



Two new species of the codling fish genus *Physiculus* from Lakshadweep, India (Gadiformes: Moridae)

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Abstract

The genus *Physiculus* is widespread in the Indo-Pacific with more than 32 valid species, and about 12 species were recorded only from the Indian Ocean. Two new species similar to each other are collected from the outer reef drop off of Kavaratti Island, Lakshadweep, India, Arabian Sea and described. *Physiculus indicus* **sp. nov.** is characterised by its light organ situated at about the middle of pelvic-fin base and anus, a small light organ, a rather forward situated anus, no scales on the gular region, dorsal-fin rays 8–9+56–60, anal-fin rays 55–60, and 52 vertebrae. This species differs from nearest congeners in lacking gular scales, anus situated closer to the light organ and slightly fewer total vertebrae. *Physiculus lakshadeepa* **sp. nov.** is characterised by a relatively high first dorsal fin (51.7–62.8% HL) and a light organ situated at the middle of the pelvic-fin base and anus. It has a small light organ, a rather forward situated anus, no scales on the gular region, dorsal-fin rays 8–9+51–59, anal-fin rays 53–59, and 49 vertebrae. *Physiculus lakshadeepa* differs from the nearest congeners in lacking gular scales, fewer anal-fin rays and fewer total vertebrae.

Key words: Pisces, Actinopterygii, Teleostei, taxonomy, Gadiformes

Introduction

Family Moridae comprises of 19 valid genera, with the description of 109 valid species globally. *Physiculus* is the widespread genus with the most number of species, among the family moridae with 43 nominal species, and reported from the Atlantic Ocean (11 species) and Indo-Pacific (32 species). Several species have restricted distribution, while others occur in broad geographic areas (Pires *et al.*, 2019).

Among these congeners, 12 species were recorded only in the Indian Ocean, including *Physiculus andriashevi* Shcherbachev 1993, *P. argyropastus* Alcock 1894, *P. beckeri* Shcherbachev 1993, *P. bertelseni* Shcherbachev 1993, *P. capensis* Gilchrist 1922, *P. fedorovi* Shcherbachev 1993, *P. marisrubri* Brüß 1986, *P. natalensis* Gilchrist 1922, *P. nielseni* Shcherbachev 1993, *P. normani* Brüß 1986, *P. roseus* Alcock 1891 and *P. sudanensis* Paulin, 1989. *Physiculus* spp. have restricted geographical distribution (Paulin, 1989), except for *Physiculus rhodopinnis* Okamura 1982, which is reported from the northwestern Pacific and the southwestern Indian Ocean, the only member with a wide distribution range that requires more investigation to check the cryptic speciation.

Ichthyofauna of Lakshadweep attained particular interest for a long time, and ichthyological explorations started in the 19th century. Some of the early accounts on fishes of this area are by Alcock in his survey during 1890. Balan (1958) documented 80 species of fishes belonging to 65 genera from Lakshadweep (Jones 1960, 1969). Jones and Kumaran (1967, 1971) and Jones *et al.* (1969, 1970) also contributed to the documentation of the ichthyofauna of Lakshadweep. Even though many studies deal with the taxonomy of marine fishes of India (Day, 1958; Munro, 1955), the fishes of the Lakshadweep Islands have received little attention.

The first concerted attempt to document fishes from these islands was made by Jones and Kumaran (1980). Their publication “*Fishes of the Laccadive Archipelago*”, an indispensable work and the most comprehensive account of the fish fauna of Lakshadweep, documented 603 species of fishes in total. However, species of the family Moridae have not been recorded from the Lakshadweep Sea so far.

Following the marine biodiversity assessment survey conducted during (2015–2018), nine *Physiculus* specimens were collected from the outer reef drop off of Kavaratti Island, Lakshadweep, India, Arabian Sea. A detailed comparison with congeners revealed two undescribed species are among these specimens. Here we formally describe these two species as new to science.

Materials and methods

Specimens were collected from a seawater sump which draws seawater by suction from a depth around 350 m at Kavaratti, Lakshadweep. Meristic and morphometric measurements were made following Hubbs & Lagler (1958), Paulin (1989) and González *et al.* (2018). Measurements related to the size and position of light organs follow Shcherbachev (1993). Abbreviations: SL, standard length; InV-af, distance between interventral line and origin of anal fin; InV-Lo, distance between interventral line and anterior margin of the light organ; Lo-An, distance between the posterior margin of light organ and anus; InV-An, distance between interventral line and anus; LoD, light organ diameter. Meristic counts were made from x-ray films or directly under a light microscope.

For diagnostic purposes, the length of the continuous tube and discontinuous tube of the lateral line and the presence and absence of gular scales have been noted in the present study (Trewavas, 1977; Okamura, 1982; Parin, 1985). Specimens examined in the present study were deposited at Marine Taxonomy Reference Laboratory, Department of Science and Technology (MTRLDST), Lakshadweep, India.

Results

Taxonomy

Family Moridae

Physiculus indicus sp. nov.

Common name: Indian Codling

Figs.1–2, Table 1

Holotype. MTRLDST 00214, 162 mm SL, 183 mm TL, India, Lakshadweep, East Coast of Kavaratti Island, 10°33'49.9"N, 72°39'4.0"E, ca. 350 m, 9 April 2018.

Paratypes. MTRLDST 00215, 128 mm SL, 148 mm TL; MTRLDST 00216, 143 mm SL, 169 mm TL; MTRLDST 00217, 154 mm SL, 169 mm TL; MTRLDST 00218, 142 mm SL, 162 mm TL; all collected with holotype.

Etymology. The specific is derived from the type locality, India.

