Zootaxa 5777 (3): 453–470
https://www.mapress.com/zt/

Article

ISSN 1175-5326 (print edition)
ZOOTAXA
ISSN 1175-5334 (online edition)

https://doi.org/10.11646/zootaxa.5777.3.3
http://zoobank.org/urn:lsid:zoobank.org:pub:D02C87D4-45F0-4244-A76F-C3EDF40EFD0F

A new species of *Careproctus* (Cottoidei: Liparidae) from the Falkland Plateau, southwestern Atlantic, with COI-based phylogenetic analysis

MARTIN L. VILLARROEL-PEREZ[1*], NATALIA V. CHERNOVA[2], JOHANNA J. N. WESTON[3], VEDRANA VUKASIN[1] & ZHANNA SHCHERBICH[1]
[1]*Falkland Islands Fisheries Department, Bypass Road, PO Box 598, Stanley, FIQQ 1ZZ, Falkland Islands*
vvukasin@naturalresources.gov.fk; https://orcid.org/0009-0004-3982-0177
zshcherbich@fisheries.gov.fk; https://orcid.org/0009-0009-7952-730X
[2]*Zoological Institute of the Russian Academy of Sciences, Universitetskaya Emb. 1, 199034 Saint Petersburg, Russia*
chernova@zin.ru; https://orcid.org/0000-0003-3955-7511
[3]*Biology Department, Woods Hole Oceanographic Institution, Woods Hole, MA 02543 USA*
johanna.weston@whoi.edu; https://orcid.org/0000-0002-7142-3081
**Corresponding author: mvillarroel@naturalresources.gov.fk; https://orcid.org/0009-0005-8168-8170*

Abstract

A new species of snailfish, *Careproctus argosgeorgiae* **sp. nov.**, is described from the northeastern Falkland Islands, within the Falkland Plateau, in the southwestern Atlantic Ocean. The specimen was collected at a depth of 1680 m during a longline fishing operation and scientific observation deployment conducted by the Falkland Islands Fisheries Department in 2024, in an area of relatively unsurveyed depths known to host Vulnerable Marine Ecosystem (VME) taxa. The new species is distinguished from all 18 known species of *Careproctus* from southern South America and adjacent subantarctic waters by the following combination of characters: strong pleural ribs; vertebrae 47; dorsal-fin rays 42, anal-fin rays 34, pectoral-fin rays 37; simple teeth; a long gill slit reaching pectoral-fin ray 18; a pelvic disk about 33% of head length; distance from disk to anus not less than the disk length; pectoral-fin upper lobe 67% HL; thick subcutaneous gelatinous tissue; and a uniform light-orange coloration with deeper orange fin and disk margins. Comparative analyses with regional congeners are presented and genetic results are discussed. These findings underscore the importance of continued deep-sea exploration to improve knowledge of the subantarctic ichthyofauna and VMEs.

Key words: snailfish**,** COI barcoding, deep sea, Falkland Islands, integrative taxonomy, longline fishery, Vulnerable Marine Ecosystems

Resumen

Se describe una nueva especie de pez caracol, *Careproctus argosgeorgiae* **sp. nov.**, del noreste de las Islas Malvinas (Falkland), en la plataforma de las Malvinas, en el océano Atlántico suroccidental. El ejemplar fue recolectado a una profundidad de 1680 m durante una operación de pesca con palangre y una campaña de observación científica realizada por el Departamento de Pesquerías de las Islas Malvinas en 2024, en una zona de profundidades relativamente inexploradas, conocida por albergar taxones de Ecosistemas Marinos Vulnerables (VMEs). La nueva especie se distingue de las 18 especies conocidas de *Careproctus* del sur de Sudamérica y de aguas subantárticas adyacentes por la siguiente combinación de características: costillas pleurales robustas; 47 vértebras; 42 radios en la aleta dorsal, 34 en la aleta anal y 37 en la aleta pectoral; dientes simples; hendidura branquial larga que alcanza el radio 18 de la aleta pectoral; disco pélvico que representa aproximadamente el 33% de la longitud de la cabeza (HL); distancia entre el disco y el ano no menor que la longitud del disco; lóbulo superior de la aleta pectoral 67% HL; tejido gelatinoso subcutáneo grueso; y coloración uniforme naranja claro, con márgenes del disco y de las aletas de un tono naranja más intenso. Se presentan análisis comparativos con congéneres regionales y se discuten los resultados genéticos. Estos hallazgos subrayan la importancia de continuar con la exploración de aguas profundas para mejorar el conocimiento de la ictiofauna subantártica y de los VMEs.

Accepted by P. Psomadakis: 5 Feb. 2026; published: 19 Mar. 2026

Introduction

The Falkland Islands are located east of South America in the southwestern Atlantic Ocean. These waters are highly productive due to the influence of the Antarctic Circumpolar Current and its interaction with the Patagonian Shelf, which gives rise to the Falkland Current (Bakun 1993). In the northeastern Falkland Islands, depth increases sharply along the Patagonian Slope, transitioning into the more level terrain of the Falkland Plateau, an area where Vulnerable Marine Ecosystem (VME) taxa have been recorded (Barker *et al.* 1983; Pearman *et al.* 2022). In this relatively unsurveyed area, a scientific observation trip was carried out between September and November 2024 as part of the Falkland Islands Fisheries Department (FIFD) associated observer program for the longline fishery targeting Patagonian toothfish, *Dissostichus eleginoides* Smitt, 1898 (Perciformes: Nototheniidae). Only a single fish of the family Liparidae Gill, 1861 was collected during the observation trip, from sets conducted at 1040–1790 m. Upon examination, it was identified as a unique specimen of the genus *Careproctus* Krøyer, 1862. Due to its rarity and broader relevance than initially anticipated, we conducted a more detailed examination of the specimen.

Snailfishes (Liparidae) are a large group distributed in temperate and cold waters of all oceans, from the littoral zone to the hadal depths. It is a diverse fish family, comprising at least 450 species from 32 genera worldwide (Chernova *et al.* 2004; Chernova 2022; Orr *et al.* 2019; Orr 2025). The most generalized snailfishes (e.g., *Liparis* Scopoli, 1777, inhabiting coastal waters) have pelvic fins modified into a large sucking disk; their teeth are typically three-lobed and form regular oblique rows on each jaw; the nostrils occur in two pairs and pseudobranchia are present; and the pectoral-fin rays are numerous (exceeding those of the anal fin), with the body color variegated and usually spotted or striped (Burke 1930 *et auctorum*). Snailfishes of the genus *Careproctus* (sea tadpoles) inhabit deeper waters and are characterized by a smaller sucking disk, a single pair of nostrils, and the absence of pseudobranchia. Their pectoral-fin rays are usually less numerous than the anal-fin rays, and body coloration is usually uniform rose, orange, or blackish due to the lack of green and brown pigments in the skin. However, species with red, white, and gray variegated body coloration are also known (Orr & Maslenikov 2007; Kai *et al*. 2018).

