Taxonomic studies on deep-sea snailfishes (Liparidae) from Suruga Bay, Japan, with aspects of the life history of *Paraliparis ruficometes* Murasaki, Takami and Fukui 2018

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Contents

I. Introduction

Snailfishes (Cottoidei: Liparidae) are a large, morphologically diverse group of marine fishes, comprising about 32 genera with over 430 species recognized worldwide (Chernova et al. 2004; Orr et al. 2019). Attaining a maximum length of about 80 cm, they are one of the most speciose fish families in the Southern, North Pacific and Arctic Oceans (Chernova et al. 2004; Nelson et al. 2016), although unevenly distributed in tidal zone to hadal zone (> 8,000 m depth) habitats (Gerringer et al. 2017). All species of snailfish have an elongate body covered by soft skin overlying more or less thick gelatinous tissue, and lack scales and a lateral line (Chernova et al. 2004). The dorsal and anal fins are usually confluent with the caudal fin, the caudal-fin rays being unbranched and the pelvic fins either transformed into a ventral sucking disk or absent (Kido 1988).

Deep-sea (>200 m depth) snailfishes probably evolved from shallow sea ancestors (Andriashev 1953), expanding to occupy benthic, epibenthic or pelagic marine layers, and accounting for ca. 70 % of total known species (Chernova et al. 2004). About 50 Japanese deep-sea species (belonging to 11 genera) are presently recognized, among an overall total of ca. 60 Japanese species (including the doubtful species *Liparis owstoni* and four new species described in this study) (Kai et al. 2011, 2018, 2019; Machi et al, 2012; Nakabo and Kai 2013; Orr et at. 2015; Matsuzaki et al. 2017; Murasaki et al. 2017, 2018, 2019a, b). Of the former, some 40 species have been recorded from northern Japan and about 10 from southern Japan including Suruga Bay (Kido 1988; Kido and Shiobara 1993; Sakurai and Shinohara 2008) (Table 1). Nevertheless, taxonomic studies of deep-sea snailfishes have lagged due to adult specimens having been rarely collected, in addition to their typically easily damaged soft body and poorly calcified bones. In addition, the life history of deep-sea snailfishes has remained almost unknown, except for two species of *Paraliparis* (Busby and Cartwright 2006; Takami and Fukui 2012), due to their larvae and juveniles not having been collected by traditional collection methods for surface to middle layer ichthyoplankton (Takami and Fukui 2012). Nevertheless, the aforementioned studies demonstrated that the life histories (e.g., development and reproduction) of deep-sea snailfishes (Busby and Cartwright 2006; Takami and Fukui 2012) differed from shallow sea forms (Aoyama 1959; Marliave and Peden 1989; Sokolovskii and Sokolovskaya 2003; Yang et al. 2010; Kojima 2014), as well as from other mesopelagic fishes (Miya and Nishida 1996). In addition, some species of the deep-sea genus *Careproctus* have a specialized spawning characteristic, laying their eggs in the gill cavities of king crabs (Gardner et al. 2014).

The purpose of this study was to elucidate the taxonomy and life history of deep-sea snailfishes collected by systematic epibenthic surveys in Suruga Bay, Japan, and to outline significant life history strategies of deep-sea snailfishes.

II. Materials and methods

1. Sampling locations and collection gear

Epibenthic surveys in Suruga Bay were conducted by the T/V *Hokuto* (Tokai University, 18 t), being monthly cruises from January 2008 to June 2019. Sampling areas were established on the continental slope and in the Suruga Trough (Fig. 1), including three stations for each: the Hagoromo Submarine Canyon (St. I: ca. 200–1,300 m depth), South Komagoe Submarine Canyon (St. J: ca. 500–1,000 m), and off the estuary of the Fuji-gawa River (St. L, including 6 horizontal transects: ca. 350, 500, 600, 700, 800, 900 m), on the continental slope, and the northern part of Ugusuoki Gorge (St. M-1: ca. 1,400–1,600 m), middle part of Ugusuoki and Senoumi Gorges (St. M-2: ca. 1,600–1,700 m), and southern part of Senoumi Gorge (St. M-3: ca. 1,900–2,200 m), in the Suruga Trough.

The collection gear used comprised ring nets [φ 1.3 m (as described by Takami and Fukui 2010) or φ 1.6 m (Fig. 2a)], mainly for the continental slope, and beam trawls [width 1.5 m × height 0.8 m (Fig. 2b) or width 1.7 m × height 1.0 m (Fig. 2c), the latter only with mesh in front of the upper and lateral aspects of the beam], mainly for the Suruga Trough. Each net was towed as follows: ring nets— (1) columnar weight in contact with seafloor (Fig. 2a), (2) net towed for ca. 5 minutes at ship speed ca. 1.7 knots, with warp released ca. 10–20 m per minute, (3) towing stopped to enable columnar weight to regain contact with seafloor, (4) sequences (2) and (3) repeated; beam trawls— (1) sled weight in contact with seafloor (Fig. 2b,c), (2) warp released until length about twice bottom depth, (3) trawl towed for ca. 5 minutes at ship speed of ca. 1.7 knots, (4) towing stopped to enable sled weight to regain contact with seafloor, (5) sequences (3) and (4) repeated. Relationships between towing depth and bottom depth are shown in Fig. 3. Ring nets and beam trawls could be effectively towed (touch the seafloor) in the epibenthic layer on the continental slope (Fig. 3a) and in Suruga Trough (Fig. 3b), respectively. However, the ring nets were less effective, sometimes lifting significantly from the seafloor, in the Suruga Trough (Fig. 3c).

2. Identification of snailfishes

A total of 464 snailfish specimens were collected by 155 survey tows in this study (Table 2). After collection, the specimens were initially maintained in iced seawater, subsequently fixed in approximately 10 % seawater-buffered formalin, and later transferred to 70 % ethanol. Specimens used for species descriptions were deposited in the Marine Science Museum, Tokai University, Shizuoka, Japan (MSM) and the National Museum of Nature and Science, Tsukuba, Japan (NSMT). In addition, 16 specimens, to serve for comparative purposes, were deposited in the Hokkaido University Museum, Hakodate, Japan (HUMZ), the Kochi University, Department of Natural Science, Faculty of Science, Kochi, Japan (BSKU), the Smithsonian Institution, National Museum of Natural History, Suitland, USA (USNM), and the Oregon State University, Faculty of Science, Museum of Natural History, Corvallis, USA (OS).

Counts and measurements followed Andriashev and Stein (1998) and Stein et al. (2001), except for the division between the upper and lower pectoral-fin ray lobes, which followed Kido (1988). Caudal-fin length was measured the longest ray, except in *Paraliparis ruficometes* Murasaki, Takami and Fukui 2018, in which the longest (= dorsalmost) ray and middle ray were measured owing to the unique caudal fin morphology in that species. Body measurements were made to the nearest 0.1 mm. Median-fin rays and vertebral counts were made from radiographs. Sensory pores were observed after staining with Cyanine Blue following Saruwatari et al. (1997). Colors of the peritoneum, stomach and pyloric caeca were noted following dissection. Ovum diameter was measured to the nearest 0.1 mm. The right pectoral girdle of some specimens was removed, and cleared and stained following Potthoff (1984), for observation of osteological characters. Developmental stage terminology generally followed Kendall et al. (1984), with a few exceptions: flexion stage—up to complete resorption of the notochord tip to a position anterior to the edge of the hypural (following Takami and Fukui 2012); juvenile stage—until anus position fixed (below gill slit). Standard length and head length are abbreviated as SL and HL, respectively.

III. Distribution and vertical separation of snailfishes in Suruga Bay

The collected specimens were found to comprise 7 species, included in two genera: genus *Careproctus* Krøyer 1862 with two species, including the new species *Careproctus surugaensis* Murasaki, Takami and Fukui 2017, and genus *Paraliparis* Collett 1879 with five species, including the three new species *Paraliparis ruficometes* Murasaki, Takami and Fukui 2018, *Paraliparis variabilidens* Murasaki, Takami and Fukui 2019 and *Paraliparis hokuto* Murasaki, Takami and Fukui 2019, and the first record from Suruga Bay of *Paraliparis atramentatus* Gilbert and Burke 1912 (Murasaki et al. 2017, 2018, 2019a, b) (Table 3). The distribution patterns based on the collecting date of 7 species clearly fell into “Continental slope” (ca. 200–1,300 m depth) (three species, 292 specimens in total) and “Suruga Trough” (ca. 1,400–2,200 m depth) (four species, 172 specimens in total) types.

“Continental slope” type— Paraliparis dipterus Kido 1988 (dominant species in the area, n = 267), *Careproctus rhodomelas* Gilbert and Burke 1912 (n = 24) and *P. atramentatus* (n = 1). *Paraliparis dipterus* and *Careproctus rhodomelas* were collected from all stations on the slope, *P. atramentatus* only from St. I. Larval *Paraliparis dipterus* totaled 65, whereas only adults of the other species were collected.

“Suruga Trough” type— Paraliparis ruficometes (dominant species in the area, n = 165), *P. hokuto* (n = 5), *Careproctus surugaensis* (n = 1) and *P. variabilidens* (n = 1). *Paraliparis ruficometes* was collected from all stations in the trough, the other three species only from St. M-1 (= northern part of Ugusuoki Gorge < 1,600 m depth). Larval *Paraliparis ruficometes* totaled 9, whereas only adults the other species were collected.

A schematic diagram of the vertical separation of deep-sea snailfishes in Suruga Bay, shown as Fig. 4, includes *Careproctus rotundifrons* Sakurai and Shinohara 2008 and *Paraliparis meridionalis* Kido 1985, previously recorded from the continental slope in Suruga Bay (Kido and Shiobara 1993; Sakurai and Shinohara 2008), but not collected by this study.

IV. Taxonomy of deep-sea snailfishes in Suruga Bay

1. Important identification characters

Snailfishes are difficult to identify due to having a soft body and poorly calcified bones, which are easily damaged during collection and problematic for observations. However, some relatively durable characters, including teeth, median-fin rays, vertebrae, and pectoral fin and gill slit conformation, are useful for species identification.

Teeth: Shape of the jaw teeth has been considered as a most important species-defining character (e.g., Burke 1930; Stein 1978; Andriashev 1986; Kido 1988), being classifiable roughly as "simple" or "trilobate". Simple teeth lack cusps, sometimes being recurved posteriorly (caniniform) (Fig. 5a). Trilobate teeth have distinct lateral cusps and are not recurved; usually more stout than simple teeth (Fig. 5b). Although jaw teeth in snailfishes usually occur as many oblique rows, some species are characterized by completely or partially uniserial teeth.

Median-fin rays and vertebrae: Counts of dorsal- and anal-fin rays, and vertebrae reflect well the posterior proportion of the body. Although sometimes subject to considerable intraspecific variation (cf. Kido 1988), these characters are usually more reliable than proportional measurements. Intraspecific variations in caudal-fin ray counts range from 0–2, being less than that of dorsal- and anal-fin rays, and vertebrae.

Pectoral fin: Pectoral fin shape (slightly notched or deeply notched) (Fig. 6a, b) and fin-ray counts are generally unequivocal in snailfishes, the fin length being unique in some species (e.g., *Careproctus zachirus* Kido 1985, *Paraliparis macropterus* Stein 2012). Andriashev (1977) demonstrated the importance of proximal radial structure as a diagnostic character for the first time.

Gill slit: Gill slit conformation is classifiable roughly as "narrow" or "wide", the former often being entirely above the pectoral-fin base, and the latter usually extending ventrally and adjacent to a number of pectoral-fin ray bases (Fig. 7a, b).

2. Key to genera of deep-sea snailfishes from Suruga Bay

1a. Ventral sucking disk present……………………………………*Careproctus* (three species)

1b. Ventral sucking disk absent…………………………………………*Paraliparis* (6 species)

Among the 9 species recorded in total from Suruga Bay, the present specimens of *Careproctus rhodomelas* and *Paraliparis dipterus* agreed closely with the original and subsequent descriptions (e.g., Kido 1988, 1993; Takami and Fukui 2012). *Careproctus rotundifrons* Sakurai and Shinohara 2008 and *Paraliparis meridionalis* Kido 1985 were not collected during the 2008–2019 T/V *Hokuto* surveys. Counts and selected characters of the above four species are included as expanded diagnoses, modified from previous studies (e.g., Kido 1988; Sakurai and Shinohara 2008), in the following sections.

3. Genus *Careproctus* Krøyer 1862

Careproctus Krøyer 1862: 253 (type by monotypy *Liparis reinhardti* Krøyer 1862).

Diagnosis. Ventral sucking disk present, pseudobranches absent, six branchiostegal rays, a single nostril on each side, no skin flaps or barbels on head, anal-fin rays generally numbering more than pectoral-fin rays, body color uniformly dark or light, rarely variegated (Burke 1930; Kido 1988; Orr and Maslenikov 2007; Stein 2012; Murasaki et al. 2017).

Key to species of *Careproctus* from Suruga Bay

1a. Teeth mixed simple and trilobate, pectoral fin slightly notched……………*C. rotundifrons*

1b. Teeth all trilobate, pectoral fin deeply notched…………………………………………….2

2a. Gill slit extending ventrally in front of 7th pectoral-fin ray base, disk large, about 30 % HL…………………………………......…..…..... *C. surugaensis*

2b. Gill slit entirely above pectoral-fin or extending ventrally in front of the 3rd ray base, disk small, about 11–13 % HL…………………………………......………....*C. rhodomelas*

***Careproctus rhodomelas* Gilbert and Burke 1912**

(Standard Japanese name: Bara-bikunin; Fig. 8)

Careproctus rhodomelas Gilbert and Burke 1912a: 365, pl. 44 (original description, type localities: Bungo Channel and Suruga Bay, Japan); Jordan et al. 1913: 307 (list); Burke 1930: 118, fig. 36 (description); Taranetz 1937: 134 (key); Okada and Matsubara 1938: 347 (key); Matsubara 1955: 1194 (key); Okamura 1982: 293, pl. 209 (description); Kido 1984b: 338, pl. 304 (brief description); Kido 1988: 198–199, fig. 37 (description); Nakabo 1993: 584 (key); Nakabo 2000: 675 (key); Chernova et al. 2004: 15 (list); Nakabo and Kai 2013: 1210 (key).

Expanded diagnosis. 58–61 total vertebrae, 53–58 dorsal-fin rays, 47–50 anal-fin rays, 28–31 pectoral-fin rays, 9–10 caudal-fin rays, 10–13 pyloric caeca, pore pattern 2-6-7-2; trilobate teeth on both jaws forming bands; gill slit entirely above pectoral-fin base or extending ventrally in front of 3rd pectoral-fin ray base; pectoral fin deeply notched, the longest ray in lower lobe almost equal to or longer than HL; disk small, 11.0–16.8 % HL; chin pores (= anteriormost mandibular pores) paired, opening separately, not in common pit;

peritoneum and stomach black (modified from Gilbert and Burke 1912a; Kido 1988).

Distribution. Known from 500 to 928 m depth in Suruga Bay, Tosa Bay and Bungo Channel, Japan.

Careproctus rotundifrons Sakurai and Shinohara 2008

(Standard Japanese name: Hime-kon'nyakuuo; Fig. 9)

Careproctus rotundifrons Sakurai and Shinohara 2008: 39–45, figs. 2, 3 (original description, type localities: off the Pacific coast of Fukushima Prefecture, Sagami Bay and Suruga Bay, Japan); Shinohara et al. 2009: 720 (list); Nakabo and Kai 2013: 1210 (key).

Expanded diagnosis. 53–56 total vertebrae, 47–50 dorsal-fin rays, 41–45 anal-fin rays, 34–40 pectoral-fin rays, 12–13 caudal-fin rays, 4 pectoral proximal radials (all unnotched), 15–28 pyloric caeca, pore pattern 2-6-7-2; mixed simple and trilobate teeth on both jaws forming bands; eye diameter 5.6–7.2 % SL; interorbital width 9.9–13.5 % SL; gill slit entirely above pectoral-fin base; pectoral fin slightly notched, scapula notch present; disk length 4.6–7.1 % SL; 2–3 paired ribs on 8–10 abdominal vertebrae; chin pores (= anteriormost mandibular pores) paired, opening separately, not in common pit; peritoneum dark brown; stomach, oral cavity, and pyloric caeca pale (modified from Sakurai and Shinohara 2008).

Distribution. Known from 521 to 1,100 m depth in the continental slope off the Pacific coast of Fukushima Prefecture, Sagami Bay and Suruga Bay, Japan.

***Careproctus surugaensis* Murasaki, Takami and Fukui 2017**

(Standard English name: Suruga snailfish; standard Japanese name: Suruga-bikunin; Figs. 10; Tables 4, 5)

Careproctus surugaensis Murasaki, Takami and Fukui 2017: figs. 1, 2; tables 1, 2 (original description, type locality: northern part of Suruga Trough, Suruga Bay, Japan)

Material examined. MSM-17-81, holotype: 82.6 mm SL, female, northern part of Suruga Trough, Suruga Bay, Japan, 34° 58.7′ N, 138° 38.2′ E–34° 55.4′ N, 138° 38.3′ E, 1,450–1,570 m, 28 Oct. 2015, T/V *Hokuto*, beam trawl (warp length 2,400 m).

Comparative materials. *Careproctus curilanus*: USNM 73341 (photograph and radiograph), holotype, off Simushir Island at Albatross station 4803, 46° 42′N, 151° 45′E. *Careproctus homopterus*: USNM 73342 (photograph and radiograph), holotype, southeast of Cape Patience, Sagalin at Albatross station 5029, 48° 22′ 30″N, 145° 43′ 30″E. *Careproctus mollis*: USNM 74383 (photograph and radiograph), holotype, off East Cape, Attu Island, Bering Sea at Albatross station 4784, 52° 55′ 40″N, 173° 26′E. *Careproctus attenuatus*: USNM 74386 (photograph and radiograph), holotype, between Petrel Bank and Agattu Island at Albatross station 4781, 52° 14′ 30″N, 174° 13′E.

Diagnosis. 50 total vertebrae, 47 dorsal-fin rays, 39 anal-fin rays, 32 pectoral-fin rays, 10 principal caudal-fin rays, 4 pectoral proximal radials (first to third with notches); trilobate teeth on both jaws, gill slit 7.1 % SL, extending in front of 7th pectoral-fin ray base; maximum body depth 19.1 % SL, disk length 7.9 % SL, anus midway between posterior margin of pelvic disk and anal-fin origin; body and fins light orange except blackish peritoneum.

Description. Counts and measurements presented in Table 4. Body covered by thick epidermis, overlying thin jelly-like tissue; flexible, elongate; greatest depth through highest point of parietal, greatest width on vertical through anus. Anus vertically below posterior margin of isosceles triangle-like opercular flap (lateral view), almost midway between posterior margin of pelvic disk and anal-fin origin (ventral view) (Fig. 10a, b). Posterior part of body (anus to caudal-fin base) elongate, length 2.36 times HL, posteriorly gradually shallowing and attenuating. Snout tip round. Dorsal contour from snout tip to parietal almost linear. Eye round, upper margin close to dorsal contour. Single nostril tube-like, horizontally level with upper margin of orbit. Mouth large, subterminal, almost horizontal when closed, posterior margin of upper jaw vertically level with eye center. All teeth sharply trilobate on both jaws, in 24–26 oblique rows of 4–7 teeth per row on each jaw (Fig. 10c). Gill slit elongate, upper origin horizontally level with eye upper margin, slightly anterior to dorsal-fin origin, lower origin in front of 7th (from dorsalmost) pectoralfin ray base. Upper origin of pectoral-fin base at ca. 1/2 body depth, lower origin below posterior margin of eye. Pectoral-fin deeply notched: 27 rays in upper lobe, 4th (from dorsalmost) longest, reaching to a vertical through 9th dorsal-fin ray base, 52.7 % of HL; 5 rays in lower lobe, extending slightly beyond anus, 60.6 % of HL. Pectoral proximal radials four; three uppermost arranged at nearly equal intervals, fourth widely separated from third; all with deformed elliptical shape, first and second with two notches, third with one; distal radials present at 2nd to 27th (from dorsalmost) pectoral-fin ray bases (Fig. 10e). Pelvic disk slightly elliptic (Fig. 10b). Anal-fin origin below 10th dorsal fin-ray base. Longest dorsal-fin ray (17th) almost equal length to that of longest anal-fin ray (24th). Dorsal- and anal-fin membranes posteriorly confluent with caudal-fin membrane. Length ratios of last dorsal-fin ray/dorsalmost caudal-fin ray and last anal-fin ray/ventralmost caudal-fin ray 0.579 and 0.500, respectively. Caudal fin slightly round at distal margin. Urogenital papilla not apparent. Pleural ribs needle-like, present only on 9th and 10th abdominal vertebrae; length of 9th pleural rib 1.33 times of 10th (Fig. 10d).

Sensory pores. Nasal pores two, maxillary pores ≥four, mandibular pores ≥5. All pores slightly smaller than nostril. Chin pores (= anteriormost mandibular pores) paired, opening separately.

Coloration when fresh. Body and fins light orange, except whitish mouth cavity and blackish peritoneum (occipital region, operculum and anterior half of tail lacking epidermis; dorsal and anal fins partly lacking membranes) (Fig. 10b).

Coloration in alcohol. Body including fins milky white, mouth cavity and peritoneum unchanged from fresh color. Stomach and pyloric caeca whitish.

Reproduction. Gonad pouch-like, translucent whitish, with ovarian eggs 0.4–0.8 mm in diameter.

Distribution. Known only from 1,450 to 1,570 m depth in northern part of Suruga Trough, Suruga Bay, Japan.