Diagnosis. A species of *Physiculus* with light organ situated at about the middle of pelvic-fin base and anus; light organ small; anus rather forward in position, closer to the light organ; gular region smooth without scales. *Physiculus indicus* differs from nearest congeners, *P. argyropastus*, in the position of the anus, and the number of total vertebrae; *P. roseus* in having the light organ closer to the anus than the pelvic-fin base; *P. rhodopinnis* by fewer rays in the second dorsal fin and fewer anal-fin rays. Although similar to each other, *P. indicus* differs from *P. lakshadeepa* in having fewer gill rakers, more caudal vertebrae, more total vertebrae, and first dorsal fin not higher than the second (vs. first dorsal fin higher with first ray filamentous)

Description. The morphometric data given in Table 1 is for the holotype, followed by the range of measurements from the paratypes in parentheses, except when otherwise indicated. Body round elongated, compressed posteriorly; head moderately large, slightly depressed anteriorly; eye large, its diameter 22.2% (19.0–25.8%) HL; interorbital space broad, its width 31.8% (26.6–34.1%) HL; snout broad and rounded, length 19.9% (19.9–28.4%)

HL, protruding slightly beyond upper jaw; mouth large; teeth equally sized; vomerine and palatine toothless; barbel on chin much shorter than orbit diameter, its length 4.7% (3.2–8.9%) HL.

Gill rakers on first gill arch small, varying from spinous tubercles to small clubs, spinous initially at tips and progressively more spinous towards the angle on the lower branch and spinous at tips on the upper branch; abdominal cavity reaching the 9th pterygiophore of the anal fin.

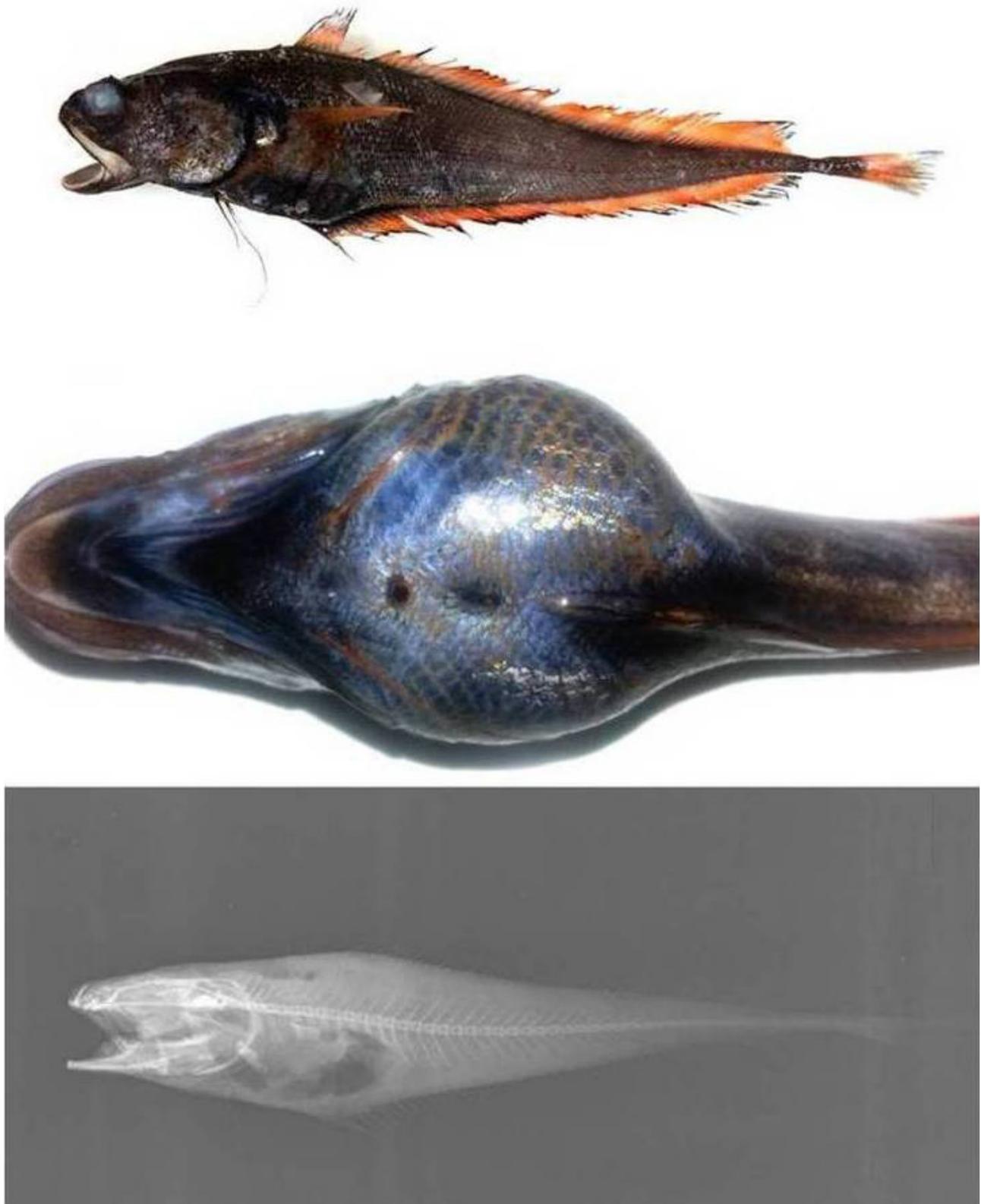


FIGURE 1. *Physiculus indicus* sp. nov., holotype, MTRL DST 00214, fresh. A. Lateral view. B. Ventral view of abdomen, showing the localities of pelvic-fin base, light organ and anus. C. Radiograph.