Careproctus includes at least 162 species and is among the three largest genera in the family (Chernova 2022). Fifteen *Careproctus* species known from the vicinity of South America at the time were included in the summarizing book “Liparid fishes of the Southern Ocean and adjacent waters” (Andriashev 2003), and three more species were described later (Stein 2006; Matallanas & Piacentino 2019). Nine of these eighteen are known from the vicinity of the Falklands: *C. falklandicus* Lönnberg, 1905; *C. aculeolatus* Andriashev, 1991; C. *atrans* Andriashev, 1991; *C. aureomarginatus* Andriashev, 1991; *C. armatus* Andriashev, 1991; *C. smirnovi* Andriashev, 1991, *C. minimus* Andriashev & Stein, 1998; *C. maculosus* Stein, 2006 and *C. stigmatogenus* Stein, 2006 (Lönnberg 1905; Andriashev 1991a, 1991b; Andriashev & Stein 1998; Stein 2006). And according to the FIFD database, only *C. falklandicus* has been recorded to date from the Falkland Islands. The present specimen differs from *C. falklandicus* and all other regional congeners and is therefore described here as a new species.

This paper describes the new species, including its cytochrome *c* oxidase subunit I (COI) barcode sequence, and compares it with congeners from the subantarctic region and the Southern Ocean (Andriashev & Stein 1998; Andriashev 2003; Balushkin 2012). COI can be useful for identifying snailfish in the Falkland Islands and surrounding waters, a region that remains poorly studied.

Material and methods

Counts of meristic characters follow Andriashev & Stein (1998), and descriptive terminology follows Stein *et al.* (2001). Morphometric measurements were taken to the nearest 0.1 mm using a caliper. Standard length (SL) is the distance from the fleshy tip of the snout to the base of the caudal (C) fin rays. Head length (HL) was measured from the tip of the snout to the tip of the opercular lobe. Mouth width was measured between the posterior tips of the mandibles; snout length from the snout tip to the anterior fleshy margin of the eye; interorbital distance as the space between the orbital margins; and postorbital distance from the posterior rim of the eye to the tip of the opercular lobe. Body depth (maximal and above the anal (A) fin origin) does not include the gelatinous tissue covering the fins. Predorsal, preanal, and precaudal distances are measured from the snout tip to the bases of the anterior rays of the dorsal (D) fin, anus, and anal fin origin, respectively. Pectoral (P) fin upper and lower lobes were measured along the longest ray of each.

Cephalic pores were visualized by injection with Mayer's hematoxylin, with nomenclature following Burke (1930), Stein & Andriashev (1990), and Stein *et al*. (2001). The specimen was fixed in buffered formalin, stored in 70% ethanol, and the right pectoral girdle stained with alizarin red (Andriashev 1977) for osteological observations.

Digital photographs were taken of the fresh and fixed specimen shortly after capture and again after fixation. Wet weight was measured on board using a motion-compensating scale. Sex and maturity were assessed visually following an 8-stage scale modified from Nikolsky (1963) and Brickle *et al*. (2005).

Radiographs were obtained before and after fixation using a ULTRA 1040HF X-ray system (Ecoray Co., Ltd.); interpretation of the hypural complex follows Andriashev (2003). Where radiographic resolution was insufficient, soft tissue was removed from the caudal region to expose the hypural complex directly.

The holotype was deposited in the Museo Nacional de Historia Natural, Santiago, Chile. Museum abbreviations are as follows: MGU—Zoological Museum of Moscow University, Moscow, Russia; MNHN—Museo Nacional de Historia Natural, Santiago, Chile; ZIN—Zoological Institute of the Russian Academy of Sciences, St Petersburg, Russia; ZPM PGU—Zoological Museum of the Perm State National Research University, Perm, Russia.

Genetic analysis. White muscle tissue preserved from the holotype in 96% ethanol was used for DNA barcoding at Macrogen Inc. (Seoul, South Korea). A fragment of the mitochondrial COI gene was amplified using the primers Liparid_WardsF1 and R1 (Ward *et al*. 2005); amplification attempts using the Folmer primers (Folmer *et al*. 1994) were unsuccessful. Laboratory procedures followed protocols commonly applied in deep-sea liparid studies (e.g., Gerringer *et al*. 2017; Linley *et al*. 2022). PCR products were bidirectionally sequenced using Sanger sequencing. Sequences were edited, trimmed, and aligned using MEGA X (Kumar *et al*. 2018). The final COI consensus sequence (660 bp) has been deposited in GenBank under accession number PV962829 and in BOLD under Process ID ZDLK001-25.

We constructed a dataset to infer the phylogenetic relationships of *Careproctus* **sp. nov.** using the COI marker, with a focus on the genera *Careproctus* and *Paraliparis*. The COI dataset comprised 63 species of *Careproctus*, *Elassodiscus* Gilbert & Burke, 1912, *Paraliparis* Collett 1879, and *Rhinoliparis* Gilbert, 1896, for which sequence data were available, with an emphasis on one record per species. Because sequences from the specimen of *Careproctus* **sp. nov.** showed >99% identity during GenBank BLAST to two records nominally identified as *C. georgianus* Lönnberg, 1905, the analysis included all other publicly available records identified as *C. georgianus* (n = 12; Table 2; Rock *et al*. 2008, Steinke *et al*. 2009; Mabragaña *et al*. 2016). *Nectoliparis pelagicus* Gilbert & Burke, 1912 and *Liparis tanakae* Gilbert & Burke, 1912 (Gilbert & Burke 1912a, 1912b) were selected as within-family outgroups, based on the COI phylogeny presented in Linley *et al*. (2022). *Aptocyclus ventricosus* Pallas, 1769 was selected as the between-family outgroup, as lumpfish (family Cyclopteridae Bonaparte, 1831) are phylogenetically close to the liparid family (Gerringer *et al*. 2017; Orr *et al*. 2019).

Electropherograms were viewed in MEGA X, where primer sequences and any ambiguous bases were trimmed. Sequence identity was confirmed using NCBI BLASTn (Altschul *et al*. 1990). Nucleotide sequences for COI were translated into amino acid sequences to check for the presence of stop codons. Nucleotide sequences were aligned with MAFFT v7 (Katoh *et al*. 2019). The final dataset comprised 77 individual sequences and an alignment length of 452 base pairs (Table 2).

