8	2.5	1.0	0.70	0.26	0.29	0.37	-	0.68	0.29	-	-	-
5.0	2.6	1.2	0.75	0.25	0.38	0.43	0.02	0.85	0.20	-	-	-
5.2	2.7	1.1	0.70	0.27	0.31	0.39	-	0.73	0.35	-	-	-
5.6	2.8	1.2	0.77	0.35	0.34	0.42	0.01	0.82	0.25	-	-	-
5.8	3.1	1.4	0.78	0.32	0.38	0.46	0.01	0.86	0.36	-	-	-
6.0	3.1	1.2	0.80	0.32	0.41	0.48	0.02	0.88	0.26	-	-	-
6.2	3.2	1.4	0.83	0.33	0.43	0.48	0.04	1.0	0.33	2.4	-	-

6.4	3.7	1.4	0.90	0.34	0.49	0.55	0.03	1.1	0.27	2.8	-	-
6.6	3.8	1.7	1.0	0.45	0.53	0.62	0.04	1.2	0.32	2.8	3.9	3.0
6.8	4.0	1.7	1.0	0.36	0.57	0.55	0.01	1.2	0.28	3.0	4.2	2.8
7.0	4.0	1.7	1.1	0.40	0.52	0.63	0.02	1.2	0.56	3.1	4.2	3.2
7.2	4.2	1.9	1.0	0.40	0.57	0.68	-	1.4	0.46	3.1	4.3	3.2
7.5	4.2	1.8	1.0	0.43	0.52	0.62	0.03	1.3	0.57	3.2	4.3	3.3
7.7	4.6	1.9	1.0	0.40	0.64	0.71	0.04	1.3	0.52	3.3	4.6	3.2

8.0	4.6	2.0	1.2	0.45	0.61	0.71	-	1.5	0.60	3.3	4.7	3.3
8.2	4.9	2.2	1.2	0.49	0.68	0.75	0.02	1.6	0.65	3.8	4.9	3.6
8.7	5.0	2.3	1.3	0.50	0.77	0.87	0.02	1.8	0.87	3.8	5.0	3.8
9.2	5.2	2.2	1.2	0.60	0.73	0.84	-	1.8	1.0	4.2	5.3	4.1
9.7	5.7	2.5	1.3	0.68	0.73	0.86	-	2.0	1.0	4.2	5.7	4.2
10.1	6.2	2.9	1.4	0.71	0.87	0.91	-	2.2	1.2	4.6	6.2	4.5
10.5	6.5	2.9	1.6	0.73	0.88	1.0	-	2.3	1.2	4.8	6.5	4.8
10.8	6.7	3.0	1.7	0.78	0.83	0.95	-	2.4	1.4	5.1	6.7	4.8
11.0	6.8	3.0	1.6	0.74	0.79	0.95	-	2.3	1.3	5.0	6.9	4.8
11.7	7.1	3.3	1.7	0.93	0.87	1.0	-	2.6	1.5	5.4	7.1	5.2
12.0	7.5	3.3	1.8	0.83	1.0	1.1	-	2.8	1.5	5.7	7.5	5.3

TABLE 1. (Continued)

Body length	Snout to anus		Head length	Head width	Snout length	Eye width	Eye length	Length of ventral eye tissue	Body depth	Pectoral fin length	Snout to origin of pelvic fin	Snout to origin of anal fin	Snout to origin of dorsal fin
	superior	inferior											
12.3	7.4	3.4	1.8	1.0	0.80	1.0	1.0	-	2.9	1.4	5.5	7.4	5.4
13.0	7.8	3.6	2.2	1.0	0.90	1.0	1.2	-	2.9	1.7	5.8	7.8	5.8
13.8	8.3	3.7	2.0	0.98	0.96	1.0	1.0	-	3.2	1.8	6.2	8.4	6.2
14.0	8.9	4.1	1.9	1.1	0.93	1.1	1.2	-	3.2	1.6	7.0	9.1	6.1
14.9*	8.8	4.0	2.2	1.1	0.95	1.1	1.2	-	3.7	2.1	6.6	8.8	6.4
14.2**	8.6	4.6	2.0	1.2	1.0	1.2	1.2	-	3.2	1.9	6.8	8.8	6.7
16.0**	9.8	5.0	2.8	1.3	0.94	1.3	1.3	-	3.5	2.5	7.2	9.9	7.1
21.2**	13.0	6.6	3.2	2.0	1.0	2.0	2.0	-	4.9	4.0	9.8	13.0	9.5

* Transforming specimen.
** Juvenile.

