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An identification guide to the larvae of lanternfishes (Teleostei: Myctophidae) from the Subtropical Convergence: subfamilies Lampanyctinae and Notolychninae

Yana Yu. Bolshakova (contact author)[1]
Artem M. Prokofiev[2]

Email address for contact author: yanusrunaa@mail.ru

[1] Shirshov Institute of Oceanology
Russian Academy of Sciences
36 Nakhimovskyi Prospekt
Moscow 117997, Russia

[2] Severtsov Institute of Ecology and Evolution
Russian Academy of Sciences
33 Leninsky Prospekt
Moscow 119071, Russia

Abstract—Descriptions of the lanternfish larvae of the subfamilies Lampanyctinae (12 species) and Notolychninae (1 species) that can be found in the Subtropical Convergence (STC) are presented: *Bolinichthys supralateralis*, *Ceratoscopelus* gr. *townsendi*, *Lampadena* sp., *Lampanyctus alatus*, *L. ater*, *L. australis*, *L.* gr. *achirus*, *L. intricarius*, *L. festivus*, *L. pusillus*, *Lampanyctus* sp. D, *Lepidophanes guentheri*, and *Notolychnus valdiviae*. Also provided is an identification key based on larval characters for all lanternfish subfamilies. We propose the use of a separate key for the postflexion larvae of all known genera of the round-eyed lanternfish subfamilies Diaphinae, Gymnoscopelinae, Lampanyctinae, and Notolychninae. For each genus, general characteristics of larval morphology are given. Species descriptions include the key characters for identification, variation in meristic characters, pigmentation, and other features important for diagnosis of Myctophidae at their larval stages. Photographs of the most important diagnostic features are provided for each species. The taxonomy of 4 problematic species in the area, *C.* gr. *townsendi*, *Lampanyctus* gr. *achirus*, *L. intricarius*, and *Lampanyctus* sp. D, is discussed. Preflexion, flexion, and postflexion stages of an unidentified *Lampadena* sp. from the northern limit of the STC are described for the first time; these larvae may belong to 1 of 3 species (*L. dea*, *L. notialis*, and *L. speculigera*) for which larvae have not yet been identified. The distribution of Lampanyctinae and Notolychninae in the STC is summarized.

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The lanternfish family Myctophidae is one of the most speciose lineages of mesopelagic fish species. It is composed of 34 genera, currently comprising over 250 valid species (Fricke et al., 2023). Lanternfish species can be found circumglobally in waters of oceanic salinity from the surface down to depths of around 2000 m and, in abundance and biomass, make up at least 30–50% of all fishes caught in mid-water trawl nets (Bekker, 1983). Larvae of myctophids are also abundant in samplings of ichthyoplankton tows, as an obligatory component of the catches in small-mesh fishing gears (Moser and Ahlstrom, 1974). A wide set of morphological features for the identification of Myctophidae at the early stages of development has been described (Moser et al., 1984), and several guides have been prepared for select areas of the world's oceans, including the Northeast Atlantic Ocean (Russell, 1976), Northwest Atlantic Ocean (Fahay, 1983, 2007), western central Atlantic Ocean (Richards, 2005), eastern central Atlantic Ocean (Rodríguez, 2023) southwest Atlantic Ocean (Bonecker and Castro, 2006), southeast Atlantic Ocean (Benguela Current Region) (Olivar and Fortuño, 1991), central North Pacific Ocean (Miller et al., 1979), eastern North Pacific Ocean (Matarese et al., 1989; Moser and Ahlstrom, 1996), western North Pacific Ocean (Ozawa, 1986; Okiyama, 1988), and Southern Ocean (Efremenko, 1983). However, the larvae have not yet been described for a number of species, and there are no guides for some areas in the tropical, southern subtropical, and temperate Indo-Pacific.

The Subtropical Convergence (STC), a frontal zone between subantarctic and tropical water masses, is one such area. Both wide-tropical and subantarctic species of myctophids can be found in the transitional or mixed water zone within and off the STC. At least 80 species of myctophids from the STC are known, but early life stages have been described for only 60% of them. Only a few previously published papers contain descriptions of lanternfish larvae from the STC (Pertseva-Ostroumova, 1977; Belyanina and Kovalevskaya, 1979; Bolshakova and Evseenko, 2015, 2020; Bolshakova et al., 2021), and a

few guides cover the border areas to the north (Olivar and Fortuño, 1991) and south (Efremenko, 1983; Kellermann, 1990) of the STC.

Herein, we combine the existing data on myctophid larvae from the STC, provide photographic illustrations of known larvae, supplementing them with descriptions and identification keys. This material will make identification of the early stages of development of this key group of mesopelagic fishes easier for a wide community of marine biologists.

The larvae of lanternfishes can be divided into 2 major groups on the basis of the shape of the eye: narrow-eyed (dorsoventrally extended elliptical eyes) and round-eyed (more or less circular eyes) (Moser and Ahlstrom, 1970, 1974). A mass of choroid tissues may develop around the eye in a member of both groups; however, such a mass is usually noticeable in narrow-eyed larvae (especially in *Centrobranchus*, *Dasyscopelus*, and *Gonichthys*) but is mostly inconspicuous, in the form of a thin crescent on the ventral side of the eye, in round-eyed larvae (except for *Lobianchia* and *Triphoturus*, with their well-developed choroid tissues). With few exceptions (*Loweina* and *Notolychnus*), the narrow- and round-eyed larvae correspond to the subfamilies Myctophinae and Lampanyctinae, respectively.

The recognition of 2 subfamilies was originally based on a wide set of morphological characters (Paxton, 1972; Bekker, 1983; Paxton et al., 1984; Stiassny, 1996; Yamaguchi, 2000) and was later supported by molecular analyses (Poulsen et al., 2013; Denton, 2014). Three tribes (Electronini, Gonichthyini, and Myctophini) have been recognized within Myctophinae, and 4 tribes (Lampanyctini, Notolychnini, Diaphini, and Gymnoscopelini) have been recognized within Lampanyctinae (Paxton, 1972). Findings from 7-locus molecular phylogeny support the recognition of these tribes, except the paraphyletic Gonichthyini and Myctophini (Denton, 2014). Results of the most recent treatment (Martin et al., 2018) support the monophyly of Diaphini and Myctophinae and raise the rank of all lampanyctine tribes to subfamilies: Diaphinae, Gymnoscopelinae, Notolychninae, and Lampanyctinae *sensu novo*. This communication covers the species from the subfamilies Lampanyctinae and Notolychninae. We plan to treat the morphologically similar larvae of the round-eyed subfamilies Diaphinae and Gymnoscopelinae and the narrow-eyed taxa (subfamily Myctophinae) in forthcoming works.

Materials and methods

Geographic coverage

The STC is almost continuously traced throughout the globe at latitudes of about 35–45°S. In fact, this area is the one between the anticyclonic circulation of the southern parts of the Atlantic, Indian, and Pacific Oceans and the cyclonic circulation of the Antarctic Circumpolar Current, which separates the warm temperate subtropical region from the cool-temperate subantarctic region. It forms the geographic limit to the influence of subantarctic surface water and consists of a strong horizontal gradient in temperature, salinity, and nutrients. The limits of the STC were discussed by Backus (1986), Deacon (1966), and McGinnis (1982) and were further summarized by Longhurst (1998). He provided a detailed overview of the oceanography, geology, and biogeography of the STC. The geographic coverage of the atlas presented herein (Fig. 1) follows the limits of the STC provided by Longhurst (2007, 543) and Sutton et al. (2017, 89).

Specimens

The original data are based on the ichthyoplankton collection housed in the Shirshov Institute of Oceanology, Russian Academy of Sciences, Moscow. The previously published descriptions of the larvae of each species known from the STC were compiled in order to estimate the range of morphological variation. Information about the studied material, including the numbers of specimens, expeditions, localities, depth, and more, and the sources of the previously published descriptions of species from the STC are summarized in Table 1. The larval stage is divided into 3 substages over the development of the caudal fin (Kendall et al., 1984): preflexion (PrF) is the larval stage before the beginning of the bending of the terminal notochord, flexion (F) is the stage of bending of the notochord, and postflexion (PoF) is the stage after the end of the bend of the notochord. We developed a complete set of diagnostic traits for larvae at the postflexion stage, and for the purposes of the atlas, we present herein the illustrations and descriptions of larvae at this stage. If descriptions of the earlier stages existed in the literature, we provide the references for them in the species description, before the "Identification" section. Details about the collection of examined specimens, such as dates and general locations, are provided in Suppl. Table.

Morphology

Counts and measurements follow the standard practice (Nafpaktitis, 1973; Fahay, 1983; Moser and Ahlstrom, 1996; Olivar and Beckley, 1997; Leis and Carson-Ewart, 2000). The scheme of measurements is shown in Figure 2. The body depth at pectoral fin base (BD) is indicated as follows: slender, BD <19% standard body length (SL); moderate, BD 19–24% SL; and deep, BD >24% SL. Eye shapes were determined according to Moser and Ahlstrom (1970). The terminology of photophores and luminous glands follows that of previous authors, notably Bolin (1939), Fraser-Brunner (1949), Nafpaktitis (1968), Paxton (1972), and Bekker (1983), and is presented in Figure 3. The pigment groups characteristic for myctophid larvae are depicted in Figure 4. Definitions of pigment groups follow Bolshakova and Prokofiev (2023).

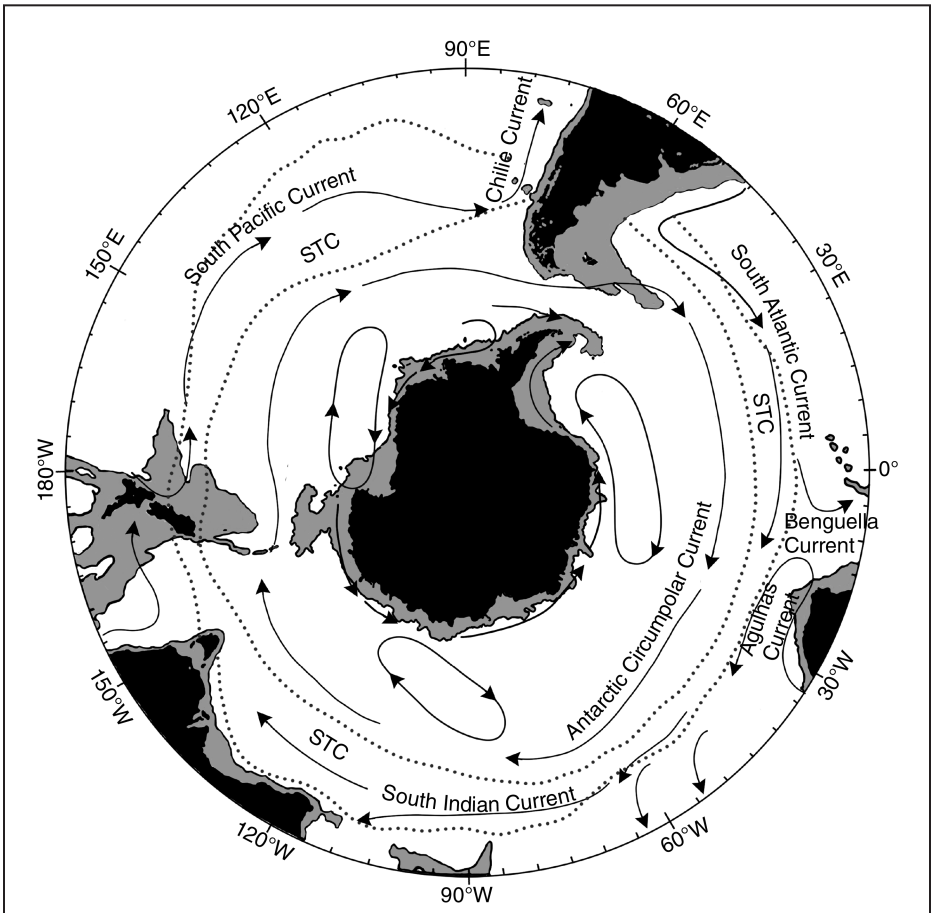

Figure 1

Schematic map of the study area showing the borders of the Subtropical Convergence (STC; dotted lines) (Deacon, 1966; Longhurst, 1998; Sutton et al., 2017), where larvae of the species of Lampanyctinae and Notolychninae examined in this study can be found. The arrows indicate the direction of the main currents (Steele et al., 2010).

Sequence of descriptions

Species descriptions In each description, the synonymic list provides all references containing morphological descriptions or figures of the larvae of a species under consideration, with indication of the substages described and the geographic area of sampling.

The "Identification" section emphasizes the key features for the identification of a species, meaning the most easily observable characters distinguishing a species from its congeners or other similar members of the family.

The "General characters" section contains meristic counts, size at which the photophores formed and sequence of their formation, size at which the fin rays developed, length at transformation, and some additional morphological characteristics of larvae useful for their identification. For genera, the most notable diagnostic features are highlighted in bold. Meristic data were taken from both the specimens studied and literature sources and include the data for the adults of the described larvae presented by Wisner (1976), Nafpaktitis et al. (1977), Hulley (1981), McGinnis (1982), Bekker (1983), and Zahuranec (2000).

The "Pigmentation" section provides a description of pigment pattern according to the nomenclature of Bolshakova and Prokofiev (2023). Before each pigment group, the number of pigment cells is indicated, if their number differs from one, and whether they are a paired or unpaired is noted. The order of each description is as follows: craniovisceral group with medullar, then medioventral group with abdominal, then mediodorsal group, lateral group, intervertebral group, and fin pigmentation.

The "General distribution" section provides information on the general distribution, with summary of the geographic range of a species under consideration, and on occurrence in the STC with clarification of the findings of a species directly in the STC.

Table 1

Number of specimens, standard body length (SL), geographic coordinates, depth layer, research vessel, expedition number, station (sta.), and date of collection for myctophid larvae in the subfamilies Lampanyctinae and Notolychninae from inside and outside the Subtropical Convergence (STC) and the sources of previously published descriptions. Original data from this study are based on the ichthyoplankton collection housed in the Shirshov Institute of Oceanology of the Russian Academy of Sciences. An asterisk (*) indicates that the specimen or specimens came directly from the STC.

