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Morphology of larvae of 6 *Lampanyctus* species in the central South Pacific Ocean with notes on their occurrence

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Abstract—Larvae of 6 species of *Lampanyctus* (family Myctophidae) collected during the 34th cruise of RV *Dmitry Mendeleev* in 1985 in the central South Pacific Ocean (27–48°S) are described. Discussed in more detail are diagnostic characters for 4 of these species, whose morphology has been insufficiently studied: cripplefin lanternfish (*L. achirus*), southern lanternfish (*L. australis*), *L. gibbsi* or *L. wisneri*, and *Lampanyctus* sp. *D*. Additional data from larvae caught during the 16th cruise of RV *Dmitry Mendeleev* (in the southwestern Pacific Ocean) and 29th cruise of RV *Akademik Ioffe* (in the South Atlantic Ocean) are incorporated in the discussion.

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Lampanyctus is one of the most species-rich genera of the family Myctophidae and includes more than 40 species (Fricke et al., 2020). There are 2 opinions about phylogenetic relationships within this genus based on both morphological and molecular data. One notion is that the genus *Nannobrachium* is a junior synonym of *Lampanyctus* (Becker, 1983; Moser and Ahlstrom, 1996; Olivar and Beckley, 1997; Denton, 2014; Kobyliansky, 2016; Martin et al., 2018). The other opinion is that both genera, *Nannobrachium* and *Lampanyctus*, are valid (Zahuranec, 2000). According to recent data (Martin et al., 2018), we consider the genus *Lampanyctus sensu lato*. Information of the larval development of *Lampanyctus* species is scarce. Descriptions of the early larval stages are available for only about half of the species (Tåning, 1918; Pertseva-Ostroumova, 1964; Moser and Ahlstrom, 1974; Miller et al., 1979; Olivar, 1985; Moser and Ahlstrom, 1996; Olivar and Beckley, 1997; Moser and Watson, 2001; Bolshakova and Evseenko, 2015, 2016, 2020).

Adults of at least 15 species of *Lampanyctus* have been found among Myctophidae collected in the western and central South Pacific Ocean (McGinnis, 1982; Becker, 1983; Becker and Evseenko, 1986; Zahuranec, 2000). Individuals of 5 of those species were caught during a complex expedition to the South Pacific Ocean in 1985, the 34th voyage of RV *Dmitry Mendeleev* (Becker and Evseenko, 1986). The collections made during this cruise include adults of the following 5 species: cripplefin lanternfish (*L. achirus*), southern lanternfish (*L. australis*), diamondcheek lanternfish (*L. intricarius*), rakery beaconlamp (*L. macdonaldi*), and pygmy lanternfish (*L. pusillus*). Here, we describe the morphology of larvae of the 6 lanternfish species found in open waters of the central South Pacific Ocean: *L. achirus*, *L. australis*, *L. gibbsi* or *L. wisneri*, *Lampanyctus* sp. *D*, *L. intricarius*, and *L. pusillus*. The morphology of all but the last 2 of these species has been insufficiently studied. These descriptions are the first ones of *Lampanyctus* larvae from this area and supplement the available data on the development of *Lampanyctus* species.

Materials and methods

Fish in early developmental stages sampled during the 34th expedition of RV *Dmitry Mendeleev* served as materials for the work in this study

Table 1

The stations, geographic coordinates, and depth layers at which, and the dates on which, larvae of *Lampanyctus* were captured during the 34th voyage of RV *Dmitry Mendeleev* in January–March 1985 in the central South Pacific Ocean. Larval specimens caught during this expedition were examined for this study. Ichthyoplankton and adult fish were collected as part of the expeditions of the RV *Dmitry Mendeleev* along 3 transects between 27°S and 48°S.

Station no.	Date	Coordinates	Depth layer (m)
3009	16 January 1985	46°50′S, 158°01′W	0–200
3010	17 January 1985	45°20′S, 157°33′W	0–200
3042	20–21 January 1985	45°31′S, 157°43′W	0–200
3043	22 January 1985	45°53′S, 158°09′W	0–200
3044	23 January 1985	41°32′S, 158°05′W	0–200
3049	4 February 1985	38°48′S, 157°54′W	0–200
3050	5 February 1985	37°15′S, 158°03′W	0–200
3051	6 February 1985	34°59′S, 158°06′W	0–200
3052	12–13 February 1985	37°56′S, 125°55′W	0–200
3054	14 February 1985	39°42′S, 126°01′W	0–200
3055	15 February 1985	41°43′S, 125°34′W	0–200
3056	16 February 1985	43°06′S, 125°42′W	0–50
3057	17 February 1985	44°29′S, 125°42′W	0–350
3067	25 February 1985	44°51′S, 134°41′W	0–200
3068	27 February 1985	40°47′S, 139°28′W	0–550
3069	28 February 1985	37°43′S, 143°00′W	0–500
3071	3 March 1985	17°13′S, 156°54′W	0–200

(Table 1). During January–March 1985, larval and adult fish were taken along 3 transects in the central South Pacific Ocean between 27°S and 48°S: 1) on 158°W, 2) on 126°W, and 3) between 135°W and 143°W (Figs. 1 and 2). In addition, materials from the collections of the 16th expedition of the RV *Dmitry Mendeleev* to the southwestern Pacific Ocean in 1976 and of the 29th expedition of the RV *Akademic Ioffe* to the South Atlantic Ocean in 2009 were used. The ichthyoplankton was sampled during these 3 expeditions by using an Isaacs-Kidd midwater trawl with the Samyshev-Aseev modification. The trawl net has a mouth opening of 6 m^2, a length of 25 m, 5-mm mesh without nodes, and cod end liner of 500-µm nylon mesh. The specimens were preserved and stored in 4% formaldehyde. The larvae were stained with alizarin following the standard procedure (Taylor and Van Dyke, 1985). Data on the adult meristic characters are presented in Table 2.

Information for the following features are included in the descriptions: standard body length (SL), head length (HL), body depth at pectoral fin base (BD), preanal length (PAL), predorsal length (PDL), snout length (SnL), horizontal diameter of the eye (ED), number of rays in dorsal fin (D), number of rays in anal fin (A), number of rays in pectoral fin (P_1), number of rays in pelvic fin (P_2), number of rays in caudal fin (C), number of branchiostegal rays (BrR), number of gill rakers (GR) on the upper and lower parts of the first gill arch, number of vertebrae (V), 3rd supraanal organ (SAO_3), and 2nd branchiostegal photophore (Br_2).