TABLE 2. Meristics from cleared and stained larvae of *Lampanyctodes hectoris*.

Length (mm)	Principal caudal fin rays		Procurent caudal fin rays		Branchiostegal rays		Pectoral fin rays		Hypural elements		Gill rakers (right arch)		Dorsal fin rays	Pelvic fin rays		Vertebrae
	superior	inferior	superior	inferior	left	right	left	right	superior	inferior	upper limb	lower limb		left	right	
7.5	7	7	-	-	-	-	-	-	-	-	-	-	-	-	-	-
7.7	10	9	0	1	3	3	5	5	-	-	-	-	-	-	-	-
8.3	10	9	-	-	3	3	4	5	-	-	-	-	-	-	-	-
8.7	10	9	2	3	4	4	7	7	1	3	-	-	7	-	-	-
9.2	10	9	3	4	5	5	9	9	2	3	-	-	11	7	-	-
9.6	10	9	4	5	6	6	10	9	4	3	-	-	13	9	4	4
10.1	10	9	5	6	7	7	12	12	4	3	-	-	14	12	5	5
10.5	10	9	6	7	7	7	11	11	4	3	-	-	15	12	7	7
11.1	10	9	7	8	8	8	11	12	4	3	-	-	16	13	7	7
11.8	10	9	7	8	8	8	13	13	4	3	0	12	16	14	8	8
12.3	10	9	-	9	7	8	-	12	4	3	5	14	16	14	8	8
12.7	10	9	9	11	9	9	13	13	4	3	8	17	14	14	8	8
13.2	10	9	9	10	9	9	12	12	4	3	4	13	16	14	8	8
14.4	10	9	8	9	10	10	13	12	4	3	10	17	16	14	8	8
15.9	10	9	10	10	9	9	13	13	4	3	10	20	16	14	8	8

Diagnostic features.—As for other species of lanternfishes, the pelagic eggs of *L. hectoris* are not known. The smallest larvae in our collection were 3.8 mm. Larvae obtain a moderate size in comparison with those of related genera. The largest larva in our collection is 14.4 mm and the smallest juvenile is 14.2 mm SL. A 14.9 mm specimen is undergoing transformation. Larvae of *L. hectoris* have a unique sequence of photophore development, beginning with the Br₂ in 6 mm larvae and followed by the Vn in 7 mm larvae, the PO₅ in 8 mm larvae, and the PLO and PO₁ in 11 mm larvae. Although several other genera develop this same complement of early-forming photophores, as explained in detail in a later section, none develops them in this sequence. Small larvae which have not developed photophores may be identified by their pattern of melanophores, the most characteristic of which are a persistent series of four to eight ventral tail melanophores, two melanophores in the foregut region, a bilateral pair at the divergence of the terminal region of the gut, a series of embedded spots above the mid-gut, and a melanistic shield above the developing gas bladder. In mid- and late-stage larvae, a bilateral series of melanophores develops on the posterior dorsum.

Morphology.—Larvae of *L. hectoris* have no striking morphological features. Body depth increases from a mean of 14 percent of the body length in preflexion larvae, to 18 percent in larvae undergoing flexion, to 22 percent in postflexion larvae and 23 percent in newly transformed juveniles (Table 1). Snout-anus length averages 50 percent of the body length in preflexion larvae, 58 percent during flexion and 60 percent in later developmental stages. Head size is moderate; relative head length increases gradually from a mean of 21 percent of body length in preflexion larvae to 25 percent during flexion, 27 percent in postflexion larvae and 31 percent in early juveniles. Relative head width decreases gradually during development; it averages 62, 58, and 54 percent of the head length for the three major larval stages and 49 percent in early juveniles. Snout length is moderate, averaging 24 percent of the head length over the entire larval period and shortens to 19 percent in early juveniles. The eye is moderately large; eye length averages 36 percent of the head length in larvae up to the completion of notochord flexion, is reduced to a mean of 33 percent in postflexion larvae and further to 27 percent in early juveniles. The eye is slightly elliptical in preflexion larvae; eye width averages

82 percent of eye length, but this increases to a mean of 89 percent in later larval stages and the eyes of early juveniles are round. There is a sliver of ventral choroid tissue that appears in larvae between 5.0 and 9.0 mm. It reaches a maximum relative depth of 8 percent of the eye length and is only slightly paler in color than the eye itself.