		Literature sources	
Species in the STC	Studied specimens (number, SL, coordinates, layer, vessel, expedition no., sta., date)	Based on records for larvae from the STC	Based on records for larvae from outside the STC
Bolinichthys indicus	Larvae unknown		
B. supralateralis	2 (4.6, 10.5 mm SL), 4°45′N, 37°09′W, 0–200 m, *Akademic Vavilov*, 43, sta. 2664, 25 October 2016 3 (11.4–11.9 mm SL), 13°52′N, 45°00′W, 0–700 m, *Professor Logachev*, 39, sta. 189, 1 March 2018 1 (8.2 mm SL), 2°02′N, 36°32′W, 0–700 m, *Akademic Vavilov*, 43, sta. 2669, 26–27 October 2016	None	Pertseva-Ostroumova (1964); Olivar et al. (1999); Bolshakova and Evseenko (2020)
Ceratoscopelus gr. *townsendi*	2* (11.0, 11.7 mm SL), 38°48′S, 157°54′W, 0–200 m, *Dmitry Mendeleev*, 34, sta. 3049, 4 February 1985 57* (9.1–19.5 mm SL), 34°59′S, 158°06′W, 200-0, *Dmitry Mendeleev*, 34, sta. 3051, 6 February 1985 2 (12.5, 13.2 mm SL), 00°01′S, 36°01′W, 0–700 m, *Akademic Vavilov*, 43, sta. 2675, 26–27 November 2016	None	Shiganova (1977); Miller et al. (1979); Belyanina (1982); Ozawa (1986); Badcock and Araújo (1988); Moser and Watson (2001); Bonecker and Castro (2006)
Lampadena anomala	Larvae unknown		
L. dea	Larvae unknown		
L. notialis	Larvae unknown		
L. speculigera	Larvae unknown		
Lampadena sp.	1* (9.8 mm SL), 35°08′S, 128°35′E, 0–500 m, *Dmitry Mendeleev*, 16, sta. 1363, 26 February 1976 18* (5.4–10.0 mm SL), 35°19′S, 128°42′E, 0–200 m, *Dmitry Mendeleev*, 16, sta. 1359, 25 February 1976	First description in this study	None
Lampanyctus gr. *achirus*	2 (8.3, 8.5+ mm SL), 36°56′S, 07°19′E, 0–550 m, *Akademic Ioffe*, 29, sta. 2193, 26 November 2009 1* (12.8 mm SL), 43°06′S, 125°42′W, 0–50 m, *Dmitry Mendeleev*, 34, sta. 3056, 16 February 1985 3* (15.0–22.0 mm SL), 39°42′S, 126°01′W, 0–200 m, *Dmitry Mendeleev*, 34, sta. 3054, 14 February 1985	Bolshakova et al. (2021)	Moser and Ahlstrom (1974)
L. ater	1 (18.5 mm SL), 32°47′S, 01°49′E, 0–1150 m, *Akademic Ioffe*, 29, sta. 2187, 22 November 2009	None	Olivar (1985); Moser and Watson, (2001)
L. alatus	2 (5.8, 9.1 mm SL), 11°02′S, 50°37′E, 0–400 m, *Akademik Kurchatov*, 36, sta. 3740, 4 April 1983 2 (7.0, 8.2 mm SL), 16°18′N, 46°41′W, 0–75 m, *Akademic Ioffe*, 29, sta. 2163, 3 November 2009	None	Olivar and Beckley (1997); Moser and Watson (2001); Bolshakova and Evseenko (2016a)
L. australis	2* (10.0, 12.5 mm SL), 39°42′S, 126°01′W, 0–200 m, *Dmitry Mendeleev*, 34, sta. 3054, 14 February 1985 1 (9.2 mm SL), 49°41′S, 148°25′E, 0–200 m, *Dmitry Mendeleev*, 16, sta. 1335, 13 February 1976 1 (12.0 mm SL), 46°50′S, 158°01′W, 0–200 m, *Dmitry Mendeleev*, 34, sta. 3009, 16 January 1985 1 (11.5 mm SL), 44°20′S, 157°33′W, 0–200 m, *Dmitry Mendeleev*, 34, sta. 3010, 17 January 1985	Bolshakova et. al. (2021)	Olivar (1988); Olivar and Beckley (1997); Bolshakova and Evseenko (2016b)
L. festivus	1 (9.5 mm SL), 29°28′S, 00°11′E, 0–2000 m, *Akademic Ioffe*, 29, sta. 2184, 19 November 2009	None	Olivar and Beckley (1997); Bolshakova and Evseenko (2016b)

(*Continued on the next page*)

Table 1 (*continued*)

Species in the STC	Studied specimens (number, SL, coordinates, layer, vessel, expedition no., sta., date)	Literature sources: Based on records for larvae from the STC	Literature sources: Based on records for larvae from outside the STC
L. intricarius	18* (9.0–19.7 mm SL), 38°48′S, 157°54′W, 0–200 m, *Dmitry Mendeleev*, 34, sta. 3049, 4 February 1985 1 (12.7 mm SL), 36°56′S, 07°19′E, 0–550 m, *Akademic Ioffe*, 29, sta. 2193, 26 November 2009	Bolshakova and Evseenko (2015)	Regan (1916); Olivar (1988)
L. lepidolychnus	Absent	None	Olivar and Fortuño (1991); Olivar and Beckley (1997)
L. macdonaldi	Larvae unknown		
L. pusillus	1 (6.4 mm SL), 36°56′S, 07°19′E, 0–550 m, *Akademic Ioffe*, 29, sta. 2193, 26 November 2009 16* (6.2–11.5 mm SL), 38°48′S, 157°54′W, *Dmitry Mendeleev*, 34, 0–200 m, sta. 3049, 4 February 1985 1 (10.2 mm SL), 29°28′S, 00°11′E, 0–2000 m, *Akademic Ioffe*, 29, sta. 2184, 19 November 2009	None	Tåning (1918); Rodríguez et al. (2017)
L. wisneri	See remarks under *L.* gr. *achirus*		
Lampanyctus sp. D	2* (11.6, 11.7 mm SL), 45°31′S, 157°43′W, 0–200 m, *Dmitry Mendeleev*, 34, sta. 3042, 20–21 January 1985 9* (7.8–10.7 mm SL), 37°56′S, 125°55′W, 0–200 m, *Dmitry Mendeleev*, 34, sta. 3052, 12–13 February 1985 10* (8.4–13.8 mm SL), 38°48′S, 157°54′W, 0–200 m, *Dmitry Mendeleev*, 34, sta. 3049, 4 February 1985	Bolshakova et al. (2021)	None
Lepidophanes guentheri	2 (10.5, 11.0 mm SL), 14°44′N, 44°55′W, 0–700 m, *Professor Logachev*, 39, sta. 183, 27 February 2018 1 (14.3 mm SL), 15°45′S, 13°13′W, 0–225 m, *Akademic Ioffe*, 29, sta. 2175, 11 November 2009	None	Moser and Ahlstrom (1972); Shiganova (1977); Moser and Watson (2001); Bonecker and Castro (2006)
Taaningichthys bathyphilus	Larvae unknown		
Notolychnus valdiviae	2 (7.8; 9.8 mm SL), 29°57′S, 168°41′E, 0–200 m, *Dmitry Mendeleev*, 16, sta. 1259, 4 January 1976 5 (7.5–10.0 mm SL), 6°12′S, 54°21′E, 0–500 m, *Academic Kurchatov*, 36, sta. 3716, 25 March 1983 10 (4.8–10.5 mm SL), 10°35′S, 50°51′E, 0–500 m, *Academic Kurchatov*, 36, sta. 3737, 2–3 April 1983	None	Tåning (1918); Pertseva-Ostroumova (1964); Moser and Ahlstrom (1974); Shiganova (1975); Moser et al. (1984); Moser and Ahlstrom (1996)

Abbreviations Abbreviations used in the text and figures for meristic characters and other features are shown in Table 2. We use the abbreviation *gr*. (for *grex*, a Latin word meaning *group*) before the species name to indicate a putative species complex or mix of different species (i.e., *Ceratoscopelus* gr. *townsendi* and *Lampanyctus* gr. *achirus*).

Results

Two identification keys are presented. The first is a key based on larval characters for all lanternfish subfamilies: Myctophinae, Notolychninae, Lampanyctinae, Gymnoscopelinae, and Diaphinae. The second key is for the postflexion larvae of all known genera of round-eyed lanternfish.

Key to subfamilies of Myctophidae based on larval characters

1a Narrow eyes; noticeable choroid tissue on ventral surface of eye usually present (except for *Loweina*, with slightly oval eyes lacking choroid tissue; *Diogenichthys* lacking choroid tissue; and some species of *Protomyctophum* and of *Hygophum* lacking choroid tissue); some have stalked eyes; number of rays in dorsal fin (D) fewer than number of rays in anal fin (A) (D<A).....**Myctophinae** (not treated here)

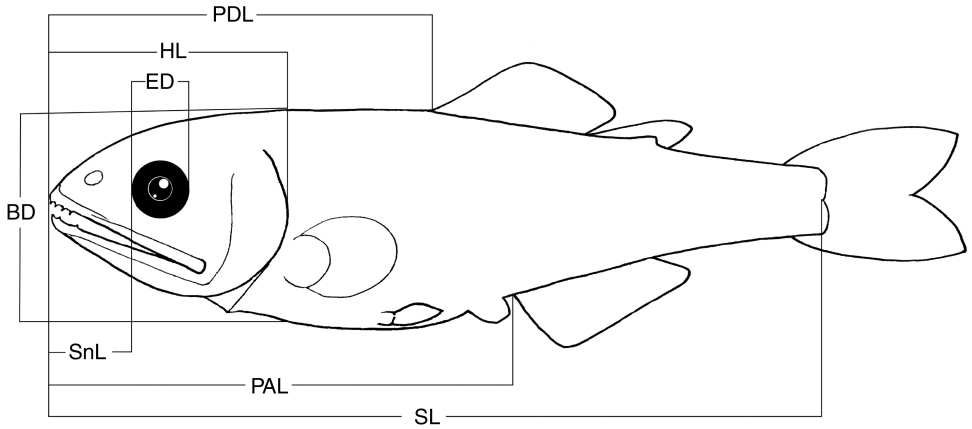

Figure 2

Scheme of measurements used for larvae in this study. The measurements include standard body length (SL), head length (HL), body depth at pectoral fin base (BD), preanal length (PAL), predorsal length (PDL), snout length (SnL), and horizontal eye diameter (ED).

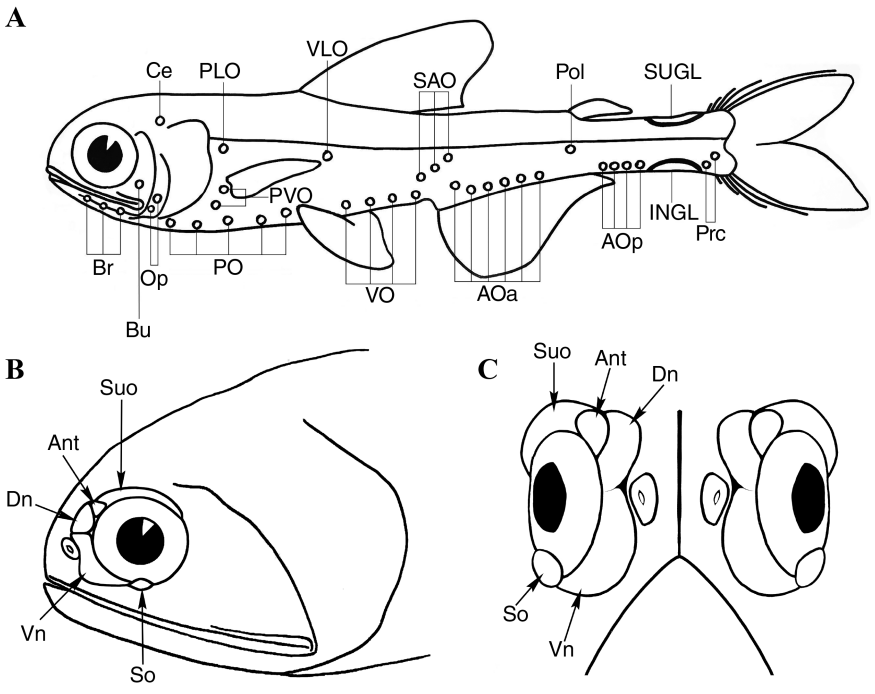

Figure 3

Illustrations showing the locations of photophores and orbital glands of larvae of the family Myctophidae: (**A**) total scheme without luminous orbital glands, (**B**) lateral view of the luminous orbital glands, and (**C**) frontal view of the luminous orbital glands. The photophores include the pectolateral (PLO), pectoventral (PVO), pectoral (PO), ventrolateral (VLO), ventral (VO), supraanal (SAO), anterior anal (AOa), posterior anal (AOp), posterolateral (Pol), precaudal (Prc), branchiostegal (Br), opercular (Op), cervical (Ce), and buccal (Bu) photophores. The luminous glands include the dorsonasal gland (Dn), anteorbital gland (Ant), suborbital gland (So), ventronasal gland (Vn), supraorbital gland (Suo), supracaudal luminous gland (SUGL), and infracaudal luminous gland (INGL).

1b Rounded or slightly oval eyes, usually without conspicuous choroid tissue (except for *Lobianchia* having ventral choroid tissue; *Notolychnus*, with eyes irregular in shape and with ventral and dorsal choroid tissue; *Triphoturus*, with oval eyes having ventral choroid tissue); always sessile; dorsal fin-ray count usually a few more than or nearly equal to anal fin-ray count (D≥A) (except for *Lampichthys* and *Lampanyctus*, with D<A) **2**

2a Short gut; preanal length (PAL) 44–53% SL; 6–7 rays in pelvic fin; larval photophores absent ..... **Notolychninae**

2b Moderate or slender gut; PAL 56–75% SL (50–54% in *Scopelopsis*; 52–58% in *Parvilux*); 8–9 (7–8 in *Scopelopsis*); pelvic-fin rays; at least 2nd branchiostegal photophore (Br_2) present, except for *Taaningichthys minimus* and *L. intricarius* **3**

3a Only Br_2 or additionally ventronasal gland or pectolateral photophore formed second in order ..... **Lampanyctinae**

3b Fifth pectoral photophores second to form **4**

4a Mediodorsal (MD) or mediolateral (ML) pigment always present ..... **Gymnoscopelinae** (not treated here)

4b Mediodorsal and ML pigment always absent ..... **Diaphinae** (except for *Diaphus ostenfeldi*, with MD pigment present) (not treated here)

Key to genera of round-eyed lanternfish based on postflexion larvae (standard length >7–12 mm)

Each genus that is not represented in the STC is marked by an asterisk (*).

1a No photophores or only 2nd branchiostegal photophore (Br_2) during the larval stage ..... **2** [*Bolinichthys*, *Lampanyctus* (except for *L. alatus*), *Notolychnus*, *Parvilux**, *Stenobrachius**, *Taaningichthys*, *Triphoturus**]

1b Additional photophores (ventronasal gland [Vn], pectolateral photophore [PLO], ventrolateral photophore [VLO], and fifth and first pectoral photophores [PO_5 and PO_1]) are formed ..... **3** [*Ceratoscopelus*, *Diaphus*, *Gymnoscopelus*, *Idiolychnus**, *Lampadena*, *Lampanyctodes*, *Lampichthys*, *Lepidophanes*, *Lobianchia*, *Notoscopelus, Scopelopsis*]

2a Body depth at pectoral fin base (BD) ≥24% standard body length (SL); upper jaw length >60% head length (HL); head large (HL 27–50% SL) ..... ***Lampanyctus***

2b Body depth at pectoral fin base ≤24% SL (up to 27% in *Bolinichthys*); jaws short, <50% HL; head small, HL 23–30% SL ..... **13** [*Bolinichthys*, *Notolychnus*, *Parvilux**, *Stenobrachius**, *Taaningichthys*, *Triphoturus*]

3a Sequence of photophore development: Br_2, PO_5, PO_1 ..... **4** [*Diaphus*, *Gymnoscopelus*, *Idiolychnus**, *Lobianchia*]

3b Sequence of photophore development different, with Vn and PLO always formed earlier than PO_1 (Br_2, PO_5, Vn, PLO/VLO or Br_2, Vn, PO_5, PLO, PO_1, or Br_2, Vn, PLO, PO_5, or Br_2, PLO, PO_5, Vn, PO_1) ..... **7** [*Ceratoscopelus*, *Lampadena*, *Lampanyctodes*, *Lampichthys*, *Lepidophanes*, *Notoscopelus*, *Scopelopsis*]

4a Body slender (BD 13–22% SL); 41–45 myomeres; mediodorsal (MD) pigment usually present; transformation at SL >20 mm SL ..... ***Gymnoscopelus***

4b Body moderate to deep (BD 19–38% SL); 31–38 myomers; MD pigment absent; transformation at SL <15 mm SL ..... **5** [*Diaphus*, except for *D. ostenfeldi*, *Idiolychnus**, *Lobianchia*]

4c Body moderate in depth (BD 24–28% SL); 37–38 myomers; MD pigment present at 9.5 mm SL; transformation at SL ~20 mm SL ..... ***Diaphus ostenfeldi***

5a Pectoral fin large, reaching to or behind anus, wing-shaped and bilobed (upper rays elongated); BD >30% SL ..... **6** [*Idiolychnus**, *Lobianchia*]

5b Pectoral fin normal, not reaching anus; BD <30% SL ..... ***Diaphus***

6a Numerous abdominal myoseptal melanophores (MSa); slightly oval eyes with ventral choroid tissue ..... ***Lobianchia***