Remarks. *Careproctus surugaensis* can be associated with 37 other species of *Careproctus* characterized by trilobate teeth on both jaws (Table 5) and a further 91 species having only simple teeth on either jaw (Gilbert 1896; Gilbert and Burke 1912a, b; Burke 1930; Schmidt 1950; Stein 1978; Kido 1984, 1985, 1988; Krasyukova 1984; Andriashev and Chernova 1989, 1997, 2010; Pitruk 1993; Geistdoerfer 1994; Tsutsui and Amaoka 1997; Matallanas 1998; Andriashev and Stein 1998; Stein et al. 2001; Imamura and Nobetsu 2002; Andriashev 2003; Chernova 2005a, b; Stein 2006; Duhamel and King 2007; Orr and Maslenikov 2007; Knudsen and Møller 2008; Sakurai and Shinohara 2008; Kai et al. 2011a, b; Machi et al. 2012; Orr 2012; Stein 2012; Chernova 2014a, b; Orr et al. 2015; Orr 2016). Of the species with trilobate teeth, 14 plus *C. surugaensis* have the gill slit opening level with the pectoral-fin base, compared with above the pectoral-fin base in 22 species (one species unknown) (Table 5). Of the former, *Careproctus kamikawai* Orr 2012 (off California) and

Careproctus lycopersicus Orr 2012 (Bering Sea) have fin ray counts close to those of *C. surugaensis*, but differ in having a robust deeper body (vs. an elongate body in *C. surugaensis*), higher gill slit length/SL ratios 12.5–15.3 % in *C. kamikawai* and 10.7–14.5 % in *C. lycopersicus* (vs. 7.1 %) and anus to anal-fin origin length/SL ratios 12.8–15.2 % in *C. kamikawai* and 11.4–18.1 % in *C. lycopersicus* (vs. 10.8 %) (Orr 2012; Murasaki et al. 2017). Although *Careproctus curilanus* Gilbert and Burke 1912 and *Careproctus simus* Gilbert and Burke 1912 from the western North Pacific and *Careproctus rhodomelas* Gilbert and Burke 1912 from only southern Japan have black peritoneal pigment, as in *C. surugaensis*, the vertebral number of the latter (50) is lower (55 in *C. curilanus*, 59–64 in *C. simus* and 61 in *C. rhodomelas*) (Table 5). The remaining nine species clearly differ from *C. surugaensis* in having pale peritoneal pigment, plus higher or lower numbers of vertebrae and/or lower anal-fin rays (Table 5). Twenty-two species, listed consecutively in Table 5, from *Careproctus attenuatus* Gilbert and Burke 1912 (Bering Sea) to *Careproctus zachirus* Kido 1985 (western North Pacific) clearly differ from *C. surugaensis* in having the gill slit entirely above the pectoral-fin base. In addition, the pectoral-fin base height differs between *C. attenuatus* and *C. surugaensis* [horizontal level of upper pectoral-fin base origin above lower orbital margin in former (Gilbert and Burke 1912b) vs. below], with the two species otherwise having similar counts and peritoneal color. *Careproctus atrans* Andriashev 1991 (Southern Ocean) (gill slit position unknown, Andriashev 2003) differs from *C. surugaensis* in eye diameter/SL ratios (7.4 % at 61 mm SL in *C. atrans* vs. 4.7 % at 82.6 mm SL in *C. surugaensis*) and upper jaw length/SL ratios (9.8 % vs. 13.4 %), pectoral- and caudalfin ray numbers (26 and 8 vs. 32 and 10, respectively), and proximal radial morphology (all lacking a notch vs. first to third with notches), although both have black peritoneal pigmentation and similar vertebral numbers (47 vs. 50). Only *C. surugaensis*, *C. simus* and *C. rhodomelas* have a combination of trilobate teeth, gill slit level with the pectoral-fin base and blackish peritoneum among the 25 congeneric Japanese species (Gilbert and Burke 1912a; Burke 1930; Stein 1978; Kido 1984, 1985, 1988; Kido and Shinohara 1997; Tsutsui and Amaoka 1997; Sakurai and Shinohara 2008; Kai et al. 2011b; Machi et al. 2012; Murasaki et al. 2017). *Careproctus surugaensis* is easily distinguishable from *C. simus* (see Kido 1985; Tsutsui and Amaoka 1997) by the level of the lower pectoral-fin base origin (below posterior margin of eye in *C. surugaensis* vs. center of margin in *C. simus*) and coloring on the postero-distal margin of the dorsal, anal and caudal fin (light orange when fresh, milky white in alcohol vs. black), and from *C. rhodomelas* (see Kido 1988) by the lower pectoral-fin lobe longest ray length /HL ratio (60.6 % vs. 100.9–116.0 %) and pelvic disc length/HL ratio (28.5 % vs. 11.0–12.7 %).

2. Genus *Paraliparis* Collett 1879

Paraliparis Collett 1879: 34 (type by monotypy *Liparis bathybii* Collett 1879).

Diagnosis. Ventral sucking disk and pseudobranchs absent, six branchiostegal rays, a single nostril on each side, no skin flaps or barbels on head, gill slit either entirely above pectoral-fin base or above it and extending ventrally over a number of fin rays, lower lobe of pectoral fin comprising more than two rays, coronal pore absent (rarely present) and one or (rarely) two suprabranchial pores on each side (Kido 1984a, 1988; Stein and Tompkins 1989; Stein et al. 2001; Stein 2012; Takami and Fukui 2012; Murasaki et al. 2018, 2019a, b).

Key to species of *Paraliparis* from Suruga Bay

1a. Teeth mixed simple and trilobate…………………………………………...*P. variabilidens*

1b. Teeth all simple……………………………………………………………………………2

2a. 12–14 pectoral-fin rays, coronal pore present, pyloric caeca absent……………*P. dipterus*

2b. 20–26 pectoral-fin rays, coronal pore absent, pyloric caeca present………....…………...3

3a. Lower part of each pectoral-fin ray completely free from the base, dorsalmost caudal-fin ray elongate, stomach black...............……………………………………...*P. ruficometes*

3b. Lower part of pectoral-fin rays connected by membrane, dorsalmost caudal-fin ray not elongate, stomach pale.......................…………………………………………………4

4a. Teeth row primarily uniserial, 6 caudal-fin rays....……………………………….…….*P. hokuto*

4b. Teeth row forming bands, 8–9 caudal-fin rays..........……………………………………...5

5a. 52–53 dorsal-fin rays, 45–46 anal-fin rays…………………………………...*P. atramentatus*

5b. 59–62 dorsal-fin rays, 54–56 anal-fin rays......………………………………...*P. meridionalis*

Paraliparis atramentatus **Gilbert and Burke 1912**

(Standard Japanese name: Inki-uo; Figs. 11, 12; Table 6)

Paraliparis atramentatus Gilbert and Burke 1912a: 377, pl. 48 (original description, type locality: off Cape Shionomisaki, east coast of Honshu, Japan); Jordan et al. 1913: 309 list); Burke 1930: 180, figs. 97, 98 (description); Taranetz 1937: 138 (key); Okada and Matsubara 1938: 348, pl. 85 (key); Matsubara 1955: 1196 (key); Kido 1984b: 326, pl. 366 (description); Kido 1985a: 366–367, figs. 4, 7, 8 (description); Yatou 1985: 603, pl. 376 (description); Kido 1988: 237–238, figs. 59, 60 (description); Nakabo 1993: 590 (key); Nakabo 2000: 677 (key); Chernova et al. 2004: 34 (list); Shinohara et al. 2005: 429 (list); Nakabo and Kai 2013: 1218 (key); Murasaki et al. 2019b: (description).

Material examined. MSM-19-200: 43.6 mm TL, 38.8 mm SL, female, Hagoromo Submarine Canyon, Suruga Bay, Japan, 35° 00.2′ N, 138° 32.6′ E–35° 00.2′ N, 138° 37.2′ E, 253–1,282 m, 24 Feb. 2010, T/V *Hokuto*, 1.3 m ring net (warp length 1,360 m).

Comparative materials. *Paraliparis atramentatus*: USNM 73345, holotype, 67.5 mm SL, male, off Cape Shionomisaki, east coast of Honshu, Japan, 33° 23' 30" N, 135° 34' E, depth 1,188 m, 30 Aug. 1906; BSKU 26438, 71 mm SL, female, the Okinawa Trough, East China Sea, 26° 20.1' N, 124° 50.7' E, depth 1,000–1,140 m, 22 Jan. 1978.

Diagnosis. 57 or 58 total vertebrae; 52 or 53 dorsal-fin rays; 45 or 46 anal-fin rays; 21–26 pectoral-fin rays; 8 or 9 caudal-fin rays; lower jaw included (lower tooth plates included entirely within posterior margin of upper tooth plate); teeth simple, with rounded or pointed tips on both jaws; gill slit entirely above pectoral-fin base; peritoneum black; stomach pale.

Description. Counts and measurements shown in Table 6. Body covered by thin, fragile epidermis lacking prickles, overlying thick jelly-like tissue; flexible, elongate; greatest depth and width near level of anus (Fig. 11a, b). Anus vertically below posterior tip of opercular flap. Body length from anus to caudal-fin base 3.41 times HL, gradually becoming shallow and attenuating posteriorly. Snout deeply rounded, slightly projecting. Dorsal contour straight from snout to nape. Single nostril tube-like, very short, horizontally level with eye center. Eye round, 0.80 times orbit length; low positioned, its counter not touching dorsal profile of head. Suborbital distance 0.70 times eye diameter. Mouth subterminal, horizontal when closed; oral cleft extending to anterior margin of pupil; suborbital fold covering ca. 3/4 of upper jaw, posterior margin of upper jaw below posterior margin of eye; lower jaw included, lower tooth plates included entirely within posterior margin of upper tooth plate. Teeth on both jaws large, stout, simple, with pointed tips (Fig. 12a); inner teeth slightly larger than outer teeth; upper-jaw teeth in about 10 rows, 3–4 teeth per row; lower-jaw teeth in about 8 rows, 3–5 teeth per row. Diastema absent on upper and lower jaw symphyses. Gill slit short, entirely above pectoral-fin base. Opercular flap rounded, supported by two posteriorly extended spines with tips level vertically. Uppermost part of pectoral-fin base at ca. 1/2 body depth, lowermost part almost below posterior margin of orbit. Pectoral fin slightly notched, shortest ray at notch greater than half length of longest ray in both lobes; 17 rays in upper lobe, each ray tips free of membrane, uppermost ray longest, reaching to below 10th dorsal-fin ray base, 59.1% of HL; 4 rays in lower lobe, free length greater than in upper lobe rays, longest ray almost reaching to below 4th dorsal-fin base, 51.1% of HL. Dorsal-fin origin vertical level with posterior tip of opercular flap. Membrane of posterior dorsal-fin rays continuous with caudal fin, overlapping 18.8% of caudal-fin length. Anal-fin origin below 9th dorsal-fin ray base. Membrane of posterior anal-fin rays continuous with caudal fin, overlapping 20.8% of caudal-fin length. Dorsal- and anal-fin ray lengths similar, both fin rays deeply buried anteriorly in gelatinous tissue. Caudal fin truncate. Epural absent. Hypural plate fused with terminal vertebral centrum, slit absent. Urogenital papilla absent. Pyloric caeca short, longest caecum ca. 20 % of HL, located on left side. Pleural ribs absent.

Sensory pores. Nasal pores 2, maxillary pores 6, mandibular pores 7, suprabranchial pore 1; pore pattern 2-6-7-1. Coronal pore absent. All pore sizes almost same size or smaller than nostril. Chin pores (= anteriormost mandibular pores) paired, opening separately, normal (not in common pit). No free neuromasts on head and body.

Color when fresh. Body and fins white; snout, lips and anterior part of head blackish; eye black; peritoneum, as seen through skin, black (Fig. 11a).

Color in alcohol. Body and fins whitish, epidermis transparent; snout, lips and anterior part of head blackish; melanophores sparsely scattered on the body musculature; eye black; peritoneum black; mouth and gill cavity dusky; stomach and pyloric caeca pale white (Fig. 11b).

Reproduction. Ovary pouch-like, translucent whitish, unripe ovarian eggs 0.3 mm in maximum diameter.

Distribution. Known from 253 to 1,282 m depth in Suruga Bay, off Cape Shionomisaki, Pacific coast of Honshu, and the Okinawa Trough, East China Sea.

Remarks. *Paraliparis atramentatus* shares a horizontal mouth, short gill slit, and low dorsal-, anal- and pectoral-fin ray counts with *Paraliparis dipterus* Kido 1988 (Suruga Bay: North Pacific), *Paraliparis penicillus* Baldwin and Orr 2010 (Bering Sea: North Pacific) and *Paraliparis australis* Gilchrist 1902 (South Atlantic off Africa) (Andriashev 1986; Kido 1988; Baldwin and Orr 2010; Takami and Fukui 2012; Murasaki et al. 2019b). However, *P. atramentatus* clearly differs from the three species in having: 52 or 53 dorsal-fin rays (vs. 54–58 in *P. dipterus*, 45–48 in *P. australis*), 45 or 46 anal-fin rays (vs. 48–54 in *P. dipterus*, 40–44 in *P. australis*), 21–26 pectoral-fin rays (vs. 12–14 in *P. dipterus*, 17–19 in *P. penicillus*, 19 in *P. australis*), 8 or 9 caudal-fin rays (vs. 6 in *P. dipterus*, 6 or 7 in *P. penicillus*) (Andriashev 1986; Kido 1988; Baldwin and Orr 2010; Takami and Fukui 2012; Murasaki et al. 2019b).

Paraliparis dipterus Kido 1988

(Standard Japanese name: Suruga-inkiuo; Fig. 13)

Paraliparis dipterus Kido 1988: 242–243, fig. 63 (original description, type locality: Suruga Bay, Japan); Nakabo 1993: 589 (key); Nakabo 2000: 675 (key); Chernova et al. 2004: 38 (list); Takami and Fukui 2012 (description); Nakabo and Kai 2013: 1216 (key).

Expanded diagnosis. 60–64 total vertebrae, 54–58 dorsal-fin rays, 48–54 anal-fin rays, 12–14 pectoral-fin rays, 6 caudal-fin rays, pyloric caeca absent, pore pattern 2-6-7-1; simple teeth on both jaws forming bands; gill slit extending ventrally in front of 1st–4th pectoral-fin ray base; pectoral fin deeply notched; coronal pore present; chin pores (= anteriormost mandibular pores) paired, opening separately, not in common pit; peritoneum and stomach black (modified from Kido 1988; Takami and Fukui 2012).

Distribution. Known only from 174 to 802 m depth in the continental slope of Suruga Bay, Japan.

***Paraliparis hokuto* Murasaki, Takami and Fukui 2019**

(Standard English name: Hokuto snailfish; standard Japanese name: Suruga-no-onibi; Figs. 14, 15; Tables 7, 8)

Paraliparis hokuto Murasaki, Takami and Fukui 2019b: figs. 1, 2, 3; tables 1, 2 (original description, type locality: Suruga Trough, Suruga Bay, Japan).

Materials examined. Two specimens. MSM-19-198, holotype: 192.7 mm SL, female, Suruga Trough, Suruga Bay, Japan, 34° 58.9′ N, 138° 37.9′ E–34° 56.1′ N, 138° 37.6′ E, 1,432–1,554 m, 7 July 2014, T/V *Hokuto*, 1.6 m ring net (warp length 1,650 m). MSM-19-199, paratype: 125.9 mm SL, male, Suruga Trough, Suruga Bay, Japan, 34° 59.1′ N, 138° 38.9′ E–34° 55.8′ N, 138° 38.4′ E, 1,462–1,562 m, 16 Nov. 2016, T/V *Hokuto*, beam trawl (warp length 2,400 m).

Comparative materials. *Paraliparis rosaceus*: holotype, USNM 48918, 135.3 mm SL, immature, off southern California, U.S.A., 32° 17' 00" N, 119° 17' 00" W, depth 1,799 m, 17 Jan. 1889; USNM 214608, 321 mm SL, female, off Oregon, U.S.A., 44° 50.2' N, 125° 32.5'

W, depth 2,758 m, 8 Mar. 1972; USNM 214609, 285 mm SL, male, off Oregon, U.S.A., 44° 57.6' N, 126° 40.0' W, depth 2,706 m, 19 Feb. 1971; USNM 214610, 82 mm SL, female, off Oregon, U.S.A., 44° 45.8' N, 131° 23.8' W, depth 3,358 m, 31 May 1970; USNM 214611, 78.5 mm SL, immature, off Oregon, U.S.A., 45° 55.5' N, 125° 38.8' W, depth 2,122 m, 20 Mar. 1970; HUMZ 77743, 305.0 mm SL, male, off Abashiri, Okhotsk coast of Hokkaido, Japan, 44° 33' N, 144° 24' E, depth 1,290–1,330 m, 24 Sept. 1978; HUMZ 78816, 292.7 mm SL, male, off Abashiri, Okhotsk coast of Hokkaido, Japan, 44° 56' N, 144° 30' E, depth 1,050–1,200 m, 8 Sept. 1978.

Diagnosis. 72 total vertebrae; 65 dorsal-fin rays; 60 or 61 anal-fin rays; 22 or 23 pectoral-fin rays; 6 caudal-fin rays; 3 pectoral proximal radials, all unnotched; 5 pyloric caeca, longest caecum ca. 60 % of HL; teeth weak, easily bent or damaged, completely uniserial in lower jaw; paired chin pores in common pit; opercular flap present; uppermost part of pectoral-fin base horizontally level with center or lower margin of eye.

Description. Counts and measurements presented in Table 7; holotype description given first, followed by those of paratype in parentheses when different. Body covered by thin, fragile epidermis lacking prickles, overlying thick jelly-like tissue; flexible, elongate; greatest depth and width slightly behind anus (Fig. 14a). Anus positioned about between the base of lowermost pectoral-fin ray and vertically below posterior tip of opercular flap. Body length from anus to caudal-fin base 5.14 (5.32) times HL, gradually becoming shallow and attenuating posteriorly. Snout deeply rounded, slightly projecting. Dorsal contour rounded from snout to nape. Single nostril tube-like, short, horizontally level with eye center. Eye round, almost equal to orbit length; low positioned, its counter not touching dorsal profile of head. Suborbital distance 0.81 (0.75) times eye diameter. Mouth subterminal, horizontal when closed; oral cleft extending to anterior margin of eye; suborbital fold covering ca. 1/2 of upper jaw, posterior margin of upper jaw below anterior margin of pupil; lower jaw included, lower tooth plates included entirely within posterior margin of upper tooth plate. Teeth on both jaws small, weak, easily bent or damaged, simple (Fig. 14b); upper-jaw teeth about 25 (20), mostly covered with skin, uniserial except irregularly biserial near symphysis; lower-jaw teeth about 60 (50), completely uniserial, more closely spaced than those of upper jaw. Diastema present on upper and lower jaw symphyses. Gill slit short, entirely above pectoral-fin base. Opercular flap small, triangular, supported by two dorsally recurved spines; upper spine stronger, shorter than lower spine. Uppermost part of pectoral-fin base horizontally level with center of eye (lower margin of eye), lowermost part below posterior margin of eye. Pectoral fin deeply notched, shortest ray at notch much shorter than half length of longest ray in both lobes; 18 (19) rays in upper lobe, 1st–14th (1st–15th) ray tips slightly prominent from membrane, 4th (3rd) ray from dorsalmost longest, reaching to below 4th (6th) dorsal-fin ray base, 72.1 (76.5) % of HL; 4 rays in lower lobe, each ray tips more prominent than in upper lobe rays, longest ray beyond vertical through dorsal-fin origin, 74.2 (72.8) % of HL. Pectoral proximal radials 3, round, lacking notches or fenestrae, two uppermost close together, third widely separated from second (Fig. 14c). Distal radials absent. Scapula with strong helve, basal notch absent. Coracoid triangular, with long slender helve. Dorsal-fin origin vertically level with posterior tip of opercular flap. First and second (first only) pterygiophores of dorsal fin without rays. Membrane of posterior dorsal-fin rays continuous with caudal fin, overlapping 48.8 (41.9) % of caudal-fin length. Anal-fin origin below 9th (8th) dorsal-fin ray base. First pterygiophore of anal fin supporting two rays. Membrane of posterior anal-fin rays continuous with caudal fin, overlapping 50.2 (45.2) % of caudal-fin length. Dorsal- and anal-fin ray lengths similar, both fins with anterior rays deeply buried in gelatinous tissue. Caudal fin truncate. Epural absent. Hypural plate fused with terminal vertebral centrum, slit absent. Minute genital papilla-like process at posterior of anus. Pyloric caeca long, longest caecum ca. 60 % of HL, located on left side. Pleural ribs absent.

Sensory pores. Nasal pores 2, maxillary pores 6, mandibular pores 7, suprabranchial pore 1; pore pattern 2-6-7-1. Coronal pore absent. All pore sizes similar to or smaller than nostril. Chin pores (= anteriormost mandibular pores) paired, opening close together in common pit. Free neuromasts about 27 (26), originating from around suprabranchial pore and extending posteriorly to about three-quarters length of body.

Color when fresh. Body dusky tan with faint blue, except black head, pectoral fin, caudal fin, and distal margins of dorsal and anal fins (all parts of body, head and fins black); eye black; peritoneum, as seen through skin, black (Fig. 15a, b).

Color in alcohol. Body, head, fins and eye similar to fresh coloration; mouth and gill cavity black; peritoneum black; stomach and pyloric caeca pale white.

Reproduction. Ovary pouch-like, yellowish, with ripe ovarian eggs 3.0 mm maximum diameter in female (testes slender, yellowish-white in male).

Distribution. Known only from 1,432 to 1,562 m depth in the northern part of the Suruga Trough, Suruga Bay, Japan.

Remarks. *Paraliparis hokuto* is most similar to *Paraliparis rosaceus* Gilbert 1890 from Japanese waters in the combination of fin ray and pectoral proximal radial counts (Table 8) and body proportions (Stein 1978; Kido 1988; Murasaki et al. 2019b). However, *P. hokuto* clearly differs from *P. rosaceus* in having weak, easily bent or damaged teeth on both jaws (vs. stout, resistant to bending or damage), the lower jaw teeth completely uniserial (vs. uniserial, except 2–5 oblique rows at symphysis), and 5 pyloric caeca (vs. 6–9) (Stein 1978; Kido 1988; Murasaki et al. 2019b).

Paraliparis hokuto is also similar to seven other species of *Paraliparis* characterized by completely uniserial teeth in the lower or both jaws as shown Table 8 (Garman 1899; Burke 1930; Andriashev 1986; Stein et al. 1991; Kido and Yabe 1995; Busby and Cartwright 2009; Stein 2012a; Murasaki et al. 2019b). Of the latter, *Paraliparis copei* Goode and Bean 1896 (four subspecies recognized from North and South Atlantic and Indian oceans) shares overlapping dorsal- and pectoral-fin ray counts, unnotched pectoral proximal radials and paired chin pores in a common pit with *P. hokuto* (Andriashev 1986; Kido and Yabe 1995; Murasaki et al. 2019b). However, *P. hokuto* has more anal-fin rays, fewer caudal-fin rays and pectoral proximal radials, and an opercular flap. *Paraliparis merodontus* Stein, Meléndez and Kong 1991 (South Pacific off Chile) has the same number and shape of pectoral proximal radials, and an opercular flap as *P. hokuto*, but differs in having fewer dorsal-, anal- and pectoral-fin rays and more caudal-fin rays. *Paraliparis alius* Stein 2012 (Ross Sea: Southern Ocean), *Paraliparis adustus* Busby and Cartwright 2009 (Bering Sea: North Pacific), *Paraliparis plicatus* Stein 2012 (Ross Sea) and *Paraliparis longicaecus* Stein 2012 (Ross Sea) have similar pectoral- and caudal-fin ray counts to *P. hokuto*, and also share the presence of an opercular flap (Busby and Cartwright 2009; Stein 2012a; Murasaki et al. 2019b). However, *P. hokuto* differs from those species in having more dorsal- and anal-fin rays, fewer pectoral proximal radials with notches lacking, paired chin pores in a common pit. *Paraliparis hokuto* also differs from *P. adustus* in the uppermost part of the pectoral-fin base being horizontally level with the center or lower margin of the eye (vs. dorsal margin of eye) (Busby and Cartwright 2009; Murasaki et al. 2019b). *Paraliparis attenuatus* Garman 1899 (North Pacific off Panama) has a similar combination of fin ray counts (except caudal-fin rays) with *P. hokuto* (Garman 1899; Murasaki et al. 2019b). However, the original illustrations of pectoral proximal radial and chin pore of this species clearly differ from those of the latter. Additionally, *P. attenuatus* apparently differs from *P. hokuto* in pyloric caeca length (short, details unknown in the former vs. long, ca. 60 % of HL in the latter) (Burke 1930; Murasaki et al. 2019b).