Ossification of some important larval features is as follows. Vertebrae begin to ossify at about 11.1 mm length and the full complement of 36 to 37 is ossifying in larvae 12.3 mm and larger. Branchiostegal rays begin to ossify in 7 mm larvae, but, the full complement of 11 as listed by Paxton (1972) is not achieved in larvae nor in the earliest juveniles.

The maxillary is ossifying in larvae as small as 3.9 mm but develops no teeth. The dentary is ossifying and bearing teeth by 5.9 mm, as is the premaxillary. Teeth are uniserial on the premaxillary with the anterior five or six teeth larger than the remainder; as many as 20 conical, usually straight teeth form on late-stage larvae. On the posterior two-thirds of each dentary bone a series of six to eight conspicuous hooked teeth form early in the larval period. The hooked part of each tooth projects anteriorly at almost right angles to the base of the tooth. They persist to transformation. The dentary teeth anterior to these, and later between and posterior to the hooked teeth, are conical, straight and uniserial anteriorly. Late-stage larvae have more than 30 such dentary teeth. The hooked and uniserial teeth present on the jaws of larvae are shed or resorbed and replaced by the wide bands of numerous small teeth at transformation.

Fin formation.—A pectoral fin with differentiated base and blade is present in our smallest larvae (3.8 mm). The base remains small and inconspicuous throughout the larval period as does the blade, which has a rounded posterior margin. At transformation the pectorals extend posteriorly to the origin of the pelvics. Rays begin to ossify in 7 mm larvae in a dorsal to ventral sequence and the full complement of 13 to 14 is present in larvae as small as 11.8 mm (Table 2).

The anlage of the caudal fin is present in larvae as small as 5.0 mm. The principal caudal rays begin to ossify in 7 mm larvae and the full complement of 10+9 rays is ossifying in a 7.7 mm specimen. Procurrent caudal rays also begin to ossify in 7 mm larvae and the full complement of 8 to 10 superior and 9 to 11 inferior rays is ossifying in 12 mm larvae. The hypural elements begin to ossify in 8 mm larvae and the full complement of four superior and three inferior elements is

ossifying in 9 mm larvae. Flexion of the notochord begins when the larvae are about 6.5 mm long and is completed at about 8.0 mm length.

The anal and dorsal fin bases begin to form during notochord flexion. Anal fin rays are beginning to ossify in a 7.7 mm larva and dorsal rays are ossifying in an 8.7 mm larva. The full complements of 16 to 17 anal and 13 to 14 dorsal rays are ossifying in larvae 10.5 mm and larger. In both the anal and dorsal fins, the rays ossify posterior and anterior from the more central rays. In both fins the last ray to form is the short anterior-most ray.

Pelvic fin buds appear at about 6.2 mm length, but, the rays do not begin to ossify until the larvae reach about 9 mm. The full complement of 8 pelvic rays is ossifying in larvae 11.8 mm and larger.

Pigmentation.—Preflexion larvae (3.8 to ca. 6.0 mm) have two pairs of pigment dashes developed on the gut. The anterior pair is on the foregut posterior to the cleithra, while the posterior pair is on the free terminal section of the gut. The most conspicuous pigment in preflexion larvae is the series of four to eight melanistic spots or dashes on the ventral midline of the tail. By the end of the preflexion stage, melanistic pigment is developing over the gas bladder. Also the anterior foregut spots have coalesced and moved forward and dorsad to form a pigment shield over the anterior part of the liver.

Flexion larvae (6.2 to ca. 7.5 mm) have essentially the same pigment as in preflexion larvae. The ventral tail spots range from three to seven (mean of 4.4 for 27 specimens). The median ventral foregut pigment spot or patch is continuously present as are the paired patches or streaks of pigment on the free terminal section of the gut. Pigment above the gas bladder increases in amount, with sometimes a pair of internal pigment spots located between the gas bladder and the termination of the gut.

A single pigment spot develops over the hind brain in some specimens; of the 27 specimens between 6.2 to 7.5 mm, only four had this head pigment spot. Two specimens in this size range, 6.5 and 7.2 mm respectively, had a double row of small dorsal pigment spots (seven to eight spots per side) extending for most of the length of the tail portion of the body.