6b Abdominal myoseptal melanophores absent; round eyes without choroid tissue ..... ***Idiolychnus****

7a Sequence of photophore development: Br_2, PO_5, Vn, PLO/VLO; number of rays in dorsal fin (D) 16–27; number of rays in anal fin (A) 18–27 ..... **8** [*Lampichthys*, *Notoscopelus*, *Scopelopsis*]

7b Another sequence of photophore development (Br_2, Vn, PO_5, PLO, PO_1; Br_2, Vn, PLO, PO_5; or Br_2, PLO, PO_5, Vn, PO_1); D 11–13; A 11–17 ..... **10** [*Ceratoscopelus*, *Lampadena*, *Lampanyctodes*, *Lepidophanes*]

8a Body depth at pectoral fin base 24–35% SL; subdorsal mediolateral melanophores (MLD) present; anteroventral foregut melanophores (FGv) absent ..... ***Notoscopelus***

8b Body depth at pectoral fin base 19–24% SL; MLD absent; FGv present ..... **9** [*Lampichthys*, *Scopelopsis*]

9a Lower-jaw symphyseal melanophores (LJS) present; posterior lower-jaw melanophores (LJP) present; D 16–18; A 21–23 ..... ***Lampichthys***

9b Lower-jaw symphyseal melanophores absent; LJP absent; D 20–24; A 23–27 ..... ***Scopelopsis***

10a Sequence of photophore development: Br_2, Vn, PLO, PO_5; subdorsal (SMD) and preadipose (PMDa) pigment always absent; basicaudal (BC) pigment always absent ..... **11** [*Ceratoscopelus*, *Lepidophanes*]

10b Another sequence of photophore development (Br_2, Vn, PO_5, PLO, PO_1 or Br_2, PLO, PO_5, Vn, PO_1); SMD or PMDa pigment always present; BC present or absent ..... **12** [*Lampadena*, *Lampanyctodes*]
11a Anteroventral foregut and otical melanophores (Ot) absent ..... ***Ceratoscopelus***
11b Anteroventral foregut melanophores and Ot present ..... ***Lepidophanes***
12a Sequence of photophore development: Br_2, PLO, PO_5, Vn, PO_1; number of gill rakers in the outer row of first gill arch (GR) <30 ..... ***Lampadena***
12b Sequence of photophore development: Br_2, Vn, PO_5, PLO, PO_1; GR ≥30 ..... ***Lampanyctodes***
13a Eyes round or slightly oval without choroid tissue ..... **14** [*Bolinichthys*, *Parvilux**, *Stenobrachius**, *Taaningichthys*]

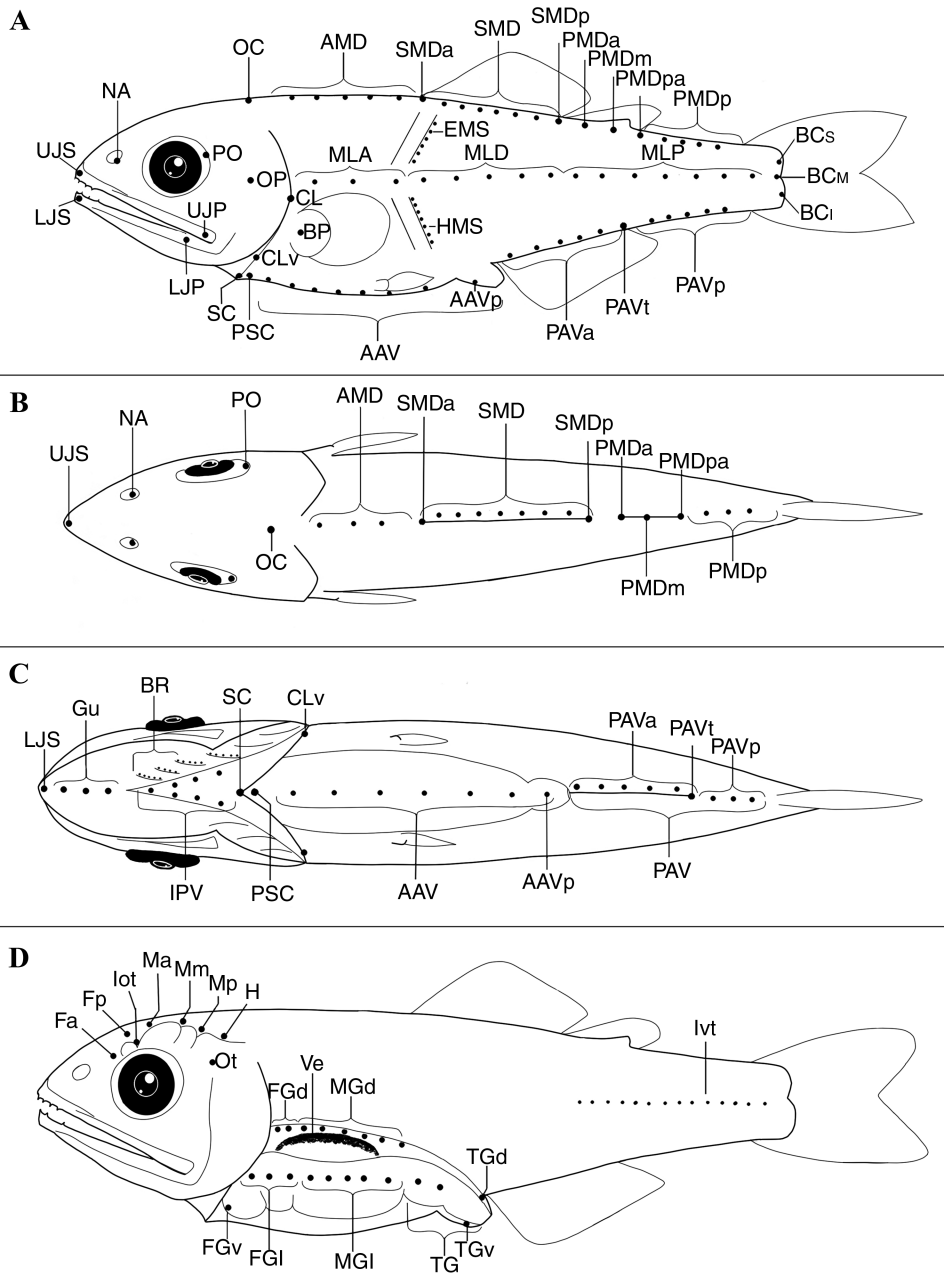

Figure 4

Scheme of the external pigmentation of larvae of the family Myctophidae: (**A**) lateral view, (**B**), dorsal view, and (**C**) ventral view. (**D**) Scheme of the internal pigmentation of larvae of this family. Abbreviations are defined in Table 2.

Table 2

Abbreviations used in the text and figures for photophores, orbital glands, meristic characters, measurements, and pigmentation. These features are part of the descriptions for species of myctophid larvae (subfamilies Lampanyctinae and Notolychninae) from the Subtropical Convergence and can be used to identify them.

Abbreviation	Name	Abbreviation	Name
	Photophores and orbital glands		
PLO	Pectolateral photophore	Br	Branchiostegal photophores
PVO	Pectoventral photophores	Op	Opercular photophore(s)
PO	Pectoral photophores	Ce	Cervical photophore
VLO	Ventrolateral photophore	Bu	Buccal photophore(s)
VO	Ventral photophores	Dn	Dorsonasal gland
SAO	Supraanal photophores	Ant	Anteorbital gland
AOa	Anterior anal photophores	So	Suborbital gland
AOp	Posterior anal photophores	Vn	Ventronasal gland
Pol	Posterolateral photophore(s)	Suo	Supraorbital gland
Prc	Precaudal photophores	SUGL	Supracaudal luminous gland
		INGL	Infracaudal luminous gland
	Meristic characters		
D	Number of rays in dorsal fin	C	Number of rays in caudal fin
A	Number of rays in anal fin	GR	Number of gill rakers in the outer row of first gill arch
P_1	Number of rays in pectoral fin	V	Number of vertebrae
P_2	Number of rays in pelvic fin		
	Measurements		
SL	Standard body length	PDL	Predorsal length
HL	Head length	SnL	Snout length
BD	Body depth at pectoral fin base	ED	Horizontal eye diameter
PAL	Preanal length		
	Pigmentation		
Mediodorsal group		Craniovisceral group	
MD	Mediodorsal	LJS	Lower-jaw symphyseal
AMD	Antedorsal	UJS	Upper-jaw symphyseal
SMD	Subdorsal	LJP	Posterior lower-jaw
SMDa	Anterior subdorsal	UJP	Posterior upper-jaw
SMDp	Posterior subdorsal	BR	Branchiostegal
PMD	Postdorsal	NA	Nasal
PMDa	Preadipose	OP	Opercular
PMDm	Subadipose	OC	Occipital
PMDp	Supracaudal	PO	Postorbital
PMDpa	Postadipose	Gu	Gular
Mediolateral group		Fin pigmentation	
ML	Mediolateral	Pp	Pectoral-fin pigmentation
MLA	Anterior mediolateral	Vp	Ventral-fin pigmentation
MLD	Subdorsal mediolateral	Cp	Caudal-fin pigmentation
MLP	Posterior mediolateral	Adp	Adipose-fin pigmentation
MS	Myoseptal	Dp	Dorsal-fin pigmentation
MSa	Abdominal myoseptal	Ap	Anal-fin pigmentation
MSc	Caudal myoseptal	DFp	Dorsal fin-fold pigmentation
EMS	Epaxial myoseptal	VFp	Ventral fin-fold pigmentation
EMSa	Epaxial abdominal myoseptal	Medullar group	
EMSc	Epaxial caudal myoseptal	Fa	Anterior forebrain
HMS	Hypaxial myoseptal	Fp	Posterior forebrain
HMSa	Hypaxial abdominal myoseptal	Ma	Anterior midbrain
HMSc	Hypaxial caudal myoseptal	Mm	Medial midbrain
CL	Lateral cleithral	Mp	Posterior midbrain
CLv	Ventral cleithral	H	Hindbrain
BP	Basipectoral	Ot	Otical
BC	Basicaudal	Iot	Transverse interorbital

(*Continued on the next page*)

Table 2 (*continued*)

Abbreviation	Name	Abbreviation	Name
		Pigmentation	
BC_S	Basicaudal superior	Abdominal group	
BC_M	Basicaudal medium	FG	Foregut
BC_I	Basicaudal inferior	FGl	Lateral foregut
Medioventral group		FGv	Anteroventral foregut
IPV	Prepectoral (isthmic)	FGd	Dorsal foregut
AAV	Preanal	MG	Midgut
AAVp	Periproctal	MGd	Dorsal midgut
PAV	Postanal	MGl	Lateral midgut
PAVa	Subanal	TG	Terminal gut section
PAVt	Terminal subanal	TGd	Dorsal terminal gut
PAVp	Infracaudal	TGv	Ventral terminal gut
SC	Symphyseal-cleithral	Ve	Vesicular
PSC	Postsymphyseal-cleithral	Intervertebral pigmentation	
		Ivt	Sagittal intervertebral

13b Eyes elliptical or irregular in shape with choroid tissue ..... **17** [*Notolychnus*, *Triphoturus*]
14a Horizontal eye diameter 36–46% SL..... **15** [*Bolinichthys*, *Parvilux*]
14b Horizontal eye diameter 17–33% SL..... **16** [*Stenobrachius*, *Taaningichthys*]
15a Preanal length >59% SL; supracaudal melanophores (PMDp) absent ..... ***Bolinichthys***
15b Preanal length <58% SL; PMDp present ..... ***Parvilux****
16a Body depth at pectoral fin base 13–18% SL; full row of sagittal intervertebral melanophores (Ivt) present; BC present; Br_2 absent..... ***Taaningichthys***
16b Body depth at pectoral fin base 17–24% SL; Ivt absent; BC absent; Br_2 form at 7 mm SL ..... ***Stenobrachius****
17a Basicaudal melanophores present; preanal (AAV) and postadipose melanophores (PMDpa) absent; eyes irregular in shape with dorsal and ventral crescent choroid mass ..... ***Notolychnus***
17b Basicaudal melanophores absent; AAV and PMDpa present; eyes elliptical with ventral lunate choroid mass ..... ***Triphoturus***

Subfamily Lampanyctinae Paxton, 1972

Identification Larvae of the lampanyctine genera, except for *Ceratoscopelus*, *Lepidophanes*, and *Lampadena*, can be distinguished from those of Gymnoscopelinae and Diaphinae by the absence of the photophores or the presence of only a 2nd branchiostegal photophore (Br_2) at their larval stages. Lampanyctinae can be separated from the Notolychninae by a greater preanal length (PAL) and more pelvic-fin rays. *Ceratoscopelus*, *Lepidophanes*, and *Lampadena* larvae can be separated from the Diaphinae and Gymnoscopelinae larvae by another sequence of photophore development (ventronasal gland [Vn] or pectolateral photophore [PLO], second to form versus fifth pectoral photophores [PO_5], respectively). Larvae of the Lampanyctinae can be distinguished from those of Myctophinae by the combination of rounded eyes without choroid tissue (except for *Triphoturus* spp. that have choroid tissue), with the number of rays in the dorsal fin a few more than or nearly equal to the number of rays in the anal fin (except for *Lampichthys* and *Lampanyctus*, with the number of rays in dorsal fin [D] fewer than the number of rays in anal fin [A]).

Genera *Bolinichthys* Paxton, 1972, *Ceratoscopelus* Günther, 1864, *Lampadena* Goode and Bean in Gill, 1893, *Lampanyctus* Bonaparte, 1840 (including *Nannobrachium* Günther, 1887), *Lepidophanes* Fraser-Brunner, 1949, *Parvilux* Hubbs and Wisner, 1964, *Stenobrachius* Eigenmann and Eigenmann, 1890, *Taaningichthys* Bolin, 1959, and *Triphoturus* Fraser-Brunner, 1949.

Bolinichthys Paxton, 1972

General characters Body moderately deep (**BD 19–27% SL**); head relatively small (head length [HL] 25–30% SL); snout short (snout length [SnL] 21–26% HL); eye large (**horizontal eye diameter [ED] >36–43% HL**); anus opens slightly behind the midbody (PAL 59–67% SL). **Only Br_2** during the larval stage or additional Vn, PLO, or PO_5 appear during transformation; Br_2 appear at 5 mm SL; transformation usually occurs at **12–13 mm SL**.

Pigmentation Pigment is sparse: posterior midbrain (Mp); otical (Ot); vesicular (Ve); postanal (PAV), only in *B. longipes*; and mediolateral (ML), only in *B. distofax*.

Similar genera *Bolinichthys* larvae similar to some *Lampanyctus* larvae lacking rostrum (i.e., *Lampanyctus* sp. D) but have a shorter snout (SnL <10% SL versus >10% SL in *Lampanyctus* larvae) and a lower anal-fin ray count (11–15 versus 14–21 in *Lampanyctus* larvae). Larvae of *Bolinichthys* are also similar to those of *Ceratoscopelus* but have larger eyes (ED 36–43% HL versus 24–32% HL in *Ceratoscopelus*), deeper body (BD 19–27% SL versus 14–19% SL), and Vn absent until transformation and to those of *Parvilux* but have a greater PAL (>59 % SL versus <58% SL in *Parvilux*) (Moser and Ahlstrom, 1974, 1996) and no supracaudal melanophores.

Remarks Adults of *B. indicus* (Hulley, 1981; Bekker, 1983) and *B. supralateralis* (Hulley, 1981; McGinnis, 1982; Bekker, 1983; Hulley and Duhamel, 2009; Roberts et al., 2015) were recorded in the STC. The larvae of the first species are unknown.

Bolinichthys supralateralis (Parr, 1928)
Stubby lanternfish
Figure 5

Lepidophanes pyrsobolus: Pertseva-Ostroumova, 1964, 88, fig. 8d (PoF); Pacific Ocean.