The topology was inferred by Bayesian evolutionary analysis by sampling trees (*BEAST) software package v1.10.4 (Suchard *et al*. 2018). The analysis was run for 40,000,000 generations and sampled every 100,000 trees with an uncorrelated relaxed clock (Drummond *et al*. 2006). The sequence evolution model was estimated using jModelTest2, and the optimal Akaike Information Criterion and Bayesian Information Criterion indicated that the General Time-Reversible (GTR) model (Gatto *et al*. 2006), with a gamma distribution and invariant sites, was the best-fit model. Two independent runs were performed with an uncorrelated relaxed clock, and outputs were assessed with Tracer v1.7 to ensure convergence (effective sample size >200). The two independent runs were combined in LogCombiner v1.8.4. With TreeAnnotator v1.8.4, the first 4,000,000 trees were discarded as burn-in, where the partition frequencies among the remaining trees gave the posterior probabilities used to provide an estimate of clade credibility. Trees were visualized using FigTree v1.4.3 (Rambaut 2012) and annotated using Inkscape 1.3.2.

Results

Careproctus argosgeorgiae sp. nov. Villarroel-Perez & Chernova

urn:lsid:zoobank.org:act:5D8A7C1A-7E7A-491C-AA8E-5184B4EEFA9D
(Figures 1–5; Table 1)

Holotype. MNHN- ICT 7645, female 294 mm TL, 255 mm SL. Falkland Plateau northeast of Falkland Islands, 50°32' S, 53°54' W, depth 1680 m, 10.10.2024 (UTC-3), F/V CFL Hunter, longline (umbrella), line 3476/station 1815, FIFD grid XL-AW; collector Martin L. Villarroel-Perez.

Diagnosis. *Careproctus argosgeorgiae* **sp. nov.** is distinguished from congeners by the following combination of characters: vertebrae 47; dorsal-fin rays 42; anal-fin rays 34; pectoral-fin rays 37; pleural ribs in three pairs, two of which are strongly developed; teeth simple; gill slit long, about half HL and reaching pectoral-fin ray 18; pelvic disk large, about 33% HL; distance from disk to anus greater than or equal to disk length; pectoral-fin upper lobe 67% HL; skin naked, with thick subcutaneous gelatinous tissue; color uniformly light orange, with deep orange margins of disk and pectoral fins.

Description. Dorsal-fin rays 42, first ray between neural spines 2 and 3. Anal-fin rays 34, with three anterior rays before the first haemal spine. Caudal-fin principal rays 12 (6 upper and 6 lower); procurrent rays 3 (2 upper and 1 lower) (Fig. 3); caudal-fin formula 15 (2+6/6+1). Hypural plate structure indistinguishable on radiographs. Vertebrae 47 (pre-caudal 12 + caudal 35, including urostylar center). Pleural ribs in three pairs: two strong pairs on vertebrae 10 and 11 (Fig. 2D); and a third pair thin and short (hardly visible) on vertebra 12. Counts and measurements are provided in Table 1.

Body stout and not humpback (Fig. 1). Head large, 3.5 in SL; pre-caudal part of body almost half of SL (48%). Maximal body depth equal to head length (99% HL), depth at A-fin origin almost equal to head depth (16 and 19% SL), depth at caudal peduncle 2% SL (8% HL).

Head not deep at occiput, depth (66% HL) somewhat less than width (74% HL). Snout, 42% HL in length, not protruding above upper jaw. Nostrils one pair; tube width 2.1% HL. Mouth horizontal, terminal; width between corners of mouth about half of head length (54% HL). Teeth simple, conical, and sharp (Fig. 2C), in numerous oblique rows, 6–7 teeth in a row near jaw symphysis. Eye small; diameter 4.6% SL (6.2 in HL); pupil round. Interorbital width 11.2% SL (2.4 times eye diameter). Postorbital length 14% SL (3.0 times eye diameter). Gill slit long, 13% SL (2.8 times eye diameter), almost equal to half the head length (45% HL) and reaching pectoral-fin ray 18, ventral end about level with mouth cleft. Opercular flap prominent, tip rounded when fresh and angled after fixation (Fig. 1C). Pore formula 2–6–7–1 (Fig. 2A). Chin pores closely spaced (~2 pore diameters), preoperculomandibular pores 2–4 separated by ~4 pore diameters.

Dorsal fin not deep, with 3 or 4 anterior rays obviously erectile, tips standing out from fin membrane (Fig. 1A). Caudal fin length 27% SL. Dorsal and anal fins overlap caudal fin by about three quarters of its length.

Pectoral fin distinctly notched, with 37 rays: 29 in upper lobe, including shortest in notch, and 8 in lower lobe. Pectoral fin upper lobe rather long (67% HL), reaching anal-fin origin; lower-lobe rays no longer than upper-lobe rays, almost reaching anus. Pectoral girdle broken, lower part missing (Fig. 4); scapula and two upper radials present; scapula and radials notched, with fenestrae in the cartilaginous plate between adjacent elements.

Pelvic disk longitudinally oval (length 1.2 times width), located below gill slit. Disk length 32.6% HL (3.1 in HL), disk width 27.2% HL. Anterior fold of disk and segmental pads in central part not differentiated, central part of disk not depressed, diameter larger than width of marginal part (Fig. 2B). Disk to anus distance about equal to disk length (10.0% and 9.2% SL). Anus opening well behind head (pre-anal length 128% HL), on vertical line near end of longest ray of the pectoral-fin. Distance from anus to anal-fin origin 1.8 times distance from posterior margin of disk to anus. Stomach and pyloric caeca not examined; otoliths not extracted.

Gelatinous subcutaneous tissue (=subdermal extracellular matrix *sensu* Eastman *et al.* 1994) quite thick when fresh; dorsal-fin rays covered by this tissue on proximal one-third of fin length; anal-fin rays completely embedded in tissue along anterior half of fin length. Skin naked, prickles absent. Female with large light-yellow eggs of approximately equal size, averaging 5 mm diameter, largest 5.7 mm.

Color when fresh uniform light orange with rose tint; margins of disk and ends of pectoral-fin rays orange. Oral cavity pale; gill cavity orange brown; gills reddish brown. Peritoneum brown with darker dispersed pigments. Coloration after fixation in formaldehyde and after preservation in alcohol pale (Fig. 1C).