***Paraliparis meridionalis* Kido 1985**

(Standard Japanese name: Ryukyu-inkiuo; Fig. 16)

Paraliparis meridionalis Kido 1985a: 364–366, figs. 4, 5, 6 (original description, type localities: Okinawa Trough and East China Sea); Yatou 1985: 605, pl. 377 (description); Kido and Shiobara 1993: 87–90, figs. 1, 2 (description); Nakabo 1993: 590 (key); Nakabo 2000: 677 (key); Chernova et al. 2004: 42 (list); Nakabo and Kai 2013: 1218 (key).

Expanded diagnosis. 66–69 total vertebrae, 59–62 dorsal-fin rays, 54–56 anal-fin rays, 21–23 pectoral-fin rays, 8 caudal-fin rays, 5–7 pyloric caeca, pore pattern 2-6-7-1; simple teeth on both jaws forming bands; gill slit entirely above pectoral-fin base; pectoral fin deeply notched; chin pores (= anteriormost mandibular pores) paired, opening closely, but not in common pit; peritoneum black, stomach pale (modified from Kido 1985; Kido and Shiobara 1993).

Distribution. Known from 600 to 932 m depth in Suruga Bay, the Okinawa Trough and the East China Sea.

***Paraliparis ruficometes* Murasaki, Takami and Fukui 2018**

(Standard English name: Long-tailed snailfish; standard Japanese name: Onaga-inkiuo; Figs. 17; Tables 9, 10)

Paraliparis ruficometes Murasaki, Takami and Fukui 2018: figs. 1, 2; tables 1, 2 (original description, type locality: Suruga Trough, Suruga Bay, Japan)

Materials examined. 28 specimens (all collected from Suruga Trough, Suruga Bay, Japan). MSM-18-69, holotype: 80.4 mm SL, female, 34° 57.8′ N, 138° 38.8′ E–34° 55.9′ N, 138° 38.3′ E, 1,510–1,560 m, 14 Jan. 2015, T/V *Hokuto*, beam trawl (warp length 2,400 m). MSM-18-70, paratype: 52.9 mm SL, male, 34° 59.4′ N, 138° 38.1′ E–34° 56.2′ N, 138° 38.2′ E, 1,430–1,550 m, 7 May 2014, T/V *Hokuto*, 1.6 m ring net (warp length 1,670 m). MSM-18-71, paratype: 65.7 mm SL, female, 34° 58.9′ N, 138° 37.9′ E–34° 56.0′ N, 138° 38.2′ E, 1,430–1,560 m, 14 May 2014, T/V *Hokuto*, 1.6 m ring net (warp length 1,750 m). MSM-18-72, paratype: 58.2 mm SL, male, collected with MSM-18-71. MSM-18-73, paratype: 67.3 mm SL, female, 34° 58.9′ N, 138° 37.9′ E–34° 56.2′ N, 138° 38.2′ E, 1,430–1,550 m, 7 July 2014, T/V *Hokuto*, 1.6 m ring net (warp length 1,650 m). MSM-18-74, paratype: 77.7 mm SL, female, 34° 49.9′ N, 138° 37.5′ E–34° 47.9′ N, 138° 37.4′ E, 1,570–1,710 m, 17 July 2014, T/V *Hokuto*, 1.6 m ring net (warp length 1,900 m). MSM-18-75, paratype: SL unknown, female, 34° 42.8′ N, 138° 34.5′ E–34° 42.0′ N, 138° 35.0′ E, 1,960–2,070 m, 24 July 2014, T/V *Hokuto*, 1.6 m ring net (warp length 2,800 m). MSM-18-76, paratype: 67.8 mm SL, female, 34° 57.8′ N, 138° 38.8′ E–34° 55.9′ N, 138° 38.3′ E, 1,510–1,560 m, 14 Jan. 2015, T/V *Hokuto*, beam trawl (warp length 2,400 m). MSM-18-77, paratype: 60.2 mm SL, male, collected with MSM-18-76. MSM-18-78, paratype: 78.9 mm SL, female, 34° 57.8′ N, 138° 38.8′ E–34° 56.3′ N, 138° 38.3′ E, 1,510–1,550 m, 20 Jan. 2015, T/V *Hokuto*, beam trawl (warp length 2,500 m). MSM-18-79, paratype: 62.7 mm SL, female, collected with MSM-18-78. MSM-18-80, paratype: 56.0 mm SL, male, 34° 56.6′ N, 138° 38.3′ E–34° 56.2′ N, 138° 38.3′ E, 1,540–1,550 m, 22 May 2015, T/V *Hokuto*, 1.6 m ring net (warp length 1,800 m). MSM-18-81, paratype: 64.0 mm SL, female, 34° 58.8′ N, 138° 39.1′ E–34° 56.3′ N, 138°

38.4′ E, 1,480–1,520 m, 2 June 2015, T/V *Hokuto*, 1.6 m ring net (warp length 2,100 m). MSM-18-82, paratype: 70.0 mm SL, female, 34° 57.9′ N, 138° 38.1′ E–34° 56.0′ N, 138° 38.2′ E, 1,490–1,560 m, 11 Nov. 2015, T/V *Hokuto*, beam trawl (warp length 2,400 m). MSM-18-83, paratype: 54.3 mm SL, male, collected with MSM-18-82. MSM-18-84, paratype: 68.3 mm SL, female, 34° 58.0′ N, 138° 38.1′ E–34° 55.9′ N, 138° 38.3′ E, 1,490–1,560 m, 2 Dec. 2015, T/V *Hokuto*, beam trawl (warp length 2,400 m). MSM-18-85, paratype: 60.1 mm SL, male, collected with MSM-18-84. MSM-18-86, paratype: 59.7 mm SL, male, collected with MSM-18-84. MSM-18-87, paratype: SL unknown, female, 34° 58.8′ N, 138° 38.5′ E–34° 55.4′ N, 138° 38.2′ E, 1,460–1,570 m, 18 Feb. 2016, T/V *Hokuto*, beam trawl (warp length 2,400 m). MSM-18-88, paratype: 66.6 mm SL, male, collected with MSM-18-87. MSM-18-89, paratype: 61.2 mm SL, male, collected with MSM-18-87. MSM-18-90, paratype: SL unknown, female, 34° 49.0′ N, 138° 37.7′ E–34° 48.1′ N, 138° 37.4′ E, 1,660–1,750 m, 30 Aug. 2017, T/V *Hokuto*, modified beam trawl (warp length 2,700 m). NSMT-P 132395, paratype: 71.3 mm SL, female, 34° 49.5′ N, 138° 37.2′ E–34° 46.6′ N, 138° 37.3′ E, 1,650–1,750 m, 17 Mar. 2016, T/V *Hokuto*, beam trawl (warp length 3,000 m). NSMT-P 132396, paratype: 66.3 mm SL, female, collected with NSMT-P 132395. NSMTP 132397, paratype: 64.0 mm SL, male, collected with NSMT-P 132395. NSMT-P 132398, paratype: 61.6 mm SL, male, collected with NSMT-P 132395. NSMT-P 132399, paratype: 59.2 mm SL, male, collected with NSMT-P 132395. NSMT-P 132340, paratype: 52.0 mm SL, male, collected with NSMT-P 132395.

Comparative materials. *Paraliparis latifrons*: OS 16714, Pacific Ocean, 45° 38.4′ N, 126° 11.3′ W; OS 16716, Pacific Ocean, 45° 09.1′ N, 126° 21.4′ W; OS 5092, off the Oregon coast, Pacific Ocean, latitude and longitude unknown.

Diagnosis. 61–64 total vertebrae; 53–59 dorsal-fin rays; 48–52 anal-fin rays; 20–25 pectoral-fin rays, lower part of each ray completely free; 6 principal caudal-fin rays, dorsalmost elongate, about 2 or 3 times length of other rays; simple teeth on both jaws; gill slit 5.9–10.0% SL, extending in front of 9th–13th pectoral-fin ray base; 4 pectoral proximal radials (all unnotched); peritoneum and stomach black.

Description. Counts and measurements presented in Table 9; holotype description given first, followed by those of paratypes in parentheses when different. Body covered by thin epidermis overlying thin jelly-like tissue; flexible, elongate; greatest depth and width at near level of anus. Anus almost vertically below upper origin of gill slit (Fig 17a). Body from anus to caudal-fin base elongate, length 4.81 (4.11–5.02) times HL, gradually becoming shallow and attenuating posteriorly. Snout short, deep. Dorsal contour from snout tip to parietal round. Eye round, diameter ca. 2/3 of horizontal length of elliptical orbit. Single nostril tube-like, very short, horizontally level with center of orbit. Mouth large, terminal, almost horizontal when closed, posterior margin of upper jaw vertically level with posterior margin of orbit. All teeth simple on both jaws, mixed caniniform and cylindrical, forming a narrow band-like row (Fig. 17c). Diastema on upper and lower jaws symphysis. Gill slit elongate, upper origin horizontally level with eye upper margin, vertically level with dorsal-fin origin, lower origin in front of 10th (9th–13th) pectoral-fin ray base. Opercular flap angular, supported by two spines from opercle. Upper origin of pectoral-fin base at ca. 2/5 body depth from ventrum, lower origin below posterior margin of eye. Pectoral fin slightly notched, shortest ray at notch slightly longer than (rarely near equal) a half of longest ray of upper lobe: 18 (16–21) rays in upper lobe, 4th (2nd–5th) ray from dorsalmost longest, reaching to below 10th (8th–14th) dorsal-fin ray base, 66.5% (55.1–82.4%) of HL; 3 (3 or 4) rays in lower lobe, extending to anal-fin origin, 67.1% (56.4–91.0%) of HL; lowermost 5 (4–6) rays completely free, others connected by fin membrane. Pectoral proximal radials four, three uppermost arranged at nearly equal intervals, fourth widely separated from third, all with deformed elliptical shape, lacking notches; interradial fenestrae and distal radial absent (Fig. 17d). Anal-fin origin below

8th (6th–9th) dorsal-fin ray base. Dorsal- and anal-fin ray lengths similar. Caudal fin distal margin slightly emarginate, dorsalmost caudal-fin ray elongate, 2.85 (2.25–2.85) times length of middle caudal-fin ray. Epural absent. Urogenital papilla absent (present in male). Pleural ribs absent.

Sensory pores. Nasal pores 2, maxillary pores 6, mandibular pores 7, suprabranchial pore 1. Coronal pore absent. All pores larger than nostril. Chin pores (= anteriormost mandibular pores) paired, opening in separate pits. Free neuromasts on head and body absent.

Coloration when fresh. Body and fins orange red; mouth, gill cavity, eye, peritoneum and stomach black; pyloric caeca yellowish-white (Fig. 17b, d).

Coloration in alcohol. Body and fins milky-white; mouth, gill cavity, eye, peritoneum and stomach black (unchanged from fresh color); pyloric caeca whitish.

Reproduction. See the chapter V.

Distribution. Known only from 1,430 to 2,070 m depth in Suruga Trough, Suruga Bay, Japan.

Remarks. *Paraliparis ruficometes* similar to 43 other species of *Paraliparis* characterized by simple teeth on both jaws and a wide gill slit (gill slit condition unknown in four species, as shown in Table 10), a further 96 species having trilobate teeth or a narrow gill slit (Goode 1881; Garman 1899; Gilbert 1915; Burke 1930; Schmidt 1950; Cohen 1968; Stein 1978, 2005, 2012a, b; Anderson et al. 1979; Merrett 1983; Kido 1984, 1988; Matallanas 1984, 1999; Stein and Fitch 1984; Andriashev 1986, 1992, 1993, 1994, 1997; Stein and Andriashev 1990; Stein et al. 1991, 2001; Kido and Shiobara 1993; Kido and Yabe 1995; Andriashev and Chernova 1997; Matallanas and Pequeño 2000; Charnova and Eastman 2001; Stein and Chernova 2002; Chernova and Duhamel 2003; Chernova 2004, 2006; Busby and Cartwright 2006, 2009; Duhamel and King 2007; Chernova and Møller 2008; Baldwin and Orr 2010; Chernova and Prut'ko 2011; Takami and Fukui 2012; Stein and Drazen 2014). The ventral position of the gill slit (relative to pectoral-fin ray base) in *P. ruficometes* overlaps that condition in the following six species among the aforementioned 43 (condition in four species unknown, as shown in Table 10): *Paraliparis albeolus* Schmidt 1950 (Sea of Okhotsk), *Paraliparis bullacephalus* Busby and Cartwright 2009 (Gulf of Alaska), *Paraliparis hureaui* Matallanas 1999 (Southern Ocean), *Paraliparis albescens* Gilbert 1915 (Eastern Pacific), *Paraliparis holomelas* Gilbert 1896 (northern North Pacific) and *Paraliparis latifrons* Garman 1899 (eastern North Pacific). However, *P. ruficometes* differs from those species as follows: 53–59 dorsal-fin rays (vs. 62–65 in *P. albeolus* and 60 in *P. bullacephalus*), 48–52 anal-fin rays (vs. 57–59 in *P. albeolus*, 53–55 in *P. bullacephalus* and 46 in *P. hureaui*), 20–25 pectoral-fin rays (vs. 17–18 in *P. albescens*), 6 caudal-fin rays (vs. 5 in *P. albeolus* and 10 in *P. hureaui*), 6–8 pyloric caeca (vs. 3 in *P. bullacephalus*), slightly notched pectoral fin [vs. deeply notched in *P. bullacephalus*, *P. holomelas* (the shortest ray at notch shorter than a half of the longest ray of upper lobe), *P. hureaui* and *P. latifrons* (the shortest ray at notch rudimentary)], each pectoral-fin ray completely free in lower part of pectoral fin (vs. connected by fin membrane in *P. bullacephalus* and *P. holomelas*), interradial fenestrae absent on pectoral girdle (vs. present in *P. bullacephalus*, *P. hureaui* and *P. holomelas*), black peritoneum (vs. clear in *P. hureaui*) and black stomach (vs. pale in *P. latifrons*, clear in *P. hureaui*) (Schmidt 1950; Stein 1978; Anderson et al. 1979; Matallanas 1999; Busby and Cartwright 2006, 2009; Murasaki et al. 2018). The remaining 37 species of the former group, in which the ventral position of the gill slit does not overlap that of *P. ruficometes*, have a different combination of meristic counts or stomach color from *P. ruficometes* (Table 10). The following four species (of unknown gill slit position) clearly also differ from *P. ruficometes* as follows: pale or brown stomach (vs. black) in *Paraliparis attenuatus* Garman 1899 (off Panama), *Paraliparis debueni* Andriashev 1986 (off Chile) and *Paraliparis carlbondi* Stein 2005 (off Peru), and 49 dorsal- and 45 anal-fin rays (vs. 53–59 and 48–52, respectively) in

Paraliparis fimbriatus Garman 1892 (off Panama) (Table 10).

Paraliparis variabilidens Murasaki, Takami and Fukui 2019

(Standard English name: Variable-toothed snailfish; standard Japanese name: Mitsuba-inkiuo; Figs. 18; Tables 11, 12)

Paraliparis variabilidens Murasaki, Takami and Fukui 2019a: figs. 1, 2; tables 1, 2 (original description, type locality: Suruga Trough, Suruga Bay, Japan)

Material examined. MSM-19-32, holotype: 52.0 mm SL, female, Suruga Trough, Suruga Bay, Japan, 34° 59.1′ N, 138° 38.9′ E–34° 55.8′ N, 138° 38.4′ E, 1,462–1,562 m, 16 Nov. 2016, T/V *Hokuto*, beam trawl (warp length 2,400 m).

Diagnosis. 67 total vertebrae, 62 dorsal-fin rays, 57 anal-fin rays, 26 or 27 pectoral-fin rays, 9 caudal-fin rays (including 2 procurrent rays), ca. 12 pyloric caeca, mixed simple and trilobate teeth on both jaws, eye diameter 18.1% HL, gill slit extending ventrally in front of 2nd pectoral-fin ray base, deeply notched pectoral fin, body dusky, peritoneum black and stomach pale.

Description. Counts and measurements shown in Table 11. Body covered by thin, fragile epidermis lacking prickles, overlying thin jelly-like tissue; flexible, elongate; greatest depth and width near level of anus (Fig. 18a, c). Anus almost vertically below highest point of parietal. Body length from anus to caudal-fin base 3.74 times HL, gradually becoming shallow and attenuating posteriorly. Snout shallow, rounded, slightly projecting. Dorsal contour from snout to parietal almost straight. Eye round, 0.67 times orbit length. Single nostril tube-like, short, almost horizontally level with dorsal margin of pupil. Mouth subterminal, horizontal when closed, oral cleft extending posteriorly to below center of pupil; posterior margin of upper jaw below posterior margin of eye. Teeth on both jaws mixed simple and trilobate; outer teeth smaller, simple, caniniform or with moderately developed lateral shoulders; inner teeth larger, trilobate; forming about 15 rows of 3–6 teeth per row (Fig. 18d). Diastema absent from upper and lower jaw symphyses. Gill slit moderately short; upper end horizontally level with dorsal margin of pupil, below dorsal-fin origin; extending ventrally in front of 2nd pectoral-fin ray base. Opercular flap angular, supported by two spines; those extending posteriorly, posterior tip equal level vertically. Uppermost part of pectoral-fin base at ca. 1/2 body depth, lowermost part almost below posterior margin of eye. Pectoral fin deeply notched, shortest ray at notch less than half the length of longest ray in both lobes; 22 rays in upper lobe (23 on right side), each ray tip free of membrane, 6th ray from dorsalmost longest, reaching to below 10th dorsal-fin ray base, 58.6% of HL; 4 rays in lower lobe, free length greater than in upper lobe rays, longest ray nearly reaching below posterior tip of opercular flap, 39.7% of HL. Anal-fin origin below 8th dorsal-fin ray base. Dorsal- and anal-fin ray lengths similar. Caudal fin truncated. Epural absent. Hypural plate fused with terminal vertebral centrum, slit absent. Minute genital papilla-like process present at posterior of anus. Pyloric caeca short, located on left side, a few individual sacs slightly damaged but no fewer than 12 in total. Pleural ribs absent.

Sensory pores. Nasal pores 2, maxillary pores 6, mandibular pores 7, suprabranchial pore 1; pore pattern 2-67-1. Coronal pore absent. All pore sizes similar to nostril, except smaller suprabranchial pore. Chin pores (= anteriormost mandibular pores) paired, opening separately, not in common pit. Free neuromasts absent.

Color when fresh. Body and fins dusky, some parts tending orange; eye black; outer peritoneum as seen through skin black (Fig. 18b).

Color in alcohol. Body and fins dusky, parts tending orange when fresh becoming pale; eye and peritoneum black; mouth and gill cavity dusky; stomach and pyloric caeca pale.

Reproduction. Ovary pouch-like, translucent whitish, with ovarian eggs 0.2 mm in maximum diameter, unripe.

Distribution. Known only from 1,462 to 1,562 m depth in the northern part of the Suruga Trough, Suruga Bay, Japan.

Remarks. *Paraliparis variabilidens* can be associated with 19 other species of *Paraliparis* characterized by trilobate teeth (or simple teeth with lateral shoulders) (Garman 1899; Burke 1930; Stein 1978, 2012b; Andriashev 1992, 1993, 2003; Matallanas 1999; Chernova and Eastman 2001; Mecklenburg et al. 2002; Chernova 2003, 2006; Chernova and Duhamel 2003; Stein and Drazen 2014). Of the latter species, those sharing a gill slit extending ventrally in front of the pectoralfin ray base, and similar peritoneal and stomach coloration with *Paraliparis variabilidens* include *Paraliparis rossi* Chernova and Eastman 2001 (Southern Ocean), *Paraliparis dactylosus* Gilbert 1896 (North Pacific), *Paraliparis trilobodon* Andriashev and Neyelov 1979 (Southern Ocean) and *Paraliparis challengeri* Andriashev 1993 (Eastern North Atlantic) (Table 12). However, *P. variabilidens* clearly differs from these as follows: 62 dorsal-fin rays (vs. 49 or 50 in *P. rossi*; 45–49 in *P. trilobodon*), 57 anal-fin rays (vs. 44 in *P. rossi*; 41–43 in *P. trilobodon*), ca. 12 pyloric caeca (vs. 0 in *P. challengeri*), eye diameter 18.1% HL (vs. 28–33% HL in *P. dactylosus*), deeply notched pectoral fin (vs. unnotched in *P. challengeri*) and dusky body in preserved specimen (vs. pale in *P. rossi*, *P. dactylosus* and *P. trilobodon*) (Stein 1978; Andriashev 1993, 2003; Chernova and Eastman 2001; Mecklenburg et al. 2002; Chernova 2003). The remaining 15 species of the former group are characterized by different combinations of meristic counts, lowermost gill slit position, or peritoneum and stomach colors (Table 12).

Paraliparis liparinus (Goode 1881), originally collected off Rhode Island and described as *Amitra liparina*, lacked information on teeth shape (see Goode 1881). The two syntypes have subsequently been lost (Andriashev 1993). Although Burke (1930) redescribed *P. liparinus* from a new (non-type) specimen, noting simple teeth with lateral shoulders, the redescription clearly differed from the original, particularly in pectoral-fin structure (= unnotched), as Andriashev (1993) pointed out. *Paraliparis variabilidens* differs from *P. liparinus* and Burke's redescription of that species as follows: 62 dorsal-fin rays (vs. 67 in the former, 58 in the latter), 57 anal-fin rays (vs. 54, 55), 26 or 27 pectoral-fin rays (vs. 23, 22), 9 caudal-fin rays (vs. 6, 4), and dusky body (vs. yellowish white, pale) (Goode 1881; Burke 1930; Murasaki et al. 2019a).

V. Life history of *Paraliparis ruficometes*

Life histories of deep-sea snailfishes, based on morphological development and reproduction, have been reported for only two species, *Paraliparis holomelas* (North Pacific) (Busby and Cartwright 2006) and *P. dipterus* (Suruga Bay, Japan) (Takami and Fukui 2012), with morphological development only reported for *Rhinoliparis barbulifer* (Pacific coast off Tohoku region, Japan) (Kido and Kitagawa 1986). According to these studies, deep-sea snailfishes undergo direct development, larvae and juveniles occupying an epibenthic habitat, and adults spawning a small number of large eggs. Other reports have variously included limited information on larval morphology or reproduction [*Careproctus reinhardti*, *Paraliparis calidus* and *Paraliparis copei* in the North Atlantic (Able et al. 1986), and *Careproctus melanurus*, *Paraliparis cephalus* and *Rhinoliparis attenuatus* in the North Pacific (Ambrose 1996) for larval morphology; *Acantholiparis opercularis*, *Careproctus melanurus*, *Careproctus oregonensis*, *Careproctus ovigerum*, *Osteodiscus cascadiae*, *Paraliparis latifrons*, *Paraliparis mento* and *Paraliparis rosaceus* in the North Pacific (Stein 1980) for reproduction]. The life history of *Paraliparis ruficometes* is described herein, with notes on reproduction based on ovarian eggs.

Material examined. Larvae and juveniles: 9 specimens (all collected from Suruga Trough, Suruga Bay, Japan). Flexion stage: four unregistered specimens 12.3, 12.8, 13.8, 14.0 mm SL, 34° 56.6′ N, 138° 38.3′ E–34° 56.2′ N, 138° 38.3′ E, 1,540–1,550 m, 22 May 2015, T/V *Hokuto*, 1.6 m ring net (warp length 1,800 m). Postflexion stage, three unregistered specimens 15.5, 17.3, 18.5 mm SL, collected with above unregistered flexion stage specimens. Juvenile stage: two unregistered specimens 21.2, 23.8 mm SL, collected with above unregistered flexion stage specimens.