Bolinichthys spp.: Olivar et al., 1999, 110, fig. 9, (PoF); Agulhas Current.

Bolinichthys supralateralis: Bolshakova and Evseenko, 2020, 137, fig. 3 (F, PoF); North Atlantic Ocean.

Negative reference: *Bolinichthys distofax* as *B. supralateralis* in Moser and Ahlstrom, 1974, 408, fig. 11D (PoF) (corrected to *B. distofax* in Moser et al., 1984).

Identification

–Large round eyes (ED 39–41% HL) versus all Myctophidae species (≤18–36% HL), except for *Notoscopelus resplendens*, *N. caudispinosus*, *Lampanyctus pusillus*, and *L. festivus* (extralimital species: large eyes also in *P. ingens* from the California Current and in *L. tenuiformis* and *L. steinbecki* from tropical and subtropical waters); and

–Lack of external pigment on the body versus pigment present in all Myctophidae larvae with round eyes, except for *Lampanyctus* sp. D.

General characters D: 12–14, A: 13–15, number of rays in the pectoral fin (P_1): 12–14, number of rays in pelvic fin (P_2): 8, number of gill rakers in the outer row of first gill arch (GR): 5–7+1+12–15, total 18–22, number of vertebrae (V): 33–34. Length at transformation >12 mm SL. At ~8 mm SL, Br_2 appear. All the rays in the fins are distinguishable in the 8.2-mm-SL larva, and the definitive number of gill rakers is noticeable to a size of 11.5 mm SL.

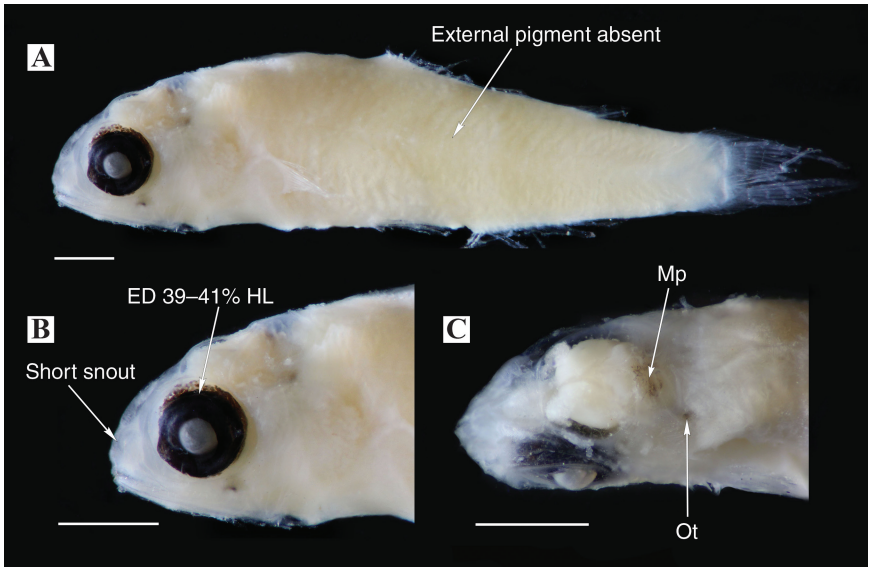

Figure 5

A larva of *Bolinichthys supralateralis* (stubby lanternfish) (11.4 mm standard body length, ID code: IORAS 04473): (**A**) lateral view, (**B**) lateral view of the head, and (**C**) dorsolateral view of the head. The ratio of horizontal eye diameter (ED) to head length (HL) is large compared to those for larvae of other myctophid species. The locations of the posterior midbrain (Mp) and otical (Ot) melanophores are shown in panel C. The scale bar in each panel indicates a length of 1 mm.

Pigmentation Paired Mp, paired Ot, dorsal terminal gut (TGd), Ve.

General distribution Tropical, subtropical, and north temperate waters in the Atlantic Ocean, the western Indian Ocean, and tropical and subtropical waters in the western Pacific Ocean. Occurrence in the STC: in the region of the northern limit of the STC in the South Atlantic and western Indian Oceans (Hulley, 1981; McGinnis, 1982; Bekker, 1983; Hulley and Duhamel, 2009; Roberts et al., 2015).

Ceratoscopelus Günther, 1864

General characters Body slender (**BD <19% SL**); head relatively small (HL 24–27% SL); snout short (SnL 19–27% HL); eye small, slightly oval (**ED >24–32% HL**); anus opens slightly behind the midbody (PAL 58–62% SL). During the larval stage, Br_2, Vn, PLO, and PO_5; Br_2 appear at 7 mm SL; **Vn appear at 7.8 mm SL**; transformation usually occurs at **17–20 mm SL**.

Pigmentation Pigment is sparse: hindbrain (H), Ve, infracaudal (PAVp) and/or supracaudal (PMDp), and terminal subanal (PAVt).

Similar genera Similar to *Lepidophanes*, but have no otical melanophores, and to *Taaningichthys* but photophores appear during larval stages at 5–7 mm SL (appear at >18 mm SL in *Taaningichthys*) and sagittal intervertebral melanophores (Ivt) are absent.

Remarks The species composition of the genus *Ceratoscopelus* is uncertain. Two or 3 valid species are recognized in that genus (Bekker and Borodulina, 1968; Bekker, 1983; Badcock and Araújo, 1988; Fricke et al., 2023). *Ceratoscopelus maderensis* (Lowe, 1839) in the North Atlantic can be easily separated by a number of characters (Nafpaktitis et al., 1977; Hulley, 1981; Bekker, 1983), but the status of the other 2 species, *C. townsendi* (Eigenmann and Eigenmann, 1889) and *C. warmingii* (Lütken, 1892), is controversial. *Ceratoscopelus townsendi* can be separated from *C. warmingii* primarily upon a single feature, the presence of a supraorbital luminous patch (Nafpaktitis and Nafpaktitis, 1969; Wisner, 1976; Bekker, 1983; Badcock and Araújo, 1988). Badcock and Araújo (1988) defined 6 morphotypes on the basis of the arrangement of luminous patches on the body but united all of them under the name *C. townsendi*. This complex is currently under study by A. Prokofiev and probably represents a complex of sibling species different in the arrangement of luminous patches and relative disposition of some photophores on the body, modal gill-raker count, details of dentition, and proportions.

The name *C. townsendi* should be restricted for the populations of the California Current. For the *Ceratoscopelus* larvae from that area, the timing of the formation of fins and photophores is somewhat different from those in other regions, but they are otherwise the same in morphology and pigmentation (Ahlstrom, 1971; Badcock and Araújo, 1988). Two other published names, *Scopelus warmingii* (Lütken, 1892) and *Lampanyctus polyphotis* (Beebe, 1932), are applicable to the populations from the North Atlantic Ocean. Populations from the STC may belong to some undescribed species (different in the Atlantic Ocean and Indo-Pacific), which cannot be evaluated by the larval characters at present.

Ceratoscopelus gr. *townsendi*

Figure 6

Myctophum (*Lampanyctus*) *elongatum*: Roule and Angle, 1930, 44, plate 2, fig. 448, 49 (PoF); Canary Islands (Northeast Atlantic Ocean).

Ceratoscopelus townsendi: Moser and Ahlstrom, 1996, 396, figure on p. 397 (PrF, F, PoF, juvenile [Juv]); California Current.

Diaphus metopoclampus: Rodríguez, 2023, 104 (PoF); central Northeast Atlantic Ocean.

Ceratoscopelus warmingii: Shiganova, 1977, 94, fig. 16G (PoF) (in part.: fig. 16, A and G); Atlantic Ocean. Miller et al., 1979, 31, fig. 37 (PrF); central North Pacific Ocean (Hawaiian Islands). Belyanina, 1982, 22, fig. 19 (PoF); tropical western Pacific Ocean. Ozawa, 1986, 155, plate 19, D and E (PrF, F), plate 20, A–D (PoF, Juv); Northwest Pacific Ocean. Badcock and Araújo, 1988, 20, fig. 4 (F, PoF); Azores front (Northeast Atlantic Ocean). Olivar et al., 1999, 111, fig. 10 (PoF); Agulhas Current. Moser and Watson, 2001, 64, figure on p. 65 (PrF, F, PoF, Juv); western central Atlantic Ocean. Bonecker and Castro, 2006, 137, figure on p. 137 (PoF); tropical southwest Atlantic Ocean. Suntsov et al., 2008, 67, fig. 6d (PoF); area unknown.

Negative reference: *Lampadena luminosa* as *C. townsendi* in Pertseva-Ostroumova, 1964, 89, fig. 9A (Northeast Pacific Ocean).

Notes: Shiganova (1977) apparently described a mix of 2 or more species: *C. warmingii* (fig. 16, A and G), *C. maderensis* (fig. 16, B–D, F), and uncertain species (fig. 16, E and H). Rodríguez (2023) erroneously identified the 8.1-mm-SL larva of *C.* gr. *townsendi* as *D. metopoclampus*. The larva has Vn, which appear in *Diaphus* larvae only during metamorphosis, and there were also no basicaudal melanophores characteristic of *Diaphus* larvae.

Identification

–Supracaudal and PAVp melanophores absent versus present in *Lepidophanes guentheri* (extralimital species: also present in *C. maderensis* from the North Atlantic Ocean);

–Mediodorsal melanophores absent versus present in *Lampadena* spp. and *Lepidophanes guentheri*;

–Anteroventral foregut and basicaudal melanophores absent versus present in *Diaphus* spp.; and

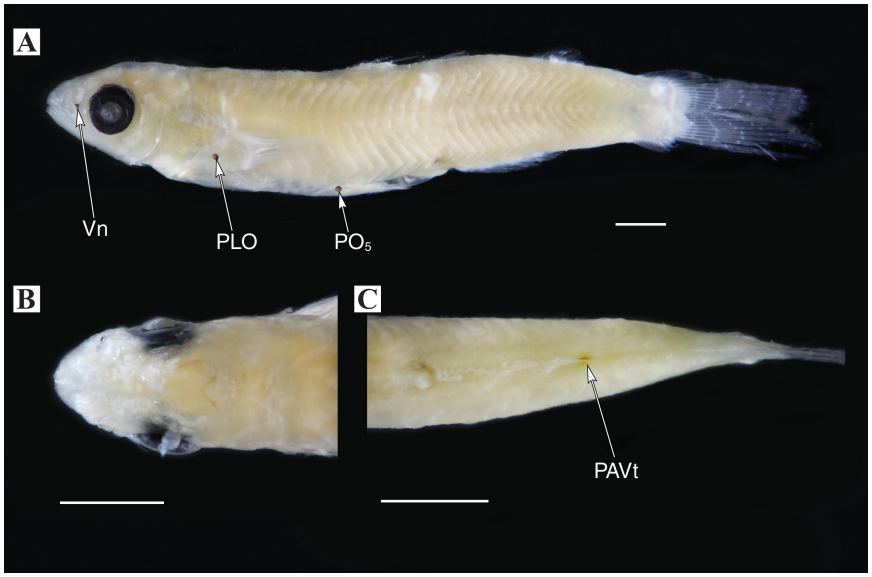

Figure 6

A larva of *Ceratoscopelus* gr. *townsendi* (13.2 mm standard body length, ID code: IORAS 04474): (**A**) lateral view, showing the location of the ventronasal gland (Vn), pectolateral photophore (PLO), and fifth pectoral photophore (PO_5); (**B**) dorsal view of the head; and (**C**) ventral view of the tail, showing the location of the terminal subanal melanophore (PAVt). The scale bar in each panel indicates a length of 1 mm.

–Ventronasal gland forming at 8 mm SL versus Vn absent in *B. supralateralis*, *Diaphus* spp., and *Taaningichnys* spp. to the transformation stage.

General characters D: 13–15, A: 13–15, P_1: 12–15, P_2: 8; GR: 3–5+1+8–10(11), total 13–15(16), V: 35–36. Length at transformation >15 mm SL. The Br_2 appear at ~5–7 mm SL, Vn and PLO appear at ~8 mm SL, and PO_5 appear at 9 mm SL. All the rays in the fins are distinguishable in the 9–10-mm-SL larva, and the definitive number of gill rakers is noticeable to a size of 13 mm SL.

Pigmentation Paired Mp, 2–3 H, TGd, PAVt, Ve, 1–4 Ivt.

General distribution Circumglobal in tropical and warm temperate waters. Occurrence in the STC: in the region of the northern limit of the STC (Parin et al., 1973; Hulley, 1981; McGinnis, 1982; Bekker, 1983; Bekker and Evseenko, 1986; Young et al., 1996; Figueroa et al., 1998; Roberts et al., 2015).

Lampadena Goode and Bean in Gill, 1893

General characters Body moderate (**BD 19–24% SL**) to moderately deep (**BD 27–28% SL**); head moderate (HL 27–31% SL); snout short (SnL 19–29% HL); eye moderately large (**ED >26–37% HL**); anus opens slightly behind the midbody (PAL 62–67% SL). During the larval stage, Br_2, PLO, PO_5, first pectoral photophores (PO_1), and Vn; Br_2 appear at 6–7 mm SL; PLO appear at 8 mm SL; transformation usually occurs at **20 mm SL**.

Pigmentation Rows of mediodorsal (MD) and PAV most prominent, occipital (OC), Ve, anteroventral foregut (FGv), dorsal foregut (FGd), dorsal midgut (MGd); some species have posterior mediolateral (MLP).

Similar genera Similar to *Taaningichthys* larvae, but photophores appear during larval stages at 6–7 mm SL (versus at >18 mm SL in *Taaningichthys*) and body is deeper (BD >19% SL versus <19% SL in *Taaningichthys*); similar to *Ceratoscopelus*, but with FGv and MD melanophores (absent in *C. warmingii*) and with PLO formed earlier than Vn; similar to *Lepidophanes*, but with deeper body (BD >19% SL versus <19% SL in *Lepidophanes*); and similar to *Diaphus* spp., but with another sequence of photophore formation (Br_2, PLO, PO_5 versus Br_2, PO_5, PO_1).

Remarks Ten valid species are recognized in the genus *Lampadena* (Fricke et al., 2023), but the early stages of development are known only for 3 of them: *L. chavesi* (Bolshakova and Evseenko, 2016a), *L. luminosa* (Pertseva-Ostroumova, 1964; Moser and Ahlstrom, 1974; Ozawa, 1986; Olivar et al., 1999), and *L. urophaos* (Moser and Ahlstrom, 1972, 1996). Fahay (1983) tentatively assigned the larvae of *Lampadena* sp. 1 (Ozawa, 1986) and *Lampadena* sp. (Moser and Watson, 2001) to

L. anomala, but this definition is not warranted because the meristic characters overlap within *Lampadena* species, and there are no photophores in the described larvae. Several types of *Lampadena* larvae were described but not identified to the species level (Moser and Ahlstrom, 1972; Miller et al., 1979; Ozawa, 1986; Bonecker and Castro, 2006).

All described *Lampadena* larvae share a combination of characters given previously herein, and we expect a similar situation for the species known in the STC. Adults of 4 species were found in the area of the STC: *L. anomala* (single record at 38°38′S in the western Atlantic Ocean: Hulley, 1981), *L. dea* (Hulley, 1981; McGinnis, 1982; Bekker, 1983; Bekker and Evseenko, 1986), *L. notialis* (Hulley, 1981; McGinnis, 1982; Bekker, 1983), and *L. speculigera* (Hulley, 1981; McGinnis, 1982; Bekker, 1983). However, none of these 4 species are identified at larval stages. The unidentified *Lampadena* larvae described herein may belong to 1 of the last 3 aforementioned species.

Lampadena sp.
Figure 7

Identification

–Anterior mediodorsal melanophore (AMD) present versus absent in *Ceratoscopelus*, *Lepidophanes*, and other *Lampadena* species (extralimital species: AMD also present in *L. urophaos* from the subtropical North Atlantic and Pacific Oceans);
–Basicaudal melanophores absent versus present in *Diaphus* spp.; and
–Ventronasal gland absent in 9.8-mm-SL larva versus Vn forming at ~8 mm SL in *Ceratoscopelus* spp. and *Lepidophanes guentheri*.