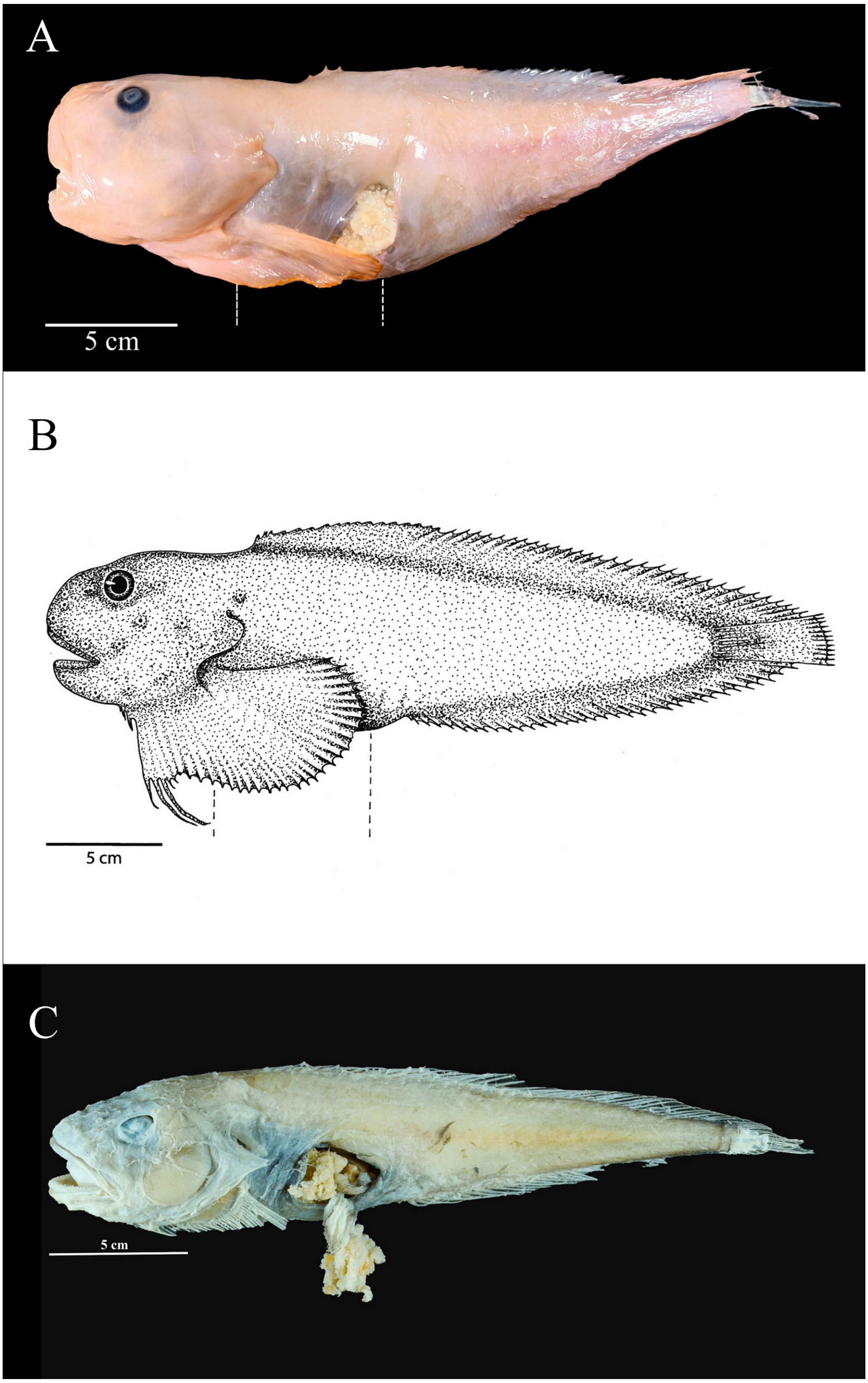

FIGURE 1. *Careproctus argosgeorgiae* **sp. nov.**, holotype MNHN-ICT 7645, female, 255 mm SL. Dashed lines indicate the location of the pelvic disk center and the anus position. (**A**) Fresh specimen. (**B**) Composite drawing from fresh and fixed specimen. Drawing by Daniela Álvarez Bravo. (**C**) Preserved specimen.

Etymology. The specific epithet argosgeorgiae honors the F/V Argos Georgia, a longliner that sank in the South Atlantic near the Falkland Islands on 22 July 2024, resulting in the loss of 13 lives and 14 survivors, including two fisheries observers. The response to the tragedy reflects the resilience and compassion of the South Atlantic islands community and underscores the human risks of deep-sea fishing in subantarctic and Antarctic waters. The epithet is a Latin feminine genitive meaning "of the Argos Georgia", commemorating the vessel, its crew, and all those connected to it.

Distribution. Known from a single specimen captured on the Falkland Plateau, northeast of the Falkland Islands, at a bathydemersal depth of 1680 m.

Capture and associated fauna. The fish was incidentally recovered during hauling of umbrella-type longline gear targeting *Dissostichus eleginoides* Smitt, 1898 in waters northeast of the Falkland Islands, at depths of approximately 1040–1790 m. The individual was unhooked at the time of collection and exhibited a ruptured abdominal wall with extruded ripe eggs. The bycatch composition (%) was dominated by deep-sea fish species, including the elasmobranchs Antarctic starry skate *Amblyraja georgiana* Norman, 1938 and butterfly skate *Bathyraja papilionifera* Stehmann, 1985 (Rajiformes: Rajidae) (41%), the Southern sleeper shark *Somniosus antarcticus*