Results

Lampanyctus achirus (Andriashev, 1962)

Distinguishing features In addition to meristic characters, larvae of this species are easy to differentiate from those of other lanternfish species by the long, toothy rostrum, preopercular spines, pigmentation of the rostrum and postorbital region, and lack of pigment above the brain. Preopercular spines have also been found in larvae of the black lantern fish (*L. niger*) and dusky lanternfish (*L. ater*) (Moser and Watson, 2001). Characteristic differences between larval *L. achirus* and larvae of these 2 species occur in pigmentation. In *L. ater*, there is pigment in the dorsal midline behind the dorsal fin; in *L. niger*, there are melanophores at the base of pectoral fins and at the rays of pelvic fins.

Morphology In our collections, 102 larvae with sizes of 9.0–22.0 mm SL were found (Fig. 3). The head and jaws are large, taking almost half of the body length in the larvae that were 11.0–16.0 mm SL (HL 46–50% SL), with an elongated toothy rostrum (SnL 50–65% HL). The head length decreases from about 50% to 38% SL as larvae grow from a length of 16.0 mm SL to a length of 21.5 mm SL. All the larvae have 3–6 small inner preopercular spines and 3 large outer preopercular spines. The length of these spines decreases with larval size. The eyes are slightly oval and become round to a length of about 15 mm SL (ED 20–23% HL). The jaws are long and end behind the vertical of the posterior margin of the eye. Body depth increases with larval size (BD 24–27% SL). The pectoral fins are large and fan-shaped. The anus opens far behind the middle of the body. The dorsal and anal fins are displaced posteriorly (PDL 58–66% SL; PAL 67–75% SL).

Meristic characters D: 15–17, A: 18–20, P_1: 14–16, P_2: 8, C: 6+11–10+6, GR: 6+1+12–14, V: 35–36, BrR: 9. 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 Pigmentation of the head includes one melanophore at the tip of the lower jaw, a row of melanophores scattered on the dorsal side of the rostrum, and a row of 3 large melanophores on the rostrum anterior to the eye. The row of 2–5 melanophores (the number of melanophores increases with larval size) at the postorbital and opercular regions is located at the level of the middle of the eye. Minute melanophores cover the base and rays of the pectoral fin. No pigmentation occurs above the brain. Pigmentation on the body appears in larvae only up to a size of 14–15 mm SL. It includes pigment on the myosepta of the oblique myotomes of the abdomen between the pectoral fin and the anus.

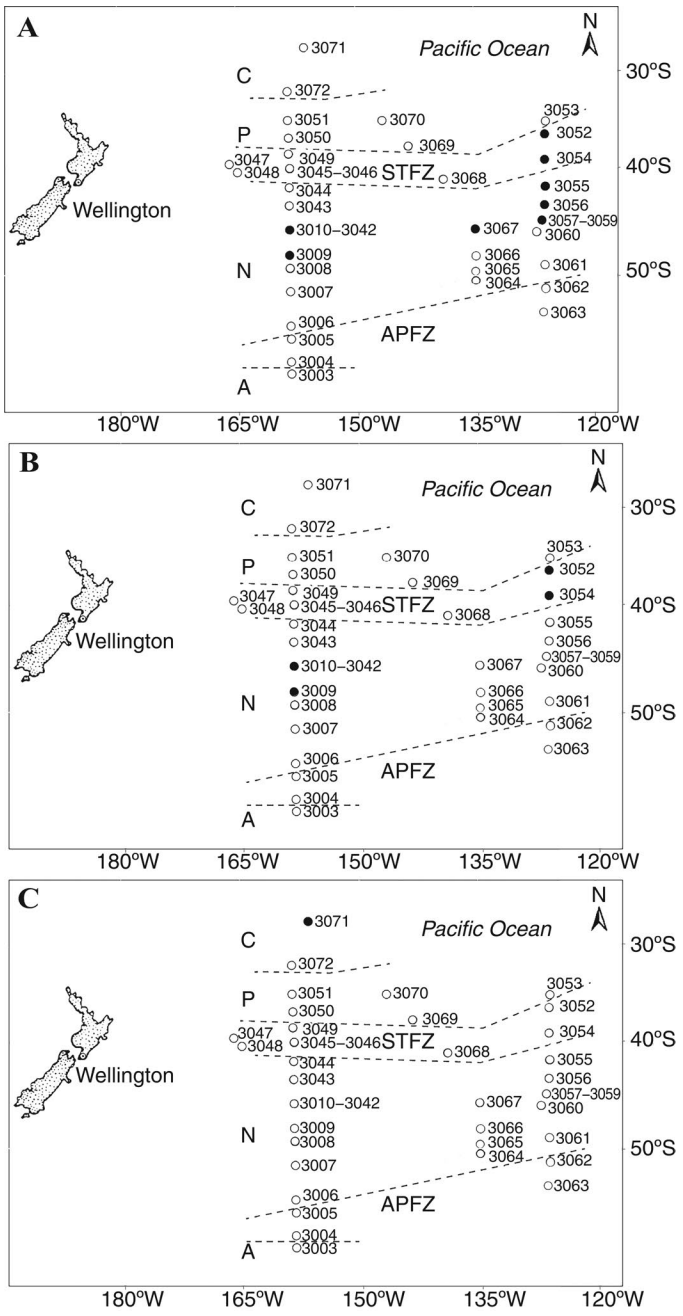

Figure 1

Schematic maps of the stations (open circles) where larvae of the following 3 species of *Lampanyctus* (black circles) were sampled during the 34th cruise of the RV *Dmitry Mendeleev* in the central South Pacific Ocean between January and March 1985: (**A**) cripplefin lanternfish (*L. achirus*), (**B**) southern lanternfish (*L. australis*), and (**C**) *L. gibbsi* or *L. wisneri*. Dashed lines indicate the positions of biogeographic borders (Becker and Evseenko, 1986) for the central water mass (C), the periphery of the central water mass (P), subtropical frontal zone (STFZ), notal zone (N), Antarctic Polar Frontal Zone (APFZ), and Antarctic (A). Station numbers are given next to station markers. For geographic coordinates of the stations and for the dates of capture of larvae, see Table 1.

Photophore formation Br_2 are noticeable on the 9.2-mm-SL larva. No other photophores appear.