Scales small and deciduous, 96 (90–102) in longitudinal series; 7 (7–8) scale rows between the base of the first dorsal fin and lateral line; scale cycloid, covered on head and body, except for branchiostegal membrane and gular region. Continuous tube of lateral line reaching 14th ray of the second dorsal fin and discontinuous tube of lateral line reaching caudal peduncle.

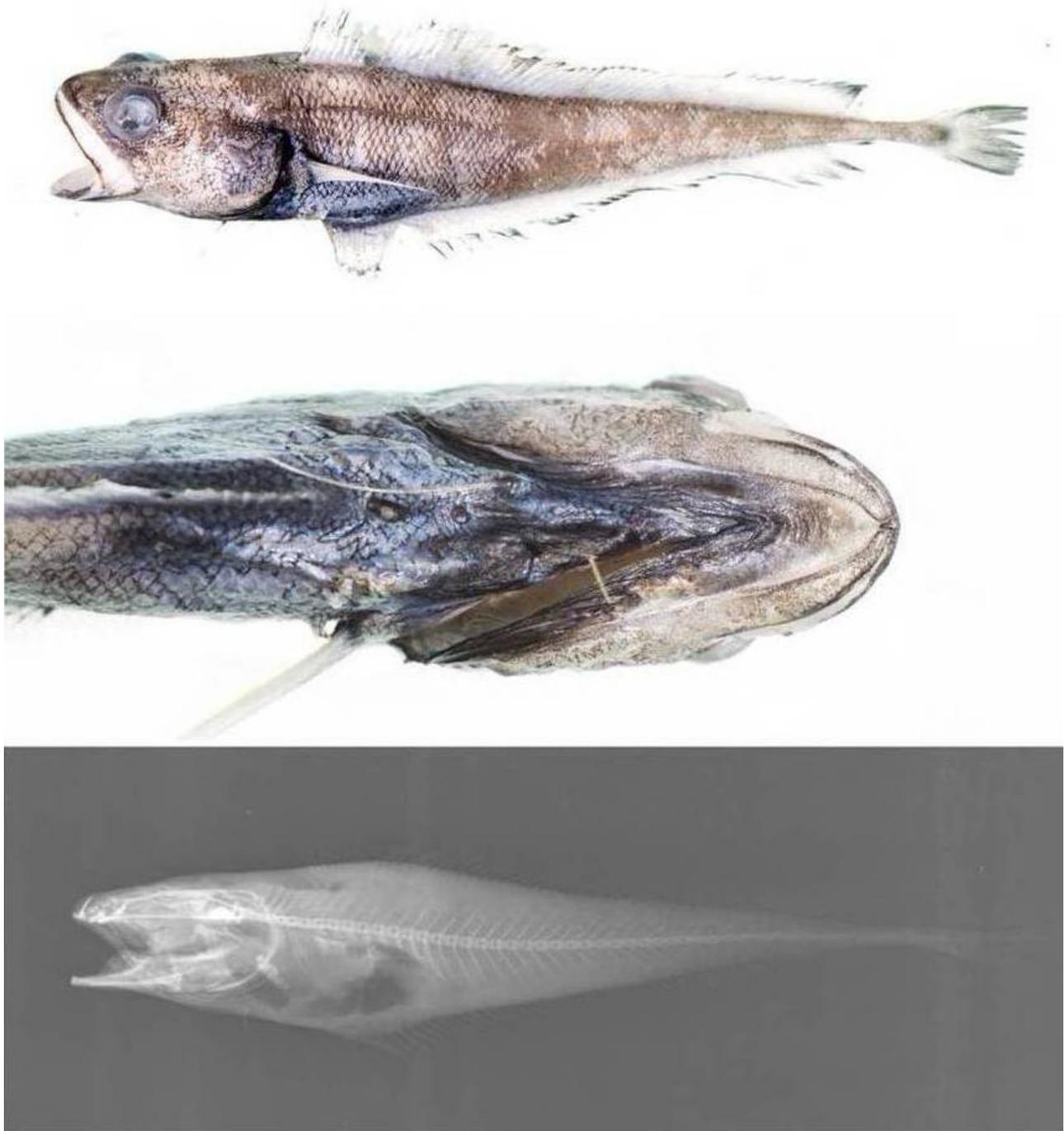


FIGURE 2. *Physiculus indicus* sp. nov., paratype, MTRLDST 00215, preserved. A. Lateral view. B. Ventral view of abdomen. C. Radiograph..

First dorsal fin higher than the second; a very small gap separating first from second dorsal fin; the origin of the first dorsal behind a vertical through pectoral fin base; the origin of the second dorsal fin at a vertical through 5th anal-fin ray; both dorsal fins not indented. The pectoral fin extends up to the 8th ray of the second dorsal fin. Pelvic fin slender, two outermost rays filamentous and extend to 3rd ray of the anal fin. Caudal fin truncate and well separated from second dorsal and anal fins. Caudal peduncle short, less than orbit diameter, its length 8.8% (8.4–10.3%) HL.

Light organ moderately sized; externally prominent as a circular scale less fossa in advance of the anus; its diameter 11.4% (6.4–12.0%) InV-af. Distance from inter ventral line to anterior margin of light organ 22.6% (18.6–29.0%) In V-af; distance from posterior margin of the light organ to anterior margin of anus 17.6% (17.6–23.8%) In V-af; and distance from the inter-ventral line to anterior margin of anus 53.6% (50.6–58.2%) InV-af.

Vertebrae: 12 (11–12) precaudal, 40 (40–41) caudal vertebrae, and 52 (52) in total.