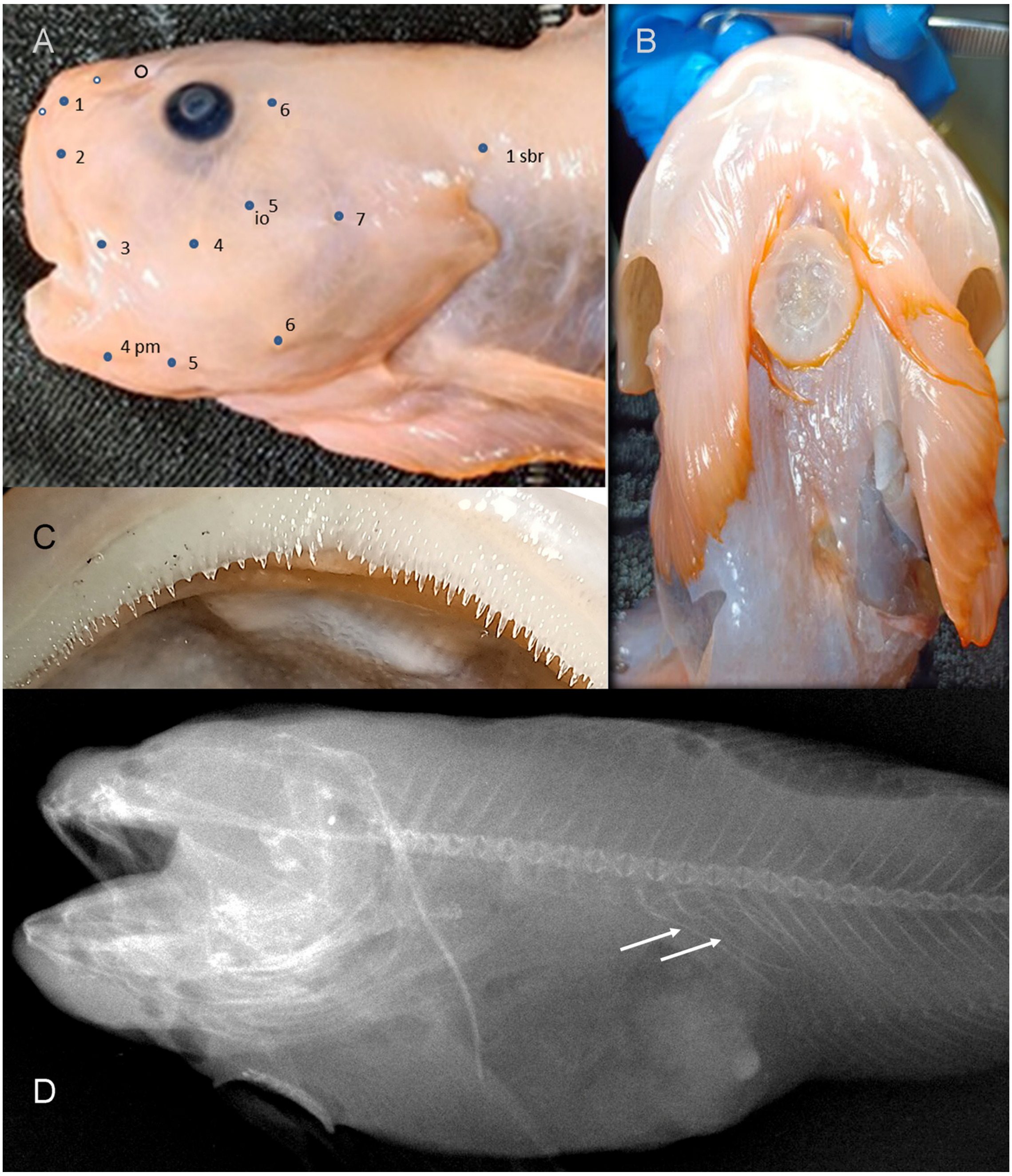

FIGURE 2. *Careproctus argosgeorgiae* **sp. nov.**, holotype. (**A**) Arrangement of cephalic pores: two nasal pores (small empty circles); other pores (solid circles): 1–6 infraorbital (io), 4–7 preoperculomandibular (pm), and one suprabranchial (sbr); large empty ring is the nostril. (**B**) Ventral view. (**C**) Upper jaw teeth. (**D**) Radiograph; arrows indicate the two pairs of sabre-like pleural ribs on posterior abdominal vertebrae.

Whitley, 1939 (Squaliformes: Somniosidae) (2%) and the osteichthyans, mainly big-eye grenadier *Macrourus holotrachys* Günther, 1878 (Gadiformes: Macrouridae) (35%) and blue antimora *Antimora rostrata* Günther, 1878 (Gadiformes: Moridae) (22%). Benthic invertebrates, including cold-water corals and sponges that are VME indicator taxa (Huvenne *et al*. 2011; Robert *et al*. 2020), together with lithodid crabs, collectively accounted for only 0.02% of the total bycatch weight recorded across all hauls.

Biology. The holotype is a ripe female (maturity stage V), weighing 392 g (wet weight at sea), with large eggs; the specimen was collected in October (Southern Hemisphere). An elongate, worm-like ectoparasite was attached to the caudal region on the left side of the body.

Comparisons. Of the eighteen species of *Careproctus* known from southern South America and adjacent waters, *C. atakamensis* Andriashev, 1998, *C. aureomarginatus*, *C. macranchus* Andriashev, 1991, and *C. magellanicus* Matallanas & Pequeño, 2000 have more vertebrae (51–59) than *C. argosgeorgiae* **sp. nov.** (47). In contrast, *C. falklandicus*, *C. fueguensis* Matallanas & Piacentino, 2019, *C. pallidus* Vaillant, 1888, and *C. patagonicus* Matallanas & Pequeño, 2000 have fewer vertebrae (36–40). Unlike *C. argosgeorgiae* **sp. nov.**, most of the other listed species lack pleural ribs, including *C. acaecus* Andriashev, 1991, *C. aculeolatus*, *C. armatus*, *C. cactiformis* Andriashev, 1990, *C. minimus* and *C. stigmatogenus.*

By the presence of two pairs of strong pleural ribs, *C. argosgeorgiae* **sp. nov.** is similar only to *C. atrans*, *C. herwigi* Andriashev, 1991, and *C. smirnovi*. It differs from *C. atrans* in having a higher number of pectoral-fin rays (37 vs. 26). Of the remaining two species, *C. argosgeorgiae* **sp. nov.** differs from *C. herwigi*, described from northern Argentina (41°13’ S, 1250 m), by the presence of simple teeth (vs. three-tuberculated teeth), a higher number of vertebrae (47 vs. 45), a longer gill slit reaching the 18th pectoral-fin ray (vs. 7–8 rays), and a gill slit approximately half of head length (vs. one-third). Additional differences include a smaller eye (6.2 in HL vs. 4.4), and a distance from disk to anus approximately equal to disk length (vs. about half of disk length).

The new species is most similar to *C. smirnovi*, which is known from waters north of the Falkland Islands at depths of 1500–1580 m based on two specimens of 204 and 186 mm SL (Andriashev 1991a, 2003; this paper: Fig. 5). *Careproctus argosgeorgiae* **sp. nov.** is larger in size and agrees with *C. smirnovi* in the presence of pleural ribs, simple teeth, a similar number of vertebrae, dorsal-, pectoral- and caudal-fin rays, a similar gill slit size (Table 1), and in the peritoneum coloration. However, it differs in having a less humpbacked occiput, an opercular flap positioned below the level of the eye, the upper pectoral-fin ray at mouth-cleft level, and a thicker, well-developed subcutaneous layer covering the origins of the dorsal and anal fins.