Comparative remarks A 13.4-mm-SL larva of *L. achirus* from the South Pacific Ocean has been described and illustrated (Moser and Ahlstrom, 1974; Moser et al., 1984), and a 6.0-mm-SL larva from the southwestern Indian Ocean has been described (Olivar and Beckley, 1997). The larvae of this species have such a characteristic appearance, especially a long rostrum, that it is quite easy to identify them. However, a detailed description and a series of developments is still absent in the literature. Our larvae do not differ in pigmentation from the previously described larvae of this species of a similar size (Moser and Ahlstrom, 1974; Moser et al., 1984), but they differ in the presence of preopercular spines. Spines in our larvae are noticeable in all studied individuals, starting at a length of 9.2 mm SL; therefore, it can be assumed that previous researchers did not notice this morphological feature. Further, on the 9.0-mm-SL larva from our collections taken in the South Atlantic Ocean (29th expedition of the RV *Akademik Ioffe*; station [st.] 2193; 36°56′S, 7°19′E), preopercular spines (both inner and outer) are also present.

Researchers have noted the possibility of the existence of 2 forms of this species that differ mainly in the number of gill rakers of the first gill arch (5+12–13 versus 6+13–14), in addition to the differences in the color of the body, the size of the vomerine tooth patch, and the position of the SAO_3 (Hulley, 1981; McGinnis, 1982; Zahuranec, 2000). These authors noticed that these characters were not always correlated; therefore, only one species is recognized, and these differences are explained as part of the mosaic pattern of variability. We found no differences in pigmentation or in meristic characters in the larvae we studied. In all larvae >16.0 mm SL, the number of gill rakers is 6+1+12–14.

Distribution Among *Lampanyctus* species in the investigated area, this species has the second-most abundant larvae. A total of 102 larvae of this species were collected at 8 stations (st. 3009, 3042, 3052, 3054, 3055, 3056, 3057, and 3067) in the notal zone of the South Pacific Ocean, from 45–46°S in the west of the study area to 37–48°S in the east of the study area. Single larvae of this species were found in the subtropical frontal zone in the South Pacific Ocean at 126°W (st. 3052 and 3054) (Fig. 1A). The presence of this species is an indicator of notal waters, although adults have a wider range and were found in the subtropical frontal zone (st. 3049) and in the periphery of the central water mass in the South Pacific Ocean (st. 3069) (Becker and Evseenko, 1986).

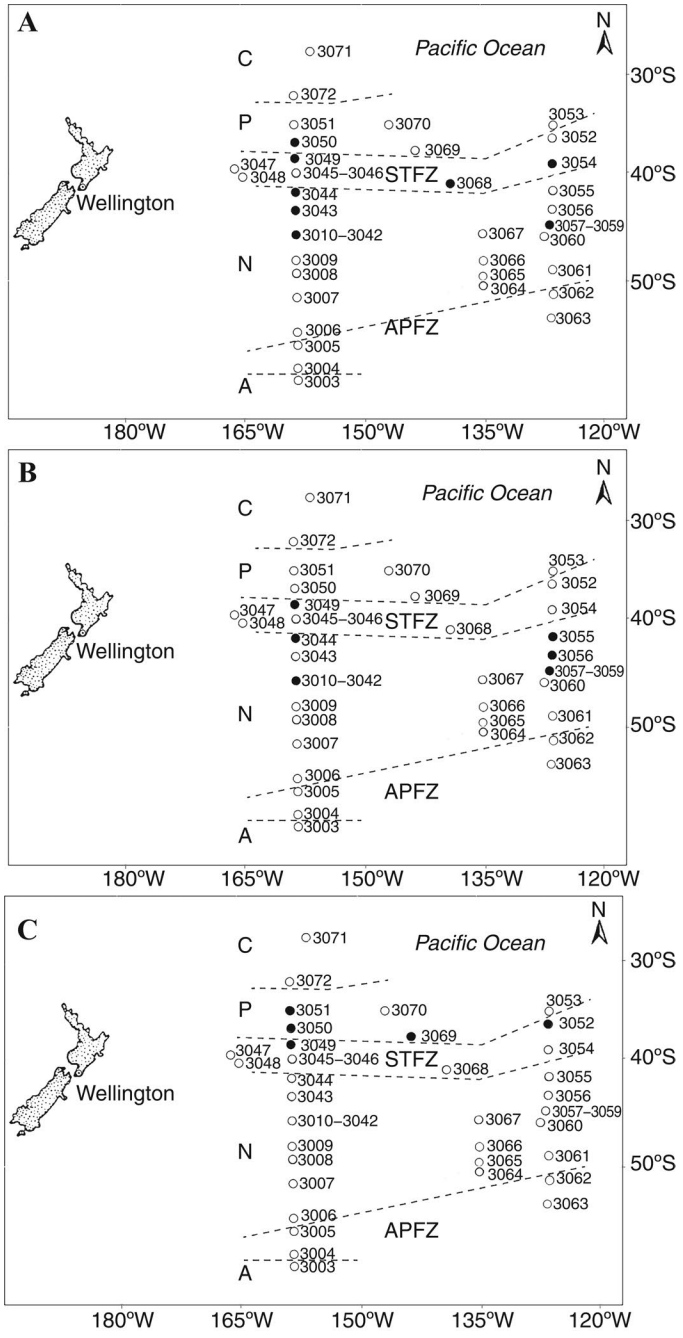

Figure 2

Schematic maps of the stations (open circles) where larvae of the following 3 species of *Lampanyctus* (black circles) were sampled during the 34th cruise of the RV *Dmitry Mendeleev* in the central South Pacific Ocean between January and March 1985: (**A**) diamondcheek lanternfish (*L. intricarius*), (**B**) *Lampanyctus* sp. *D*, and (**C**) pygmy lanternfish (*L. pusillus*). Dashed lines indicate the positions of biogeographic borders (Becker and Evseenko, 1986) for the central water mass (C), the periphery of the central water mass (P), subtropical frontal zone (STFZ), notal zone (N), Antarctic Polar Frontal Zone (APFZ), and Antarctic (A). Station numbers are given next to station markers. For geographic coordinates of the stations and for the dates of capture of larvae, see Table 1.

Lampanyctus australis Tåning, 1932

Distinguishing features Larvae of *L. australis* are intensely pigmented and characterized by the presence of a broad vertical band of pigment posterior to the pectoral fin, distinguishing it from larvae of all other known lanternfish species in the area. Among all known species of *Lampanyctus*, 2 other species have a broad stripe of pigment at the larval stage: the jewel lanternfish (*L. crocodilus*) and noble lampfish (*L. nobilis*) (Moser and Watson, 2001). Larvae of *L. australis* differ from those of *L. crocodilus* in the presence of melanophores on the cleitrum and at the tip of the lower jaw. Larvae of *L. nobilis* have no melanophores between the dorsal and adipose fins, and a row of melanophores on the isthmus is present.