Coloration. When fresh, the head and body, pinkish tan; abdomen, silvery blue; branchiostegal membranes black; vertical fin membrane dark brown. Colour when preserved head and body light brown and abdomen silvery.

Distribution. *Physiculus indicus* is known from the type series collected off Kavaratti Island, Lakshadweep, India, at a depth of ca. 350 m.

***Physiculus lakshadeepa* sp. nov.**

Common name: Lakshadweep codling

Figs. 3–5, Table 1

Holotype. MTRL DST 00112, 164 mm SL, 192 mm TL, India, Lakshadweep, East Coast of Kavaratti Island, 10°33'49.9"N, 72°39'4.0"E, from 350 m depth, 9 April 2018.

Paratypes. MTRL DST 00113, 125 mm SL, 143 mm TL; MTRL DST 00114, 183 mm SL, 224 mm TL; both collected with holotype.

Etymology. The specific name is derived from the type locality, Lakshadweep.

Diagnosis. A species of *Physiculus* with light organ situated at about the middle of pelvic-fin base and anus; light organ small, anus rather forward in position, closer to the light organ; gular region smooth without scales; *Physiculus lakshadeepa* differs from the Indian congeners in having relatively high first dorsal fin, with first ray filamentous, except for that of *P. capensis*, *P. beckeri* and *P. roseus*; *P. lakshadeepa* differs from *P. capensis* in having scales on snout (vs snout smooth) and teeth in equally sized (vs in graded series); from *P. beckeri* in having 84–95 scales in longitudinal series (vs 115–130) and less tall first dorsal fin; and from *P. roseus* in having fewer second dorsal-fin rays and more gill rakers. Compared with the other species in the Pacific Ocean, *P. lakshadeepa* resembles only *P. chigodarana*, which has the first dorsal fin distinctly higher than the second. However, *P. lakshadeepa* differs from the latter in lacking gular scales (vs present in *P. chigodarana*), fewer second dorsal-fin rays; fewer anal fin rays; light organ situated rather backward; anus situated rather backward (InV-An 41.7–58.2% InV-af vs 38.7–43.7%); more gill rakers, and fewer vertebrae.

Description. The morphometric data given in Table 1 is for the holotype, followed by the range of measurements from the paratypes in parentheses, except when otherwise indicated. Body slender and long, compressed posteriorly; head moderately small, depressed anteriorly; eye large 24.7% (19.1–28.5%) in HL; interorbital space broad, 30.1% (25.4–30.7%) in HL; snout broad and rounded, length 24.7% (24.7–25.9%) in HL, protruding slightly beyond the upper jaw. Mouth large, gape extending to a vertical through posterior margin of eye, teeth small, equally sized; vomerine and palatine toothless. Barbel on chin much shorter than orbit diameter, length 7.5% (3.2–11.6%) in HL.

Gill rakers on the first gill arch small, varying from spinous tubercles to small clubs, spinous initially at tips and progressively more spinous towards the angle on lower branch and spinous at tips on the upper branch. Abdominal cavity reaching the 13th pterygiophore of the anal fin.

Scales small and deciduous, 90 (84–95) in longitudinal series; 7 (6–7) scale rows between the first dorsal-fin base and lateral line. Cycloid scales cover the head and body, except for the branchiostegal membrane and the gular region are completely scaleless. Continuous tube of lateral line reaching 10th ray of the second dorsal fin, followed by discontinuous short tubes on the lateral line reaching caudal peduncle. Caudal fin rounded and fan-shaped, well separated from dorsal and anal fins. Caudal peduncle short than orbit diameter, its length 17.1% (17.1–19.7%) HL.

First dorsal fin higher than second, first dorsal-fin ray elongated and filamentous, its length 62.8% HL (51.7% in 1 paratype and broken in another one). A very small gap separates the first from the second dorsal fins. Origin of first dorsal fin slightly behind a vertical through the pectoral-fin base; the origin of the second dorsal fin at a vertical through 4th anal-fin ray. Pelvic fin slender, two outermost rays slightly filamentous, extending to 7th ray of the anal fin. The pectoral fin extends up to the 7th ray of the second dorsal fin.



FIGURE 3. *Physiculus lakshadeepa* sp. nov., holotype, MTRLDST 00112, preserved. A. Lateral view. B. Ventral of the abdomen. C. Radiograph.

Ventral light organ small in size, externally prominent as a circular scale less fossa in advance of the anus, its diameter 6.0% (6.0–9.6%) InV-af; distance from inter ventral line to anterior margin of light organ 29.0% (24.4–29.0%) InV-af; distance from posterior margin of the light organ to anterior margin of anus 22.6% (17.4–22.6%) InV-af, and distance from inter ventral line to anterior margin of anus 58.2% (41.7–58.2%) InV-af.