In postflexion larvae (7.7 to 13.9 mm) the pigment areas already described either persist or are more consistently present, and additional pigment develops on the head, back, and in the caudal region. The pigment over the gas bladder increases

in extent and begins to spread laterally. Melanistic pigment is present on the cleithral margin forward of the pectoral base on most larvae 9.2 mm and larger. The ventral midline of pigment spots becomes imbedded and sometimes faint, but was absent on only four specimens. The number of pigment spots ranges between two and five (mean of 3.6 spots on 43 specimens). The imbedded pigment spot on the hind brain occurs on about $\frac{1}{3}$ of the larvae between 7.7 and 8.7 mm, but thereafter is consistently present. By about 10 mm, two spots form over the cerebellum and are usually present on larvae larger than this. The double row of dorsal tail pigment spots is only sporadically present on larvae under 10.5 mm, but consistently present on larger larvae. The rows extend from about the termination of the dorsal fin, almost to the procurent caudal rays; the usual count is seven or eight spots per side, but the range is from two to thirteen spots. Internal pigment forms over the hypurals, usually adjacent to the ural centrum; this pigment, first observed on a 7.7 mm specimen, is infrequently present on larvae under 10.5 mm. Pigment also forms at the hypural edge of the caudal fin. It was first observed on a 7.2 mm larva and was sporadically present until 10.5 mm. On older specimens this pigment becomes almost continuous along the hypural edge. The 14.9 mm transforming specimen added a line of dorsal pigment spots to the nape and trunk; however, a 14.2 mm juvenile had pigment over the entire body and the peritoneum was conspicuously black.

Photophore development.—A number of photophores form on larvae of *Lampanyctodes* prior to transformation. As is usual in myctophids, the Br_2 pair is the first to form; it was consistently present on specimens 6.6 mm and larger. The V_n , the second pair to form, was first observed on a 7.5 mm specimen and was consistently present by 7.8 mm. The third pair, PO_5 , was present by 8.7 mm. A specimen 11.2 mm had two additional pairs, the PLO and PO_1 ; however, specimens 11.7 and 11.8 mm had added only the PLO pair, indicative that it forms somewhat sooner than the PO_1 . Specimens 12.0 mm and larger consistently had both these pairs. A 12.7 mm specimen had three additional pairs faintly formed, the VLO, OP_2 , and PO_2 ; however, none of these was present on a 13.7 mm specimen, and only the VLO pair was present on a 13.8 mm and a 14.4 mm specimen. A transforming specimen 14.9 mm long had the majority of photophores formed. The initial five pairs to form, the Br_2 , V_n , PO_5 , PLO and PO_1 became conspicuous photophores soon after their formation. This was not the case for the three other pairs

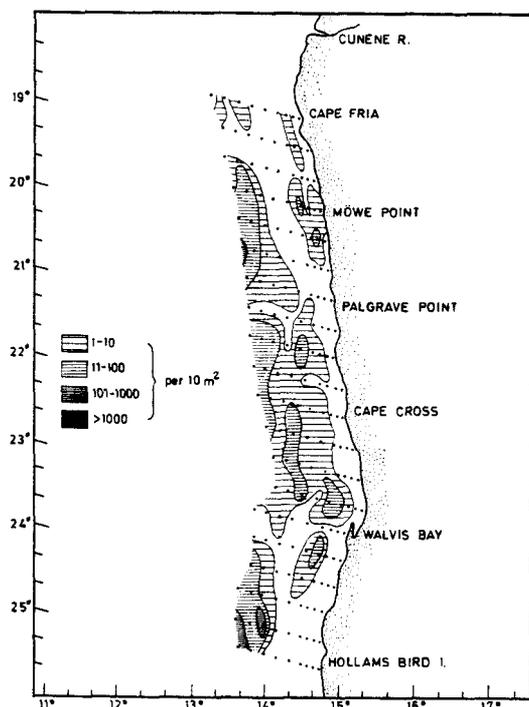


Figure 5. Distribution and abundance of larvae of *Lampanyctodes hectoris* on SWAPELS Survey 1 (August 1972 to March 1973). Numbers represent cumulative standard haul totals.