Morphology In our collections, 15 larvae with sizes of 10.0–15.1 mm SL were identified, including specimens from the 34th expedition of the RV *Dmitry Mendeleev* and a 9.2-mm-SL larva from the 16th expedition of the RV *Dmitry Mendeleev* (st. 1335; 49°41′S, 148°25′E) (Fig. 4). Larvae are moderately deep bodied (BD 30–34% SL). The head length decreases from 33% to 27% SL as size increases from 9.2 mm SL to 15.1 mm SL. Larvae have a comparatively short snout (SnL 28–33% HL) and almost round eyes (EL 28–33% HL). The jaws are relatively prominent and extend behind the level of the posterior margin of the orbit. The dorsal fin originates approximately in the middle of the body (PDL 46–54% SL), and the anal fin begins under the 10–12 ray of the dorsal fin (PAL 58–66% SL). The PDL and PAL indicate the negative relationship with SL.

Meristic characters D: 13–14, A: 16–19, P_1: 13–14, P_2: 8, C: 8+10–9+8, GR: 6(7)+1+14(13), V: 36–37, BrR: 9. Fin rays are formed in all fins at 10.0 mm SL, and larvae have a definitive number of gill rakers at 10.2 mm SL. Larvae have 36–37 myomeres.

Pigmentation Larvae are intensely pigmented. Pigmentation of the head includes paired melanophores anterior to the midbrain, unpaired melanophores above the forebrain, one melanophore between the midbrain and the hindbrain, and one melanophore posterior to the hindbrain. There is one melanophore at the tip of the lower jaw. Melanophores are located on the cleithrum, on the inner surface of the base of the pectoral fins, and on its rays. One minute melanophore is located ventrally on the gut terminus. One conspicuous melanophore is on the dorsal midline between the dorsal and adipose fins. Internal melanophores are noticeable on the myosepta between the pectoral and pelvic fins and dorsally at the terminal gut section.

Table 2

Meristic characters of adults of the *Lampanyctus* species that have been found in the South Pacific Ocean. These data are from Wisner (1976), Hulley (1981), McGinnis (1982), Becker (1983), and Zahuranec (2000). A question mark (?) indicates that no data have been reported, and a dash (–) indicates that no fins have been observed. *Lampanyctus* sp. *A*, *L.* sp. *B*, *L.* sp. *C*, and *L.* sp. *D sensu* McGinnis (1982).

Species	Dorsal rays	Anal rays	Pectoral rays	Gill rakers	Vertebrae
L. achirus	14–16	16–20	–	5–6+1+11–13	35–36
L. alatus	11–13	16–18	11–13	3–4+1+9 (8)	33–35
L. ater	14–16	16–20	–	5 (4)+1+10–12	36 (35)
L. australis	12–14	17–19	13–15	6 (7)+1+13–14 (15)	35 (36–37)
L. festivus	14–15	19–21	15–17	4+1+9 (8–10)	35 (34)
L. gibbsi	13–14	18–19	13–14	3–4+1+8–10	37–38
L. intricarius	14–16	18–20	13–15	4+1+10 (9–11)	38 (37)
L. lepidolychnus	14–16	18–20	12–13	4+1+10 (8–11)	36–37
L. macdonaldi	14–16	17–18	12–13	8 (9–10)+1+17–18	34–35
L. pusillus	11–13	14–15	13–14	3+1+8 (9)	31–32
L. wisneri	14–15	17–19	–	4-5+1+10-11	36–37
L. sp. *A*	14–16	16–20	–	4+1+11–13	35–36
L. sp. *B*	15	21	17	?	?
L. sp. *C*	12–13	16–18	14–15	?	?
L. sp. *D*	12–13	16–18	14–15	?	?

Photophore formation Only Br_2 are formed in all individuals.

Comparative remarks Morphology of 5.5- and 6.4-mm-SL larvae of *L. australis* from the southwestern Indian Ocean (Olivar and Beckley, 1997) and of 8.3-, 9.3-, 10.1-, and 10.7-mm-SL larvae from the southeastern Atlantic Ocean (Bolshakova and Evseenko, 2016) have been described. In general, the morphology of our larvae is similar to that given previously. Larvae of a similar size from the Pacific Ocean and Atlantic Ocean do not differ in proportions. There is some variability in pigmentation between specimens from these oceans—2 larvae (8.3 and 10.1 mm SL) from the Atlantic Ocean lack the melanophore behind the dorsal fin, and all larvae from the Pacific Ocean have such a melanophore. Our description of larvae examined in our study complements the developmental series of this species.

Distribution A total of 14 larvae of this species were found in the study area (st. 3009, 3010, 3042, 3052, and 3054) between 37°S and 46°S in the subtropical frontal zone and the notal zone of the South Pacific Ocean (Fig. 1B). Adults of *L. australis* have a much broader range, with isolated specimens occurring down to 52°S (st. 3063) (Becker and Evseenko, 1986).

Lampanyctus gibbsi or *L. wisneri*

Distinguishing features Meristic characters are useful in separating the larva of either *L. gibbsi* or *L. wisneri* examined in this study from the larvae of other *Lampanyctus* species. The prominent jaw and the forward direction of teeth at the tip of the upper jaw distinguish this specimen from the larvae of *Lampanyctus* species with short rostrums. The larva is also well distinguished from the larvae of other long-rostrum species of *Lampanyctus*. These differences are clearly visible in pigmentation. In *L. ater* and the pinpoint lampfish (*L. regalis*), there is a melanophore between the dorsal and adipose fins. In *L. cuprarius* and *Nannobrachium* sp. 1 (Bolshakova and Evseenko, 2020, fig. 5), there is pigment at the midline of the body. In *L. niger*, there are melanophores at the base of pectoral fins and at the rays of pelvic fins. All these melanophores are absent in larvae of *L. gibbsi* and *L. wisneri*. The larvae of *L. lineatus* have a smaller body depth, and the larvae of *L. achirus* have a longer and more noticeable rostrum. The larva differs from larvae of *L. ater* in the absence of the preopercular spines.