Adults: 28 type specimens listed in chapter IV and 16 unregistered specimens (all collected from Suruga Trough, Suruga Bay, Japan) listed below: 2 males, 31.0, 52.3 mm SL, 34° 58.9′ N, 138° 38.0′ E–34° 56.0′ N, 138° 38.2′ E, 1,434–1,570 m, 23 April 2014, T/V *Hokuto*, 1.6 m ring net (warp length 1,700 m); 2 males, 37.4, 41.2 mm SL and a female, 42.0 mm SL, 34° 59.4′ N, 138° 38.1′ E–34° 56.2′ N, 138° 38.2′ E, 1,430–1,550 m, 7 May 2014, T/V *Hokuto*, 1.6 m ring net (warp length 1,670 m); male, 46.2 mm SL, 34° 58.9′ N, 138° 37.9′ E–34° 56.0′ N, 138° 38.2′ E, 1,430–1,560 m, 14 May 2014, T/V *Hokuto*, 1.6 m ring net (warp length 1,750 m); 2 males, 29.2, 47.6 mm SL and a female, 32.4 mm SL, 34° 57.8′ N, 138° 38.8′ E–34° 55.9′ N, 138° 38.3′ E, 1,510–1,560 m, 14 Jan. 2015, T/V *Hokuto*, beam trawl (warp length 2,400 m); female, 41.1 mm SL, 34° 57.8′ N, 138° 38.8′ E–34° 56.3′ N, 138° 38.3′ E, 1,510–1,550 m, 20 Jan. 2015, T/V *Hokuto*, beam trawl (warp length 2,500 m); female, 43.3 mm SL, 34° 58.0′ N, 138° 38.1′ E–34° 55.9′ N, 138° 38.3′ E, 1,490–1,560 m, 2 Dec. 2015, T/V *Hokuto*, beam trawl (warp length 2,400 m); male, 37.1 mm SL, 34° 58.8′ N, 138° 38.5′ E–34° 55.4′ N, 138° 38.3′ E, 1,458–1,568 m, 18 Feb. 2016, T/V *Hokuto*, beam trawl (warp length 2,400 m); 2 males, 35.3, 43.4 mm SL and 2 females, 39.3, 44.1 mm SL, 34° 58.8′ N, 138° 38.5′ E–34° 55.4′ N, 138° 38.2′ E, 1,460–1,570 m, 18 Feb. 2016, T/V *Hokuto*, beam trawl (warp length 2,400 m).

1. Morphological development

(Standard lengths at each developmental stage, and counts and measurements are presented in Table 13.) Body covered by thin loose epidermis overlying thin jelly-like tissue at 12.3 mm SL, epidermis becoming looser with further development. Head and trunk short, thick, tail elongate and remarkably compressed posteriorly. Body depth greatest at parietal region, becoming gradually shallower posteriorly; maximum body depth slightly less than head length. Snout short, deep. Mouth large, terminal, almost horizontal when closed, posterior margin of upper jaw vertically level with posterior margin of orbit. Teeth simple, almost uniserial on upper and lower jaws in flexion stage (12.3–14.0 mm SL), uniserial or biserial in postflexion stage (15.5–18.5 mm SL), and forming irregular bands in juvenile (21.2, 23.8 mm SL) and adult stages (29.2–80.4 mm SL). Single nostril tube-like, very short, horizontally level with center of eye. Eye round, diameter ca. 2/3 of horizontal length of elliptical orbit. Upper origin of gill slit almost horizontally level with upper margin of orbit; lower origin slightly over uppermost pectoral-fin base in flexion and postflexion stages, extending in front of 9th–13th pectoral-fin ray bases in juvenile and adult stages. Opercular flap angular, supported by two spines from opercle. Anus position moving slightly more anteriorly with development until end of juvenile stage. Dorsal-fin origin vertically level with or slightly posterior to dorsal margin of gill slit. Anal-fin origin below 6th–9th dorsal-fin rays. Dorsal, anal and caudal-fins with full adult ray complements at 12.3 mm SL. Upper origin of pectoral-fin base horizontally level with lower margin of orbit; lower origin below posterior margin of eye or orbit. Pectoral-fin rays apparent at 12.3 mm SL, but full adult complement not attained until 21.2 mm SL; rays of upper part connected by membrane to each other, lowest 4–6 rays entirely without interconnecting membrane; all rays elongating with development during flexion and postflexion stages. Dorsalmost caudal-fin ray elongate in adult stage (39.3 mm SL) (condition unknown in specimens less than 39.3 mm SL due to poor condition).

Head sensory pores. Full adult complement, comprising nasal pores (2), maxillary pores (6), mandibular pores (7) and suprabranchial pore (1), apparent at 12.3 mm SL. Chin pores (= anteriormost mandibular pores) paired, opening separately. Coronal pore absent. All pore sizes similar to or smaller than nostril in flexion stage, larger than nostril except similar nasal and suprabranchial pores in postflexion, juvenile and adult stages.

Melanophores and coloration. Melanophores progressively increasing with development during flexion and postflexion stages, being scattered posteriorly on head (especially around gill cover) and dorsal region of abdominal cavity in flexion stage (Fig. 19a). Melanophores newly develop on entirety of head and trunk, and anterior half of tail in postflexion stage (Fig. 19b), subsequent increases in melanophore number becoming irregular. A juvenile specimen (23.8 mm SL) had fewer melanophores than found on a postflexion specimen (Fig. 19c). Abdominal cavity almost jet black at 12.3 mm SL. Body color of fresh adult specimens (35.3–80.4 mm SL) changing with growth, from dusky light yellow to orange red (Fig. 20a–e).

Body proportions. Body proportions remaining constant with growth included: head length to SL, maximum head depth to SL, maximum head width to SL, maximum body depth to SL, body depth at anal-fin origin to SL, predorsal-fin length to SL, preanal-fin length to SL, upper jaw length to HL, snout length to HL, eye diameter to HL, and gill slit length to HL (Fig. 21a). Increasing proportions included: lengths of upper and lower pectoral-fin lobes to HL (Fig. 21b). The anterior lower jaw margin to anus distance to HL was the only proportion that decreased with growth (Fig. 21c).

Remarks. *Paraliparis ruficometes* undergoes direct development, similar to *P. holomelas* (see Busby and Cartwright 2006), *P. dipterus* (see Takami and Fukui 2012) and *Rhinoliparis barbulifer* (see Kido and Kitagawa 1986). The smallest specimen (12.3 mm SL, flexion stage) observed of *Paraliparis ruficometes* had already acquired the following adult characters: all fin-ray complements, except upper part of pectoral fin (59 dorsal, 52 anal and 6 caudal), head sensory pore patterns (2-6-7-1), simple teeth on both jaws, wide gill slit, lower pectoral fin rays completely free, and black peritoneum. Onset of the juvenile stage (21.2 mm SL) was taken as the completion of the pectoral-fin ray complement, there being no other clear morphological changes occurring during the transition period from postflexion to juvenile. Eleven body proportions were constant with development, three other body proportions gradually changing until the end of juvenile stage (anus moving slightly anteriorly, and upper and lower pectoral-fin rays becoming more elongate).

The larvae and juveniles of *Paraliparis ruficometes* were distinguishable from those of five other species of *Paraliparis*, based on the combination of several adult diagnostic characters: 53–59 dorsal-fin rays; 48–52 anal-fin rays; 6 caudal-fin rays; lowermost 4–6 pectoral-fin rays completely free. In addition, the caudal region melanophore patterns clearly differed between known *Paraliparis* larvae as follows: on anterior 1/2 in *P. ruficometes* vs. absent in *P. copei* (see Able et al. 1986); only along dorsal-fin base in *P. calidus* (see Able et al. 1986), on anterior 4/5 in *P. dipterus* (see Takami and Fukui 2012) and entirely covering in *P. cephalus* and *P. holomelas* (see Ambrose 1996; Busby and Cartwright 2006). Other distinctive adult characters of *Paraliparis ruficometes*, including counts of vertebrae and pectoral fin proximal radials, stomach color and length of the dorsalmost caudal-fin ray, could not be assessed due either to the paucity of specimens for comparison or their poor condition.

The relationship between maximum size in adults (Y) and the size at onset of postflexion (X) in known species of *Paraliparis* is expressed as Y = 0.789X – 1.849 ($R^2 = 0.7496$, $p < 0.01$) (Fig. 22). An increase in size at the onset of postflexion in some species appeared to be associated with increasing adult maximum size.

2. Reproduction

Forty-four adult specimens included 21 females (32.4–80.4 mm SL) and the remainder males (29.2–66.6 mm SL). The ovaries in females < 60 mm SL were not enlarged, but were swollen so as to occupy most of the abdominal cavity in larger specimens. Male testes were slender and smooth. In larger females > 60 mm SL, the maximum diameter of ovarian eggs (e.g., 3.2 mm at 77.7 and 80.4 mm SL) had increased significantly with fish size, among 14 examined females (Fig. 23). Ova numbered 197 and 338 at 61.7 and 77.7 mm SL, respectively, ranging from 146 to 338 (average ± standard deviation: 202.4 ± 69.9) in five females (41.1–77.7 mm SL). Such ova were characterized as “undeveloped” (0.1–0.9 mm diameter classes, translucent to milky-white in color) or “developed” (1.0–3.2 mm, bright yellow to yellow). Notably, the “developed” group comprised plural peaks (Fig. 24), at 2.3, 2.5 and 3.2 mm diameter, including 3, 5 and 8 ova, respectively. The smallest specimen (61.5 mm SL) with “developed” ovarian eggs (≥ 1.0 mm) (Fig. 23) had been collected in April, other females with similar stage eggs occurring in January, July, September and November.

Remarks. The maximum ovarian egg diameter in *Paraliparis ruficometes* (3.2 mm) was about midway between 12 other known species of *Paraliparis* (2.0–4.5 mm) (Stein 1980; Able et al. 1984; Busby and Cartwright 2006; Takami and Fukui 2012), the number of ovarian eggs in the former (146–338) being fewer than in *P. dipterus* (322–735), the only other *Paraliparis* species for which batch fecundity is known (see Takami and Fukui 2012). Nevertheless, ovarian eggs, including both “undeveloped” and “developed” groups with single or multiple size distributions, have been noted among a number of deep-sea snailfishes, including species of *Paraliparis* (Stein 1980). Stein (1980) recognized three egg types, based on maximum egg numbers included in each aggregation of “developed” groups, relating them to spawning patterns: type I, <10 eggs (e.g., *Paraliparis latifrons*); type II, 11–100 eggs (e.g., *Paraliparis megalopus*); type III, >100 eggs (e.g., *Paraliparis rosaceus*). Types I and II were characteristic of continuous spawning and type III, periodic spawning. *Paraliparis ruficometes* is included in type I *sensu* Stein (1980), due to the low egg numbers (3–8) in each aggregation of “developed” groups (Fig. 24), and is therefore expected to be a continuous spawner. The periods during which adults possessing “developed” eggs were found (January, April, July, September and November) also suggested that *P. ruficometes* spawns year-round. Continuous year-round spawning has also been shown in *P. dipterus* (Takami and Fukui 2012).

VI. Discussion —life history strategies of deep-sea snailfishes

Life history strategies of deep-sea snailfishes, which probably have secondarily evolved from shallow marine to deep sea habitats, became moderately clear during the present study, certain aspects differing remarkably between 10 known shallow water species [e.g., *Liparis tanakae* (see Aoyama 1959; Kojima 2014) and *Liparis ochotensis* (see Sokolovskii and Sokolovskaya 2003; Yang et al. 2010)] and three deep water species [*Paraliparis holomelas* (see Busby and Cartwright 2006), *P. dipterus* (see Takami and Fukui 2012) and *P. ruficometes* (this study)]. Morphological development, larval habitat and reproduction (ovarian egg size and number) of representative species, *Liparis tanakae* (a shallow water species inhabiting depths of ca. 50–130 m), *Paraliparis dipterus* (a deep water species inhabiting continental slope depths of ca. 180–800 m) and *P. ruficometes* (a deep water species found in the Suruga Trough in depths of ca. 1,400–2,100 m), are summarized in Fig. 25.

Morphological development: metamorphic changes characteristic of *L. tanakae* vs. direct development in *P. dipterus* and *P. ruficometes*. Some shallow water species (e.g., *L. fucensis*) demonstrate a unique larval morphology as "bubble-morphs" (the head and trunk skin becoming enlarged and bubble-like) (Marliave and Peden 1989). However, the morphology of deep water species remains almost constant with development, being unchanged during transition through larval to juvenile stages (Busby and Cartwright 2006; Takami and Fukui 2012; this study).

Larval habitat: planktonic, inhabiting the surface water layer, compared with the near bottom habitat of adults in *L. tanakae* vs. epibenthic, as in adults, in *P. dipterus* and *P. ruficometes*.

Reproduction: ovarian egg size in *Liparis tanakae* < *Paraliparis dipterus* < *P. ruficometes* and ovarian egg number (= batch fecundity) in *L. tanakae* > *P. dipterus* > *P. ruficometes*. Egg size and number tend to increase and decrease, respectively, with increasing habitat depth. The spawning season is seasonal in *Liparis tanakae* [December to February in Sendai Bay, northern Japan (Aoyama 1959)], versus year-round in *Paraliparis dipterus* and *P. ruficometes* (Takami and Fukui 2012; this study). Snailfishes tend to conform to the K selection theory compared with other marine fishes [e.g., *Pagrus major* and *Katsuwonus pelamis* (see Matsuura 1972; Ashida et al. 2008)], this tendency becoming more pronounced in the increasingly stable environment of deeper water. However, the spawning patterns and batch fecundity described by Stein (1980) demonstrate the complexity and reproductive diversity of deep-sea snailfishes. The year-round spawning of a small number of large-sized eggs and direct development recognized in the deep-sea snailfishes are similar to features found in other epibenthic deep-sea fishes from Suruga Bay, including the genus *Leptoderma* (Family Alepocephalidae, Argentinoidei) (derived from deep sea habitats) (Takami and Fukui 2010), but radically different from those of mesopelagic fishes. It is not yet clear whether or not *Paraliparis dipterus* and *P. ruficometes* have developed specialized spawning methods, such as found in *Careproctus melanurus* and *C. colletti*, which deposit their eggs in the gill cavities of crabs (Gardner et al. 2014), because crabs from Suruga Bay have not been examined.

Teeth morphology: teeth shape and row number are more variable in deep-sea snailfishes compared with shallow-sea taxa. Such variability appears to be related to differences in feeding behavior in the former, as pointed by Stein (1978). Elsewhere in Pisces, morphological diversification due to differences in feeding behavior is recognized as the driver for sympatric speciation in African cichlids (e.g., Schluter 2000; Ford et al. 2016).

The significance of the life history strategies of deep-sea snailfish can be summarized as follows. Direct development of larger larvae (hatched from larger eggs) is likely effective in the early settlement of larvae and reduced larval mortality. Whereas the planktonic larvae of shallow water species are generally subject to dispersal, such is less likely for epibenthic larvae. Furthermore, the lower numbers and larger sizes of ovarian eggs in deep-sea species is offset by year-round spawning and reduced early larval mortality. Such strategies of deep-sea snailfish are more appropriate for survival in the harsh deep-sea environment (e.g., high water pressure, low water temperature, reduced food, and relatively strong tidal currents). Reduced larval dispersal may also emphasize geographical isolation leading to speciation, viz. the allopatric speciation. In addition, the morphological variations evident in teeth number and structure, probably related to differences in feeding behavior, may also be consistent with sympatric speciation. The enormous species diversity (ca. 70 % of all species) of deep-sea snailfishes and their uneven distribution seems to have resulted from such isolation and reduced larval mortality.

VII. Summary

1) This study clarified the taxonomy and aspects of the life history (based on morphological development and reproduction) of deep-sea snailfishes (Cottoidei: Liparidae) collected during a systematic survey of the epibenthic layer in Suruga Bay, southern Japan. Significant life history strategies of deep-sea snailfishes were detailed.

2) The survey, conducted by the T/V *Hokuto* (Tokai University, 18 t), comprised monthly cruises (January 2008–June 2019) over the continental slope and Suruga Trough, at three stations established for each: the Hagoromo Submarine Canyon (ca. 200–1,300 m depth), South Komagoe Submarine Canyon (ca. 500–1,000 m) and off the estuary of the Fuji-gawa River (ca. 350, 500, 600, 700, 800, 900 m) on the continental slope, and the northern part of Ugusuoki Gorge (ca. 1,400–1,600 m), middle part of Ugusuoki and Senoumi Gorges (ca. 1,600–1,700 m) and southern part of Senoumi Gorge (ca. 1,900–2,200 m) in the Suruga Trough. Collection gear utilized included ring nets and beam trawls.

3) A total of 464 snailfish specimens, collected from 155 tows, were found to represent two genera with 7 species: genus *Careproctus* with two species, including the new species *C. surugaensis*, and genus *Paraliparis* with five species, including three new species, *P. ruficometes*, *P. variabilidens* and *P. hokuto*, and the first record from Suruga Bay of *P. atramentatus*. The distribution patterns of the seven species were consistent with "Continental slope" (ca. 200–1,300 m depth) and "Suruga Trough" (ca. 1,400–2,200 m) types.

4) A total of two genera with 9 species (including two species that were not collected during this study) of deep-sea snailfishes from Suruga Bay were described, and a key to genera and species provided. Intraspecific variations in teeth tip shape due to ontogenetic development in *Paraliparis atramentatus* were reported for the first time in the genus.

5) The life history of the new species *Paraliparis ruficometes* was described on the bases of

morphological development and reproduction. *Paraliparis ruficometes* undergoes direct development, spawns a low number of large eggs, and year-round spawning as described in two other species of *Paraliparis*.

6) The life history strategy of deep-sea snailfishes differed significantly from that of shallow water species, the former being characterized by direct development (vs. metamorphic in the latter), similar larval and adult habitats (vs. different), low numbers of large eggs spawned (vs. small eggs in large numbers), and year-round spawning (vs. seasonal). The enormous species diversity and uneven distribution of deep-sea snailfishes may have been caused by the above life history strategies.

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Figures and tables

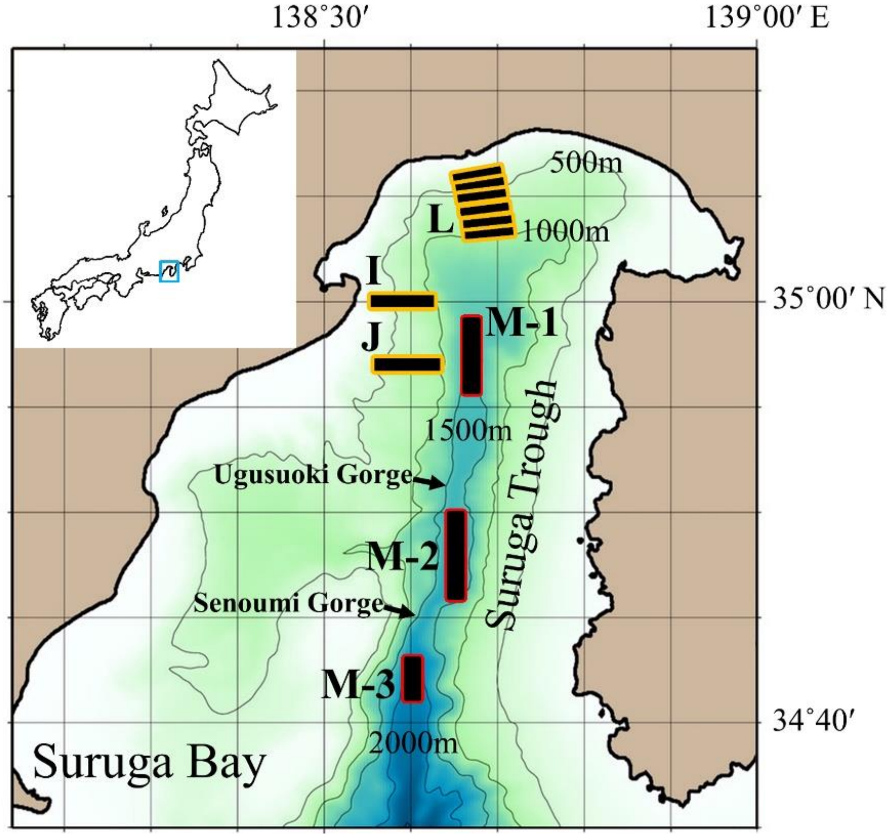

Fig. 1 Sampling locations in Suruga Bay. *Closed rectangles* indicate areas trawled (*yellow frames*: continental slope, *red frames*: Suruga Trough)

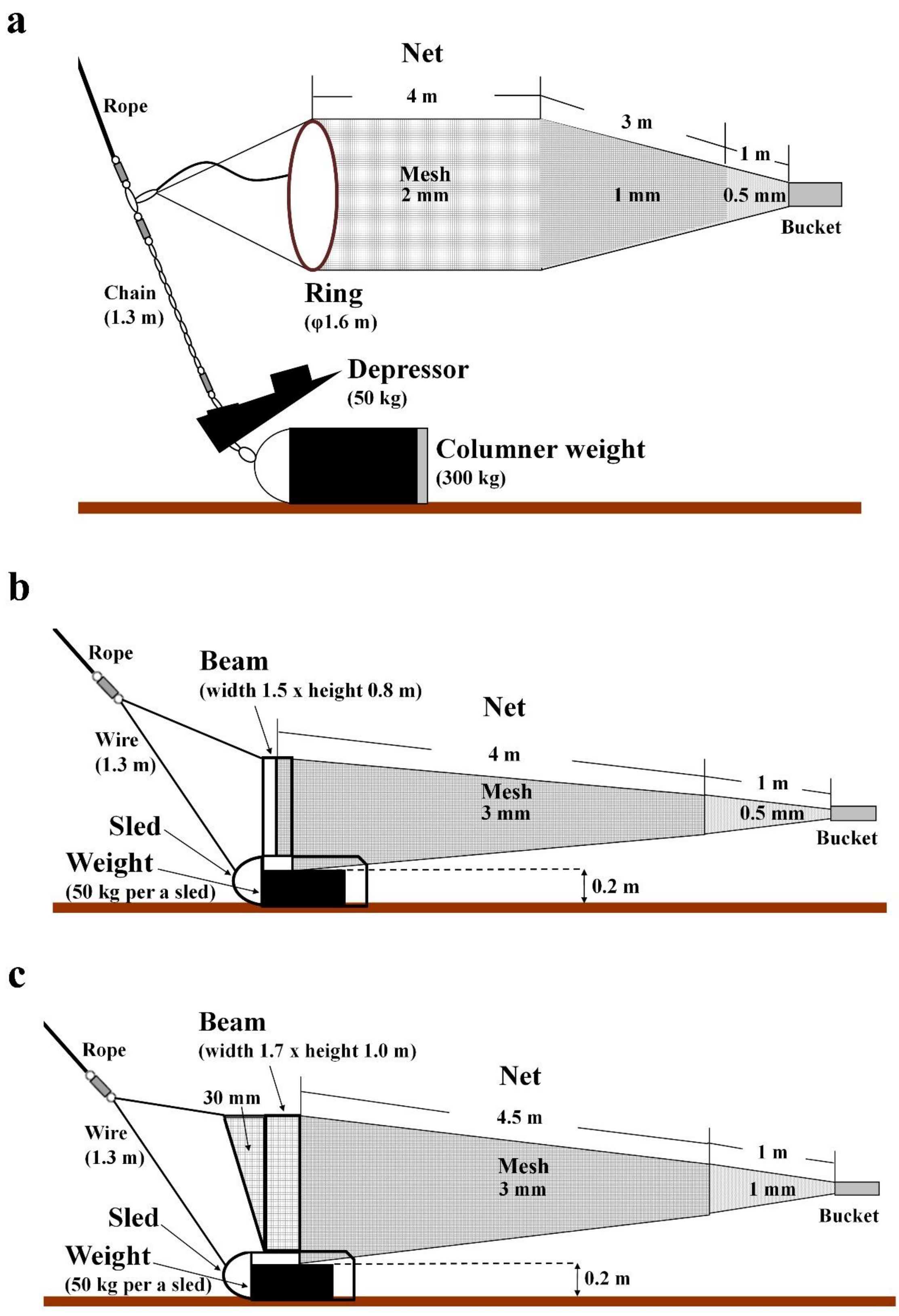

Fig. 2 Schematic illustrations of collection gear. **a** ring net (φ 1.6 m); **b** beam trawl (wide 1.5 m × height 0.8 m); **c** beam trawl (wide 1.7 m × height 1.0 m)