General characters D: 12–13, A: 12–14, P_1: ~11 (have not yet fully formed), GR: 6+1+15+ (have not yet fully formed), total 22+, V: 39–40. Flexion at 6.0–6.2 mm SL; length at transformation >10 mm SL. The Br_2 appear at ~6–7 mm SL, PLO appear at 8–9 mm SL; PO_5 appear after PLO at ~8–9 mm SL. All the rays in the fins are distinguishable in the 9–10-mm-SL larvae, and the number of gill rakers is not definitive at a size of 9.8 mm SL.

Pigmentation Preflexion: single AMD; paired posterior subdorsal (SMDp); 3–4 unpaired PMDp (in the form of stripes); paired TGd; 6–7 PAV, Ve; F: the same; PoF: single Mp, single H, single AMD, paired SMDp, 3–4 unpaired PMDp, paired TGd, 1–2 PAVp (often immersed), Ve.

General distribution Larvae were found in samples off the southern coast of Australia, where the northern border of the STC lies.

Remarks The larvae have a set of features (proportions, sequence of photophore formation, pigmentation) characteristic for moderate-bodied *Lampadena* larvae. These larvae differ from those already described in the literature by the presence of an AMD melanophore located on 3rd to 4th trunk myomere. This melanophore appears in the PrF stage and remains in 10-mm-SL larvae. The formation of gill rakers is not yet completed, but about 22 rakers are already present on the first arch in the 3 largest larvae (8.6–10.0 mm SL), greatly exceeding the range known for *L. anomala* (GR: 16–18). The remaining 3 species (*L. dea*, *L. notialis*, and *L. speculigera*) reported off the southern coast of Australia have similar meristic characters; therefore, further identification is difficult.

Lampanyctus Bonaparte, 1840

General characters Body deep (**BD >24% SL**); head large (**HL >27% SL**) (50% SL in *L. achirus*); snout moderate (SnL 26–38% HL) or large (38–56% HL) (65% SL in *L. achirus*); **jaws long with prominent teeth**, ≥60% HL at PoF stage; eye moderately large (ED >24–39% HL); anus opens slightly behind the midbody (PAL 58–65% SL) or shifted posteriorly (65–78% SL). **Only Br_2** during the larval stage, except for *L. alatus* (Vn or PO_5 present) and *L. intricarius* (Br_2 absent during the larval stage); Br_2 appear at 5–11 mm SL; transformation usually occurs at **20 mm SL** (*L. alatus* and *L. pusillus* to 11 mm SL). In addition, see main characters of the larval types.

Pigmentation Medullar pigment in most species; most diverse pigment pattern among all genera.

Similar genera Some *Lampanyctus* larvae similar to *Bolinichthys* but have a longer snout (SnL >10% SL versus <10% SL in *Bolinichthys* larvae) and more numerous anal-fin rays (14–21 versus 11–15 in *Bolinichthys* larvae).

Note that larvae of *Lampanyctus* can be grouped into 2 types:

Larvae with long rostrum: main characters

–Snout produced into rostrum with large jaws: SnL ≥15% SL;
–Dorsal fin displaced posteriorly: predorsal length (PDL) ≥55% SL;
–Teeth at tip of upper jaw pointing slightly upward; and
–Relatively large gut in PoF stage: PAL ≥65% SL.

Larvae without rostrum: main characters

–Relativity short snout: SnL <15% SL;
–dorsal fin located anterior to or near mid-body: PDL <55% SL (except for *L. pusillus*, *L. steinbecki*, and *L. tenuiformis*);
–No teeth at tip of upper jaw pointing upward (except for *L. festivus*); and
–Moderate or short gut in PoF stage: PAL <65% SL (except for *L. pusillus*, *L. steinbecki*, and *L. tenuiformis*).

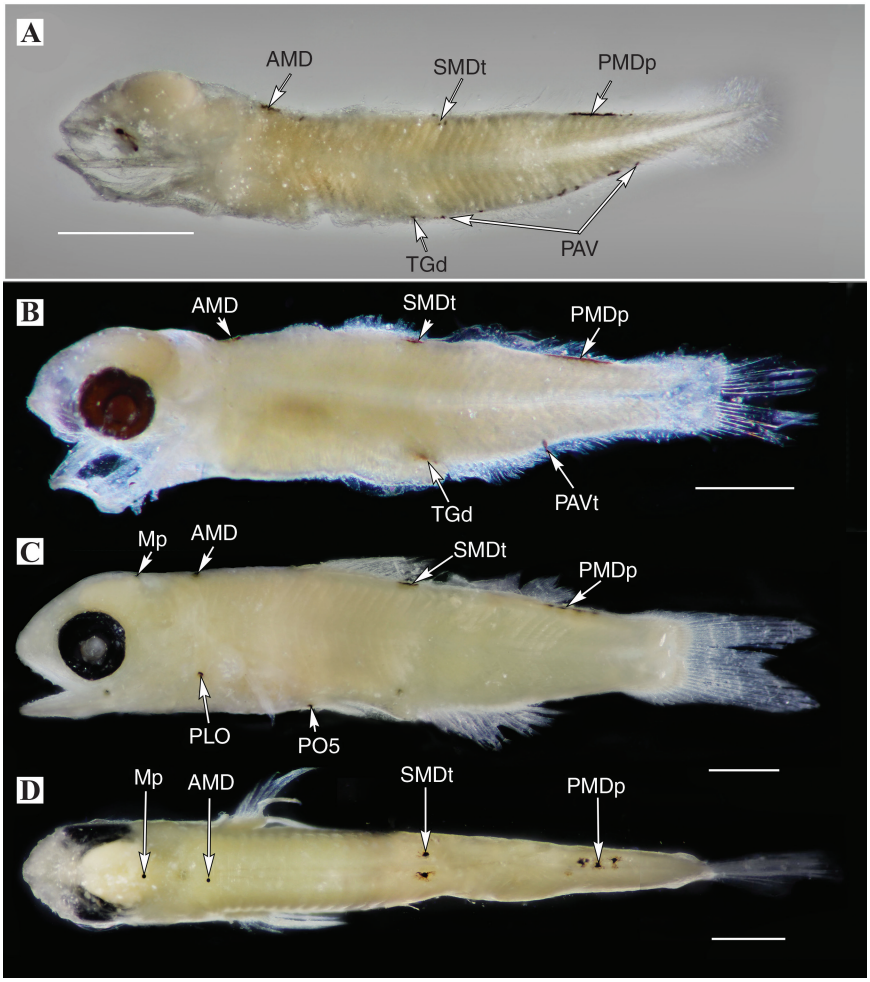

Figure 7

Larvae of *Lampadena* sp.: (**A**) 6.2 mm standard body length (SL), ID code: IORAS 04491; (**B**) 7.5 mm SL, IORAS 04490; (**C**) 9.8 mm SL, IORAS 04489 (lateral view); and (**D**) 9.8 mm SL, IORAS 04489 (dorsal view). The following melanophore pigment groups and photophores are shown: antedorsal (AMD), posterior subdorsal (SMDp), supracaudal (PMDp), dorsal terminal gut (TGd), postanal (PAV), posterior midbrain (Mp), pectolateral photophore (PLO), and fifth pectoral photophore (PO_5). The scale bar in each panel indicates a length of 1 mm.

Remarks Adults of 10 described and 3 undescribed species were recorded from the STC: *Lampanyctus achirus* (Hulley, 1981; McGinnis, 1982; Bekker, 1983; Bekker and Evseenko, 1986; Zahuranec, 2000; Roberts et al., 2015), *L. ater* (Hulley, 1981; McGinnis, 1982; Bekker, 1983; Zahuranec, 2000; Roberts et al., 2015), *L. alatus*, *L. australis*, *L. festivus*, *L. lepidolychnus* (Hulley, 1981; McGinnis, 1982; Bekker, 1983; Roberts et al., 2015), *L. intricarius*, *L. macdonaldi*, *L. pusillus* (Hulley, 1981; McGinnis, 1982; Bekker, 1983; Bekker and Evseenko, 1986; Roberts et al., 2015), *L. wisneri* (Hulley, 1981; McGinnis, 1982; Zahuranec, 2000), and *Lampanyctus* sp. B, C, and D (McGinnis, 1982).

The systematic position of the larvae identified as *L. lepidolychnus* (Olivar and Beckley, 1997) requires further study (see the "Remarks" section for *L. intricarius*). The early stages of development of *L. macdonaldi* and *Lampanyctus* sp. B are unknown, adults of the latter species are most similar in meristic features to *L. festivus*. *Lampanyctus* sp. C can be identical with *L. australis* because the meristic characters of these species match, and a characteristic vertical band of pigment was noted for juvenile *Lampanyctus* sp. C at <30 mm SL (McGinnis, 1982; Bolshakova et al., 2021). *Lampanyctus* sp. D is an undescribed species abundant in the western and central South Pacific Ocean (McGinnis, 1982).

Larvae with long rostrum

Lampanyctus gr. *achirus*
Figure 8

Lampanyctus sp. (possibly *L. achirus*): Moser and Ahlstrom, 1974, 406, fig. 10D (PoF).
Lampanyctus achirus: Olivar and Beckley, 1997, 49 (description without illustration); Agulhas Current (southwestern Indian Ocean). Bolshakova et al., 2021, 113, fig. 3 (F, PoF); southwest Pacific Ocean.

Identification

–Longest toothy rostrum (SnL 50–65% HL) versus ≤50% HL among all Myctophidae species;
–Preopercular spines present versus absent in most *Lampanyctus* larvae except for *L. ater* (extralimital species: also present in *L. niger* from the central and western Pacific Ocean); and
–Lack of medullar pigment versus present in all *Lampanyctus* larvae (extralimital species: medullar pigment also absent in *L. idostigma* from the eastern Pacific Ocean).

General characters D: 15–17, A: 18–20, P_1: 14–16, P_2: 8; GR: 5–6+1+11–13, total 17–19, V: 35–36. Length at transformation >22 mm SL. The Br_2 appear at 9 mm SL. All the rays in the fins are distinguishable in the 14.5-mm-SL larva, and the definitive number of gill rakers is noticeable to a size of 16.0 mm SL.

Pigmentation Upper-jaw symphyseal (UJS) in a row, lower-jaw symphyseal (LJS), 1–3 nasal, 1 postorbital (PO), 1–4 opercular (OP), TGd, numerous basipectoral (BP), hypaxial abdominal myoseptal (HMSa), pectoral-fin pigmentation (Pp).

General distribution Circumglobal in subantarctic zone. Occurrence in the STC: throughout the area (Hulley, 1981; McGinnis, 1982; Bekker, 1983; Bekker and Evseenko, 1986; Zahuranec, 2000; Roberts et al., 2015).

Remarks Two very similar species, *L. achirus* and *L. wisneri* (as *Lampanyctus* sp. A: McGinnis, 1982; as *Nannobrachium wisneri*: Zahuranec, 2000), are known in the STC. *Lampanyctus wisneri* differs from *L. achirus* in the lower gill raker count (4+11–12, total 15–16, versus 5–6+13, total 18–19), greater PDL, absence of pectoral fins in the specimens larger than 35 mm SL, and smaller maximum size (~80 mm SL in *L. wisneri* versus ~160 mm SL in *L. achirus*) (Zahuranec, 2000).

Of all aforementioned features, only the number of gill rakers can be estimated on larvae. By this character, the described larvae (Bolshakova et al., 2021; this study) agree with *L. achirus* (5+12 (4), 5+13 (2), 5+14 (3), and 6+13 (3)). However, *L. achirus* is a subantarctic species that is distributed between the STC in the north and the Antarctic Polar Front to the south (McGinnis, 1982), whereas all the described larvae were obtained from an area north of 46°S and have never been caught south of this latitude. This boundary corresponds to the southernmost limit of the distribution of *L. wisneri*.

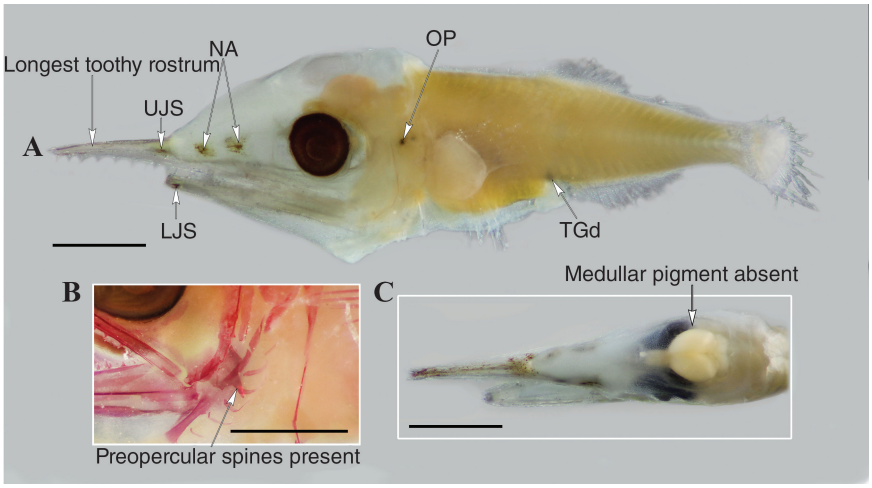

Figure 8

Larvae of *Lampanyctus* gr. *achirus*: (**A**) 8.3 mm standard body length (SL), ID code: IORAS 04475; (**B**) 12.8 mm SL, IORAS 04476 (preopercular spines), and (**C**) 8.3 mm SL, IORAS 04475 (dorsal view of the head). The upper-jaw symphyseal (UJS), lower-jaw symphyseal (LJS), nasal (NA), opercular (OP), and dorsal terminal gut (TGd) melanophore pigment groups are shown in panel A. The scale bar in each panel indicates a length of 1 mm.

Therefore, identification of the described larvae becomes controversial.

The presence of the larvae morphologically congruent with the subantarctic species (*L. achirus*) in the area of distribution of its closest relative (*L. wisneri*) and the absence of the larvae referable to *L. wisneri* in the same area raise a question on the validity of the latter species. On the other hand, all larvae attributed to *L. achirus* were collected from the area of distribution of *L. wisneri* (Olivar and Beckley, 1997; Bolshakova et al., 2021), except for a larva that Moser and Ahlstrom (1974, fig. 10D) figured without indicating an origin. Therefore, all descriptions of *L. achirus* may belong to *L. wisneri*, the larvae of true *L. achirus* may not be known, and the variation in gill-raker count in both species may be greater than indicated by Zahuranec (2000) and may not warrant the separation of these species. This problem requires further study, and for the purposes of our work, we treat these larvae as *L.* gr. *achirus*.

Lampanyctus ater Tåning, 1928
Dusky lanternfish
Figure 9

Nannobrachium atrum: Moser and Watson, 2001, 102, (PrF, F, PoF); western central Atlantic Ocean.

Lampanyctus ater: Olivar, 1985, 285, fig. 5.46 (PrF, PoF); Benguela Current (southeast Atlantic Ocean). Olivar, 1988, 406 (single larval stage without illustration); Benguela Current. Rodríguez, 2023, 122 (PrF, PoF), 123 (PrF, F, PoF); central Northeast Atlantic Ocean.

Identification

–Preopercular spines present versus absent in most *Lampanyctus* larvae except for *L. achirus* (extralimital species: also present in *L. niger* from the central and western Pacific Ocean);

–Poorly pigmented larvae: only preadipose (PMDa) and terminal gut melanophores present on body versus different pigmentation in all other *Lampanyctus* larvae (extralimital species: pigment also is sparse in *L. nobilis* from the tropical zone of 3 oceans and in *L. acanthurus* from the North Pacific).

General characters D: 14–16, A: 16–20, P_1: 11–12, P_2: 8; GR: 4–5+1+11 (10–12), total 15–18, V: 35–36. Length at transformation >15 mm SL. The Br_2 appear at 6 mm SL. All the rays in the fins are distinguishable in the 14.5-mm-SL larva.