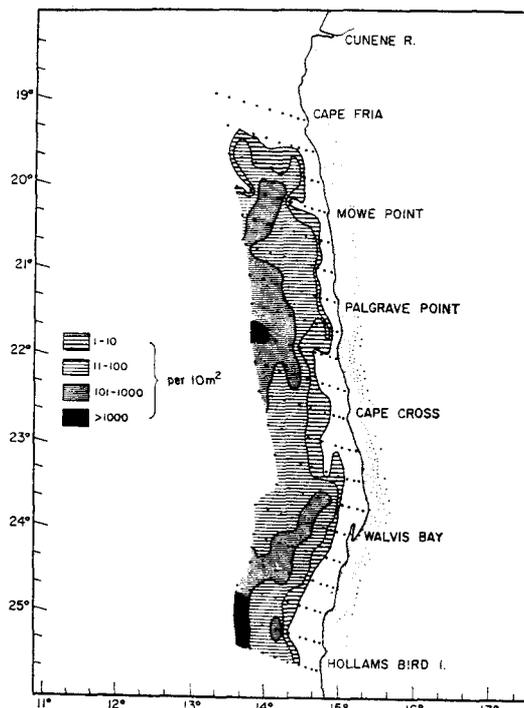


Figure 6. Distribution and abundance of larvae of *Lampanyctodes hectoris* on SWAPELS Survey 2 (August 1973 to April 1974).

mentioned above which, at best, were but faintly developed on late-stage larvae prior to transformation.

DISTRIBUTION

Lampanyctodes hectoris is a neritic species associated with land masses in the vicinity of the subtropical convergence. It is known from South Africa, New Zealand, Southern Australia, and Chile, but apparently does not occur in the western Atlantic off Argentina (McGinnis, 1974). Where it occurs, it is highly abundant, as demonstrated by the fishery off South Africa. It may occur in commercial abundance in other southern ocean areas.

There are no available data on the distribution and abundance of the larvae in the area of the fishery off South Africa, but SWAPELS provides larval data from an area just to the north of the fishery. Results from the two year survey show that larvae of the family Myctophidae formed 9.75 percent of all the fish larvae taken and larvae of *L. hectoris* comprised over 85 percent of all

myctophid larvae. This species was widely distributed between latitudes 19° and 25° S (Figs. 5 and 6). Larvae were found at distances of 8 to 112 km from the coast but were most abundant in offshore waters especially between Möwe Point (20°20' S) and Cape Cross (22° S) and between Walvis Bay (23° S) and Hollams Bird Island (25° S). Approximately 93 percent of all larvae were taken during the months of August, September, October, and November of both years. Early larval stages (those less than 5.0 mm in length) were common from August to October, but were most abundant in the plankton in August particularly in the region west of Hollams Bird Island. Over 62 percent of all early larval stages were taken during this month. The larvae of *L. hectoris* were found at surface temperatures ranging from 13.9° to 21.5° C. However, over 60 percent of all larvae occurred at mean surface temperatures of 14.0° to 15.5° C.

SYSTEMATIC RELATIONSHIPS

Although the photophores of *L. hectoris* were not mentioned in the original description of the species

(Günther, 1876), Fraser-Brunner (1949) was well aware of the unique arrangement of the light organs and, accordingly, created the genus *Lampanyctodes* for this species. He noted the marked ventral placement of the two longitudinal series of photophores, a feature which he thought was more characteristic of the "primitive" myctophine lanternfishes than of the lampanyctine genera to which it was obviously allied on the basis of morphological characters. He mentioned particularly the horizontal positioning of the two PVO photophores, an arrangement found only in the myctophine genera *Protomyctophum*, *Dio-genichthys*, and *Benthoosema*. His view of *Lampanyctodes* as a primitive lampanyctine genus is demonstrated by the statement, "this genus is clearly indicative of the form from which *Lampanyctus*, *Gymnoscopelus* and their allies have been derived." He did not elaborate on the relationships of *Lampanyctodes* with other lampanyctine genera nor did he construct a higher classification for lanternfishes.

It remained for Paxton (1972) to formally recognize the two subfamilies Myctophinae and Lampanyctinae and to construct a higher classification that included six tribes, two in the Myctophinae and four in the Lampanyctinae. In the latter subfamily he recognized the monotypic tribe Notolychnini, the tribe Lampanyctini consisting of eight genera, Diaphini with two genera, and Gymnoscopelini with eight genera. *Lampanyctodes* was important in his tribal arrangement as shown by his statement "the Diaphini and Gymnoscopelini are closely related, for the most primitive genus of each group, *Lobianchia* of the Diaphini and *Lampanyctodes* of the Gymnoscopelini, share a number of characters. Each form has widely ossified pubic plates, a relatively low number of ventral procurrent rays, well-developed caudal glands, one or two elevated PO photophores, and an arched or elevated series of VO photophores . . ." He viewed *Lampanyctodes* as an essentially intermediate form that branched from the main line of gymnoscopeline evolution soon after the divergence of this tribe from the Diaphini.