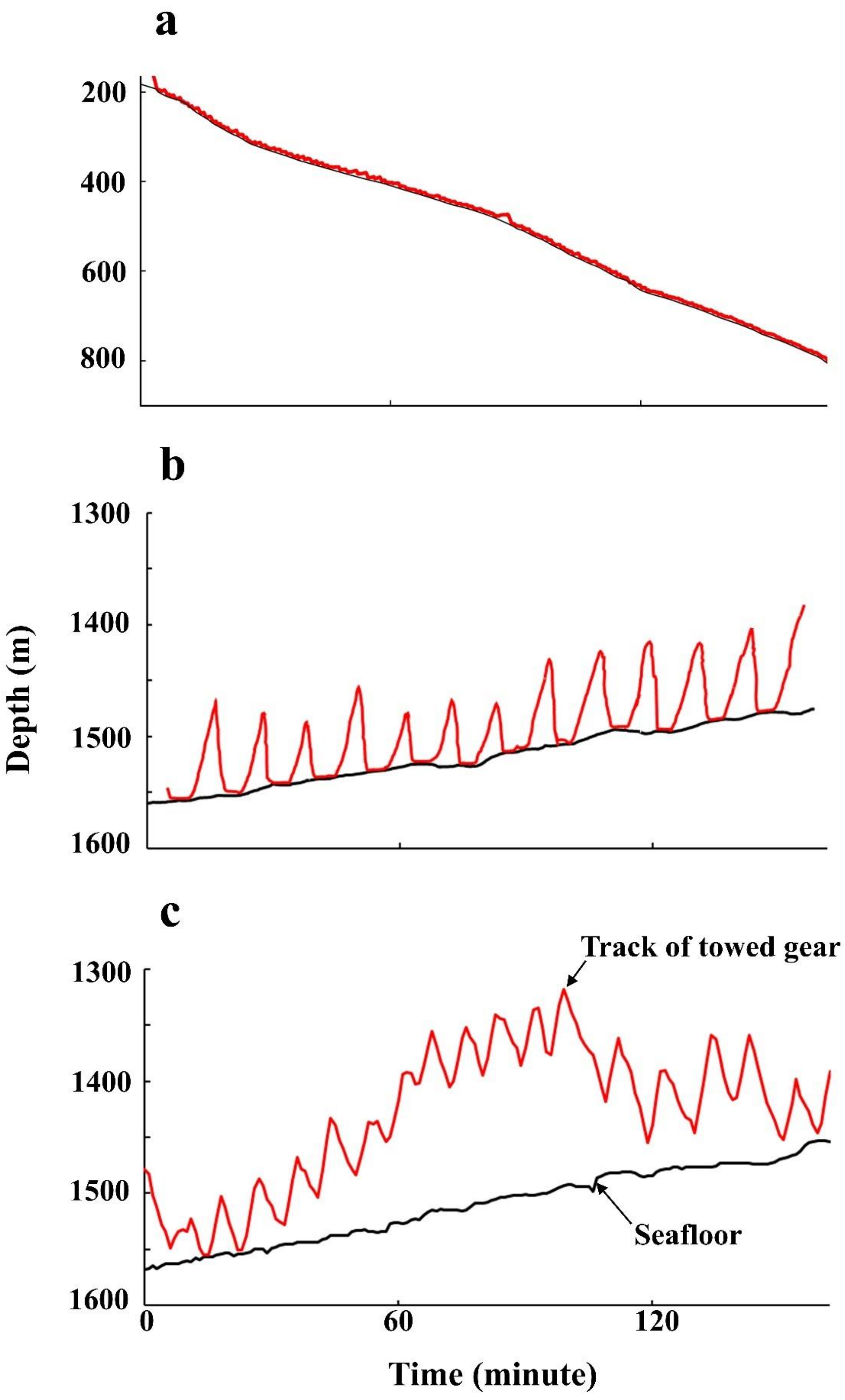

Fig. 3 Relationships between the towing and bottom depths. **a** Towed by ring net on continental slope (St. I, 8 April 2009); **b** towed by beam trawl in Suruga Trough (St. M-1, 16 November 2016); **c** towed by ring net in Suruga Trough (St. M-1, 7 July 2014)

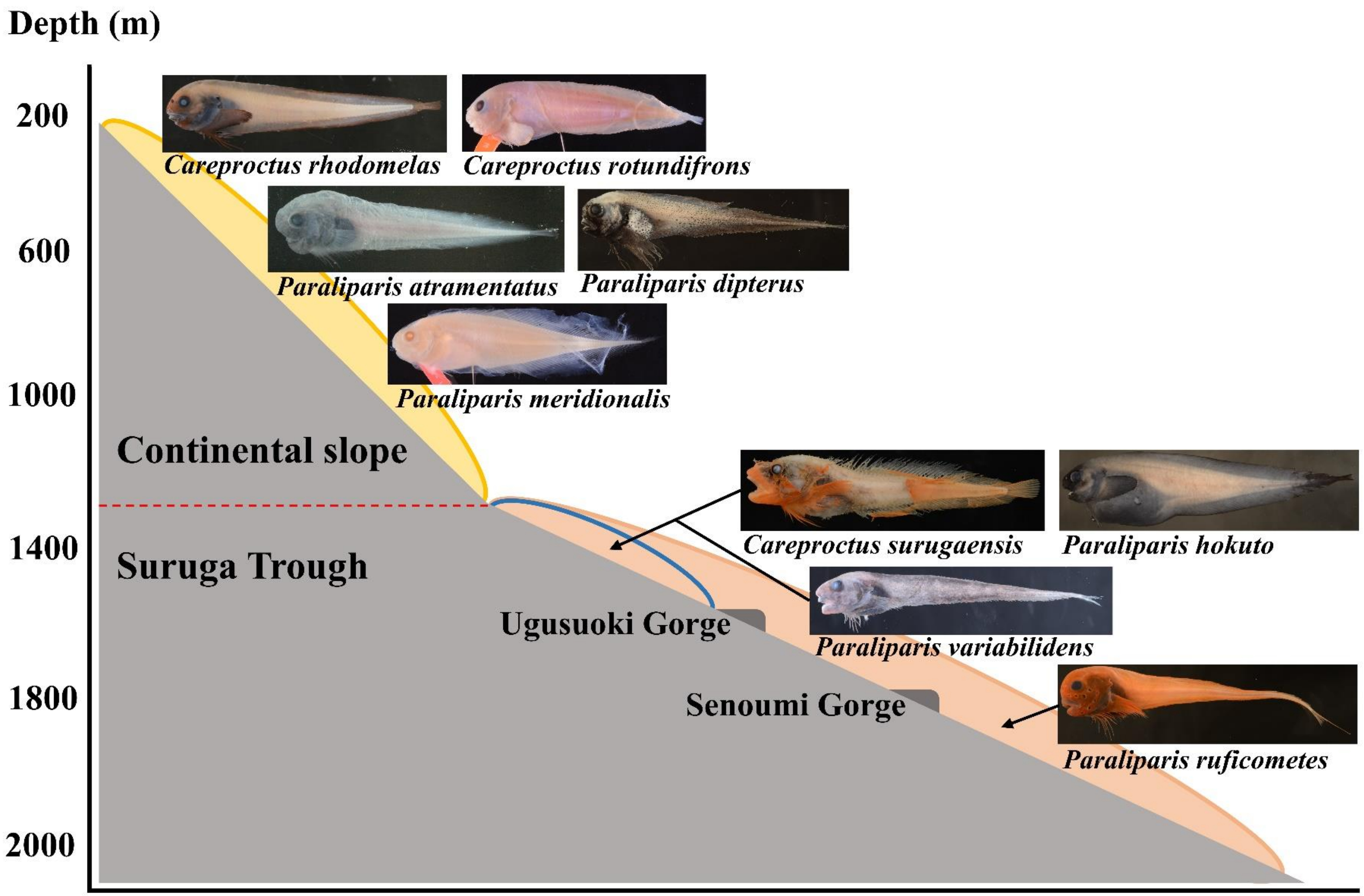

Fig. 4 Vertical separation of deep-sea snailfishes in Suruga Bay. *Careproctus rotundifrons* and *Paraliparis meridionalis* (both continental slope species) (Kido and Shiobara 1993; Sakurai and Shinohara 2008) were not collected during this study

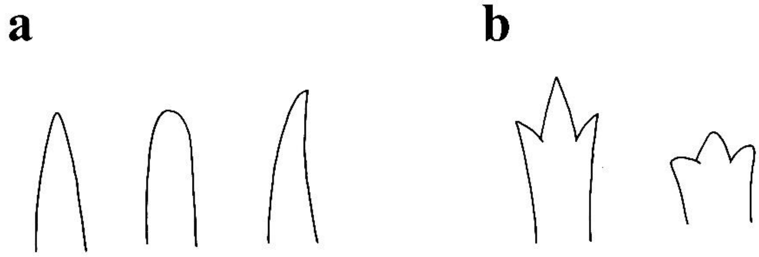

Fig. 5 Snailfish jaw teeth shapes **a** simple; **b** trilobate

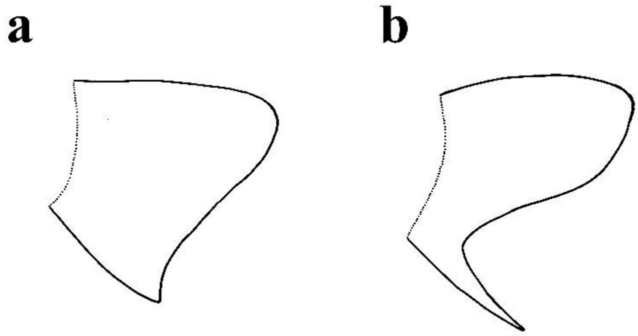

Fig. 6 Snailfish pectoral fin shapes **a** slightly notched; **b** deeply notched

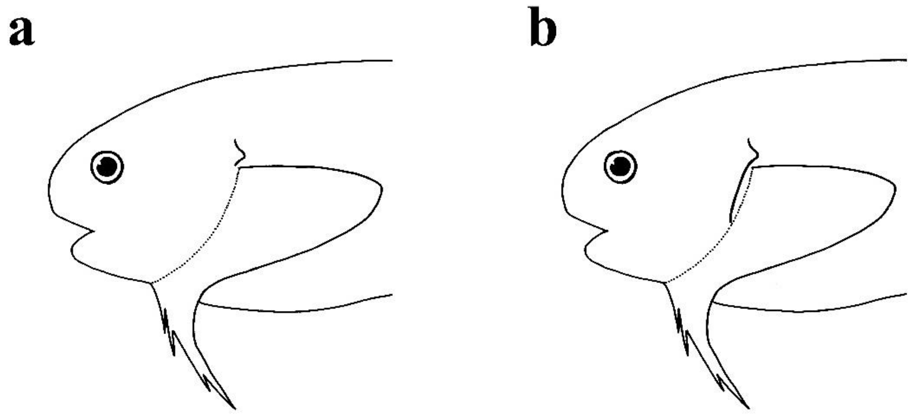

Fig. 7 Snailfish gill slit lengths **a** narrow; **b** wide

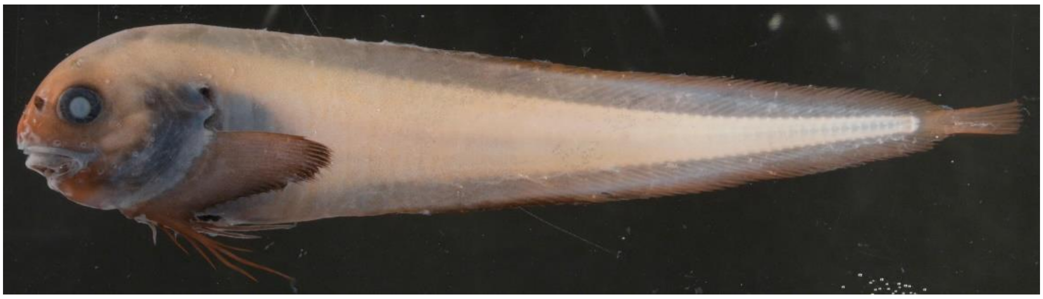

Fig. 8 Photograph of fresh specimen of *Careproctus rhodomelas*, unregistered specimen, 78.1 mm SL, sex unknown

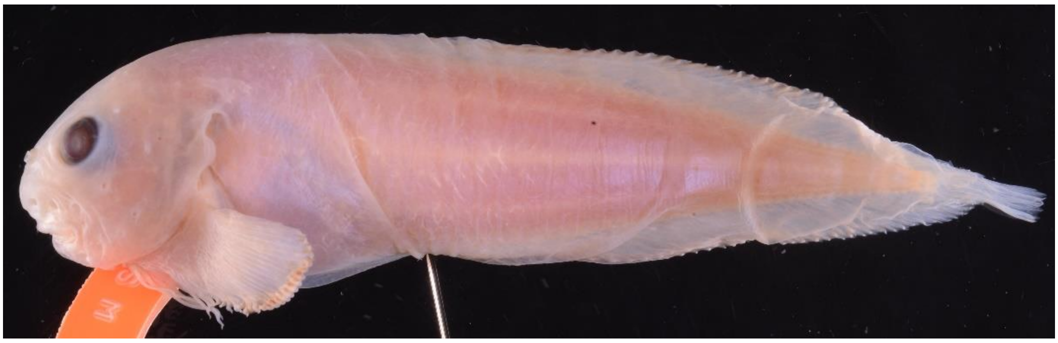

Fig. 9 Photograph of preserved specimen of *Careproctus rotundifrons*, MSM-15-81, 99.0 mm SL, sex unknown

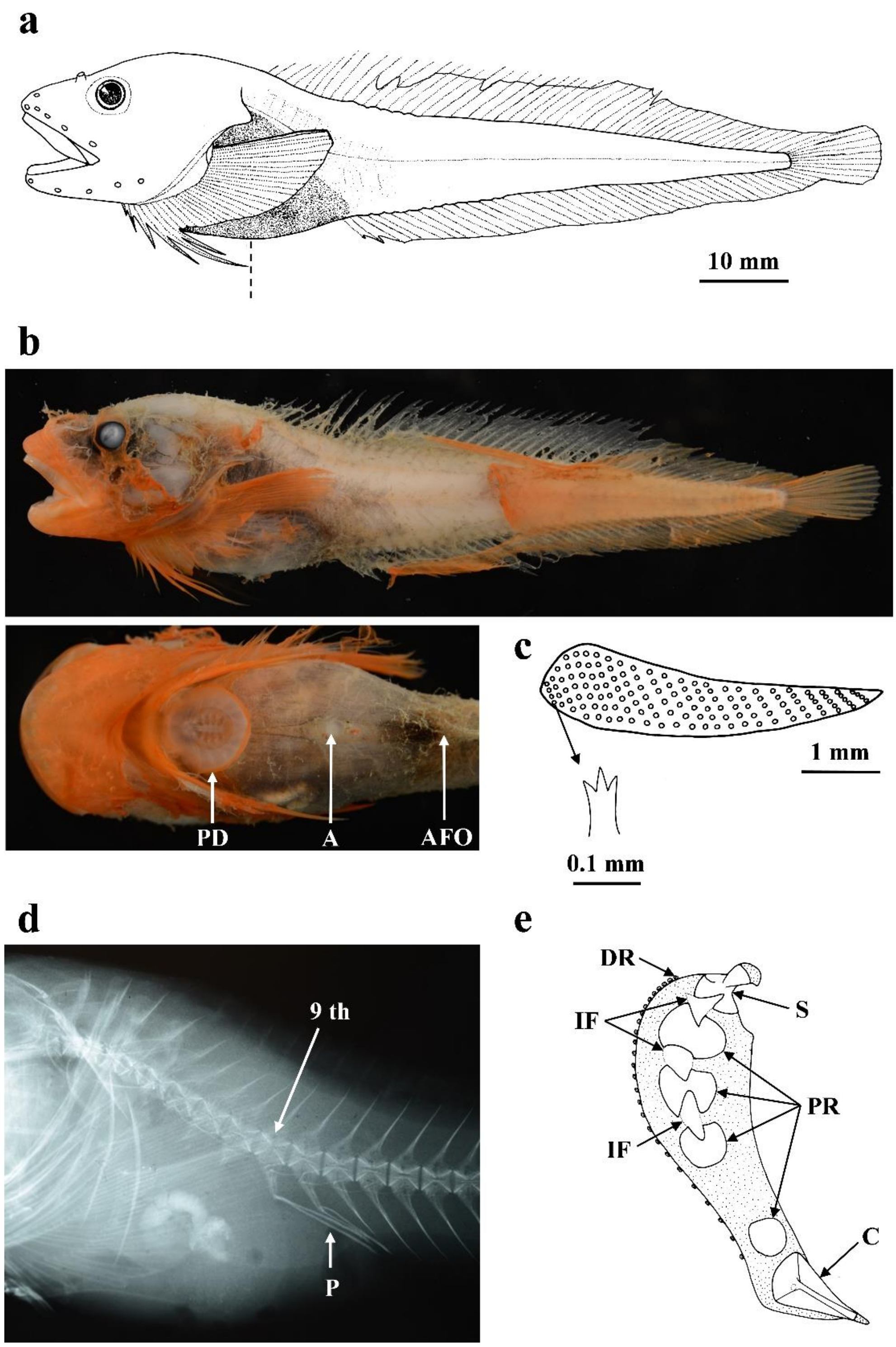

Fig. 10 *Careproctus surugaensis*, MSM-17-81, holotype, 82.6 mm SL. **a** lateral view of body, sketched during preservation in 10 % seawater formalin; **b** lateral view of body and ventral view of abdominal region, respectively, photographed about three hours after collection; **c** sketch of upper jaw teeth (right side); **d** radiograph of abdominal vertebrae; **e** sketch of cleared-and-stained pectoral girdle (right side). *A* anus, *AFO* anal-fin origin, *C* coracoid, *DR* distal radial, *IF* interradial fenestra, *P* left and right pleural ribs, *PD* pelvic disk, *PR* proximal radial, *S* scapula, *9th* 9th abdominal vertebrae

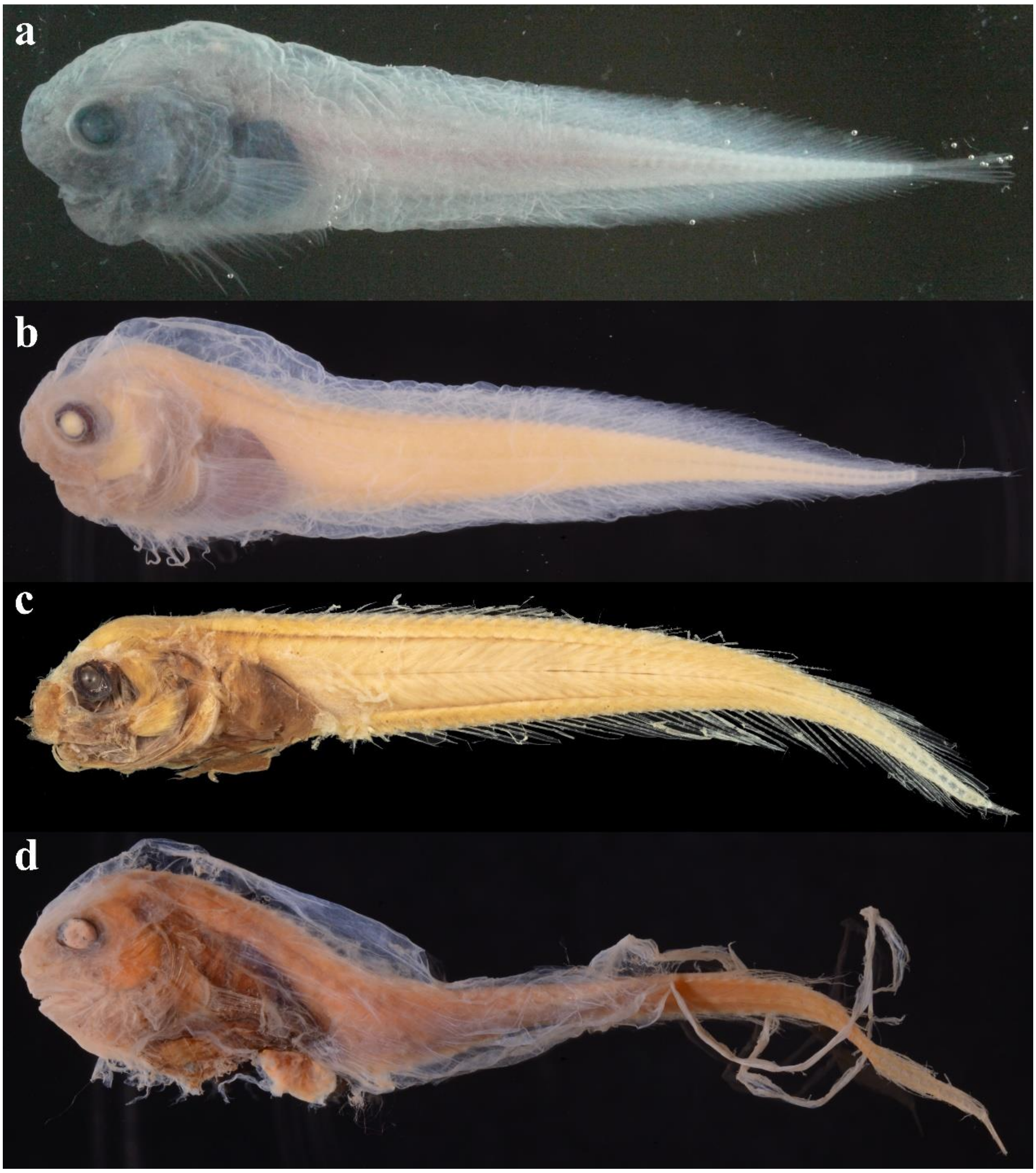

Fig. 11 Photographs of *Paraliparis atramentatus*. **a** MSM-19-200, 43.6 mm TL, 38.8 mm SL, female (taken when fresh); **b** MSM-19-200 (taken after preservation); **c** holotype, USNM 73345, TL unknown, 67.5 mm SL, male (preserved specimen), taken by S. Raredon (USNM); **d** BSKU 26438, TL unknown, 71 mm SL, female (preserved specimen)