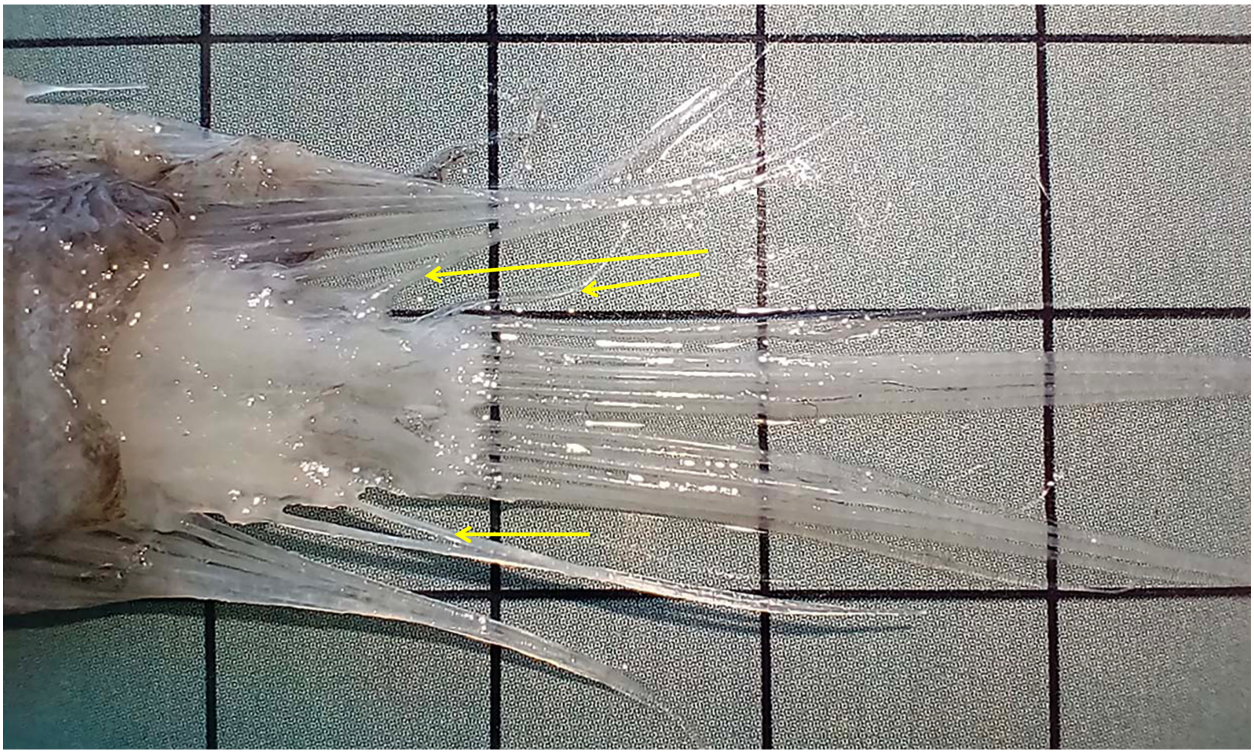

FIGURE 3. *Careproctus argosgeorgiae* **sp. nov.**, holotype. Caudal-fin secondary rays (shown by arrows): two upper and one lower. Scale indicated by grid squares (1 cm).

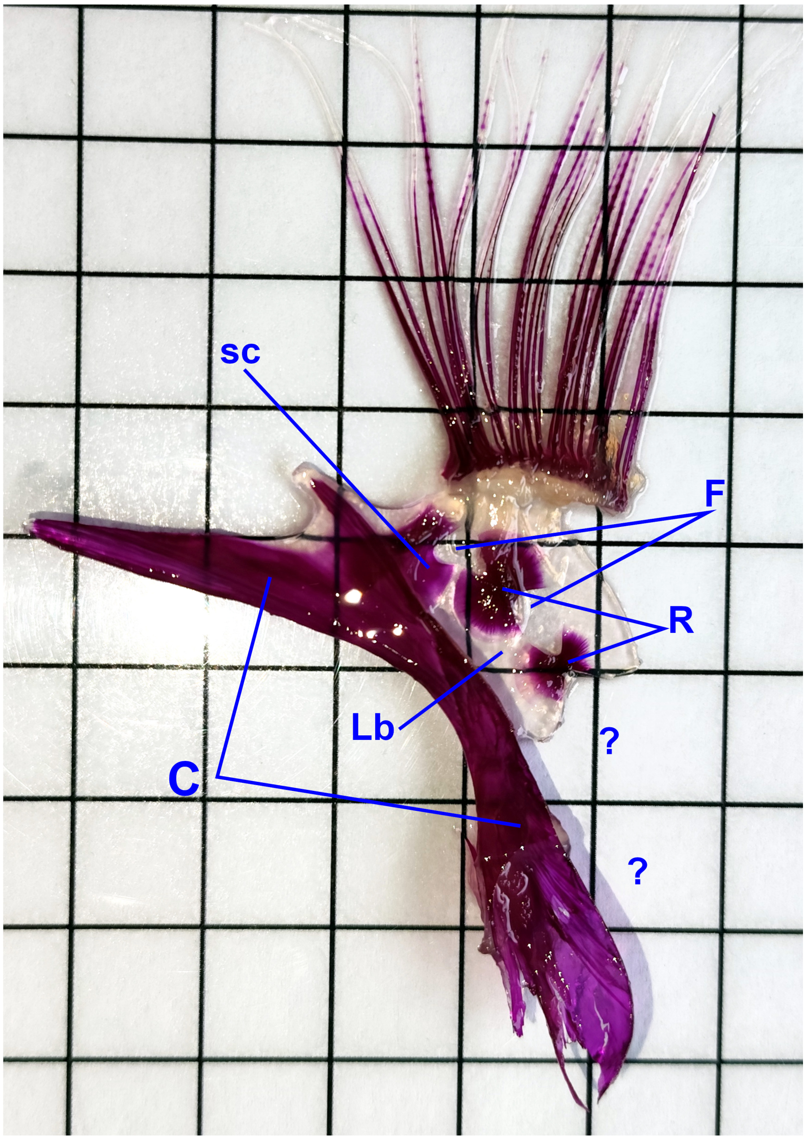

FIGURE 4. Right pectoral girdle and fin of *Careproctus argosgeorgiae* **sp. nov.**, holotype. Abbreviations: C—cleithrum; Lb—basal cartilaginous plate; sc—scapula; R—two radials; F—two fenestrae; ?—indicating missing parts damaged during processing. Scale indicated by grid squares (1 cm).