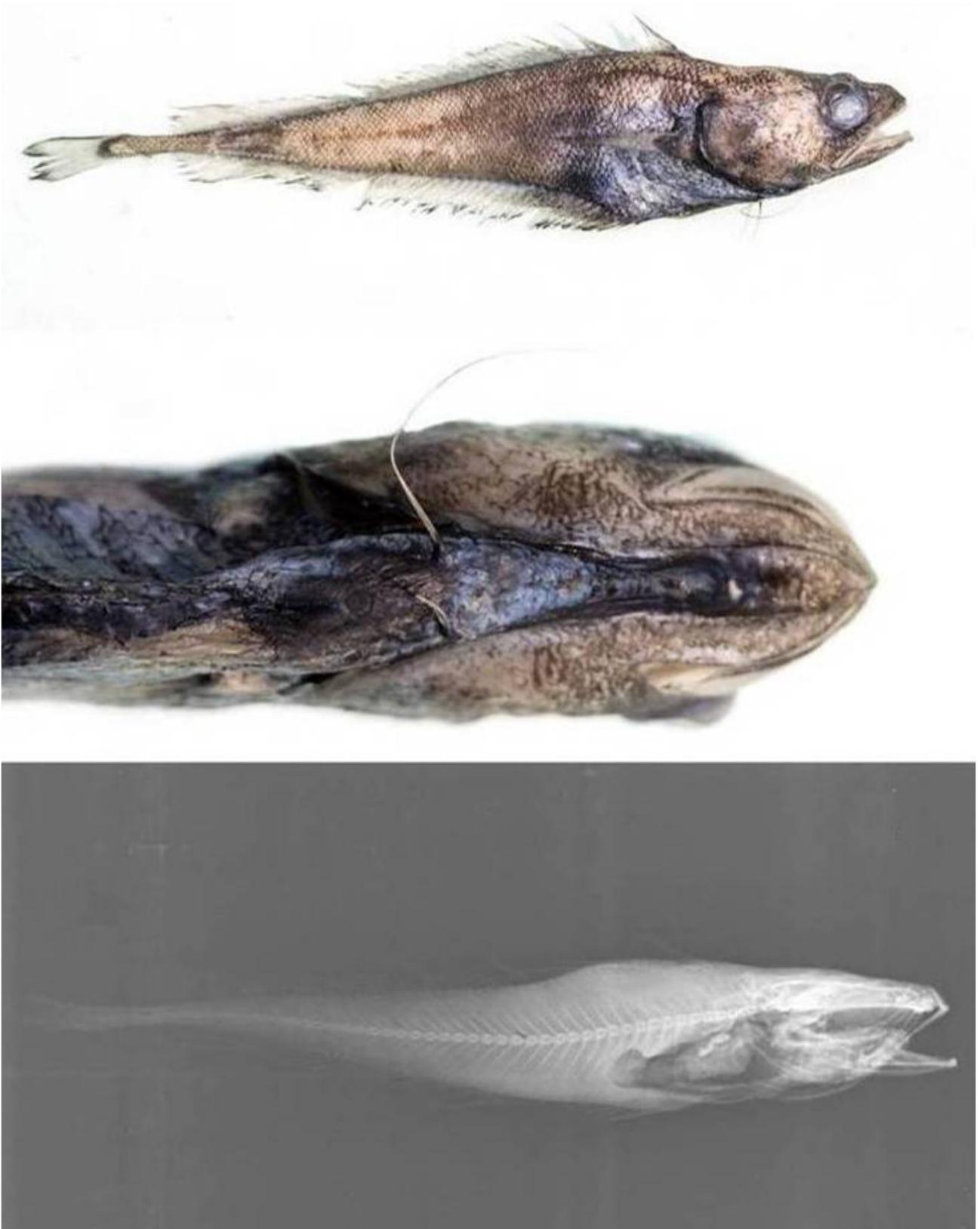


FIGURE 4. *Physiculus lakshadeepa* sp. nov., paratype, MTRLDST 00113, preserved. A. Lateral view. B. ventral view of abdomen. C. Radiograph.