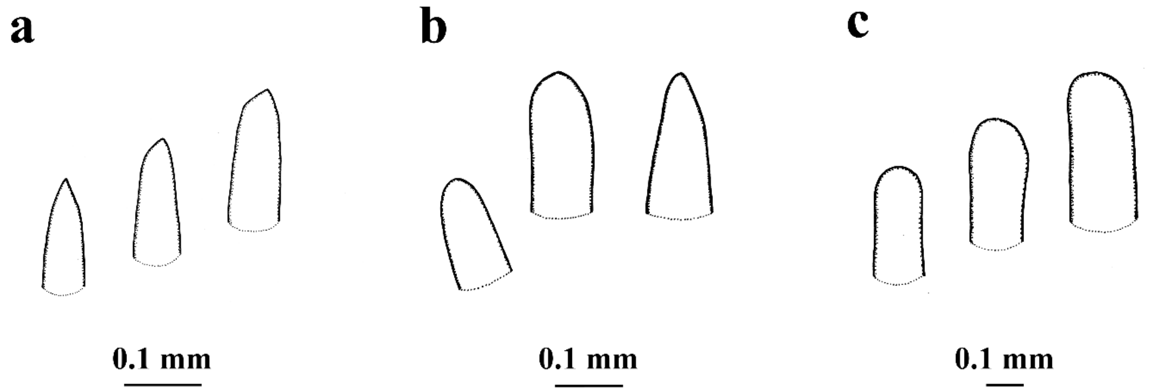

Fig. 12 Sketches of upper-jaw teeth (right side) of *Paraliparis atramentatus* Gilbert and Burke 1912. **a** MSM-19-200, 43.6 mm TL, 38.8 mm SL, female; **b** holotype, USNM 73345, TL unknown, 67.5 mm SL, male; **c** BSKU 26438, TL unknown, 71 mm SL, female

Fig. 13 Photograph of fresh specimen of *Paraliparis dipterus*, unregistered specimen, 48.7 mm SL, sex unknown

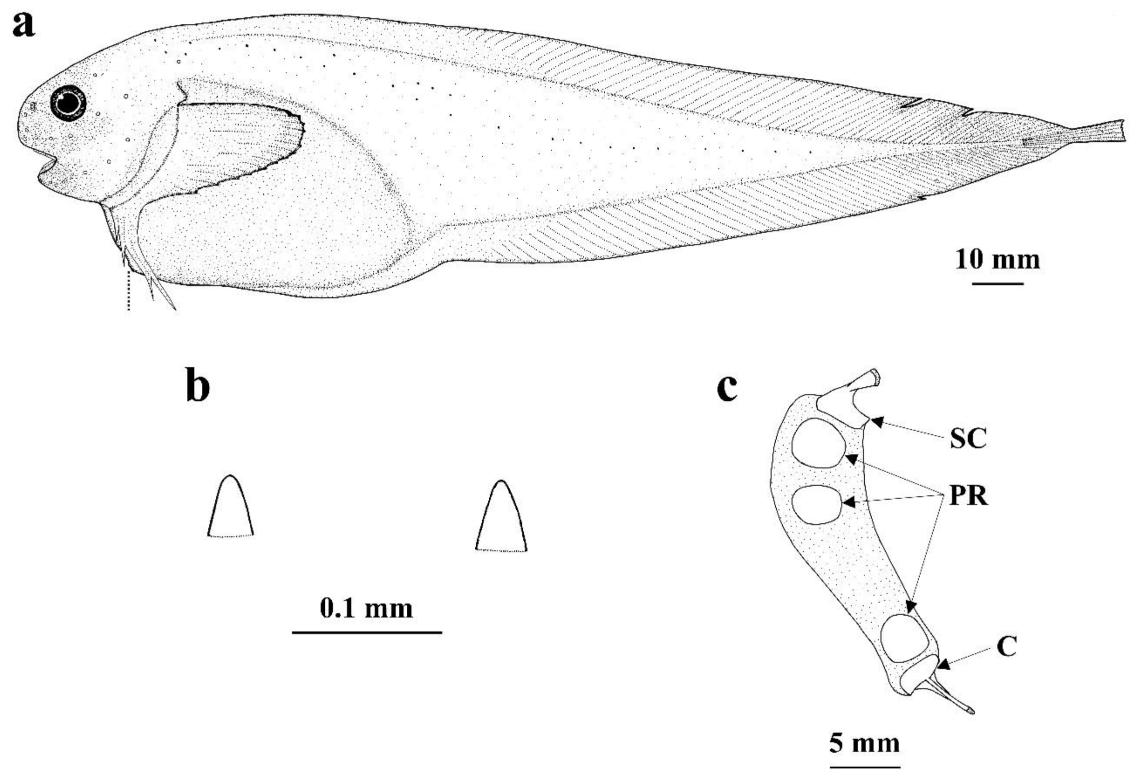

Fig. 14 Sketches of *Paraliparis hokuto*, holotype, MSM-19-198, 212.8 mm TL, 192.7 mm SL, female. **a** Lateral view; **b** upper-jaw teeth (right side); **c** pectoral girdle (right side). *C* coracoid, *PR* proximal radial, *SC* scapula

Fig. 15 Photographs of fresh specimens of *Paraliparis hokuto*. **a** Holotype, MSM-19-198, 212.8 mm TL, 192.7 mm SL, female; **b** paratype, MSM-19-199, 138.3 mm TL, 125.9 mm SL, male

Fig. 16 Photograph of preserved specimen of *Paraliparis meridionalis*, MSM-11-264, 163.5 mm SL, sex unknown

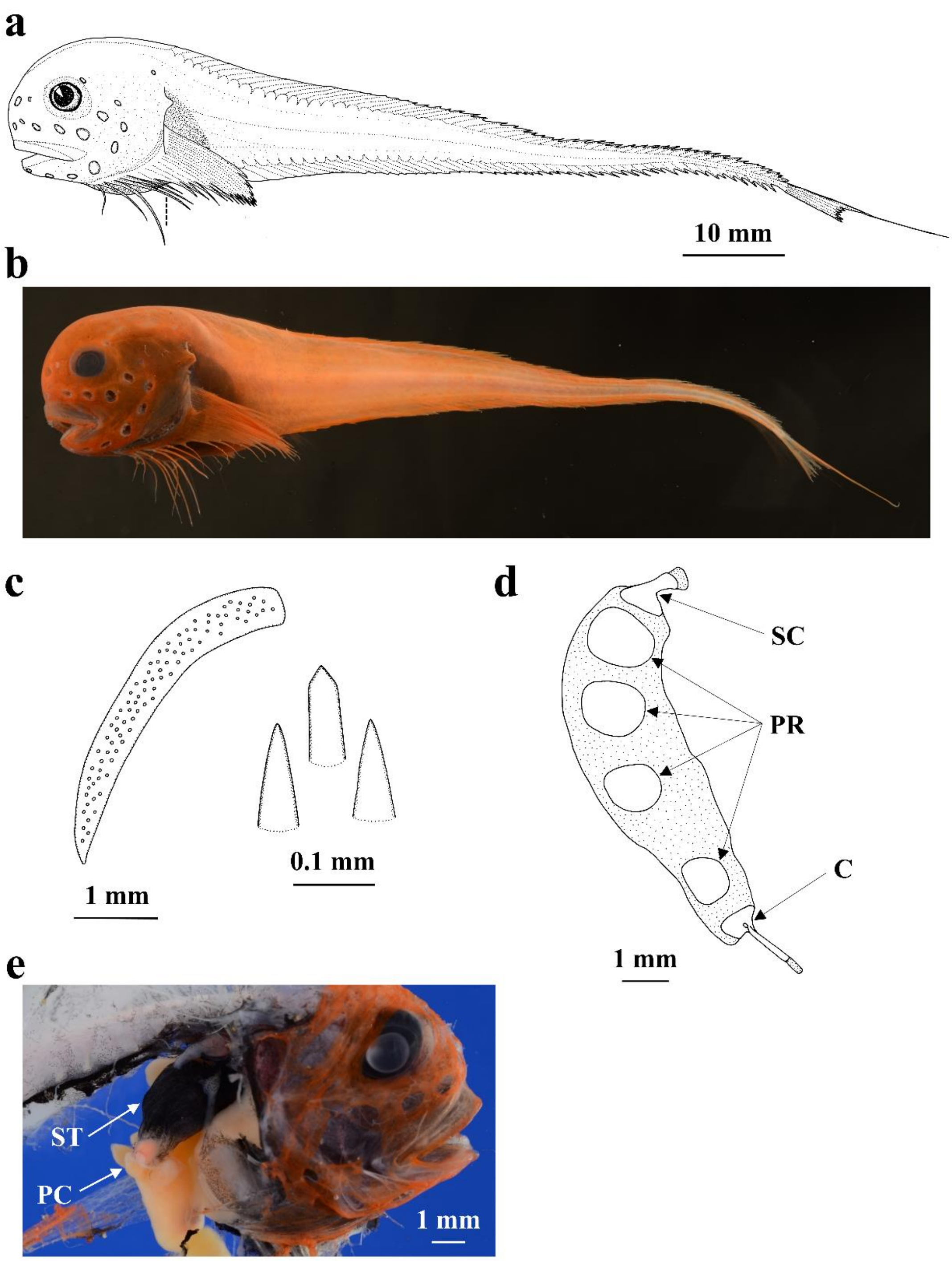

Fig. 17 *Paraliparis ruficometes*. **a** Lateral view of holotype, sketched during preservation in 70 % ethanol, MSM-18-69, 80.4 mm SL, female; **b** lateral view of holotype, photographed ca. three hours after collection, MSM-18-69, 80.4 mm SL, female; **c** sketch of upper jaw teeth (right side), MSM-18-76, paratype, 67.8 mm SL, female; **d** sketch of cleared-and-stained pectoral girdle (right side), MSM-18-76, paratype, 67.8 mm SL, female; **e** stomach and pyloric caeca, photographed ca. three hours after collection, MSM-18-90, paratype, SL unknown, female. *C* coracoid, *PC* pyloric caeca, *PR* proximal radial, *SC* scapula, *ST* stomach

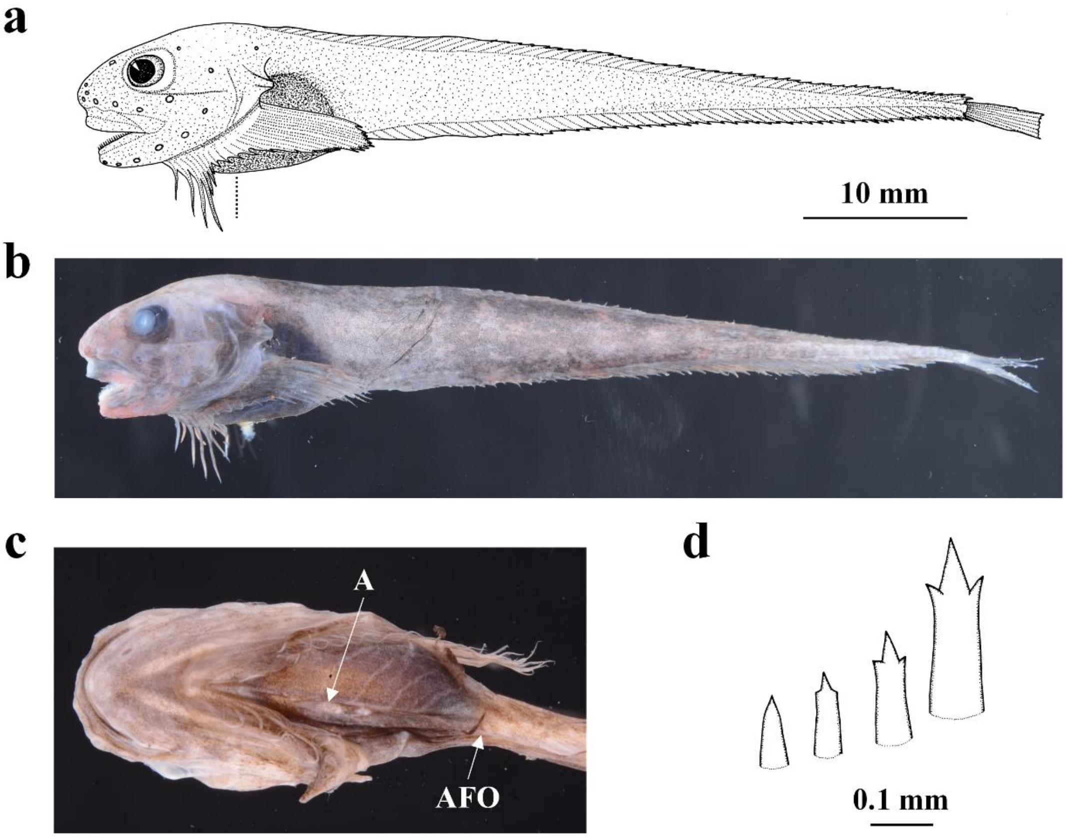

Fig. 18 *Paraliparis variabiliden*, holotype, MSM-19-32, 55.9 mm TL, 52.0 mm SL, female. **a** Lateral view, sketched after preservation in 70% ethanol; **b** lateral view, photographed ca. three hours after collection; **c** ventral view of abdominal region, photographed after preservation in 70% ethanol; **d** sketch of upper jaw teeth (right side). *A* anus, *AFO* anal-fin origin

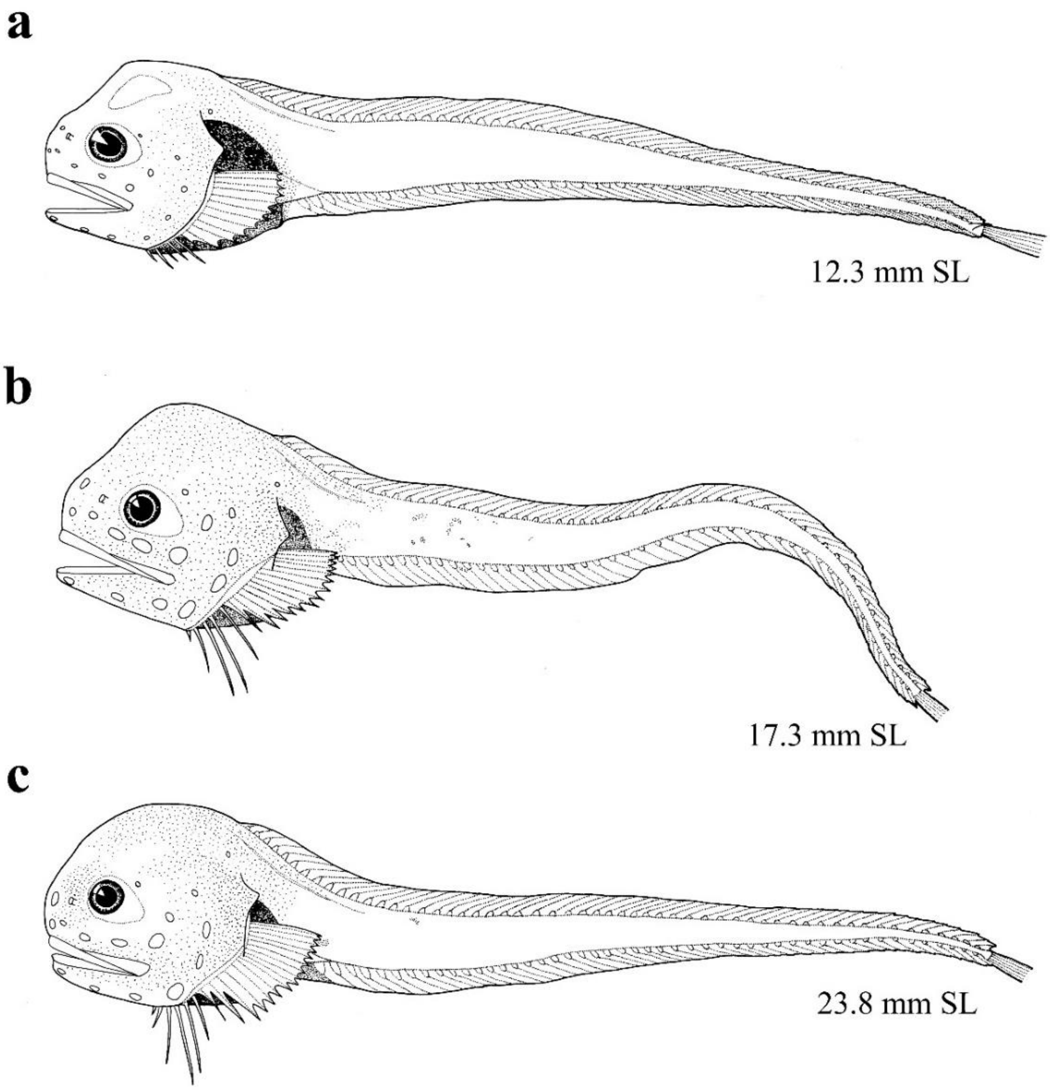

Fig. 19 Larvae and juveniles of *Paraliparis ruficometes*. **a** Unregistered specimen, 12.3 mm SL, flexion stage; **b** unregistered specimen, 17.3 mm SL, postflexion stage; **c** unregistered specimen, 23.8 mm SL, juvenile stage

a

b

c

d

e

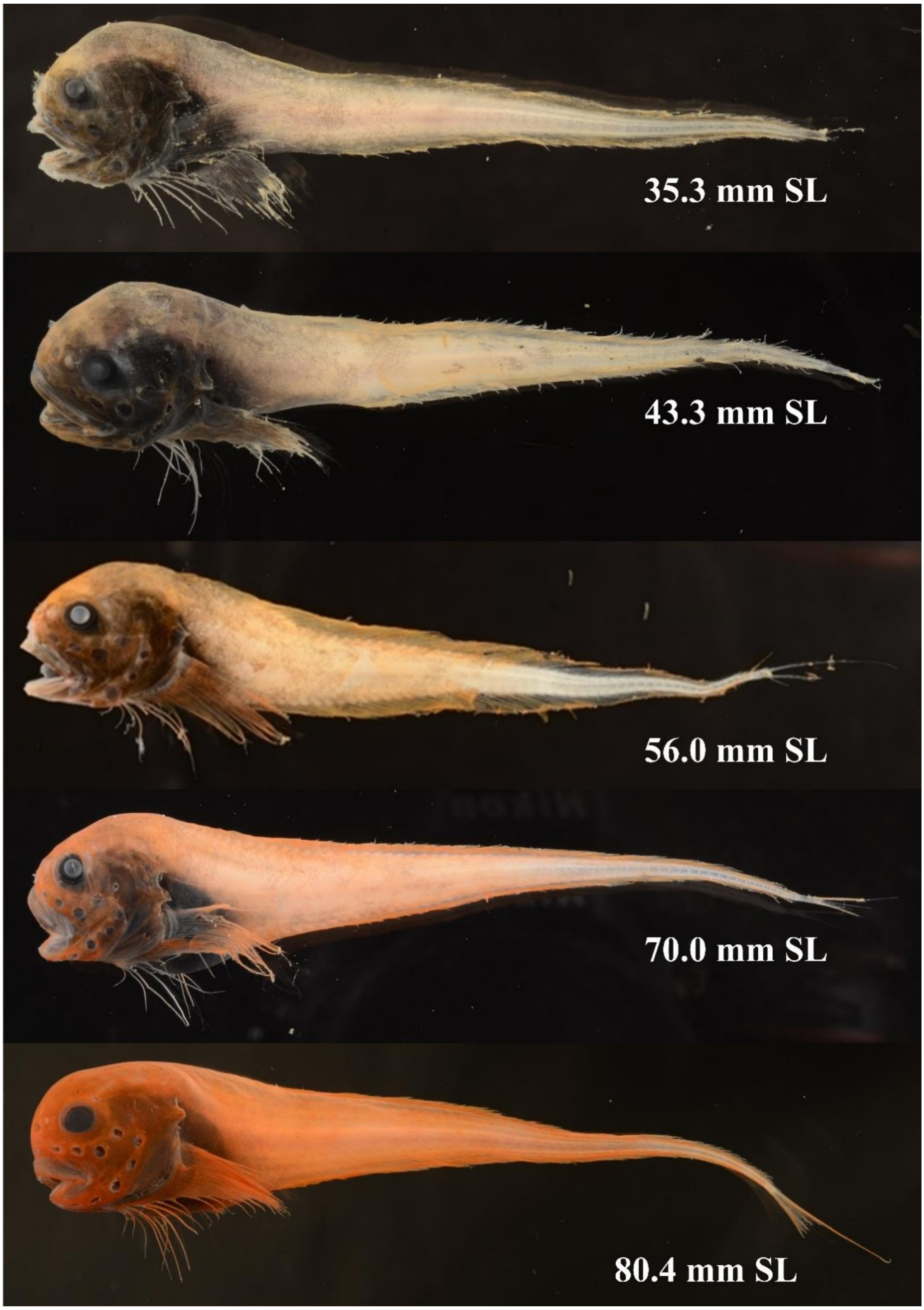

Fig. 20 Fresh specimens of *Paraliparis ruficometes* in adult stage. **a** Unregistered specimen, 35.3 mm SL, male; **b** unregistered specimen, 43.3 mm SL, female; **c** MSM-18-80, 56.0 mm SL, male; **d** MSM-18-82, 70.0 mm SL, female; **e** MSM-18-69, 80.4 mm SL, female