Pigmentation Lower-jaw symphyseal, UJS, paired Mp, FGv, paired TGd, PMDa.

General distribution Tropical and subtropical Atlantic, South Pacific, and Indian Oceans. Occurrence in the STC: throughout the area except in the Pacific Ocean east of 165°W (Hulley, 1981; McGinnis, 1982; Bekker, 1983; Young et al., 1996; Zahuranec, 2000; Roberts et al., 2015).

Larvae without rostrum

Lampanyctus alatus Goode and Bean, 1896
Winged lanternfish
Figure 10

Lampanyctus alatus: Olivar and Beckley, 1997, 49, fig. 1 (PrF, PoF); Agulhas Current. Moser and Watson, 2001, 82 (PrF, PoF, Juv); western central Atlantic Ocean. Bolshakova and Evseenko, 2016b, 526, fig. 4 (PoF); tropical South Atlantic Ocean.

Figure 9

A larva of *Lampanyctus ater* (dusky lanternfish) (18.5 mm standard body length, ID code: IORAS 04477): (**A**) lateral view, showing the locations of the lower-jaw symphyseal (LJS) and upper-jaw symphyseal (UJS) melanophores, and (**B**) dorsal view of the tail, showing the location of the preadipose (PMDa) melanophore. The scale bar in each panel indicates a length of 1 mm.

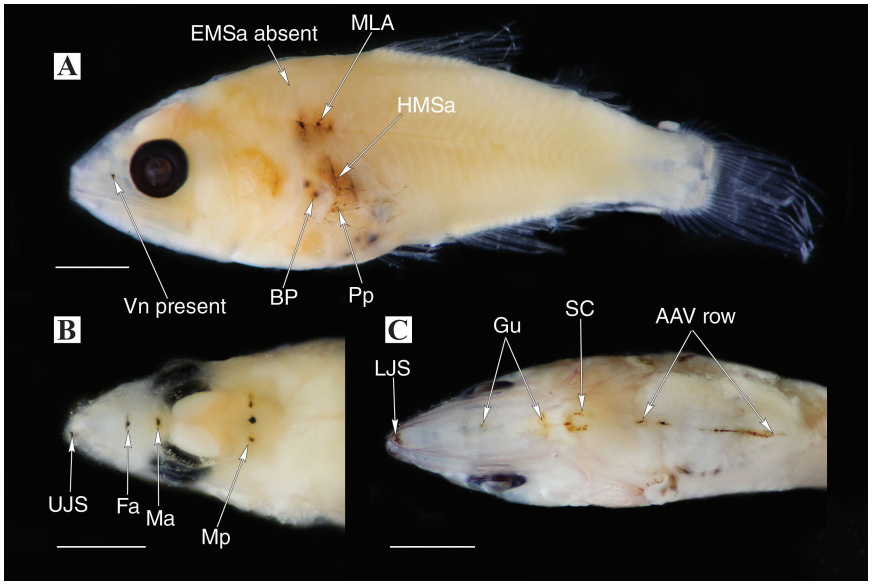

Figure 10

A larva of *Lampanyctus alatus* (winged lanternfish) (9.1 mm standard body length, ID code: IORAS 04478): (**A**) lateral view, (**B**) dorsal view of the head, and (**C**) ventral view of the body. The following melanophore pigment groups and photophore are shown: anterior mediolateral (MLA), hypaxial abdominal myoseptal (HMSa), basipectoral (BP), pectoral-fin pigmentation (Pp), upper-jaw symphyseal (UJS), anterior forebrain (Fa), anterior midbrain (Ma), posterior midbrain (Mp), lower-jaw symphyseal (LJS), gular (Gu), symphyseal-cleithral (SC), preanal (AAV), and ventronasal gland (Vn). Epaxial abdominal myoseptal (EMSa) pigmentation is absent. The scale bar in each panel indicates a length of 1 mm.

Identification

–A series of 4–6 preanal (AAV) melanophores present versus absent in all *Lampanyctus* larvae except for *L. pusillus* and *L. intricarius*; and
–The PO_5 or Vn form at 8–10 mm SL versus no PO_5 and Vn in all other *Lampanyctus* species during the larval stage.

General characters D: 11–12, A: 16–18, P_1: 11–13, P_2: 8; GR: 3–4+1+8–9, total 12–14, V: 33–35. Length at transformation ~12 mm SL. The Br_2 appear at 4.5–5.0 mm SL. All the rays in the fins are distinguishable in the 7-mm-SL larva.

Pigmentation Lower-jaw symphyseal, UJS, 1–2 gular (Gu), anterior forebrain (Fa), anterior midbrain (Ma), paired and unpaired Mp, H, symphyseal-cleithral (SC), 4–6 AAV, TGd, MGd, paired lateral cleithral (CL), 1–2 inner BP, 2–5 anterior mediolateral (MLA), HMSa, Pp.

Similar species in the STC Similar to larvae of *L. australis* but lack PMDa melanophore and broad vertical band of pigment. Similar to *L. pusillus* but moderately slender body (BD 28–33% SL) versus deep body in *L. pusillus* (BD 35–43% SL).

General distribution The tropical and subtropical Atlantic Ocean and Indo-Pacific. Occurrence in the STC: from north of the STC to 38°S in the western South Atlantic, in the region of the northern limit of the STC in the eastern South Atlantic and Indian Oceans, and in the western Pacific Ocean (to 180°E) in the region of the northern limit of the STC (Hulley, 1981; McGinnis, 1982; Bekker, 1983; Young et al., 1996; Roberts et al., 2015).

Lampanyctus australis Tåning, 1932
Southern lanternfish
Figure 11

Lampanyctus sp. 1: Olivar, 1988, 410, fig. 11 (PrF, F, PoF); Benguela Current.
Lampanyctus australis: Olivar and Beckley, 1997, 52, fig. 3 (F, PoF); Agulhas Current. Bolshakova and Evseenko, 2016a, 852, fig. 4 (PoF); Walvis Ridge (southeast Atlantic Ocean). Bolshakova et al., 2021, 115, fig. 4 (PoF); southwest Pacific Ocean.

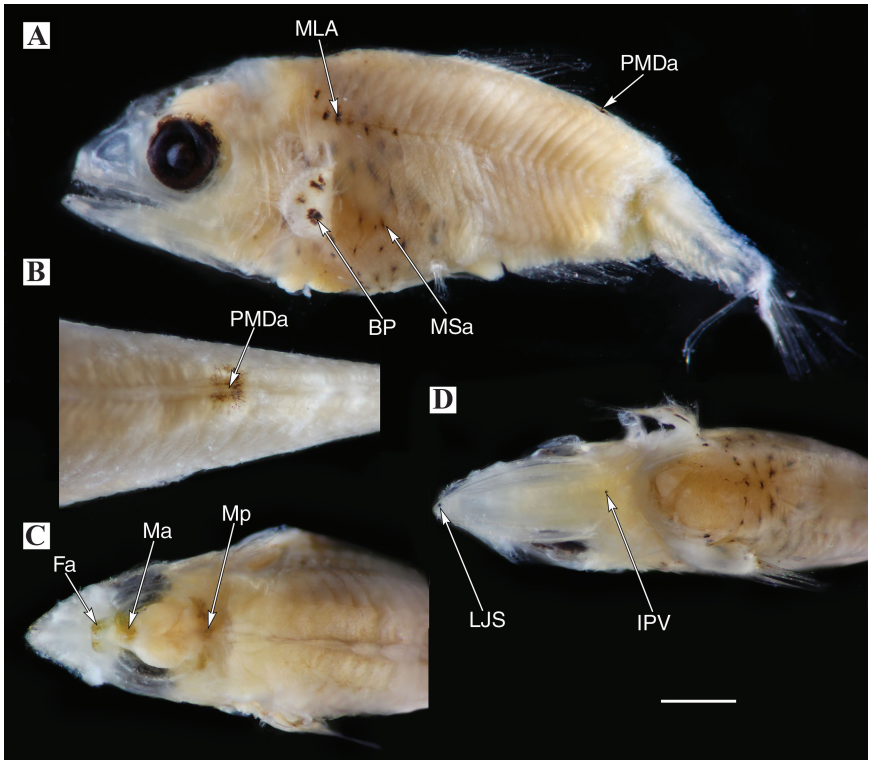

Figure 11

A larva of *Lampanyctus australis* (southern lanternfish) (10.0 mm standard body length, ID code: IORAS 04479): (**A**) lateral view, (**B**) dorsal view of the tail, (**C**) dorsal view of the body, and (**D**) ventral view of the body. The following melanophore pigment groups are shown: anterior mediolateral (MLA), preadipose (PMDa), basipectoral (BP), abdominal myoseptal (MSa), anterior forebrain (Fa), anterior midbrain (Ma), posterior midbrain (Mp), lower-jaw symphyseal (LJS), and prepectoral (isthmic) (IPV). The scale bar indicates a length of 1 mm.

Identification A broad vertical band of pigment posterior to the pectoral fin present versus absent in other *Lampanyctus* larvae (extralimital species: also present in *L. crocodilus* from the North Atlantic Ocean and *L. nobilis* from the tropical zone of 3 oceans).

General characters D: 12–14, A: 16–19, P_1: 13–15, P_2: 8; GR: 6(7)+1+14(13), total 19–21, V: 35–37. Length at transformation >15 mm SL. The Br_2 appear at 5.5 mm SL. All the rays in the fins are distinguishable in the 10.0-mm-SL larva.

Pigmentation Lower-jaw symphyseal; sometimes UJS; paired Ma; unpaired: Fa, Mp, H; sometimes single prepectoral (isthmic) (IPV); periproctal (AAVp); TGd; often PMDa; inner CL; 2–3 inner BP; abdominal myoseptal (broad vertical band); 4–6 MLA; Pp.

Similar species in the STC Similar to *L. alatus* but have no preanal series of melanophores and have more GR: 19–21 versus 12–14 in *L. alatus*.

General distribution Circumglobal in Southern Hemisphere south to 30°S. Occurrence in the STC: throughout the area except the central Pacific sector (Parin et al., 1973; Hulley, 1981; McGinnis, 1982; Bekker, 1983; Young et al., 1996; Roberts et al., 2015).

Lampanyctus festivus Tåning, 1928
Festive lanternfish
Figure 12

Lampanyctus sp. B: Olivar and Beckley, 1997, 57, fig. 8 (PrF, F, PoF); Agulhas Current.
Lampanyctus festivus: Bolshakova and Evseenko, 2016a, 854, fig. 5 (PoF); Walvis Ridge.

Identification

–Postorbital and opercular melanophores present versus absent in other *Lampanyctus* larvae, except for *L. achirus* and *L. pusillus* (extralimital species: also present in *L. regalis* from the North Pacific Ocean);

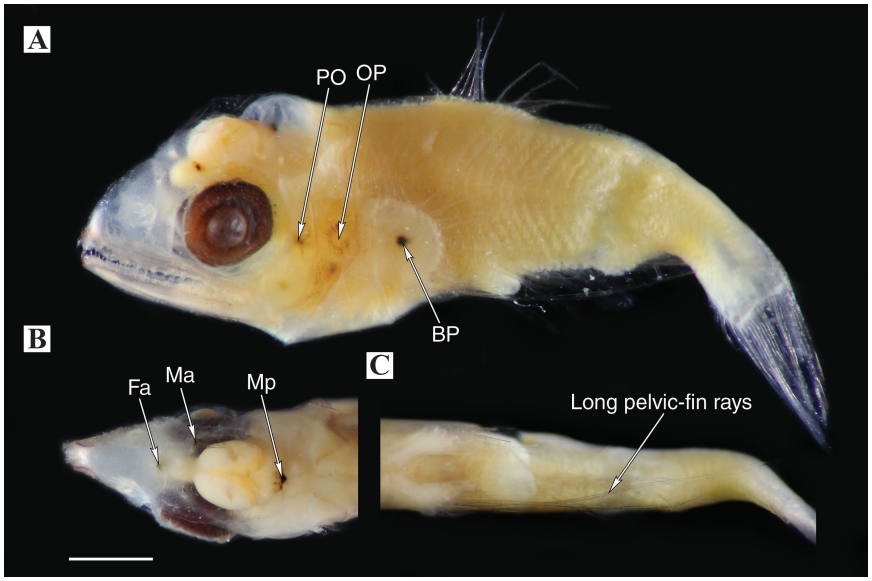

Figure 12

A larva of *Lampanyctus festivus* (festive lanternfish) (9.5 mm standard body length, ID code: IORAS 04481): (**A**) lateral view, (**B**) dorsal view of the head, and (**C**) ventral view of the body and tail, showing a long ray on the pelvic fin. The following melanophore pigment groups are shown: postorbital (PO), opercular (OP), basipectoral (BP), anterior forebrain (Fa), anterior midbrain (Ma), and posterior midbrain (Mp). The scale bar indicates a length of 1 mm.

–Single large BP melanophore versus several or lacking in other *Lampanyctus* larvae (extralimital species: single melanophore also in *L. niger* from the tropical and subtropical North Pacific Ocean);
–No TGd pigmentation and PMDa melanophore versus at least one of those present in other *Lampanyctus* larvae except for *L. achirus*; and
–Long pelvic-fin rays: rays reach from middle to end of anal fin base at ≥4.7 mm SL versus rays do not reach the middle of the anal fin in other *Lampanyctus* larvae.

General characters D: 13–16, A: 18–22, P_1: 15–17, P_2: 8; GR: 4+1+8–10, total 13–15, V: 36–37. Length at transformation >10 mm SL. The Br_2 appear at 4.7 mm SL. All the rays in the fins are distinguishable in the 8.9-mm-SL larva.

Pigmentation Postorbital, 1–3 OP, Fa, paired Ma, single Mp, FGv, MGd, BP, Pp.

General distribution Bipolar subtropical distribution in the Atlantic and Pacific Oceans and equatorial waters of the Indian Ocean. Occurrence in the STC: eastern and western sectors of the South Atlantic and Pacific Oceans (Hulley, 1981; McGinnis, 1982; Bekker, 1983; Young et al., 1996; Roberts et al., 2015).

Lampanyctus intricarius Tåning, 1928
Diamondcheek lanternfish
Figure 13

Myctophum benoiti: Regan, 1916, 139, plate 6, figs. 1 and 2 (PrF, PoF); southwest Atlantic Ocean.
Lampanyctus? isaacsi: Olivar, 1988, 407, fig. 9 (PrF, F, PoF); Benguela Current.
? *Lampanyctus lepydolichnus*: Olivar and Beckley, 1997, 53, fig. 4 (PrF, F, PoF); Agulhas Current.
Lampanyctus intricarius: Bolshakova and Evseenko, 2015, 596, figs. 2–4 (PoF); southwest and southeast Pacific and southeast Atlantic Oceans. Bolshakova et al., 2021, 117 (description without illustration); southwest Pacific Ocean.