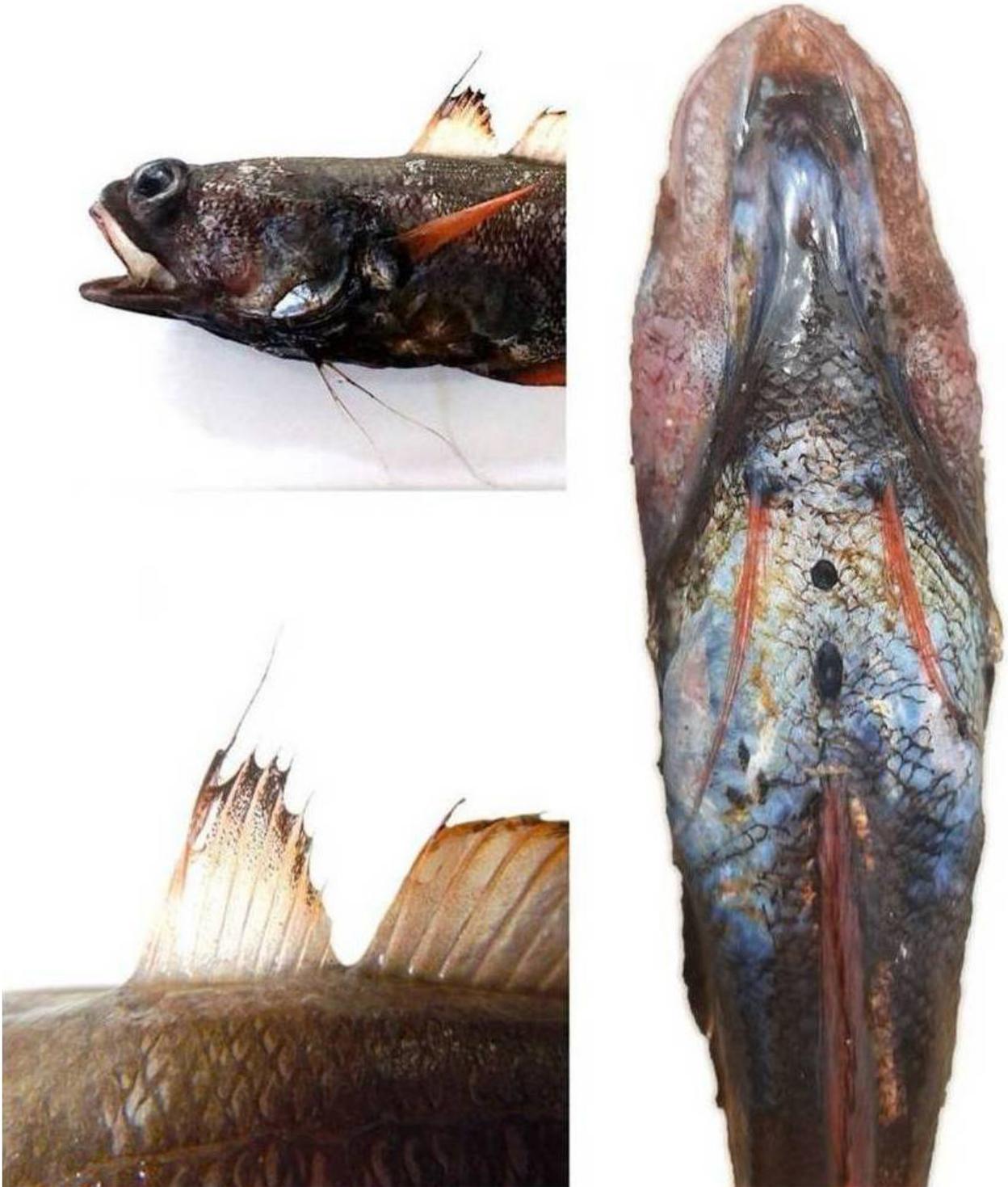


FIGURE 5. *Physiculus lakshadeepa* **sp. nov.**, fresh condition, from the holotype???. **A.** Lateral view of anterior body, fresh condition. **B.** Close-up of high first dorsal fin with first ray filamentous. **C.** Ventral view of abdomen showing the pelvic-fin base, light organ and anus.

Vertebrae: 12 (11–12) precaudal, 37 (37–38) caudal, and 49 (49) in total.

Colouration. When fresh, head and body dark brown, slightly reddish on tail, caudal fin base dark brown and abdomen silvery blue. Branchiostegal membranes black; first dorsal fin pink, with broad black margin; second dorsal fin pink, gradually becoming red posteriorly, with narrow black margin; pectoral fin red with black base; pelvic fin dark brown; anal fin red with black margin; caudal fin deep red with posterior third black. Colour when preserved, head and body light brown and abdomen silvery.

TABLE 1. Morphometric and meristic data of *Physiculus indicus* sp. nov. and *Physiculus lakshadeepa* sp. nov.

Morphometric Measurement	<i>P. indicus</i>		<i>P. lakshadeepa</i>			
	Holotype	All types	Holotype		All types	
Total length (mm)	183	183 (149–183)	192	192 (143–224)		
Standard length (mm)	162	162 (128–162)	164	164 (125–183)		
First dorsal rays	9	9 (8–9)	9	9 (8–9)		
Second dorsal rays	57	57 (56–60)	59	59 (51–59)		
Pelvic soft rays	7	7	7	7		
Pectoral fin rays	22	22 (14–22)	18	18 (14+–18)		
Caudal fin rays	19	19 (17–24)	14	14 (14–22)		
Anal soft rays	60	60 (55–60)	56	56 (53–59)		
scales in longitudinal series	96	96 (90–102)	90	90 (84–95)		
Scales between first dorsal-fin base and lateral line	7	7 (7–8)	7	7 (6–7)		
Gill rakers	4+9	13 (12–13)	5+12	14 (14–17)		
Total vertebrae	52	52	49	49		
Precaudal vertebrae	12	12 (11–12)	12	12 (11–12)		
Caudal vertebrae	40	40 (40–41)	37	37 (37–38)		
in % SL		Mean (Range)	SD		Mean (Range)	SD
Body depth	22.8	20.7 (18.0–22.8)	1.8	21.5	20.2 (19.3–21.5)	1.1
Caudal peduncle depth	1.8	2.1 (1.8–2.5)	0.3	2.3	2.2 (1.5–2.7)	0.6
Head length	25.1	25.7 (24.8–27.7)	1.2	24.3	24.3 (23.0–25.5)	1.3
Head width	18.4	18.0 (16.2–19.8)	1.4	15.8	16.1 (15.8–16.5)	0.4
Predorsal length	27.8	28 (26.1–29.8)	1.3	29.1	29.3 (28.2–30.5)	1.2
Pre-pectoral length	23.0	26.9 (23.0–29.4)	2.6	26.7	28.1 (26.7–30.5)	2.1
Pre-pelvic length	16.9	20.7 (16.9–22.9)	2.3	21.1	19.8 (16.6–21.6)	2.8
Pre-anal fin length	27.5	31.7 (27.5–34.2)	2.5	32.6	32.4 (31.6–33.2)	0.8
Pre anus length	21.6	27.4 (21.6–30.4)	3.4	30.8	29.5 (26.9–30.8)	2.2
First dorsal fin height	6.3	8.2 (6.3–9.7)	1.5	9.6	9.4 (9.2–9.6)	0.3
First dorsal fin base length	6.5	7.7 (6.5–9.0)	0.9	6.5	6.8 (6.5–7.1)	0.3
Pectoral fin length	17.8	18.4 (15.7–20.8)	2.1	17.1	17.5 (16.9–18.5)	0.9
Pelvic fin length	19.2	18.3 (17.0–19.2)	1.2	21.5	20.2 (18.9–21.5)	1.8
in % HL						
Orbital diameter	22.2	22.9 (19.0–25.8)	2.6	24.7	24.1 (19.1–28.5)	4.7
Snout length	19.9	23.4 (19.9–28.4)	3.5	24.7	25.3 (24.7–25.9)	0.6
Maxilla length	51.8	48.8 (44.9–51.8)	3.3	50.3	51.2 (48.3–54.9)	3.4
Bony inter orbital width	31.8	29.8 (26.6–34.1)	3.1	30.1	28.7 (25.4–30.7)	2.9
Barbel length	4.7	6.1 (3.2–8.9)	2.5	7.5	7.4 (3.2–11.6)	4.2
First dorsal fin height	25.1	32.5 (25.1–39.1)	5.8	62.8	57.2 (51.7–62.8)	7.8
Caudal peduncle length	8.8	9.4 (8.4–10.3)	0.8	17.1	18.1 (17.1–19.7)	1.4
%InV–af						
LoD	11.4	9.5 (6.4–12.0)	2.9	6.0	7.6 (6.0–9.6)	1.8
InV–Lo	22.6	23.3 (18.6–29.0)	3.7	29.0	26.8 (24.4–29.0)	2.3
Lo–An	17.6	21.3 (17.6–23.8)	2.9	22.6	19.7 (17.4–22.6)	2.6
InV–An	53.6	53.9 (50.6–58.2)	3.5	58.2	51.4 (41.7–58.2)	8.7