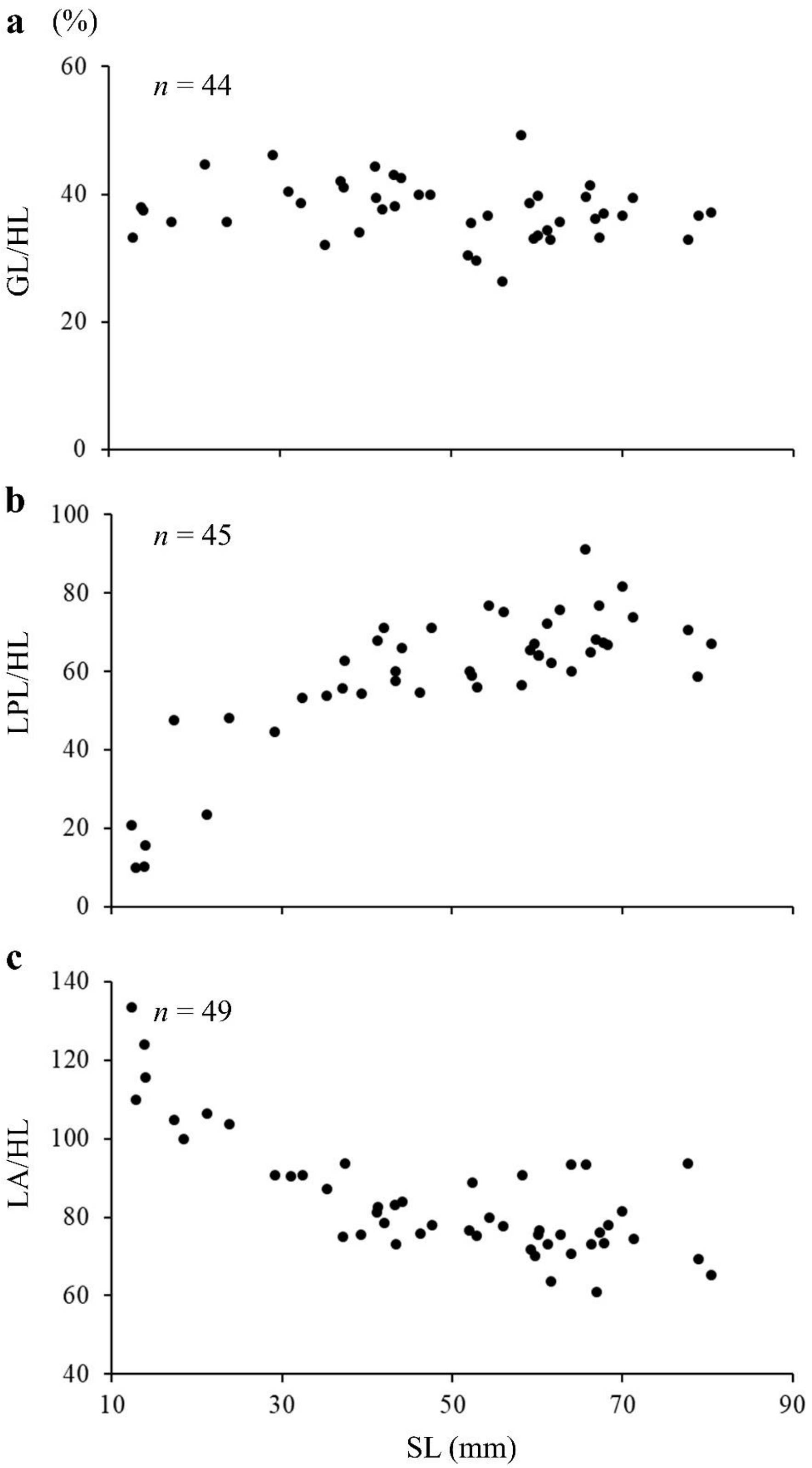

Fig. 21 Relationships between standard length (SL) and selected body proportions. **a** Gill slit length to head length (GL/HL); **b** longest pectoral-fin ray length in lower lobe to head length (LPL/HL); **c** anterior lower jaw margin to anus distance to head length (LA/HL)

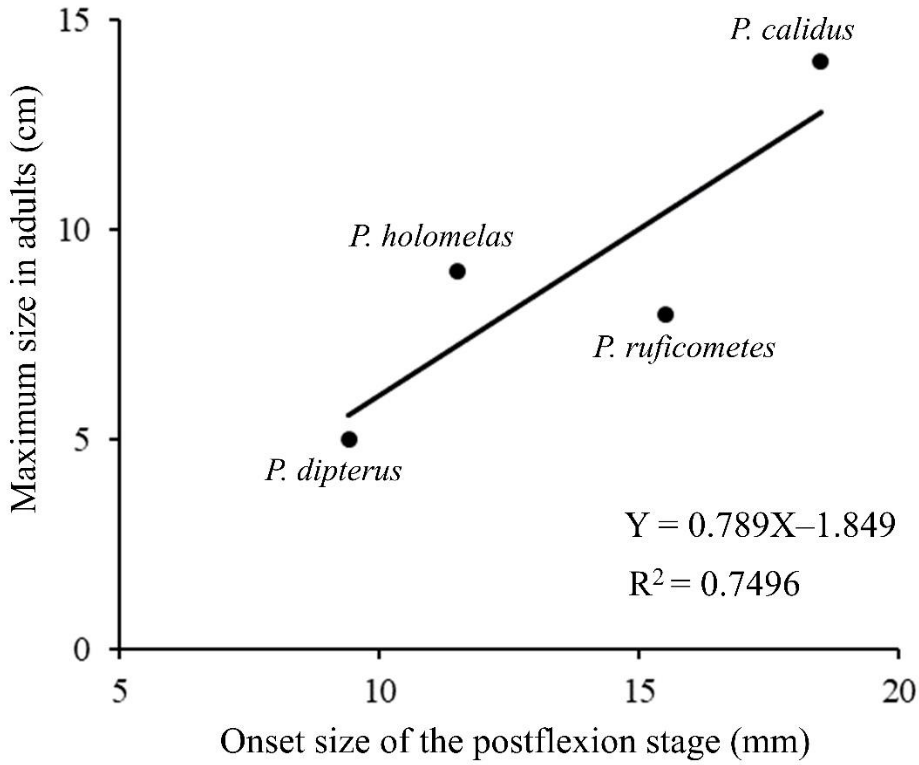

Fig. 22 Relationships between maximum size in adults (*Paraliparis dipterus* 5 cm, *P. ruficometes* 8 cm, *P. holomelas* 9 cm and *P. calidus* 14 cm) and onset size of postflexion stage (*Paraliparis dipterus* 9.4 mm, *P. ruficometes* 15.5 mm, *P. holomelas* 11.5 mm and *P. calidus* 18.6 mm) in some *Paraliparis* species

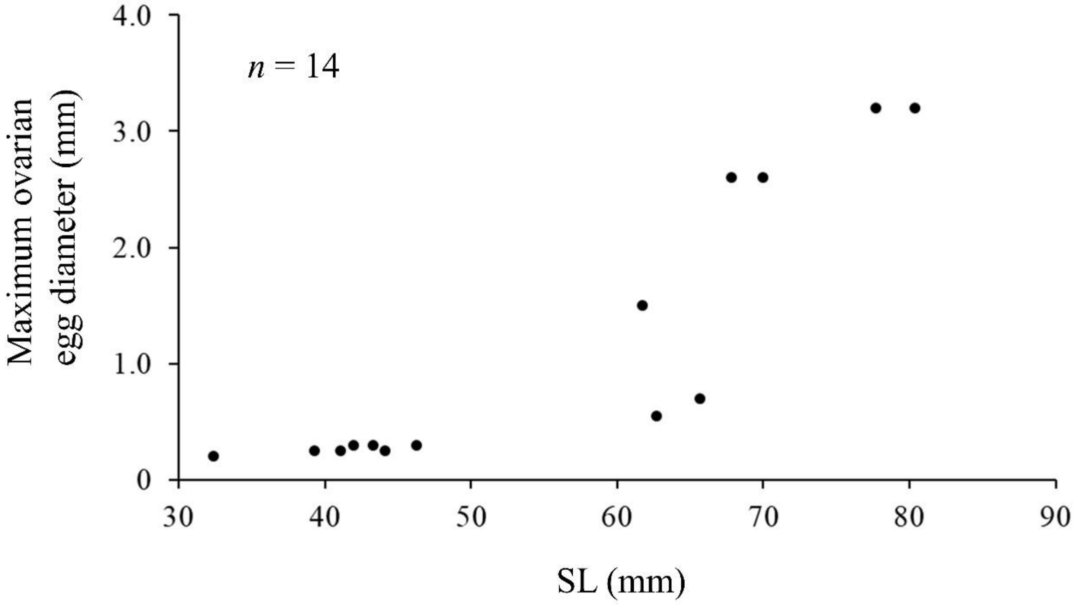

Fig. 23 Relationship between standard length and maximum ovarian egg diameter in female specimens of *Paraliparis ruficomete*

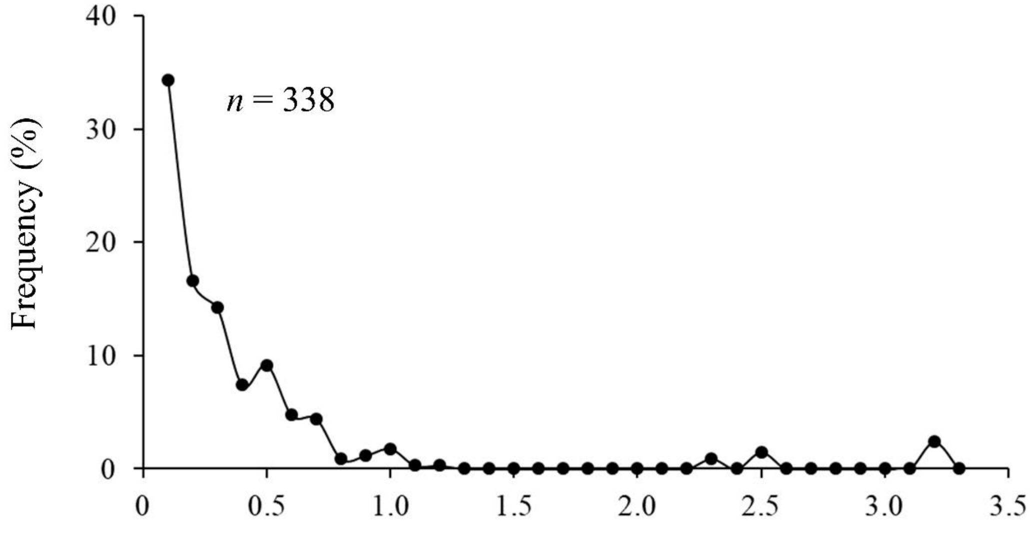

Fig. 24 Relationship between ovarian egg diameter and frequency distribution of ovarian egg diameters in female specimen of *Paraliparis ruficometes* (MSM-18-74, 77.7 mm SL)

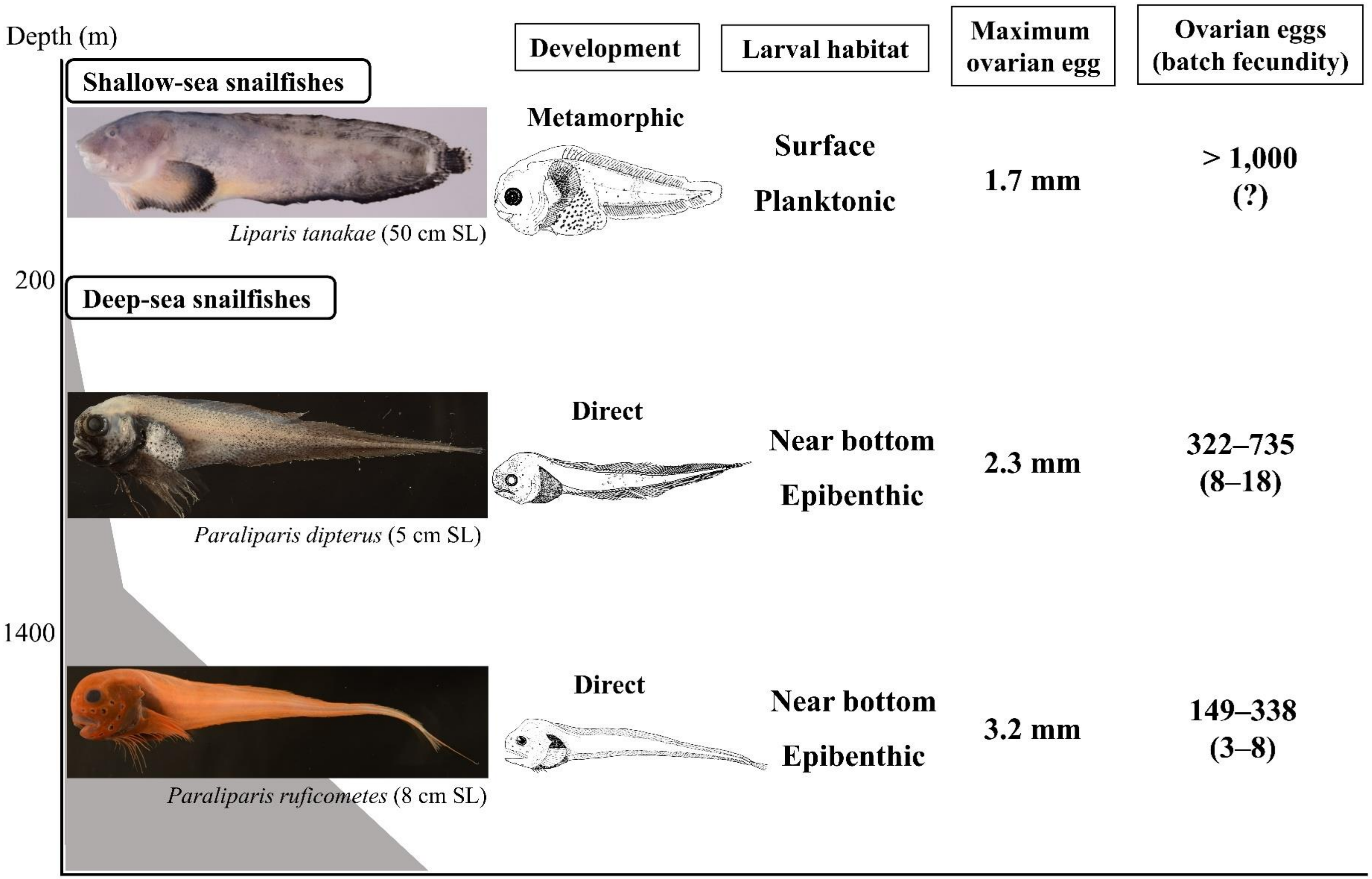

Fig. 25 Comparison of snailfish life histories. Data for *Liparis tanakae* from Aoyama (1959) and Kojima (2014), *Paraliparis dipterus* from Takami and Fukui (2012), and *Paraliparis ruficometes* from this study

Table 1 List of currently known Japanese snailfishes

	Vertical habitat	Area		
		Northern Japan	Southern Japan	
			Suruga Bay	Others
Genus *Liparis*				
L. miostomus	S	○		
L. punctulatus	S	○	○	○
L. burkei	S	○		○
L. frenatus	S	○		
L. bikunin	S	○		
L. owstoni *	S			○
L. tanakae	S	○		○
L. tessellatus	S, D	○		
L. ochotensis	S	○		
L. agassizii	S	○		
L. latifrons	S	○		
Genus *Crystallichthys*				
C. matsushimae	D	○		
Genus *Squalolipsris*				
S. dentatus	D	○		
Genus *Pseudoliparis*				
P. amblystomopsis	D	○		
P. belyaevi	D	○		
Genus *Allocareproctus*				
A. jordani	D	○		
Genus *Careproctus*				
C. rhodomelas	D		○	○
C. rotundifrons	D		○	○
C. marginatus	D	○		
C. simus	D	○		
C. melanurus	D	○		
C. segaliensis	D	○		
C. sinensis	D	○		
C. homopterus	D	○		
C. mederi	D	○		
C. parvidiscus	D	○		
C. macrodiscus	D	○		
C. cyclocephalus	D	○		
C. rastrinus	D	○		
C. trachysoma	D	○		
C. acanthodes	D	○		
C. pellucidus	D	○		

Table 1 (continued)

	Vertical habitat	Area		
		Northern Japan	Southern Japan	
			Suruga Bay	Others
C. bathycoetus	D	○		
C. nigricans	D	○		
C. colletti	D	○		
C. roseofuscus	D	○		
C. furcellus	D	○		
C. cypselurus	D	○		
C. notosaikaiensis	D	○		
C. rausuensis	D	○		
C. zachirus	D	○		
C. iacchus	D	○		
C. lycopersicus	D	○		
C. surugaensis **	D		○	
Genus *Elassodiscus*				
E. tremebundus	D	○		
E. obscurus	D	○		
Genus *Nectoliparis*				
N. pelagicus	D	○		
Genus *Rhinoliparis*				
R. barbulifer	D	○		
Genus *Lipariscus*				
L. nanus	D	○		
Genus *Paraliparis*				
P. dipterus	D		○	
P. mandibularis	D			○
P. grandis	D	○		
P. pectoralis	D	○		
P. rosaceus	D	○		
P. entochloris	D	○		
P. melanobranchus	D	○		
P. atramentatus ***	D		○	○
P. meridionalis	D		○	○
P. ruficometes **	D		○	
P. variabilidens **	D		○	
P. hokuto **	D		○	

S shallow sea, *D* deep sea

* Doubtful species, ** newly described during present study, *** first record from Suruga Bay

Table 2 Towing data and individual numbers of deep-sea snailfishes in Suruga Bay

	Towing distance (km)	Towing numbers	Total towing distance (km)	Individual snailfish numbers
Continental slope				
St. I	6.7	65	435.5	284
St. J	7.2	20	144.0	5
St. L	6.0	11	66.0	3
Suruga Trough				
St. M-1	6.0	33	198.0	147
St. M-2	7.0	14	98.0	19
St. M-3	3.5	12	42.0	6
Total		155	983.5	464

Table 3 Individual numbers of deep-sea snailfishes at each sampling station

	Continental slope				Suruga Trough			
	St. I	St. J	St. L	Total	St. M-1	St. M-2	St. M-3	Total
Genus *Careproctus*								
C. rhodomelas	19	3	2 ***	24				
C. surugaensis *					1			1
Genus *Paraliparis*								
P. atramentatus **	1			1				
P. dipterus	264 (65)	2	1 ****	267 (65)				
P. ruficometes *					140 (13)	19	6	165 (13)
P. variabilidens *					1			1
P. hokuto *					5			5
Total	284 (65)	5	3	292 (65)	147 (13)	19	6	172 (13)

* new species, ** first record from Suruga Bay, *** 500 and 900 m depth transects, **** 350 m depth transects

Number in parentheses indicates larval individuals

Table 4 Counts and measurements of *Careproctus surugaensis*

Standard length (mm)	82.6
Counts	
Dorsal-fin rays	47
Anal-fin rays	39
Pectoral-fin rays	32
Principal caudal-fin rays	10
Procurrent caudal-fin rays	2 (= 1 + 1)
Vertebrae (= abdominal + caudal)	50 (= 10 + 40)
Branchiostegal rays	6
Gill rakers	0 + 8
Pyloric caeca	9
Measurements	
Measurements in percent of standard length	
Head length	27.7
Maximum head depth	18.3
Maximum head width	15.5
Maximum body depth	19.1
Body depth at anal-fin origin	13.9
Body depth at caudal-fin base	2.3
Snout length	8.2
Upper jaw length	13.4
Lower jaw length	12.1
Maximum upper jaw width	14.4
Orbit diameter	6.2
Eye diameter	4.7
Interorbital width	10.3
Gill slit length	7.1
Longest pectoral-fin ray length (upper lobe)	14.6
Pectoral-fin ray length at notch	6.7
Longest pectoral-fin ray length (lower lobe)	16.8
Pelvic disk length	7.9
Pelvic disk width	8.4
Caudal-fin length	13.3
Predorsal-fin length	29.7
Snout to pelcic disk length	17.2
Preanus length	31.6
Preanal-fin length	40.1
Lower jaw to pelvic disk length	13.1
Lower jaw to anus length	28.8
Pelvic disk to anus length	8.6
Anus to anal-fin origin length	10.8
Dorsal-fin origin to anal-fin origin length	20.7

Table 5 Comparison of counts and two characters of 38 species of *Careproctus* with trilobate jaw teeth

	Counts					Lowermost gill slit	Color of
	D	A	P_1	C	V	opening relative to PF	peritoneum
C. surugaensis [a*]	47	39	32	10	50 (= 10 + 40)	7th ray	blackish
C. kamikawai [b]	43–45	36–38	33–35	11	48–50 (= 10–11 + 38–39)	8th–12th ray	black
C. lycopersicus [b]	42–45	34–38	33–38	11	45–50 (= 10–12 + 34–39)	8th–12th ray	pale
C. curilanus [c]	49	43	34	10	55 (= 11 + 44) [w]	1st–2nd ray	black
C. simus [d*]	54–60	47–53	31–37	10	59–64 (= 10–11 + 48–53)	above PF–5th ray	black
C. rhodomelas [e*]	56	48–50	29–31	9	61 (= 9–10 + 51–52)	above PF–3rd ray	black
C. rausuensis [f*]	50–54	45–48	34–37	10–11	56–59 (= 10–11 + 45–48)	7th–11th ray	pale
C. comus [g]	50–56	44–50	33–39	10–13	56–61 (= 9–11 + 45–51)	above PF–5th ray	pale
C. notosaikaiensis [h*]	52	46–47	35–37	10	57–58 (= 10–12 + 46–48)	4th–7th ray	pale
C. bowersianus [i]	51–54	46–48	34–38	10–11	57–59 (= 9–10 + 47–50)	above PF–3rd ray	pale
C. mollis [j]	51	47	35	10	58 (= 11 + 47) [x]	3rd–4th ray	pale
C. homopterus [c*]	55	49	32–34	10	58 (= 10 + 48) [y]	1st ray	pale
C. staufferi [k]	40–42	33–37	36–44	11–13	44–46 (= 10 + 34–36)	above PF–2nd ray	pale
C. cypseluroides [l]	53	50	35	10	*ND*	7th ray	pale
C. seraphimae [l]	52	48	34	10	*ND*	2nd ray	pale
C. attenuatus [c]	48	40	34	unknown	ca. 49 (= 11 + ca. 38) [z]	above PF	black
C. leptorhinus [m]	50	44	23	9	55 (= 9 + 46)	above PF	black
C. marginatus [n*]	47–50	40–43	25–29	10	52–55 (= 9–10 + 42–45)	above PF	black
C. melanurus [o*]	53–61	47–55	27–33	9–11	57–67	above PF	black
C. novaezelandiae [m]	47–48	40–43	37–38	10	53–54 (= 10 + 43–44)	above PF	black
C. oregonensis [p]	61–67	55–57	19–23	7–8	65–69	above PF	black
C. paxtoni [q]	53–54	46–47	34–35	9	58–59 (= 10 + 48–49)	above PF	black
C. tricapitidens [m]	52	46	25	8	57 (= 8 + 49)	above PF	black
C. albescens [r]	54–58	48–52	31–35	10	60–63	above PF	brown
C. credispinulosus [m]	46–50	41–44	34–35	10	50–54 (= 8–9 + 42–45)	above PF	brown
C. rotundifrons [s*]	47–50	41–45	34–40	10	53–56 (= 10–11 + 42–46)	above PF	brown
C. canus [i]	51–53	43–46	33–36	11	55–58 (= 11–12 + 44–47)	above PF	pale
C. ectenes [t]	48–51	44	29–32	8	ND	above PF	pale
C. falklandicus [m]	34–36	27–30	29–31	10	38–40 (= 9–10 + 29–30)	above PF	pale
C. faunus [g]	47–51	41–45	32–38	11–12	52–56 (= 9–11 + 42–45)	above PF	pale
C. nelsoni [k]	39–41	33–35	32–37	11	44–45 (= 10 + 34–35)	above PF	pale
C. pallidus [r]	29–31	24–26	24–27	10	36–37 (= 9–10 + 26–28)	above PF	pale
C. pycnosoma [i]	42–45	36–39	38–39	11–12	46–49 (= 10+ 36–39)	above PF	pale
C. ranula [u]	55	49	27–28	11	60 (= 9 + 51)	above PF	pale
C. segaliensis [v*]	61	53	24–25	6	66 (= 10 + 56)	above PF	pale
C. sinensis [n*]	53	47	33	10	58 (= 11 + 47)	above PF	pale
C. zachirus [i]	51–53	43–45	28–31	11	56–58 (= 12–13 + 44–46)	above PF	pale
C. atrans [r]	44	38	26	8	47 (= 9 + 38)	unknown	black