Additional differences between *C. argosgeorgiae* **sp. nov.** and *C. smirnovi* include fewer anal-fin rays (34 vs. 36–37), a greater maximal body depth (28.0 vs. 25.8–26.2% SL), a shorter pre-dorsal length (32.3 vs. 34.4–35.0% SL), greater distances from chin to disk (15.3 vs. 13.3–14.0% SL) and from chin to anus (32.1 vs. 26.5–30.1% SL), and a longer upper lobe of the pectoral-fin (67 vs. 58–60% HL). The anus is positioned more posteriorly, with the distance from disk to anus larger (10.0 vs. 3.5–7.5% SL) and exceeding disk length (vs. less than disk diameter). In addition, the central part of the disk by diameter is larger than the width of its marginal part (vs. smaller than the marginal part), and the interorbital width is greater (39.7 vs. 34.2–35.8% HL). Color differences are also distinct with the body uniformly light orange and the disk and pectoral fins having deep orange margins (vs. rose-lilac coloration, darker posteriorly).

Some of the observed differences between *C. argosgeorgiae* **sp. nov.** and *C. smirnovi* may be influenced by specimen condition at fixation, particularly pre-dorsal-fin length and chin-to-disk distance. Nevertheless, most characters are interpreted as interspecific differences, supporting the recognition of *C. argosgeorgiae* **sp. nov.** as a distinct species.

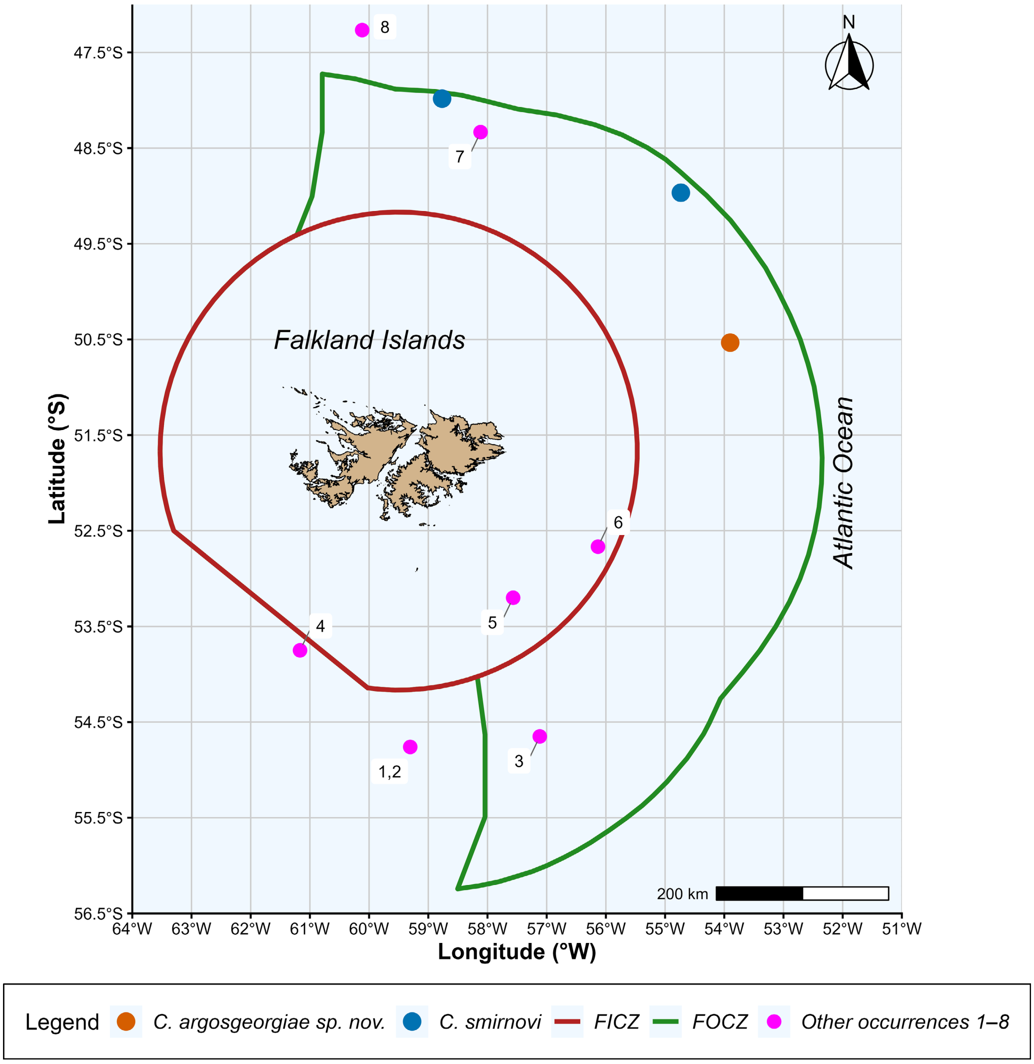

FIGURE 5. Map of Falkland Islands showing capture localities of *Careproctus argosgeorgiae* **sp. nov.** (holotype), *C. smirnovi* (holotype left and paratype right), and other *Careproctus* species reported from the area: **1,2**—*C. maculosus* and *C. stigmatogenus*; **3**—*C. minimus*; **4**—*C. falklandicus*; **5**—*C. armatus*; **6**—*C. aureomarginatus*; **7**—*C. atrans*; and **8**—*C. aculeolatus*. Species coordinates taken from original descriptions. Falkland Islands inner (FICZ) and outer (FOCZ) conservation zones also shown.

A comparison is also provided with *C. solovjevae* Balushkin, 2012, originally described in the genus *Volodichthys* Balushkin, 2012, because it was considered by its author to be closest to *C. smirnovi* (Balushkin 2012), to which the new species is also most similar. Available data (Table 1) indicate that *Careproctus argosgeorgiae* **sp. nov.** resembles *C. solovjevae* in vertebral number and the presence of pleural ribs, but differs in having a gill slit reaching anterior to the 18th pectoral-fin ray (vs. 10–13), a smaller eye (16.2 vs. 20.6–25.2% HL), a smaller disk (32.6 vs. 37.2–42.4% HL), a shorter distance from anus to anal-fin origin (17.9 vs. 20.2–20.4% SL), and distinct coloration (body light orange vs. gray-lilac, darker posteriorly; peritoneum brown vs. brown with a greenish tint).

Except as noted above, six other species of *Careproctus* possessing two or three pairs of long pleural ribs are known from the Southern Hemisphere, all of which differ from *C. argosgeorgiae* **sp. nov.** Three species have higher vertebral counts: *C. albescens* Barnard, 1927 from South Africa (60–63), *C. novaezelandiae* Andriashev, 1990 from bathyal depths of the New Zealand Plateau (53–54), and *C. paxtoni* Stein, Chernova & Andriashev, 2001 from waters off New South Wales (58–59). Two species have similar vertebral (46–47) but differ in tooth morphology (three-lobed or with shoulders) and in having a shorter gill slit reaching only to the 5th–6th pectoral-fin rays in *C. catherinae* from the Ross Sea, or to the 7–11th rays in *C. parini* from the South Shetland Islands (Andriashev 2003).