Discussion

Taking into account that *Physiculus* species have relatively restricted geographical distributions (Paulin, 1989). No known species of *Physiculus* are occurring in more than one ocean basin (Froese & Pauly, 2017). Therefore, we compared the two new species with their Indian Ocean congeners, except for other indications.

Table 2 provides the selected data for comparison. Notably, some data provided in Paulin (1989) and Shcherbachev (1993) are not consistent and are both listed. The differences between these two publications suggested a chance for the occurrence of more species. Shcherbachev (1993) included *P. andriashevi* under the key item with InV-Lo <15% InV-af, however, he provided InV-Lo 21.0–28.4% InV-af in the text, which is likely a mistake, and here we follow the value in the text.

By using the keys provided in Paulin (1989) and Shcherbachev (1993), the two new species can be excluded from *P. beckeri*, *P. bertelseni*, *P. fedorovi*, *P. natalensis*, *P. roseus* and *P. dalwigkii* by having InV-LO >15% InV-af and from *P. marisrubri*, *P. normani* and *P. nielseni* by having InV-LO <30% InV-af; and from *P. capensis* and *P. nielseni* by having scales covered on the snout. In addition, *P. andriashevi* has numerous scales in longitudinal series, dorsal- and anal- fin rays and vertebrae and can easily be separated from the two new species.

As a consequence, the new species are most similar to *P. argyropastus* and share with it in having (1) similar position and size of the light organ; (2) jaw teeth small and equally sized; (3) continuous tube of lateral line not reaching beyond the midpoint of second dorsal fin; (4) similar number of scales in longitudinal series; (5) similar numbers of gill rakers. These new species also resemble the ancestral form postulated by Bruss (1986) with large scales, undifferentiated teeth, relatively low numbers of fin rays and vertebrae and a moderately small light organ, as suggested by Paulin (1989).

Physiculus indicus differs from *P. argyropastus* in lacking gular scales (gular scales present in *P. argyropastus*), anus situated closer to the light organ (Lo-An 17.6–23.8 % vs 22.8–32.6% InV-Af), and slightly fewer total vertebrae (52 vs 53–56). *Physiculus lakshadeepa* differs from *P. argyropastus* in lacking gular scales (gular scales present in *P. argyropastus*), fewer anal-fin rays (53–59 vs 58–65), clearly fewer total vertebrae (49 vs 53–56).

Physiculus indicus is also similar to *P. roseus* in lacking gular scales, a similar number of gill rakers, similar size of the light organ and general appearance. *P. indicus* can be differentiated from *P. roseus* in having the light organ closer to the anus than the pelvic-fin base, InV-LO 18.6–29.0% InV-af (vs 4.9–8.1 in *P. roseus*) and Lo-An 17.64–23.8 % InV-af (vs 31.3–45.4), fewer rays in the second dorsal fin (56–60 vs 58–65), and fewer anal-fin rays (55–60 vs 63–65). In comparison with the other species from the Indo-Pacific, *P. indicus* is also similar to *Physiculus rhodopinnis* Okamura 1982 from Japan in the size and position of the light organ but can be distinguished by lacking gular scales (vs scale present), fewer rays in the second dorsal fin (56–60 vs 68–76) and fewer anal-fin rays (55–60 vs 70–80).

Physiculus lakshadeepa can be distinguished from most Indian congeners in having relatively high first dorsal fin (51.7–62.8% HL), with first ray filamentous, except for that of *P. capensis* (53.5–61.6% HL), *P. beckeri* (75–106% HL) and *P. roseus* (54.2–57.8% HL). *Physiculus lakshadeepa* differs from *P. capensis* in having scales on the snout (vs snout smooth) and teeth in equally sized (vs in graded series); from *P. beckeri* in having 84–95 scales in longitudinal series (vs 115–130) and less tall first dorsal fin (vs fin much taller); and from *P. roseus* in having 53–59 second dorsal-fin rays (vs 63–65) and 14–17 gill rakers (vs 9).

Compared with the other species in the Pacific Ocean, *P. lakshadeepa* resembles only *P. chigodarana*, which has the first dorsal fin distinctly higher than the second. However, *P. lakshadeepa* differs from the latter in lacking gular scales (vs presents in *P. chigodarana*), fewer second dorsal-fin rays (51–59 vs 67–70); fewer anal-fin rays (53–59 vs 67–76); light organ situated rather backward (InV-Lo 24.4–29.0% InV-af vs 9.7–14.4%); anus situated rather backward (InV-An 41.7–58.2% InV-af vs 38.7–43.7%); more gill rakers (14–17 vs 10–12), and fewer vertebrae (49 vs 52–55).