D dorsal-fin rays, *A* anal-fin rays, P_1 pectoral-fin rays, *C* principal caudal-fin rays, *V* total vertebrae (= abdominal + caudal), *PF* pectoral fin, *ND no data*

a This study, *b* Orr 2012, *c* Gilbert and Burke 1912b, *d* Kido 1985; Tsutsui and Amaoka 1997, *e* Gilbert and Burke 1912a; Kido 1988, *f* Machi et al. 2012, *g* Orr and Maslenikov 2007, *h* Kai et al. 2011b, *i* Kido 1985, *j* Gilbert and Burke 1912b; Burke 1930, *k* Orr 2016, *l* Schmidt 1950, *m* Andriashev and Stein 1998, *n* Kido 1988, *o* Burke 1930; Stein 1978; Kido and Shinohara 1997, *p* Stein 1978, *q* Stein et al. 2001, *r* Andriashev 2003, *s* Sakurai and Shinohara 2008, *t* Gilbert 1896; Burke 1930, *u* Chernova 2005b, *v* Kido 1984, 1988, *w* USNM 73341, *x* USNM 74383, *y* USNM 73342, *z* USNM 74386

* Known from Japan

Table 6 Counts and measurements of *Paraliparis atramentatus*

Counts	
Dorsal-fin rays	52
Anal-fin rays	45
Pectoral-fin rays	21
Principal caudal-fin rays	8 (= 4 + 4)
Procurrent caudal-fin rays	1 (= 1 + 0)
Vertebrae (= abdominal + caudal)	57 (= 9 + 48)
Branchiostegal rays	6
Gill rakers	Undetermined
Pyloric caeca	5
Head sensory pore pattern	2-6-7-1
Measurements in percent of standard length	
Head length	22.7
Maximum head depth	20.4
Maximum head width	19.6
Maximum body depth	17.5
Body depth at anal-fin origin	12.9
Body depth at caudal-fin base	1.0
Snout length	5.4
Upper jaw length	9.3
Lower jaw length	7.7
Maximum upper jaw width	15.2
Orbit length	6.4
Eye diameter	5.2
Interorbital width (fresh)	14.7
Interorbital width (bony)	7.7
Gill slit length	4.1
Longest pectoral-fin ray length (upper lobe)	13.4
Pectoral-fin ray length at notch	10.3
Longest pectoral-fin ray length (lower lobe)	11.6
Caudal-fin length	12.4
Predorsal-fin length	23.7
Preanus length	20.1
Preanal-fin length	31.2
Anterior margin of lower jaw to anus length	16.2
Anus to anal-fin origin length	11.6
Dorsal-fin origin to anal-fin origin length	16.8

Table 7 Counts and measurements of *Paraliparis hokuto*

	Holotype	Paratype
Counts		
Dorsal-fin rays	65	65
Anal-fin rays	61	60
Pectoral-fin rays	22	23
Principal caudal-fin rays	6	6
Procurrent caudal-fin rays	0	0
Vertebrae (= abdominal + caudal)	72 (= 11 + 61)	72 (= 11 + 61)
Branchiostegal rays	6	6
Gill rakers	0 + 12	0 + 10
Pyloric caeca	5	5
Head sensory pore pattern	2-6-7-1	2-6-7-1
Measurements in percent of standard length		
Head length	17.3	16.9
Maximum head depth	13.3	14.1
Maximum head width	13.6	11.7
Maximum body depth	22.2	17.7
Body depth at anal-fin origin	19.3	14.9
Body depth at caudal-fin base	0.9	0.7
Snout length	4.8	5.9
Upper jaw length	6.0	6.4
Lower jaw length	5.8	6.3
Maximum upper jaw width	8.3	7.8
Orbit length	4.7	4.8
Eye diameter	4.4	4.5
Interorbital width (fresh)	7.8	8.1
Interorbital width (bony)	2.1	2.5
Gill slit length	2.4	2.1
Longest pectoral-fin ray length (upper lobe)	12.5	12.9
Pectoral-fin ray length at notch	2.1	2.9
Longest pectoral-fin ray length (lower lobe)	12.8	12.3
Caudal-fin length	10.4	9.8
Predorsal-fin length	18.7	21.9
Preanus length	14.8	14.1
Preanal-fin length	40.4	32.2
Anterior margin of lower jaw to anus length	11.9	12.1
Anus to anal-fin origin length	28.3	20.3
Dorsal-fin origin to anal-fin origin length	29.7	21.0

Table 8 Comparison of fin ray counts and selected characters of 9 species of *Paraliparis*

	D	A	P_1	C	PR numbers	PR notches	Chin pores	Opercular flap	References
P. hokuto	65	60–61	22–23	6	3	Absent	In common pit	Present	This study
P. rosaceus	57–69	54–60	18–22	6–8	3	ND	Usually in common pit	Present	Stein (1978); Kido (1988)
P. copei	57–65	50–59	20–23	7–8	4	Absent	In common pit	Absent	Andriashev (1986); Kido and Yabe (1995)
P. merodontus	55–60	50–52	20–21	8	3	Absent	ND	Present	Stein et al. (1991)
P. alius	63	57	20	6	4	Absent	Normal	Present	Stein (2012a)
P. adustus	64	56	24	6	ND	ND	Normal*	Present	Busby and Cartwright (2009)
P. plicatus	56	51	21	7	4	Absent	Fold	Present	Stein (2012a)
P. longicaecus	59	52	21	7	4	1st, 3rd	Fold	Present	Stein (2012a)
P. attenuatus	66	57	24	ND	4 or 5*	Absent*	Normal*	Present?*	Garman (1899); Burke (1930)

D dorsal-fin rays, *A* anal-fin rays, P_1 pectoral-fin rays, *C* caudal-fin ray, *PR* pectoral proximal radial, *ND* no data

* Taken from figures in original description

Table 9 Counts and measurements of *Paraliparis ruficometes*

	Holotype	Paratypes	n^*
Standard length (mm)	80.4	52.0–78.9	25
Counts			
Dorsal-fin rays	56	53–59	25
Anal-fin rays	49	48–52	25
Pectoral-fin rays	21	20–25	27
Principal caudal-fin rays	6	6	25
Procurrent caudal-fin rays	0	0	25
Vertebrae (= abdominal + caudal)	64 (= 9 + 55)	61–64 (= 9–10 + 52–55)	25
Branchiostegal rays	6	6	28
Gill rakers	0 + 11	0 + 10–12	28
Pyloric caeca	7	6–8	28
Head sensory pore pattern	2-6-7-1	2-6-7-1	27
Measurements			
Mesurements in percent of standard length			
Head length	20.8	19.9–24.3	25
Maximum head depth	17.7	15.6–18.9	25
Maximum head width	16.3	12.2–19.0	25
Maximum body depth	17.8	16.2–18.7	25
Body depth at anal-fin origin	12.4	10.2–15.1	25
Body depth at caudal-fin base	1.0	0.8–1.5	25
Snout length	7.7	6.2–8.3	25
Upper jaw length	10.9	10.4–12.2	25
Lower jaw length	10.3	9.6–12.1	25
Maximum upper jaw width	14.3	9.4–15.2	25
Orbit length	6.9	5.0–6.3	25
Eye diameter	4.4	3.4–4.5	25
Interorbital width	11.4	8.3–11.3	25
Gill slit length	7.7	5.9–10.0	22
Longest pectoral-fin ray length (upper lobe)	13.8	12.3–18.0	22
Pectoral-fin ray length at notch	9.2	6.2–10.6	21
Longest pectoral-fin ray length (lower lobe)	13.9	11.3–18.6	24
Caudal-fin length (dorsalmost ray)	20.9	16.4–24.9	7
Caudal-fin length (middle ray)	7.3	7.3–11.1	18
Predorsal-fin length	21.1	18.4–23.3	25
Preanus length	17.7	14.1–21.5	25
Preanal-fin length	24.6	22.4–31.7	25
Anterior margin of lower jaw to anus length	13.6	12.6–20.8	25
Anus to anal-fin origin length	11.1	5.8–12.3	25
Dorsal-fin origin to anal-fin origin length	16.4	13.6–20.4	25

*Including holotype

Table 10 Comparison of counts and selected characters of 48 species of *Paraliparis*

	Counts							Lowermost gill slit	Color of peritoneum	Color of stomach	Reference
	D	A	P_1	C	V	R	PC	opening relative to PF			
P. ruficometes	53–59	48–52	20–25	6	61–64 (= 9–10 + 52–55)	4	6–8	9th–13th ray	Black	Black	This study
P. albeolus	62–65	57–59	20	5	ND	ND	ND	12th–13th ray	Blackish	ND	Schmidt 1950
P. bullacephalus	60	53–55	20–21	6–7	63–64 (= 10 + 53–54)	4	3	11th–13th ray	Darkish	Darkish	Busby and Cartwright 2009
P. hureaui	53	46	25	10	ND	4	6	9th ray	Clear	Clear	Matallanas 1999
P. albescens	49–57	44–53	17–18	4–6	54–61 (= 8–9 + 46–52)	ND	6–10	6th–12th ray	Dusty	Dusty	Gilbert 1915; Anderson et al. 1979
P. holomelas	57–61	52–55	19–23	6–7	60–65 (= 9–10 + 50–55)	3	7–10	8th–15th ray	Dark	Dark	Busby and Cartwright 2006
P. latifrons	54–57	48–50	21–24	5–6	ca. 61	ND	6–10	9th–15th ray	Black	Pale	Stein 1978
P. macropterus	60–62	<53–55	14–15	8–9	66–67 (= 9–10 + 56–57)	4	<5	14th–15th ray	Black	Pale	Stein 2012a
P. andriashevi	55–58	50–52	24–25	9–10	60–64 (= 9–10 + 51–54)	4	8–11	7th–8th ray	Dark brown or black	Pale	Stein 2012a
P. meganchus	52–58	46–52	24–27	10–11	58–63 (= 9–10 + 49–54)	4	6–8	16th–20th ray	Brown	Blackish-grey	Andriashev 1986
P. antarcticus	61–65	55–60	23–28	9–10	67–74 (= 8–10 + 57–64)	3–4	ND	15th–20th ray	Pale or brownish	Dark	Stein 2012a
P. molinai	61	56–57	24	4	64–65	4	8	6th ray	Black	Pale yellow	Stein et al. 1991
P. orbitalis	57	51	22–24	9	65 (= 9 + 56)	4	5<	ca. 6th ray	Black	Pale	Stein 2012a
P. leucoglossus	62	56	22	8	68 (= 8 + 60)	4	Unknown	5th–6th ray	Black	Light	Andriashev 1986
P. kocki	47–50	45	17–18	6	57–59 (= 11 + 46–48)	4	7	4th–6th ray	Dark brown	Pale	Chernova 2006
P. eltanini	58–60	51–52	18–21	4	64–65	4	ND	5th ray	Dark brown	Blackish	Stein and Andriashev 1990
P. somovi	54–57	49–52	22–26	9	60–63 (= 8–9 + 52–55)	4	6–7	4th–5th ray	Black	Blackish	Andriashev 1986
P. magnoculus	55<	50<	23–24	Unknown	61< (= 10 + 51<)	4	6	4th–5th ray	Black	Pale	Stein 2012a
P. valentinae	54–57	49–53	21–25	9–10	59–63 (= 8–9 + ND)	4	9–10	3rd–5th ray	Black	Pale	Andriashev 1986
P. coracinus	54<	50<	21–22	Unknown	62< (= 11 + 51<)	4	5	4th ray	Black	Pale	Stein et al. 2001
P. mexicanus	69	62	29	7	76 (= 11 + 65)	2	4	4th ray	Black	Pale	Chernova 2006
P. incognita	48–50	43–45	22–23	10	54–58	3	6	2nd–4th ray	Dark brown	Pale	Stein and Andriashev 1990
P. terraenovae	48–50	43–45	22–23	10	54–58 (= 8–9 + ND)	3	6	2nd–4th ray	Dark brown	Pale	Andriashev 1986
P. dipterus *	54–58	48–54	12–14	6	60–64 (= 8 + 52–56)	ND	0	1st–4th ray	Black	Black	Kido 1988; Takami and Fukui 2012

Table 10 (continued)

P. grandis *	71–82	64–76	31–39	7–8	75–86 (= 10–11 + 65–74)	ND	25–41	1st–4th ray	Black	Pale	Kido 1988
P. hystrix	51–60	47–54	16–21	7–8	56–64 (= 7–9 + 47–55)	2	4–8	1st–4th ray	Black	Pale	Merrett 1983
P. macrocephalus	49	43	20	9	56 (= 10 + 46)	3	6	2nd–3rd ray	Black	Pale	Stein 2012a
P. kreffti	64–66	59–60	16–18	4–5	71–77 (= 8–9 + 62–68)	2	7–9	1st–3rd ray	Black	Black	Andriashev 1986, 1992
P. gracilis	58–66	56–63	15–17	8	68–74 (= 9 + 59–65)	4	0	1st–3rd ray	Black	Dark brown	Andriashev 1986
P. leobergi	48–50	43–45	24–27	10	55–57 (= 8–9 + ND)	4	5	1st–3rd ray	Light	Light	Andriashev 1986
P. anthracinus	60	55	22	8	68 (= 11 + 57)	4	6	2nd ray	Black	Pale	Stein et al. 2001
P. charcoti	51–52	44–47	20–21	9	57–58 (= 9 + 48–49)	3	6	2nd ray	Black	Pale	Chernova 2006
P. dactyloides	72	62	30	Unknown	ND	ND	ND	2nd ray	Black	ND	Schmidt 1950
P. bipolaris	72	65	16–17	4	76–77 (= 9–10 + 67)	2	5–7	1st–2nd ray	Black	Black	Andriashev 1997
P. pectoralis *	55–59	49–52	28–32	7–8	61–66 (= 10–11 + 51–56)	ND	6–10	1st–2nd ray	Black	Pale	Stein 1978; Kido 1984, 1993
P. tetrapteryx	68–73	63–66	26–31	7	76–81 (= 11–12 + 65–69)	2	6	1st–2nd ray	Black	Pale	Andriashev 1986
P. amerismos	66	61	22	7	74 (= 11 + 63)	ND	ND	1st–2nd ray	Black	ND	Stein 2012a
P. wolffi	70	63–66	16	Unknown	75–76 (= 9–10 + 65–67)	2	6	1st ray	Black	Black	Duhamel and King 2007
P. gomoni	ca. 62	ca. 56	23	8	69 (= 11 + 58)	3	5	1st ray	Black	Pale	Stein et al. 2001
P. penicillus	51–55	46–49	17–19	6–7	56–60 (= 9–10 + 47–49)	4	5–10	Above PF–4th ray	Black	Pale	Baldwin and Orr 2010
P. megalopus	66–71	63–65	16–19	4	ca. 76 (= 9 + 67)	ND	6–8	Above PF–2nd ray	Black	Black	Stein 1978
P. mawsoni	62–67	56–62	23–24	6–7	71–75 (= 9–10 + 61–65)	2–4	4–6	Above PF–2nd ray	Black	Greyish-black	Andriashev 1986, 1992
P. fuscolingua	61–63	54–57	24–25	8	67–68 (= 9 + 58–59)	4	8–9	Above PF–2nd ray	Black	ND	Stein 2012a
P. posteroporus	60	54	20	ca. 6	69 (= 13 + 56)	4	5<	Above PF–1st ray	Black	Pale	Stein 2012a
P. attenuatus	66	57	24	ND	ND	ND	Few	Unknown	Black	Pale	Garman 1899; Burke 1930
P. debueni	55	49	21	8	63 (= 9 + 54)	3	3	Unknown	Blackish-brown	Brown	Andriashev 1986
P. carlbondi	54<–ca. 57	49–ca. 52	24–26	ca. 6	60–64 (= 10 + 50–54)	ND	6–7	Unknown	Dark brown	Pale	Stein 2005
P. fimbriatus	49	45	24	ND	ND	ND	Unknown	Unknown	Black	ND	Garman 1899; Burke 1930

D dorsal-fin rays, *A* anal-fin rays, P_1 pectoral-fin rays, *C* caudal-fin ray, *V* total vertebrae (= abdominal + caudal), *R* radial, *PC* pyloric caeca, *PF* pectoral fin, *ND* no data

*Known from Japan

Table 11 Counts and measurements of *Paraliparis variabilidens*

Standard length (mm)	52.0
Counts	
Dorsal-fin rays	62
Anal-fin rays	57
Pectoral-fin rays	26, 27
Principal caudal-fin rays	7
Procurrent caudal-fin rays	2 (= 1+1)
Vertebrae (= abdominal + caudal)	67 (= 9 + 58)
Branchiostegal rays	6
Pyloric caeca	ca. 12
Head sensory pore pattern	2-6-7-1
Measurements	
Measurents in percent of standard length	
Head length	22.3
Maximum head depth	15.2
Maximum head width	12.7
Maximum body depth	14.4
Body depth at anal-fin origin	11.0
Body depth at caudal-fin base	0.8
Snout length	6.2
Upper jaw length	10.0
Lower jaw length	9.6
Maximum upper jaw width	9.8
Orbit length	6.0
Eye diameter	4.0
Interorbital width	9.6
Gill slit length	5.2
Longest pectoral-fin ray length (upper lobe)	13.1
Pectoral-fin ray length at notch	2.3
Longest pectoral-fin ray length (lower lobe)	8.8
Caudal-fin length	7.5
Predorsal-fin length	22.1
Preanus length	18.7
Preanal-fin length	28.1
Anterior margin of lower jaw to anus length	16.9
Anus to anal-fin origin length	10.4
Dorsal-fin origin to anal-fin origin length	13.8

Table 12 Comparison of counts and selected characters of 20 species of *Paraliparis*

	Counts						Number of PF ray(s)*	Color of	Color of	Reference
	D	A	P_1	C	V	PC	covered by gill slit	peritoneum	stomach	
P. variabilidens	62	57	26, 27	9	67 (= 9 + 58)	ca. 12	2nd	Black	Pale	This study
P. rossi	49–50	44	20–22	9	54–56 (= 9 + 45–47)	7	2nd–3rd	Black	Pale	Chernova and Eastman 2001
P. dactylosus	54–61	49–55	28–30	8	59–67	17–23	2nd–4th	Black	Pale	Stein 1978; Mecklenburg et al. 2002
P. trilobodon	45–49	41–43	25–27	10	51–55 (= 9 + 42–46)	4–5	2nd–4th	Brown	Pale	Andriashev 2003
P. challengeri	64–65	58–60	16	10	69–70 (= 9–10 + 59–61)	0	1st–4th	Black	Light	Andriashev 1993; Chernova 2003
P. hubbsi	50–55	47–49	21–25	9	57–60	12–13	3rd–7th	Black	White	Andriashev 2003
P. exilis	60	54	ca. 20	8	66 (= 10 + 56)	2≤	Above fin	Black	Pale	Stein 2012b
P. freeborni	62	52	20	6	66 (= 10 + 56)	4	Above fin	Black	Pale	Stein 2012b
P. hawaiiensis	62	55	20–21	7	68–69	6	Above fin	Black	Pale	Stein and Drazen 2014
P. pearcyi	59	56	20	8	67 (= 9 + 58)	6	Above fin	Black	Pale	Stein 2012b
P. porcus	47	41	26	9	52 (= 9 + 43)	5	Above fin	Black	Pale	Chernova 2006
P. tompkinsae	59–63	ca. 46–56	22–27	8–9	64–67 (= 9 + 55–58)	7≤	4th–8th	Black	Pale	Andriashev 1992; Chernova 2006
P. diploprora	54	50	25	10	60 (= 8 + 52)	10	7th–8th	Black	Light	Andriashev 2003
P. angustifrons	57	53	37	ND	ND	6	Unknown	Black	Pale	Garman 1899; Burke 1930
P. leucogaster	46–49	41–44	24–28	10	52–56 (= 9 + 43–47)	6	1st–5th	Light	Light	Andriashev 2003
P. balgueriasi	48	43	23	11	ND	6	15th–16th	Light	Light	Matallanas 1999
P. operculosus	52–58	47–53	19–22	10	58–64 (= 8–9 + 50–55)	5–7	2nd–3rd	Black	Black	Andriashev 2003
P. thalassobathyalis	49–54	44–47	15–19	5–6	56–62	6–8	Above fin–2nd	Black	Black	Andriashev 2003
P. obliquosus	49	44	19	5	56 (= 9 + 47)	7	3rd–4th	Black	Black	Chernova and Duhamel 2003
P. deani	56–57	44–48	18–22	ca. 6	ND	ca. 8–9	10th–13th	Silvery	Black	Burke 1930; Stein 1978

D dorsal-fin rays, *A* anal-fin rays, P_1 pectoral-fin rays, *C* caudal-fin ray, *V* total vertebrae (= abdominal + caudal), *PC* pyloric caeca, *PF* pectoral fin, *ND* no data

* Pectoral fin ray(s) adjacent to lowermost part of gill slit (or gill slit above fin)

Table 13 Counts and measurements of *Paraliparis ruficometes* at each developmental stage

	Larvae		Juveniles	Adults
	Flexion	Postflexion		
	(*n* = 4)	(*n* = 3)	(*n* = 2)	(*n* = 44)
Standard length	12.3–14.0	15.5–18.5	21.2, 23.8	29.2–80.4
Counts				
Dorsal-fin rays	55–59	55–57	55, 58	53–59
Anal-fin rays	49–52	48–51	49, 52	48–52
Pectoral-fin rays	(15–17)	(14–19)	20, 22	20–25
Caudal-fin rays	6	6	6	6
Branchiostegal rays	6	6	6	6
Head sensory pore pattern	2-6-7-1	2-6-7-1	2-6-7-1	2-6-7-1
Measurements				
In % of standard length				
Head length	19.5–23.4	24.3	22.2, 23.5	19.7–24.5
Maximum head depth	19.6–25.0	22.7–23.1	21.0, 23.1	15.6–21.4
Maximum head width	17.1–21.4	17.9–21.1	16.5, 18.9	12.2–19.5
Maximum body depth	15.5–18.8	15.7–18.5	19.3, 19.8	15.4–19.6
Body depth at anal-fin origin	10.1–11.7	10.8–11.6	11.3, 13.9	10.2–15.1
Predorsal-fin length	21.0–22.7	21.6–23.7	21.0, 22.6	20.6–23.3
Preanal-fin length	26.8–30.0	27.6–28.9	28.2, 28.8	20.9–31.7
In % of head length				
Upper jaw length	44.8–58.3	55.6–59.5	51.1, 53.6	47.3–61.5
Snout length	18.8–20.8	22.2–33.3	21.3, 26.8	21.8–38.3
Eye diameter	15.6–20.8	14.3–17.8	14.9, 16.1	12.8–23.5
Gill slit length	33.3–37.9	35.7	35.7, 44.7	26.4–49.6
Longest pectoral-fin ray length (upper lobe)	33.3–46.9	35.7–48.9	37.5, 42.6	41.5–87.7
Longest pectoral-fin ray length (lower lobe)	10.0–20.8	47.6	23.4, 48.2	44.6–91.0
Anterior margin of lower jaw to anus length	110.0–133.3	100.0–104.8	103.6, 106.4	60.9–93.6

Counts in parentheses indicate incompletely formed elements