Identification

–Both PDL and AAV unpaired series of melanophores present versus absent or paired in other *Lampanyctus* larvae;
–Caudal myoseptal melanophores present versus absent in other *Lampanyctus* larvae, except for *Lampanyctus* sp. D (extralimital species: also present in *L. lineatus* from the tropical and subtropical Atlantic, South Pacific, and Indian Oceans); and

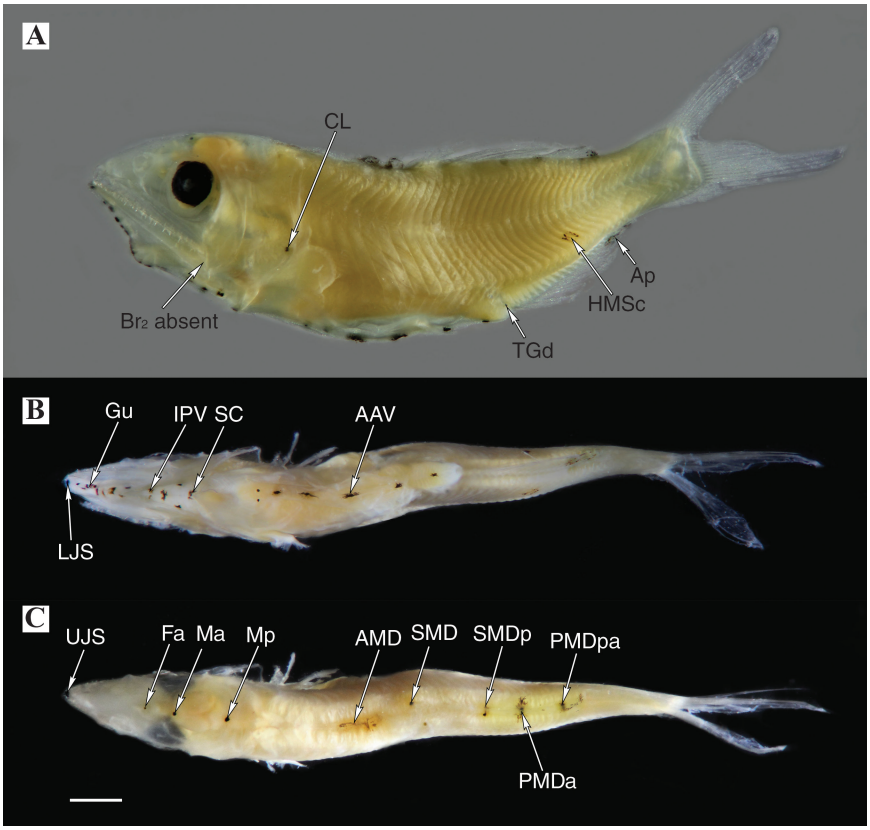

Figure 13

A larva of *Lampanyctus intricarius* (diamondcheek lanternfish) (12.7 mm standard body length, ID code: IORAS 04480): (**A**) lateral view, (**B**) ventral view, and (**C**) dorsal view. The following melanophore pigment groups are shown: lateral cleithral (CL), dorsal terminal gut (TGd), hypaxial caudal myoseptal (HMSc), anal-fin pigmentation (Ap), lower-jaw symphyseal (LJS), gular (Gu), prepectoral (isthmic) (IPV), symphyseal-cleithral (SC), preanal (AAV), upper-jaw symphyseal (UJS), anterior forebrain (Fa), anterior midbrain (Ma), posterior midbrain (Mp), antedorsal (AMD), subdorsal (SMD), posterior subdorsal (SMDp), preadipose (PMDa), and postadipose (PMDpa). The 2nd branchiostegal photophores (Br_2) are absent. The scale bar indicates a length of 1 mm.

–No photophores developed during the larval stage versus at least Br_2 are present in other *Lampanyctus* larvae.

General characters D: 14–16, A: (17)18–20, P_1: 13–15, P_2: 8; GR: 4+1+9–11, total 14–16, V: 37–38. Length at transformation >25 mm SL. No photophores developed during the larval stage. All the rays in the fins are distinguishable in the 7-mm-SL larva. Larvae have dorsal and ventral fin folds. The body of larvae is laterally compressed.

Pigmentation Lower-jaw symphyseal, few UJS, row of Gu, Fa, Ma, Mp, paired irregular row of IPV, SC, single row of AAV, 1–2 paired subanal (PAVa), PAVt, TGd, single row of AMD, 1–2 paired SMD, posterior subdorsal, PMDa, paired or unpaired postadipose, 1–2 CL, 1–2 hypaxial caudal myoseptal, dorsal-fin pigmentation, anal-fin pigmentation, Pp, ventral-fin pigmentation, adipose-fin pigmentation.

General distribution Circumglobal in the Southern Hemisphere south of 20° S to the STC; North Atlantic Ocean in temperate region. Occurrence in the STC: throughout the area (Parin et al., 1973; Hulley, 1981; McGinnis, 1982; Bekker, 1983; Bekker and Evseenko, 1986; Young et al., 1996; Roberts et al., 2015).

Remarks Larvae of *L. intricarius* described from the southwest and southeast Pacific Ocean and the southeast Atlantic Ocean (Bolshakova and Evseenko, 2015) and larvae from the Agulhas (Olivar and Beckley, 1997) and Benguela Current regions (Olivar and Fortuño, 1991) in the southeast Atlantic Ocean identified as *L. lepidolychnus* show no differences in meristic characters,

pigmentation pattern, and body proportions. Olivar and Beckley (1997) referred the larvae from the Agulhas Current region to *L. lepidolychnus* the basis of meristic characters and simultaneous catches of the adults of that species. Although initially identified as *L. isaacsi* (Olivar and Fortuño, 1991), the larvae from the Benguela Current region were later considered indistinguishable from those in the Agulhas Current and possibly belonging to 1 of 2 closely related species: *L. lepidolychnus* or *L. intricarius* (Olivar and Beckley, 1997). *Lampanyctus lepidolychnus* prefers the coastal waters and has not been recorded in the southwest Pacific Ocean east of 165°W (Hulley, 1981; McGinnis, 1982; Bekker, 1983; Bekker and Evseenko, 1986), where some of the larvae described as *L. intricarius* (Bolshakova and Evseenko, 2015; Bolshakova et al., 2021) were caught. Adults of these 2 species differ mainly in their body proportions and position of photophores but do not differ in meristic characters (Hulley, 1981). It is not clear if all these larvae belong to the same species, or differences between *L. lepidolychnus* or *L. intricarius* at larval stages have not yet established.

Lampanyctus pusillus (Johnson, 1890)
Pigmy lanternfish
Figure 14

Lampanyctus alatus: Tåning, 1918, 108, fig. 42 (F, PoF, Juv); Mediterranean Sea.

Lampanyctus pusillus: Olivar, 1985, 292 (description without illustration); Benguela Current. Olivar, 1988, 410 (short description without illustration); Benguela Current. Rodríguez et al., 2017, 68, 69 (PrF, F, PoF); Mediterranean Sea. Bolshakova et al., 2021, 121 (description without illustration); southwest Pacific Ocean.

Identification

–Paired MD and ML and numerous myoseptal (MS) melanophores present versus absent in other *Lampanyctus* larvae;
–Both TGd and AAVp melanophores present versus absent in other *Lampanyctus* larvae, except for *L. australis* and *L. intricarius* (extralimital species: also present in *L. tenuiformis* from the tropical zone of 3 oceans); and
–Number of vertebrae 30–32 versus ≥33 in other *Lampanyctus* larvae (extralimital species: also 32–34 in *L. cuprarius* from the tropical and subtropical Atlantic Ocean and *L. idostigma* from the eastern Pacific Ocean).

General characters D: 11–13, A: (13)14–15, P_1: 13–14, P_2: 8; GR: 3+1+8(9), total 12(13), V: 30–32. Length at transformation ~12 mm SL. The Br_2 appear to 5 mm SL. All the rays in the fins are distinguishable in the 8.5-mm-SL larva. Larvae have moderately deep body (BD 35–43% SL) and blunt snout. Most heavily pigmented larvae within genus.

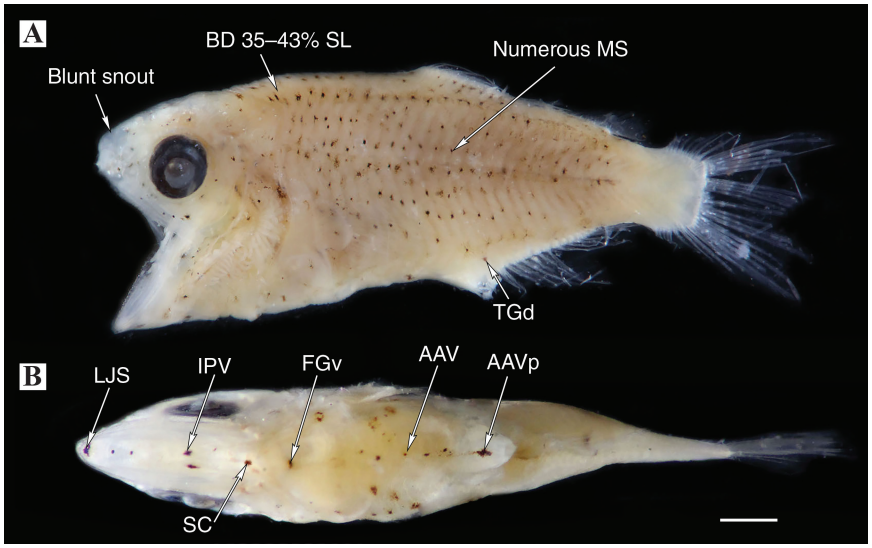

Figure 14

A larva of *Lampanyctus pusillus* (pigmy lanternfish) (11.5 mm standard body length [SL], IORAS 04482): (**A**) lateral view and (**B**) ventral view. The following melanophore pigment groups are shown: myoseptal (MS), dorsal terminal gut (TGd), lower-jaw symphyseal (LJS), prepectoral (isthmic) (IPV), symphyseal-cleithral (SC), anteroventral foregut (FGv), preanal (AAV), and periproctal (AAVp). The scale bar indicates a length of 1 mm. BD=body depth at pectoral fin base.

Pigmentation Several UJS, LJS, posterior lower-jaw (LJP), 1–3 Gu, Fa, Ma, paired and unpaired Mp, H, 1–2 paired Ot, a few PO, a few OP, paired row of IPV, SC, unpaired row of AAV, AAVp, several paired PAVa, 1–2 paired FGv, 2–3 clusters MGd, TGd, CL, 2 or more BP, row of ML, paired row of MD, numerous MS.

General distribution Circumglobal in the Southern Hemisphere north of 46°S; North Atlantic Ocean in temperate and subtropical regions. Occurrence in the STC: northern limits of the area (Parin et al., 1973; Hulley, 1981; McGinnis, 1982; Bekker, 1983; Bekker and Evseenko, 1986; Young et al., 1996; Roberts et al., 2015).

Lampanyctus sp. D
Figure 15

Lampanyctus nobilis: Olivar and Beckley, 1997, 56, fig. 6 (PoF); Agulhas Current.
Lampanyctus sp. D: Bolshakova et al., 2021, 119, figs. 6 and 7 (F, PoF); southwest Pacific Ocean.

Identification Only medullar and TGd pigmentation versus more pigment present in other *Lampanyctus* larvae (extralimital species: also poorly pigmented in *L. nobilis* from tropical region of all oceans).

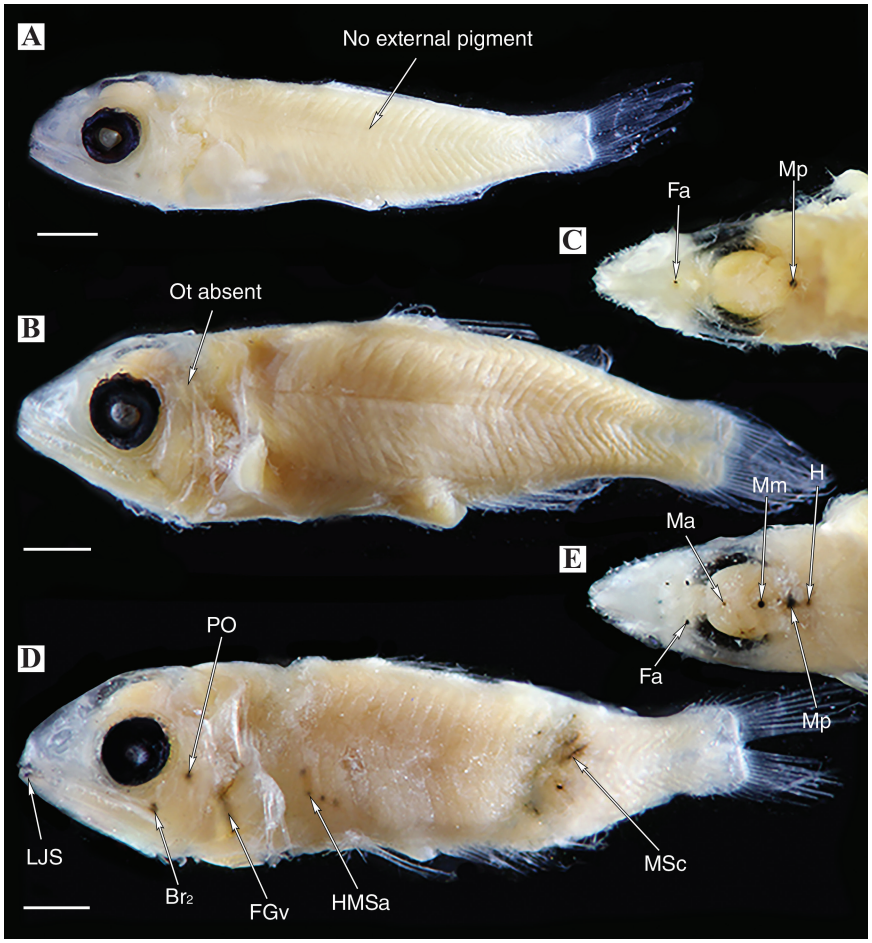

Figure 15

Larvae of *Lampanyctus* sp. D: (**A**) 10.0 mm standard body length (SL), ID code: IORAS 04485 (lateral view); (**B**) 11.6 mm SL, IORAS 04483 (lateral view); (**C**) 11.6 mm SL, IORAS 04483 (dorsal view of the head); (**D**) 11.7 mm SL, IORAS 04484 (lateral view); and (**E**) 11.7 mm SL, IORAS 04484 (dorsal view of the head). The following melanophore pigment groups and photophore are shown: anterior forebrain (Fa), posterior midbrain (Mp), lower-jaw symphyseal (LJS), anteroventral foregut (FGv), hypaxial abdominal myoseptal (HMSa), caudal myoseptal (MSc), anterior midbrain (Ma), medial midbrain (Mm), hindbrain (H), postorbital (PO), and 2nd branchiostegal photophores (Br_2). Otical (Ot) pigmentation is absent. The scale bars in panels indicate a length of 1 mm.

General characters D: 13–15, A: 16–17, P_1: 13–14, P_2: 8; GR: 4(5)+1+10, total 15(16), V: 35–36. Length at transformation >17.0 mm SL. The Br_2 appear to 9.5 mm SL. All the rays in the fins are distinguishable in the 10.3-mm-SL larva, and the number of gill rakers is definitive in the 13.0-mm-SL larva.

Pigmentation Anterior forebrain; paired Ma; Mp; TGd; FGv; FGd; often: inner PO, 1 or 2 CL; sometimes: caudal myoseptal; rarely: LJS, 1 or 2 unpaired medial midbrain, H, HMSa.

General distribution The central and western South Pacific Ocean. Occurrence in the STC: between 38°S and 42°S in the Pacific Ocean (McGinnis, 1982; Bolshakova et al., 2021).

Remarks The larva of *Lampanyctus* sp. D described from the Agulhas Current region by Olivar and Beckley (1997) belongs to *L. indicus* (Bolshakova et al., 2021). *Lampanyctus* sp. D in the sense described herein is identical to the undescribed *Lampanyctus* sp. D established by McGinnis (1982) on adults from the Southern Ocean.

The larvae described as *L. nobilis* (Olivar and Beckley, 1997) are similar in pigmentation, proportions, and meristic characters to our specimens of *Lampanyctus* sp. D. They differ from the typical larvae of *L. nobilis* (Moser et al., 1984; Moser and Ahlstrom, 1996) in the absence of a row of the isthmic and Gu melanophores (not specified in the description and not marked on the figure) and in the lower counts of D, A, and V.

Lepidophanes Fraser-Brunner, 1949

General characters The larvae have a slender body (**BD <19% SL**); head moderate (HL 25–27% SL); snout short (SnL 23–25% HL); eye moderately small (**ED 21–29% HL**); anus opens slightly behind midbody (PAL 63–67% SL). During the larval stage, Br_2, Vn, PO_5, and PLO; Br_2 appear at 5.6 mm SL (in *L. guentheri*) or at 12.3 mm SL in *L. gaussi*; transformation usually occurs at **13 mm SL**.