Morphology A single larva was collected: 13.1 mm SL (Fig. 5). The larva has a deep body (BD 30% SL) and a large head (HL 31% SL) with long jaws extending under the vertical of the eye posterior margin. The snout is long (SnL 41% HL), and the eye is round (ED 32% HL). The dorsal fin begins at about the middle of the body (PDL 54% SL). The anal fin starts under the 9–10 ray of the dorsal fin (PAL 70% SL).

Meristic characters D: 15, A: 19, P_1: 13, P_2: 8, C: 6+10–10+5, GR: 4+1+10, V: 37, BrR: 9. Rays in all fins are fully formed.

Pigmentation Pigmentation of the head includes a melanophore at the tip of the lower jaw, a paired melanophore above the midbrain and located posterolaterally to the hindbrain. There is one melanophore on the cleithrum.

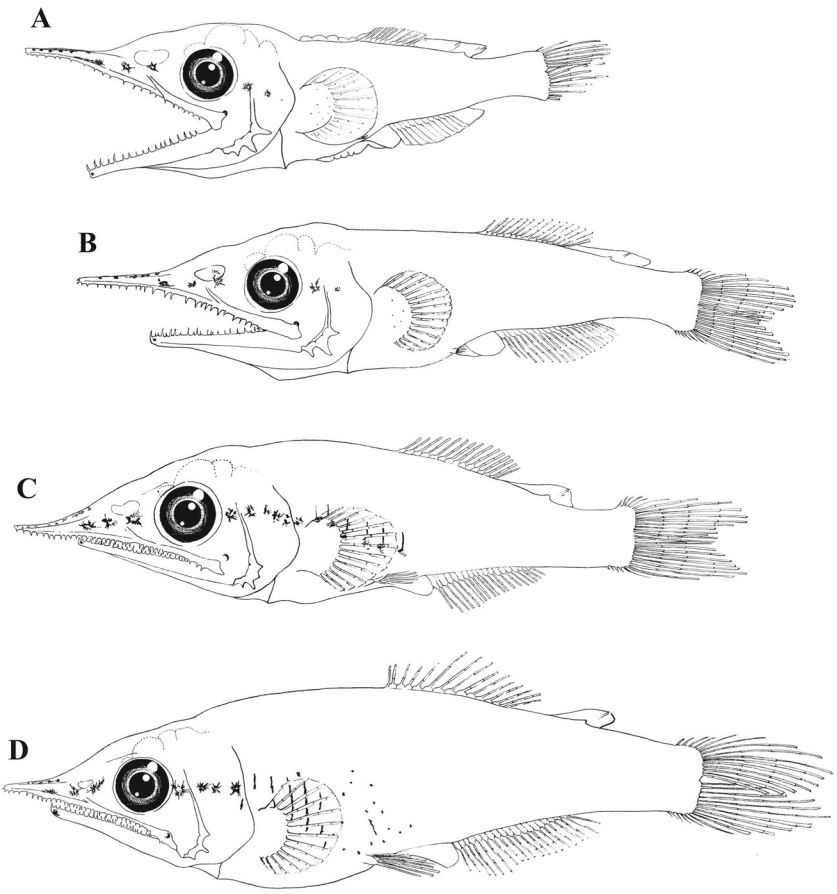

Figure 3

Illustrations of 4 early developmental stages of larval cripplefin lanternfish (*Lampanyctus achirus*) caught in the central South Pacific Ocean in 1985 (**A**) at station 3056 (9.2 mm standard body length [SL]), (**B**) at station 3056 (13.5 mm SL), (**C**) at station 3054 (15.0 mm SL), and (**D**) at station 3054 (22.0 mm SL).

Internal melanophores are visible in front of the liver, and some pigment is embedded in the peritoneal region on the myosepta between the pectoral and pelvic fins.

Photophore formation Only Br_2 are formed.

Comparative remarks On the basis of a number of characters, including elongated jaws, patch of teeth on the tip of upper jaw, long rostrum, large head, large pectoral fins, and posteriorly displaced dorsal fin (Moser et al., 1984; Zahuranec, 2000), we assign this larva to the group of long-rostrum *Lampanyctus* larvae (formerly *Nannobrachium*). Among the species that inhabit the central South Pacific Ocean, *L. macdonaldi*, *L. gibbsi*, and *L. wisneri* have not had their early stages of development described. *Lampanyctus macdonaldi* has a significantly higher number of gill rakers and lower number of vertebrae (GR: 25–28 versus 15; V: 34–35 versus 37). The meristic features of the remaining 2 types overlap (Table 2). Therefore, this larva may belong to one of these 2 species: *L. gibbsi* or *L. wisneri*.

Distribution The larva of this type was the only one with these characteristics collected in the central South Pacific Ocean. It was caught on the northernmost point of the study area (st. 3071). This station was located in the central water mass at 17°S (Fig. 1C).

Lampanuctus intricarius Tåning, 1928

Distinguishing features Larvae of this species have a highly compressed body; the larvae <14 mm SL have dorsal and ventral finfolds. The larvae are characterized by the presence of a series of prominent melanophores along the margins of dorsal and ventral finfolds and by an intensely pigmented caudal region. Among all known species of *Lampanyctus* from the Pacific Ocean, no larvae have finfolds that are so prominent at the postflexion stage. Larvae of

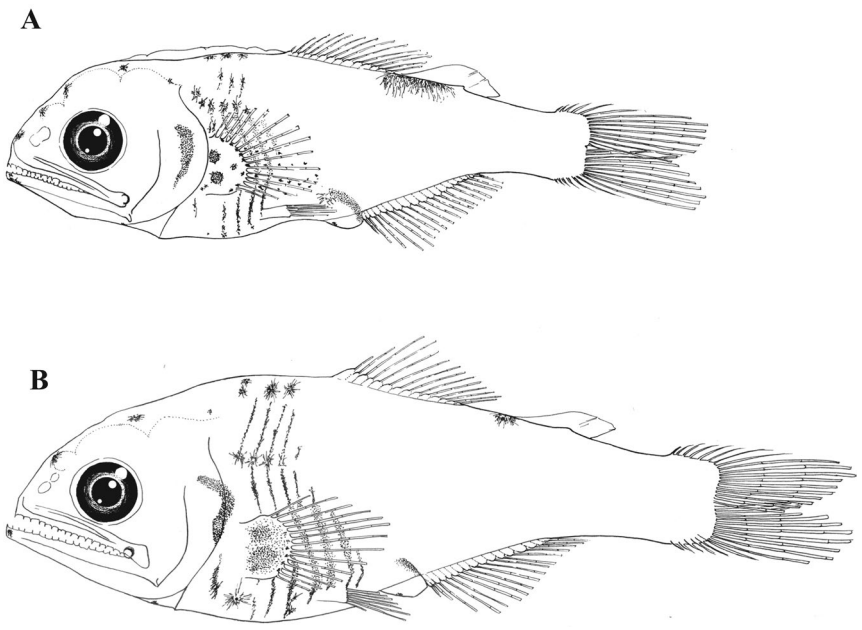

Figure 4

Illustrations of 2 early developmental stages of larval southern lanternfish (*Lampanyctus australis*) caught (**A**) during the 16th voyage of the RV *Dmitry Mendeleev* to the southwestern Pacific Ocean in 1976 at station 1335 (9.2 mm standard body length [SL]) and (**B**) during the 34th voyage of the RV *Dmitry Mendeleev* to the central South Pacific Ocean in 1985 at station 3054 (12.2 mm SL).