Although similar to each other, *Physiculus indicus* differs from *P. lakshadeepa* in having fewer gill rakers (12–13 vs 14–17), more caudal vertebrae (40–41 vs 37–38), more total vertebrae (52 vs 49), and first dorsal fin not higher than the second (vs first dorsal fin higher with first ray filamentous) (Fig. 5).

Comparative materials: *Physiculus argyropastus*: BM(NH) 1901.1.30.19–21; *P. chigodarana*: USNM 59594; *P. rhodopinnis*: BSKU 30343; *P. roseus*: BM(NH) 1898.7.13.7. Other materials, as listed in Yu & Ho (2012).

TABLE 2. Comparison of the new species with their Indian Ocean congeners and two closely similar species from western Pacific Ocean. Those cells with overlapped values of new species are shaded in gray. Data sources: A: this study. B. Shcherbachev (1993). C. Paulin (1989).

Taxon	In V-LO/ In V-af (%)	LO/ In V-af (%)	Scale series	Pelvic- fin rays	Dorsal- fin rays (2 nd)	Anal- fin rays	Pectoral- fin rays	Vertebrae	Gill rakers	1st Dorsal-fin height (% HL)	Other characters	Data sources
<i>P. indicus</i> sp. nov.	18.6–29.0	6.4–12.0	90–102	7	56–60	55–60	~22	52	12–13	25.1–39.1	Teeth equal in size; snout scaled	A
<i>P. lakshadheepa</i> sp. nov.	24.4–29.0	6.0–9.6	84–95	7	51–59	53–59	~18	49	14–17	51.7–62.8	Teeth equal in size; snout scaled	A
<i>P. capensis</i>	19.0–19.7	15.1–15.8	98–110	7	54–57	60–62	26–28	49–50	12–13	53.5–61.6	Jaw teeth in a graded series; snout naked.	B C
	20.4–30.6	5.4–10.0	105–110		53–62	58–65	24–25	48–51	2–3+9			
<i>P. andriashevi</i>	21.0–28.4	11.9–18.2	124–140	5	72–80	73–80	21–23	59–60	13–18	26.7–38.1		B
<i>P. rhodopinnis</i> (Indo-W Pacific)	24.3–26.7	11.2–16.4	120–130	5	71–76	76–79	23	57–58	11–14	34.9–36.3		B
	21.3–27.2	10.1–15.9	120–140		68–76	70–80		53–56	3–4+7–12			C
<i>P. argyropastus</i>	31.7–41.7	9.2–14.1	93–99	6–7	55–61	60–67	21–24	50–54	14–19	33.1–51.1		B
	23.0–36.0	4.6–9.8	ca. 90–95		56–60	58–65		53–56	2–3+9–11			C
<i>P. marisrubri</i>	31.4–38.0	12.9–15.2	75–80	5	58–63	62–68	21–25	52–53	22–24	41.8–44.6		B
	32.9–36.9	8.0–8.9	ca. 80		58–63	63–68		55	5+12–14			C
<i>P. normani</i>	39.0–39.1	7.6–11.0	86–97	5	59–66	64–70	23–24	50–53	10–12	30.4	Jaw teeth in a graded series; snout naked	B C
	34.9–38.2	7.1–9.4	86–95		60–63	67–70		51	2–3+8–9			
<i>P. nielsenii</i>	39.1	10.80	105	5	65+	64+	24	48+	12–14	30.5	Snout naked	B
<i>P. fedorovi</i>	[–8.5]	25.7	126	7	62	68	23–24	52	10–11	35.1		B
<i>P. dahwigkii</i>	0.0–2.4	17.5–20.0	119–126		63–68	66–75	/	52–55	2–3+7–9		Jaw teeth in a graded series	C
	7.0–9.4	14.4–24.5	127–135	5	64–65	68–71	24–26	56	10–13	39.4–40.6		B

.....continued on the next page

TABLE 2. (Continued)

Taxon	InV-LO/ InV-af (%)	LO/ InV-af (%)	Scale series	Pelvic- fin rays	Dorsal- fin rays (2 nd)	Anal- fin rays	Pectoral- fin rays	Vertebrae	Gill rakers	1st Dorsal-fin height (% HL)	Other characters	Data sources
<i>P. sudanensis</i> (= <i>P. dabwigkii</i>)	0.0–7.9	14.4–21.6	ca. 120–130		64–69	70–77	21–23	52	2–3+6–8		Jaw teeth in a graded series	C
<i>P. natalensis</i>	0.0–5.9	11.5–17.2	100–110	7	64–66	67–68	21–23	53–54	3–4+9–11			C
<i>P. beckeri</i>	3.4–6.1	11.4–17.4	115–130	7	57–65	57–65	21–24	50–54	11–17	75–106		B
<i>P. roseus</i>	4.9–8.1	13.4–18.0	92–97	7	58–65	63–65	23–24	52–53	9	54.2–57.8		B
<i>P. bertelseni</i>	11.5–13.2	20.0–26.2	140–148	5	66–68	71–73	25–27	54–58	10–13	34.2–42.3		B
<i>P. chigodarana</i> (Pacific)	9.0–10.1	14.8–18.0	92–94	7	64–65	66–68	24	52–53	12–14	93.6–94.9	Teeth subequal in size	B
	9.7–14.4	8.3–8.5	98–100		67–70	67–76		55	2–3+8–9			C

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