Using the combination of larval and adult characters, Moser and Ahlstrom (1972) proposed a phylogenetic scheme for the subfamily Lampanyctinae that recognized the four tribes of Paxton (1972) but differed in the placement of certain genera in the Lampanyctini and Gymnoscopelini. We believe that the triad of genera, *Bolinichthys*, *Ceratospelus* and *Lepidophanes* belong in the

Gymnoscopelini whereas Paxton placed them in the Lampanyctini. Also, we would include two other of Paxton's lampanyctine genera, *Lampadena* and *Taaningichthys*, in the Gymnoscopelini. These form a triad with the recently described *Dorsadena*. Our conception of tribal and generic relationships in the subfamily Lampanyctinae based on a combination of larval and adult characters is shown in the dendrogram (Fig. 7). Essentially the tribe Gymnoscopelini consists of the two above mentioned triads, the triad of *Lampichthys*, *Notoscopelus* and *Scopelopsis*, the well differentiated genus *Gymnoscopelus* and two monotypic isolated genera, *Hintonia* and *Lampanyctodes*. Based on Paxton's adult characters, and the larval characters given below and in Moser and Ahlstrom (1972), the genus *Gymnoscopelus* is closest to the Diaphini and in a direct line from the original tribal split. We have not yet identified the larvae of *Hintonia* and accept the view of Paxton that the genus has no distinct relationship to any member of the tribe and that this form split off early from the ancestral stock.

The genus *Lampanyctodes* is the most problematic and, phylogenetically, the most intriguing genus in the tribe. Its photophore arrangement is so unusual that it warrants a brief review. All photophores are relatively low on the body, including the PLO, VLO, 3rd SAO, POL and terminal Prc, all of which are well below the lateral line. Both a Dn and Vn pair of eye photophores are formed, although the Dn develops quite late. This feature is shared with *Lampichthys*, *Scopelopsis*, *Notoscopelus*, *Hintonia*, *Diaphus* (usually) and *Gymnoscopelus* among the Lampanyctinae and with most genera of Myctophinae.

Of particular interest is the horizontal arrangement of the two PVO photophores, an arrangement not found in any other genus of the Lampanyctinae, but present in three myctophine genera, as previously noted.

Although *Lampanyctodes* has the usual number of PO photophores, five, it is unique in having the PO₃ elevated rather than the PO₄. *Lampanyctodes* also has the usual number of VO photophores for Lampanyctinae, five, but has the series evenly arched, an unusual arrangement also found in some *Lampanyctus*. None of the AO series is elevated, the usual arrangement in most kinds of lanternfishes. The presence of a single POL is shared with all genera of *Myctophinae* except *Hygophum*, and with a half dozen genera of Lampanyctinae (*Diaphus*, *Lobianchia*, *Taaningichthys*, *Lampadena*, *Gymnoscopelus* and *Steno-*