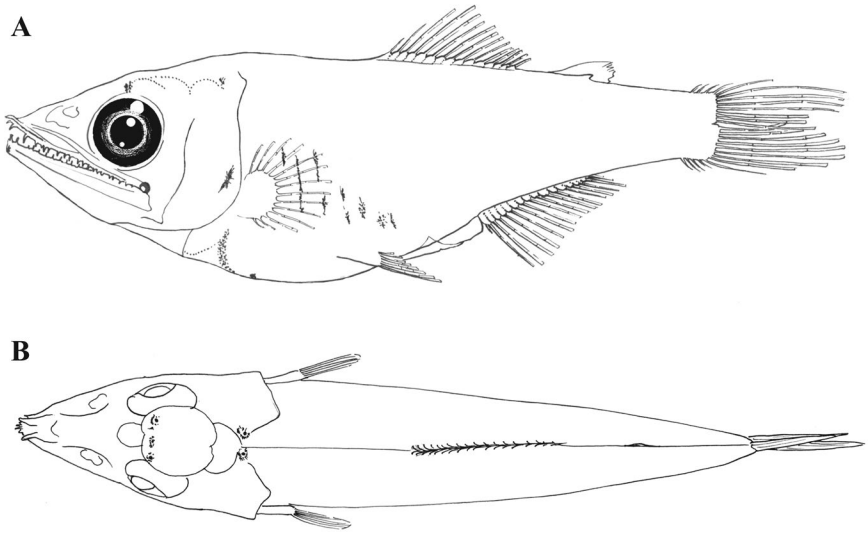

Figure 5

Illustration of one early developmental stage of larval *Lampanyctus gibbsi* or *L. wisneri*, based on a larva that could be one of those species, has a standard body length of 13.1 mm, and was caught in the central South Pacific Ocean in 1985 at station 3071.

L. intricarius are similar in pigmentation to larvae of *Lampanyctus* cf. *L. photonotus* (Moser and Watson, 2001) from the western Atlantic Ocean and differ from them in body proportions. Differences between larvae of *L intricarius* and of *Lampanyctus* cf. *L. photonotus* are found in body depth, head length, and diameter of the eye.

Morphology In our collections, 102 larvae with sizes of 6.9–20.4 mm SL were found. The larvae from the collections of the 34th expedition of RV *Dmitry Mendeleev* have been described in detail previously (Bolshakova and Evseenko, 2015).

Photophore formation All larvae 6.9–20.4 mm SL have only Br_2.

Pigmentation See Bolshakova and Evseenko (2015).

Meristic characters D: 15–16, A: 18–20, P_1: 13–14, P_2: 7–8, C: 6+10–9+6, GR: 4+1+(9)10, V: 38–39, BrR: 8.

Distribution Larvae of *L. intricarius* were collected at 9 stations (st. 3042, 3043, 3044, 3049, 3050, 3052, 3054, 3057, and 3068) between 37°S and 46°S in the notal zone and in the subtropical frontal zone of the South Pacific Ocean (Fig. 2A).

Lampanyctus sp. *D* (*sensu* McGinnis, 1982)

Distinguishing features The main feature of the larvae of this species is the almost complete absence of pigment on the body. Pigmentation is present in all larvae only in the head region above the brain and above the terminal gut section. A lack of or a small amount of pigment on the body is also noted for the larvae of *L. nobilis*, the slender lanternfish (*L. tenuiformis*), and *L. idostigma*. Larvae of *L. nobilis* have a row of melanophores on the istmus. Larvae of *L. tenuiformis* have one melanophore anterior to the anus and have a blunt snout. Larvae of *L. idostigma* have no melanophores above the brain.

Morphology In our collections, 110 larvae with sizes of 7.2–17.0 mm SL were found (Figs. 6 and 7). Larvae have relatively slender bodies (BD 24–29% SL) with large heads (HL 27–33% SL). Eyes are round and large (ED 24–34% HL) and decrease in proportion to body size during development. The jaws reach the vertical of the eye posterior margin in large larvae (SnL 26% HL), and there are teeth on both jaws. The dorsal fin originates near the middle of the body (PDL 47–56% SL). The anus opens behind the middle of the body (PAL 58–65% SL). Metamorphosis occurs at a size >17.0 mm SL.

Meristic characters D: 13–15, A: 16–17, P_1: 13–14, P_2: 8, C: 6+10–11+5, GR: 4(5)+1+10, V: 35–36, BrR: 8. 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 The pigmentation of larvae varies considerably, even among larvae of the same size from the same sample. The pigmentation that is present in almost all studied larvae includes the following: inner melanophores

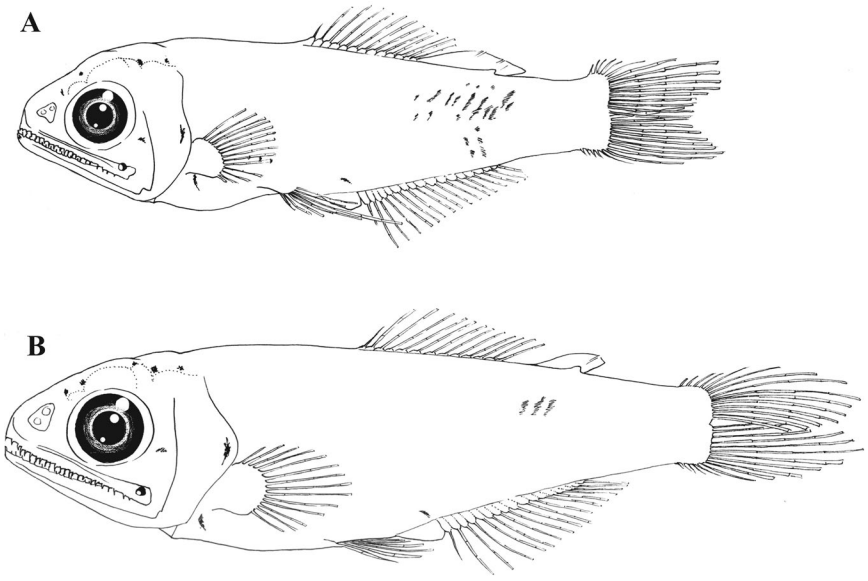

Figure 6

Illustrations of 2 early developmental stages of larval *Lampanyctus* sp. *D* caught in the central South Pacific Ocean in 1985 (**A**) at station 3042 (9.7 mm standard body length [SL]) and (**B**) at station 3049 (12.5 mm SL).