Pigmentation Occipital, Ot, usually 2 pairs PMDp, 1–2 PAVp, Ivt series.

Similar genera Similar to *Ceratoscopelus* and *Taaningichthys*, see descriptions of these genera for details.

Remarks Adults of *L. guentheri* have been recorded in the STC (Hulley, 1981; McGinnis, 1982; Bekker, 1983).

Lepidophanes guentheri (Goode and Bean, 1896)
Largemouth lampfish
Figure 16

Lepidophanes guentheri: Moser and Ahlstrom, 1972, 551, fig. 8 (PoF, Juv); Northeast Atlantic Ocean. Shiganova, 1977, 88, fig. 14 (F, PoF, Juv); Atlantic Ocean. Moser and Watson, 2001, 94, figure on p. 95 (PrF, F, PoF, Juv); western central Atlantic Ocean. Bonecker and Castro, 2006, figure on p. 148 (PoF, Juv); tropical southwest Atlantic Ocean.

Identification

–Supracaudal and infracaudal melanophores present versus absent in all Myctophidae larvae except for *Lampadena* spp. (extralimital species: also present in *C. maderensis* from the North Atlantic Ocean, *T. minimus* from subtropical waters, and *Lepidophanes gaussi* from the subtropical Atlantic Ocean); and

–Ventronasal gland present at 8 mm SL versus Vn absent in *Lampadena* spp. larvae <13.5 mm SL.

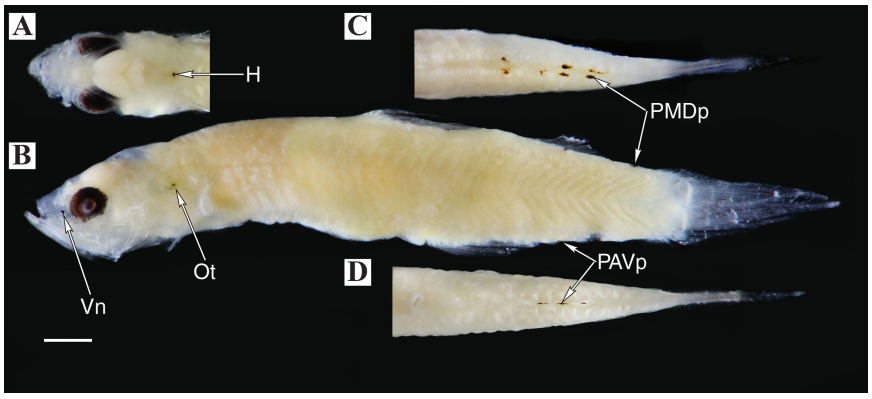

Figure 16

A larva of *Lepidophanes guentheri* (largemouth lampfish) (14.3 mm standard body length, ID code: IORAS 04486): (**A**) dorsal view of the head, (**B**) lateral view, (**C**) dorsal view of the tail, and (**D**) ventral view of the tail. The following melanophore pigment groups and photophore are shown: hindbrain (H), otical (Ot), supracaudal (PMDp), infracaudal (PAVp), and ventronasal gland (Vn). The scale bar indicates a length of 1 mm.

General characters D: 13–15, A: 13–15(16), P_1: (11)12–14, P_2: 8; GR: 4+1+8–10, total 13–15, V: 36. Length at transformation ~14 mm SL. The Br_2 appear at ~5.6 mm SL, Vn and PO_5 appear at ~7.5 mm SL, and PLO appear at ~9.0 mm SL. All the rays in the fins are distinguishable in the 10-mm-SL larva, and the definitive number of gill rakers is noticeable to a size of 11–12 mm SL.

Pigmentation Hindbrain, Ot, 3–4 PAVp, TGd, 3–4 Ve, 2–4 PMDp.

General distribution The tropical and subtropical Atlantic Ocean. Occurrence in the STC: in the region of the northern limit of the STC in the eastern Atlantic Ocean and throughout the STC in the sector of the western Atlantic Ocean (Hulley, 1981; McGinnis, 1982; Bekker, 1983; Figueroa et al., 1998).

Taaningichthys Bolin, 1959

General characters Body slender (**BD <19% SL**); head moderate (HL 21–26% SL); snout short (SnL 21–26% HL); eye moderately small (ED >26–29% HL); anus opens slightly behind midbody (PAL 60–65% SL). **No photophores** during the larval stage (Br_2 form at transformation stage); transformation usually occurs at **21 mm SL**.

Pigmentation Medullar melanophores, SMD, postdorsal and PAV series, Ivt series.

Similar genera Similar to *Lampadena*, *Lepidophanes*, and *Ceratoscopelus*, but photophores appear only toward the end of the larval stage (during the transformation) at >18 mm SL (versus early in the larval stage at 5–7 mm SL); more slender than *Lampadena* (BD <19% SL versus >19% SL); saggital intervertebral melanophores present (versus absent in *Lampadena* and *Lepidophanes*); subdorsal pigment present (versus absent in *Lepidophanes* and *Ceratoscopelus*).

Remarks This genus contains 3 species (Fricke et al., 2023): *T. bathyphilus*, *T. minimus*, and *T. paurolychnus*. The early stages of development are known only for *T. minimus* (Pertseva-Ostroumova, 1964, 86, fig. 7, as *Lampadena* sp.; Moser and Ahlstrom, 1972, 1996; Ozawa, 1986). The slender body, present MD and PAV pigment, and the absence of photophores, even Br_2, until transformation, characterize the described larvae. Adults of *T. bathyphilus* alone have been recorded in the STC (Hulley, 1981; McGinnis, 1982; Bekker, 1983). The early stages of development of *T. bathyphilus* are unknown, but we expect that the larvae of *Taaningichthys* species have similar diagnostic characters, especially the late appearing photophores.

Subfamily Notolychninae Paxton, 1972

Diagnosis Larvae of Notolychninae can be distinguished from the larvae of the subfamilies Diaphinae, Gymnoscopelinae (except for *Scopelopsis*), and Lampanyctinae by their short gut, absence of larval photophores, and lower number of pelvic-fin rays. Notolychninae can be further separated from all diaphine, gymnoscopeline, and lampanyctine larvae except for *Triphoturus* spp. by the eye shape (elliptical or trapezoidal versus round). Notolychninae larvae can be separated from Myctophinae larvae by the absence of larval photophores (versus at least Br_2 in Myctophinae larvae).

Genera Monotypic.

Notolychnus Fraser-Brunner, 1949

General characters Diagnostic characters are described later in the description of the only species in this genus.

Notolychnus valdiviae (Brauer, 1904)
Topside lanternfish
Figure 17

Myctophum valdiviae: Tåning, 1918, 151, fig. 47 (PoF, Juv); Mediterranean Sea.

Notolychnus valdiviae: Pertseva-Ostroumova, 1964, 85, fig. 6 (PoF); Pacific Ocean. Moser and Ahlstrom, 1974, 409, fig. 12e (PoF); area unknown. Shiganova, 1975, 78, fig. 4 (PrF, F, PoF, Juv); Northwest Atlantic Ocean. Moser et al., 1984, 234, fig. 120a (PoF); California Current?. Moser and Ahlstrom, 1996, 426, figure on p. 427; Northeast Pacific Ocean. Olivar et al., 1999, 109 (description without illustration); Agulhas Current.

Identification

–No photophores during the larval stage versus at least Br_2 present in Myctophidae larvae, except for *Taaningichthys minimus*; and

–Preanal length 44–53% SL versus 56–75% SL in other Lampanictinae larvae except for *Scopelopsis* (extralimital species: 52–58% SL in *P. ingens* from the California Current).

General characters D: 10–12, A: 12–15, P_1: 12–15, P_2: 6–7, GR: 2+8–9, total 10–11, V: 27–31. Body slender (BD 16–23% SL); head relatively small (HL 25–31% SL); snout moderate (SnL 32–39% HL); **eye small, elliptical or trapezoidal** with dorsal (in PrF larvae) and ventral choroid tissue (**ED 18–25% HL, in width, and 27–38% HL, in height**); anus opens near the middle of the body (**PAL 44–53% SL**). Length at transformation ~10 mm SL. No photophores during the larval stage, even Br_2. All photophores appear almost simultaneously at a 9–10 mm SL. All the rays in the fins are distinguishable in the ~7–8-mm-SL larva, and the definitive number of gill rakers is noticeable to a size of 7–8 mm SL.

Pigmentation Three to 4 PAVa, 1 PAVt, 1–2 PAVp, 1–2 basicaudal medium, paired TGd, 3–4 paired lateral midgut, Ve, Cp.

General distribution Circumglobal in tropical and subtropical waters. Occurrence in the STC: in the region of the

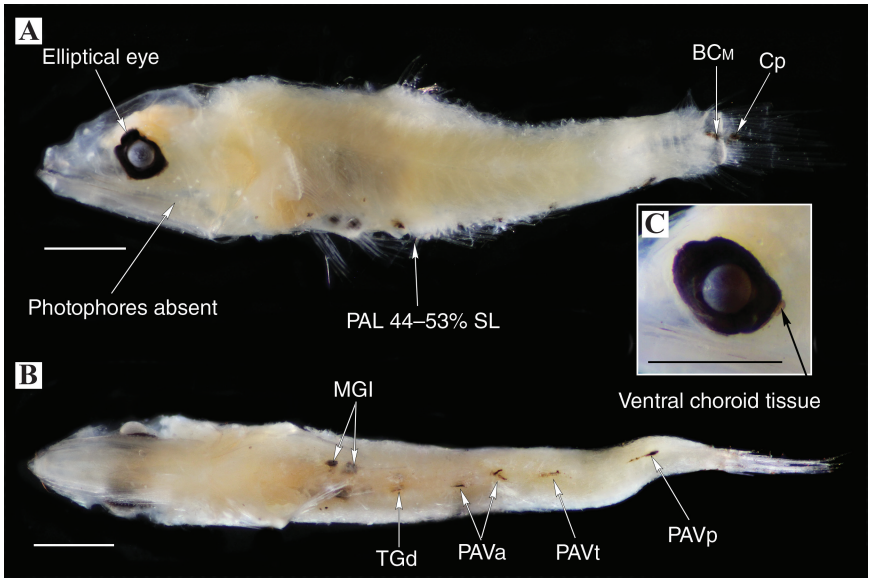

Figure 17

Larvae of *Notolychnus valdiviae* (topside lanternfish): (**A**) lateral view and (**B**) ventral view of a larvae with an 8.5 mm standard body length (SL) (ID code: IORAS 04487). (**C**) Close up of the eye of a 6.2-mm-SL specimen (IORAS 04488). The following melanophore pigment groups are shown: basicaudal medium (BC_M), caudal-fin pigmentation (Cp), lateral midgut (MGl), dorsal terminal gut (TGd), subanal (PAVa), terminal subanal (PAVt), and infracaudal (PAVp). The scale bar in each panel indicates a length of 1 mm. PAL=preanal length.

northern limit of the STC (Nafpaktitis et al., 1977; Hulley, 1981; McGinnis, 1982; Bekker, 1983).

Discussion

Notolychninae is monotypic and includes a single species, *N. valdiviae*, with a broad tropical, circumglobal distribution between 40°N and 40°S (Paxton, 1972; Nafpaktitis et al., 1977; Bekker, 1983). In the STC, it is known by a single record east of New Zealand at 44°S, 173°E (McGinnis, 1982). The subfamily Lampanyctinae consists of 9 genera (*Bolinichthys*, *Ceratoscopelus*, *Lampadena*, *Lampanyctus*, *Lepidophanes*, *Taaningichthys*, *Parvilux*, *Stenobrachius*, and *Triphoturus*), and all but the last 3 genera occur in the STC (Paxton, 1972; Hulley, 1981; McGinnis, 1982; Paxton et al., 1984; Denton, 2014; Martin et al., 2018). Some species of these genera are distributed in tropical and subtropical waters: *B. indicus*, *B. supralateralis*, *C. warmingii*, *Lampanyctus alatus*, *L. ater*, *L. festivus*, *L. pusillus*, and *Lepidophanes guentheri*. Larvae of these species are found only sporadically along the northern border of the STC. *Lampanyctus achirus* is a subantarctic species; although its larvae are often recorded in the STC (Bolshakova et al., 2021), those larvae may represent misidentified larvae of *L. wisneri* (see the "Remarks" section in the species description for *L.* gr. *achirus*).

McGinnis (1982) listed 21 transitional species, 8 of which belong to Lampanyctinae: *Lampadena notialis*, *Lampanyctus australis*, *L. intricarius*, *L. iselinoides*, *L. lepidolychnus*, *L. macdonaldi*, *Lampanyctus* sp. A (=*L. wisneri*), and *Lampanyctus* sp. D. Hulley (1981) indicated 15 myctophid species from the Atlantic Ocean belonging to a convergence subpattern (4 of them are Lampanyctinae: *Lampadena dea*, *L. notialis*, *Lampanyctus australis*, and *L. lepidolychnus*), and Zahuranec (2000) noted 2 *Nannobrachium* (=*Lampanyctus*) species (*L. achirus* and *L. wisneri*) that are distributed in and near the STC. We do not include *L. iselinoides* (larvae unknown) in the species of the STC because this species is restricted to the coastal waters of Chile between 30°S and 50°S, an area located in the Chilean Current, but does not belong to the STC. *Lampadena dea*, *L. notialis*, *Lampanyctus australis*, *L. intricarius*, *L. lepidolychnus*, *L. wisneri*, and *Lampanyctus* sp. D are apparently true convergence species (i.e., species that appear to be distributed only in oceanic waters in the region of and slightly north of the STC). Larvae of *L. australis*, *L. intricarius*, and *Lampanyctus* sp. D are found in a narrow range between 38°S and 42°S in the South Pacific Ocean, where they are very numerous in sample collections (Bolshakova et al., 2021). In general, the distribution of the larvae of the lampanyctine species known from the STC coincides with the distribution of adults, but larvae of this group have been found in a

narrower range of latitudes (Bekker and Evseenko, 1986; Bolshakova et al., 2021).

Resumen

Se presentan descripciones de las larvas de peces linterna de las subfamilias Lampanyctinae (12 especies) y Notolychninae (1 especie) que pueden encontrarse en la Convergencia Subtropical (CST): *Bolinichthys supralateralis*, *Ceratoscopelus* gr. *townsendi*, *Lampadena* sp., *Lampanyctus alatus*, *L. ater*, *L. australis*, *L.* gr. *achirus*, *L. intricarius*, *L. festivus*, *L. pusillus*, *Lampanyctus* sp. D, *Lepidophanes guentheri* y *Notolychnus valdiviae*. También se proporciona una clave de identificación basada en caracteres larvarios para todas las subfamilias de peces linterna. Proponemos el uso de una clave separada para las larvas postflexión de todos los géneros conocidos de las subfamilias de peces linterna de ojos redondos Diaphinae, Gymnoscopelinae, Lampanyctinae y Notolychninae. Para cada género se indican las características generales de la morfología larvaria. Las descripciones de las especies incluyen los caracteres clave para la identificación, la variación en los caracteres merísticos, la pigmentación y otras características importantes para el diagnóstico de Myctophidae en sus fases larvarias. Se proporcionan fotografías de las características diagnósticas más importantes de cada especie. Se discute la taxonomía de 4 especies problemáticas de la zona, *C.* gr. *townsendi*, *Lampanyctus* gr. *achirus*, *L. intricarius* y *Lampanyctus* sp. D. Se describen por primera vez los estadios de preflexión, flexión y postflexión de una *Lampadena* sp. no identificada del límite norte del CST; estas larvas pueden pertenecer a 1 de las 3 especies (*L. dea*, *L. notialis* y *L. speculigera*) cuyas larvas aún no han sido identificadas. Se resume la distribución de Lampanyctinae y Notolychninae en el CST.

Acknowledgments

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