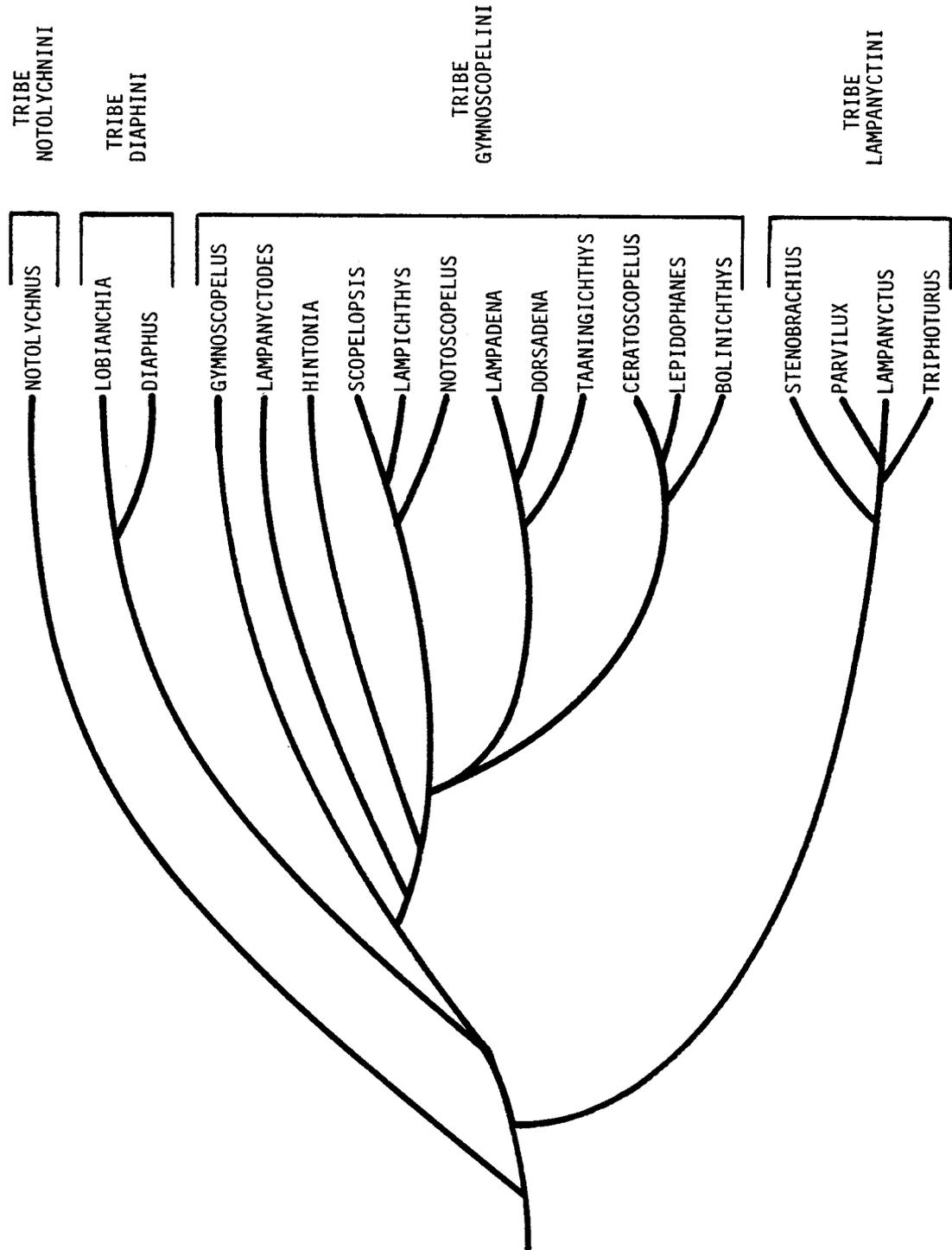


Figure 7. Dendrogram showing the generic relationships and tribal division of the subfamily Lampanyctinae based on a combination of larval and adult characters.

TABLE 3. Size at formation and sequence of early forming photophores for 10 genera of *Lampanyctinae*.

	Size at transformation (mm)	Br ₂	Vn	PO ₅	PLO	PO ₁
<i>Lampanyctodes hectoris</i>	14-15	6.6 (1)	7.8 (2)	8.7 (3)	11.7 (4)	Ca 12.0 (5)
<i>Ceratoscopelus townsendi</i>	16.5-18	7.0 (1)	7.8 (2)	9.0 (4)	8.7 (3)	-
<i>Lepidophanes guentheri</i>	-	< 9.5	< 9.5	< 9.5	< 9.5	-
<i>Notoscopelus resplendens</i>	19-21	4.2 (1)	9.2 (3)	6.2 (2)	Ca 15.0 (4)	-
<i>Lampichthys rectangularis</i>	19-21	< 7.0 (1)	9.8 (3)	8.4 (2)	Ca 16.0 (4)	16.4 (5)
<i>Lampadena urophaos</i>	17-21	6.2 (1)	13.4 (4-5)	9.8 (3)	7.3 (2)	13.4 (4-5)
<i>Scopelopsis multipunctatus</i>	16.5-17.5	5.4 (1)	11.3 (3)	10.8 (2)	-	-
<i>Gymnoscopelus aphyia</i>	Ca 30	< 23.5 (1)	-	< 23.5 (2-3)	-	< 23.5 (2-3)
<i>Diaphus theta</i>	10-11	6.0 (1)	-	6.2 (2)	-	7.6 (3)
<i>Lobianchia gemellari</i>	-	5.5 (1)	-	7.0 (3)	-	6.2 (2)

brachius). The possession of five Prc's is unusual, as is their arrangement in an ascending line that terminates well below the lateral line.