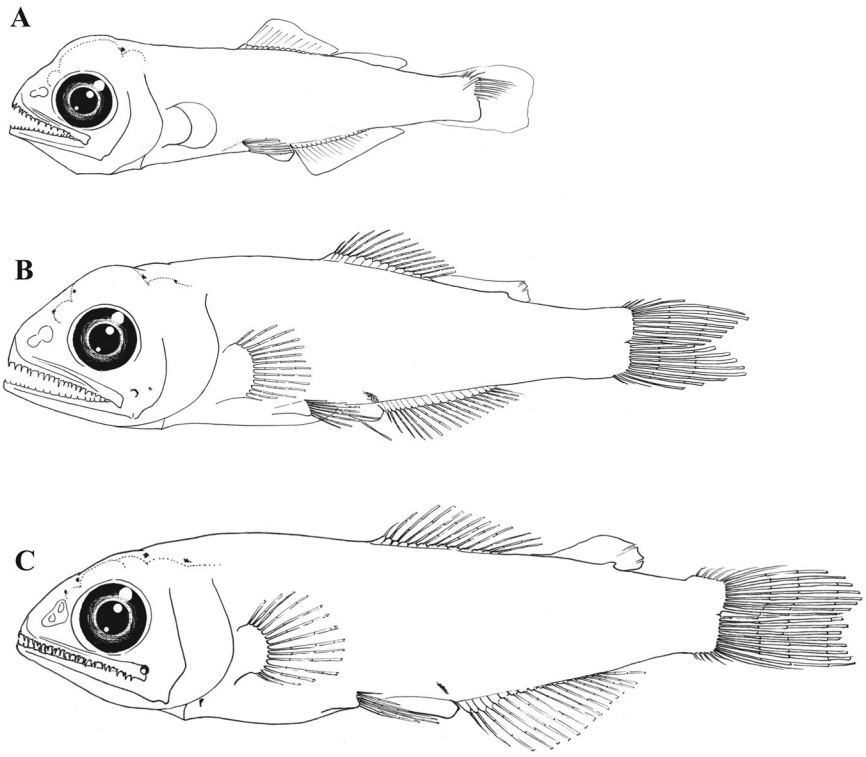

Figure 7

Illustrations of 3 early developmental stages of larval *Lampanyctus* sp. *D* caught in the central South Pacific Ocean in 1985 at station 3052: (**A**) 7.8 mm standard body length (SL), (**B**) 9.5 mm SL, and (**C**) 12.9 mm SL.

located dorsally in the intestine terminus and anterior at the liver, one unpaired melanophore anterior to the forebrain, paired melanophores between the forebrain and midbrain, one melanophore posterior to the midbrain, and one melanophore posterior to the hindbrain (Fig. 6). In addition, most larvae have 1 or 2 melanophores on the cleithrum at the level of the pectoral fin. In about half of all studied specimens, a single melanophore is visible on the inner side of the operculum at the level of the pectoral fin, and internal pigmentation occurs at the myosepta of the epaxial and hypaxial myomers in the middle part of the tail at the level of the adipose fin (Fig. 7). Less than a third of the larvae have melanophores on the tip of the lower jaw. Sometimes melanophores are present above the brain: 1 or 2 unpaired in the middle of the midbrain, on both sides or only on one side anterior to the hindbrain. The peritoneum is pigmented with large melanophores in all larvae; in some larvae, this pigment appears on the myosepta above the gut.

Photophore formation Br_2 are noticeable on the 9.5-mm-SL larva.

Comparative remarks Among the species inhabiting the study area, *L. macdonaldi*, *L. gibbsi*, and *L. wisneri* are the only species for which larvae are unknown. The meristic characters of the adults of these 3 species differ from the meristic features indicated for the larvae of *Lampanyctus* sp. *D* described here. *Lampanyctus* sp. *D* is 1 of 4 more species of *Lampanyctus* that McGinnis (1982) noted occur in the central South Pacific Ocean, with the other species being *Lampanyctus* sp. *A*, *Lampanyctus* sp. *B*, and *Lampanyctus* sp. *C*. *Lampanyctus* sp. *C* and *Lampanyctus* sp. *D* are characterized by a lower number of fin rays compared with the number for *Lampanyctus* sp. *A* and *Lampanyctus* sp. *B* (P: 14–15, D: 12–13, A: 16–18 versus P: 17, D: 14–16, A: 16–21) (Table 2). Meristic characters of *Lampanyctus* sp. *C* and *Lampanyctus* sp. *D* are similar to those described for the larvae examined in our study. Adults of these 2 species differ from each other in the relative position of unpaired fins and in the morphology of the supracaudal luminous gland; therefore, we will not be able to use these features to identify larvae examined in our study. However, McGinnis (1982) suggested that juveniles of *Lampanyctus* sp. *C* less than 30 mm SL are characterized by the presence of a large vertical band of pigment posterior to the pectoral fin. Among all the species of the southwestern Pacific Ocean whose larval development is already known, *L. australis* is the only species whose larvae have such pigmentation. Our larvae do not have such pigmentation at least up to a size of 17 mm SL; therefore,

we suppose that they may belong to *Lampanyctus* sp. *D*. Adults of *Lampanyctus* sp. *D* have been found in the central South Pacific Ocean approximately between 40°S and 50°S (McGinnis, 1982), and larvae sampled between 38°S and 45°S were found in our collections.

Distribution Among the *Lampanyctus* species in the collections of the 34th expedition of the RV *Dmitry Mendeleev*, this species has the most abundant larvae. A total of 110 larvae were collected in the central South Pacific Ocean. Larvae of *Lampanyctus* sp. *D* were found at 7 stations (st. 3010, 3042, 3044, 3049, 3055, 3056, and 3057) in a narrow range between 38°S and 42°S in the subtropical frontal zone and the northern part of the notal zone in the South Pacific Ocean (Fig. 2B).