Lampanyctodes is among the genera that develops accessory patches of luminous tissue on the body, a character shared with most members of the tribe *Gymnoscopelini*, as we interpret it, and with *Diaphus* (most species) and *Lampanyctus* (some species). None of the myctophine genera develops accessory luminous tissue other than the supra and infracaudal glands. In *Lampanyctodes* the luminous tissue develops at the bases of the dorsal, anal, pectoral and pelvic fins, before and behind the dorsal fin, and on the dorsal surface of head; this pattern is suggestive of that developed on *Ceratoscopelus* and *Bolinichthys*. No secondary photophores are developed.

The fact that, in its arrangement of light organs, *Lampanyctodes* shares so many characters with so many other genera of *Lampanyctinae*, and even shares a fundamental character (the horizontal PVO's) with some genera of the Myctophinae has produced an understandable confusion as to the position of this genus. We would agree with Fraser-Brunner (1949) and Paxton (1972) that the genus has had a long and independent evolution but do not consider it a primitive genus. We believe it is a highly specialized form and that the ventral and basically linear placement of photo-

phores is related to its mode of life in shallow neritic waters. Our thesis that the arrangement of ventrally placed, well developed linear series of photophores, such as is found in most Myctophinae, is an adaptation for countershading in shallow-living lanternfishes has been stated in detail in previous papers (Moser and Ahlstrom, 1972, 1974).

The relationships of *Lampanyctodes* to other genera of *Gymnoscopelini* is seen more clearly from an examination of larval characters. It develops the dorsal series of pigment spots found in so many members of this tribe and, more importantly, forms several of the same photophores during the larval period (Table 3).

In an attempt to analyze the position of *Lampanyctodes* in the subfamily *Lampanyctinae* we selected 10 larval characters and 10 adult characters of this genus and compared them with all other genera in the subfamily. *Dorsadena* and *Hintonia* were excluded since their larvae are unknown. Two groups of larval characters were selected, those related to early forming photophores, and those related to pigment patterns. Adult characters were based mostly on photophore arrangements, presence or absence of luminous caudal glands, accessory luminous tissue, secondary photophores, sexual dimorphism, keel or ridge on fifth circumorbital bone, and a supra-

maxillary. Presence of a character was rated as a "plus" and absence as a "dash". Because of variability occurring among species in some genera, some characters had to be rated both "plus" and "dash" (Table 4). In making a summation, characters rated as both "plus" and "dash" were weighted $\frac{1}{2}$.

We do not assume that these 20 characters are of equal phylogenetic importance, even though none is trivial. We selected characters that are present or absent, hence had to ignore equally relevant characters that can not be so rated. Among the adult characters chosen, luminous glands on the caudal peduncle (supra and infra) probably are the most problematical, in that their presence or absence may not be as important phylogenetically as are the structural and functional differences in these glands among genera. These differences cannot be simply rated by this technique.

As noted earlier, the initial five pairs of photophores to develop on *Lampanyctodes* during the larval period are Br₂, Vn, PO₅, PLO, and PO₁. As indicated in table 4, all five pairs are also developed on *Lampichthys* and *Lampadena*, although not in the same sequence as in *Lampanyctodes*. Four of the above pairs are early forming on *Notoscopelus*, *Ceratoscopelus*, and *Lepidophanes*, three of the above pairs in *Scopelopsis*, *Gymnoscopelus*, *Diaphus* and *Lobianchia* and the remaining seven genera lack early forming photophores other than the Br₂ pair. We consider the striking similarity of these early forming pairs among genera as evidence of close relationship.

The other characters selected for larvae involve pigment patterns, including the presence or absence of a row of ventral midline pigment spots on the tail of preflexion and late-stage larvae, and the development of pigment on the back of the head, along the dorsal margin of the body, or at the base of the caudal fin of postflexion larvae.

Certain relationships emerge when the characters in the table are summed. *Lampanyctodes* is found to be most closely related to *Lampichthys* (17 points), then to *Scopelopsis* (13), *Gymnoscopelus* (13), *Notoscopelus* (12½), *Lampadena* (12), *Ceratoscopelus* (11), and *Lepidophanes* (11). These genera are among those we place in the tribe Gymnoscopelini. Although it is true that larval characters strongly influence this rating, so do several of the adult characters, such as the presence of a supramaxillary, Dn and Vn photophores, and accessory luminous tissue. *Lampanyctodes* is close to three genera that Paxton

(1972) and Moser and Ahlstrom (1972) have previously shown to be closely allied (*Lampichthys*, *Scopelopsis*, and *Notoscopelus*), but also to *Gymnoscopelus*, and must have split off from the ancestral line of the triad soon after it diverged from the *Gymnoscopelus* line.

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