Lampanyctus pusillus (Johnson, 1890)

Distinguishing features Larvae of this species have a deep, stout body with a blunt snout. The larvae have characteristic pigmentation: the body is almost completely covered with melanophores, with a series of melanophores along the dorsum, a midlateral series on trunk and tail, and a series midventrally below the gut.

Morphology In our collections, 37 larvae with sizes of 6.8–13.0 mm SL were found. The morphology of the larvae examined in our study is significantly similar with the morphology that has been described earlier for larvae from the Atlantic Ocean (Tåning, 1918) and from the Indian Ocean (Olivar and Beckley, 1997).

Distribution Larvae of *L. pusillus* were collected at 5 stations (st. 3049, 3050, 3051, 3052, and 3069) between 34°S and 38°S in the periphery of the central water mass and in the subtropical frontal zone in the South Pacific Ocean (Fig. 2C).

Discussion

Larvae of at least 11 species of *Lampanyctus* have been found in the southwestern Pacific Ocean. These species are *L. achirus*, the winged lanternfish (*L. alatus*), *L. ater*, *L. australis*, the festive lanternfish (*L. festivus*), *L. gibbsi*, *L. intricarius*, the mermaid lanternfish (*L. lepidolychnus*), *L. macdonaldi*, *L. pusillus*, and *L. wisneri* (Wisner, 1976; Hulley, 1981; McGinnis, 1982; Becker, 1983; Zahuranec, 2000). Among these listed species, *L. macdonaldi* is the only species for which the early stages of development are unknown. The status of the larva that we identified as *L. gibbsi* or *L. wisneri* and the larvae of *L. lepidolychnus* (Olivar and Beckley, 1997) is not clear. *Lampanyctus lepidolychnus* is known to prefer coastal waters and has not been recorded in the southwestern Pacific Ocean east of 165°W. (Hulley, 1981; Becker and Evseenko, 1986), where all the larvae that we identified as *L. intricarius* were caught. At the same time, the larvae of *L. lepidolychnus* (Olivar and Beckley, 1997) and *L. intricarius* (Bolshakova and Evseenko, 2015) are similar. Adults of these 2 species differ mainly in the location of photophores, and they do not differ in meristic characters. For this reason, the species identification for larvae of *L. lepidolychnus* and *L. intricarius* is still questionable.

Although larvae of *L. lepidolychnus* and *L. intricarius* are similar, larvae of the 9 other species of *Lampanyctus* that occur in the southwestern Pacific Ocean differ well in pigmentation, body proportions and shape, morphological features (e.g., preopercular spines), length and shape of the rostrum, and time of metamorphosis. An additional factor for the identification of larvae of these species can be the region of capture. For example, *L. alatus* and *L. gibbsi* do not occur in the open waters of the southwestern Pacific Ocean south of 30°S (McGinnis, 1982; Zahuranec, 2000). The distribution of *L. achirus*, in contrast, extends as far north as 30°S, the latitude that corresponds with the southern border of the region of the Subtropical Convergence (a frontal zone between subantarctic and tropical water masses) in the Pacific Ocean. The distributions of *L. ater*, *L. australis*, *L. festivus*, *L. intricarius*, *L. lepidolychnus*, *L. macdonaldi*, and *L. pusillus* are associated with the Subtropical Convergence. In general, for the species found in the southwestern Pacific Ocean, the distribution of larvae coincides with the distribution of adults.

McGinnis (1982) noted the existence of 4 more species of *Lampanyctus* in the South Pacific Ocean: *Lampanyctus* sp. *A*, *Lampanyctus* sp. *B*, *Lampanyctus* sp. *C*, and *Lampanyctus* sp. *D*. *Lampanyctus* sp. *A* is closely related with *L. achirus*, and they have similar meristic features (Table 2). We did not find any significant differences among our larval specimens of *L. achirus* either in larval characters (i.e., pigmentation, body proportions, and formation rates for fin rays) or in the number of gill rakers of the first gill arch. *Lampanyctus* sp. *B*, in meristic features, is most similar to *L. festivus* and has high counts of pectoral-fin, dorsal-fin, and anal-fin rays (P: 17, D: 15, A: 21). *Lampanyctus* sp. *C* may be close to *L. australis* because the meristic characters of these species match; in addition, a vertical band of pigment posterior to the pectoral fin has been noted in juvenile *Lampanyctus* sp. *C*. The finding of larvae of *Lampanyctus* sp. *D* in the examination of our collections confirms the existence of an undescribed species of *Lampanyctus* in the central South Pacific Ocean.

Conclusions

Larval characters, together with the morphology of adults, may clarify the intergeneric relationships in the family Myctophidae. Comparison of the larval characters of representatives of the genus *Lampanyctus sensu lato* can confirm the possible paraphilia of this group (Denton, 2014; Martin et al., 2018). At the moment, the use of the larval characters in phylogenetic systematics are limited to a small number of species of *Lampanyctus sensu lato* for which detailed descriptions of larval stages are available (about half of them). We believe that the descriptions presented in this article will help clarify the taxonomic status of species within the genus *Lampanyctus sensu lato*.

Acknowledgments

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In memoriam

Sergei A. Evseenko was a world-renowned scientist, doctor of biological sciences, and head of the Laboratory of Oceanic Ichthyofauna of the Shirshov Institute of Oceanology, Russian Academy of Sciences. The main scientific interests of S. Evseenko included the taxonomy and ecology of the early stages of development of fish. He developed an ecological classification of flounder species, described for the first time the larvae of several dozen species of oceanic fish, and revealed the patterns of distribution of ichthyoplankton in the upwelling areas of the eastern Pacific Ocean and frontal zones of the World Ocean. He described several species and genera of marine fish. S. Evseenko described a new family of armless flounders of the Southern Ocean—the family Achiropsettidae—and clarified the morphology, anatomy, individual development, and evolution of this new family. In collaboration with N. Parin and E. Vasilyeva, he published a collective monograph, *Fish of the Russian Seas: Annotated Catalogue*. Overall, S. Evseenko published about 170 scientific works. On 15 October 2020, he died suddenly. S. Evseenko was working on this manuscript just before his death. Everyone who is fortunate enough to have known this wonderful person and outstanding scientist will keep a bright memory of him.

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