TABLE 1. Counts and measurements of *C. argosgeorgiae* **sp. nov.** and the type specimens of *C. smirnovi* and *C. solovjevae*; diagnostic characters of the new species are marked in bold. F=female; M=male.

Characters	*C. argosgeorgiae* **sp. nov.**	*C. smirnovi*		*C. solovjevae*	
	Holotype	Holotype	Paratype	Holotype	Paratype
Museum number	MNHN- ICT 7645	ZIN 49589	MGU 13688	ZIN 55054	ZPM PGU 393
SL, sex	254.8, F	204, M	186, F	332 F	343 F
Vertebrae	47 (12+35)	48 (11+37)	48 (11+37)	48 (13+35)	49 (12+37)
Pleural ribs, pairs	3	3	–	3	–
Dorsal-fin rays	42	43	43	43	44
Anal-fin rays	**34**	37	36	36	37
Pectoral-fin rays	37 (29+8)	37 (29+8)	37 (29+8)	35–37 (6–8+28–29)	35, 36
Caudal-fin rays	15 (2+6/6+1)	14 (2+5/6+1)	13(14?)	14 (2+5/6+1)	14
Gill slit reaching to in front of pectoral-fin ray	**18**	14	17	13	10
Pores	2–6–7–1	2–6–7–1	–	2–6–7–1	–
As % SL:					
Head length	28.3	29.4	30.1	30.7	28.9
Head width	20.9	22.1	20.5	22.9	23.3
Body depth	**28.0**	26.2	25.8	20.5	21.3
Depth at A-fin origin	**15.9**	20.6	ca. 18	23.5	26.2
Pre-dorsal length	**32.3**	34.4	35.0	–	–
Pre-caudal length	47.9	44.0	52.6	–	–
Chin to disk	**15.3**	13.3	14.0	14.2	11.5
Chin to anus	32.1	26.5	30.1	34.0	32.6
Disk	9.2	10.3	9.1	8.7 / 11.4[1]	12.2
Disk to anus	**10.0**	3.5	7.5	9.3	9.8
Anus to anal-fin origin	17.9	12.8	18.8	20.2	20.4
Pectoral-fin upper lobe	**19.0**	17.2	18.3	14.7	15.4
Pectoral-fin lower lobe	**16.1**	15.7	15.6	14.2	13.4
Snout	11.8	11.8	12.9	13.2	15.2
Gill slit, length	12.8	13.8	15.1	13.8	12.8
As % HL					
Head width	73.8	75.0	Ca.78	–	–
Eye	**16.2**	20.0	16.2	20.6	25.2
Interorbital	39.7	34.2	35.8	39.2	44.0
Gill slit, length	45.1	46.7	50.0	45.1	44.4
Disk	32.6	35.0	30.2	37.2	42.4
Pectoral upper lobe	**67**	58.4	60.4	–	–
Color of body	**Light orange**	Rose-lilac, darker posteriorly	Darker than the holotype	Grey-lilac, darker posteriorly	Grey-lilac, darker posteriorly
Peritoneum	Brown	Light brown	Light brown	Brown with greenish tint	Brown with greenish tint
Data from	This study	Andriashev (1991, 2003)		Balushkin (2012)	

[1] Balushkin (2012) gives different data for length of the disk of the holotype of *V. solovjevae* in his diagnosis and Table 2.

TABLE 2. GenBank accession numbers and references for all samples included in the analysis of the COI barcoding gene. Some identifications present in GenBank are outdated or incorrect; those updated in this study and in Orr *et al*. (2019, 2020), are shown, with the original GenBank identifications in parentheses. Asterisks denote unpublished data.

Species	GenBank Accession Number	References
Family: Cyclopteridae		
Aptocyclus ventricosus	AP004443	Miya *et al*. (2003)
Family: Liparidae		
Careproctus acanthodes	LC380018	Kai*
Careproctus ambustus	MN126594	Orr *et al*. (2020); as *C*. cf. *melanurus* Orr *et al*. (2019)
***Careproctus argosgeorgiae* sp. nov.**	**PV962829**	**Present Study**
Careproctus georgianus	EU326327	Rock *et al*. (2008)
Careproctus longifilis (*attenuates*)	FJ164428	Steinke *et al*. (2009)
Careproctus barbatulus	LC773198	Kai *et al*. (2024)
Careproctus sp. nov. (*canus*)	FJ164432	Steinke *et al*. (2009); Orr (in preparation)
Careproctus colletti	LC337287	Kai*
Careproctus continentalis	HQ712898	Dettai *et al*. (2011)
Careproctus cyclocephalus	LC337280	Kai*
Careproctus cypselurus	KY570326	Elz *et al*.*
Careproctus furcellus	LC437091	Matsuzaki *et al*. (2020)
Careproctus gilberti	MH715569	Orr *et al*. (2019)
Careproctus iacchus	LC349296	Kai *et al*. (2018)
Careproctus io	LC789195	Kai *et al*. (2024)
Careproctus longibarbatus	LC773195	Kai *et al*. (2024)
Careproctus longidigitus	LC495314	Kai & Matsuzaki (2020)
Careproctus longipectoralis	HQ712900	Dettai *et al*. (2011)
Careproctus macrodiscus	LC380009	Kai*
Careproctus marginatus	LC379996	Kai*
Careproctus melanurus	MH715572	Orr *et al*. (2019)
Careproctus cf. *melanurus*	MH715571	Orr *et al*. (2019)
Careproctus mederi	LC773185	Kai *et al*. (2024)
Careproctus notosaikaiensis	LC380012	Kai*
Careproctus ostentum	MH715573	Orr *et al*. (2019)
Careproctus ovigerus (*georgianus*)	FJ164449	Steinke *et al*. (2009)
Careproctus ovigerus (*georgianus*)	FJ164448	Steinke *et al*. (2009)
Careproctus pellucidus	LC380014	Kai*
Careproctus rastrinus	JF952697	Zhang & Hanner (2011)
Careproctus rausuensis	LC412486	Matsuzaki *et al*. (2020)
Careproctus reinhardti	HQ712338	Mecklenburg *et al*. (2011)
Careproctus rhomboides	LC773204	Mori *et al*. (2025)
Careproctus roseofuscus	LC380011	Kai*
Careproctus scottae	MH715574	Orr *et al*. (2019)
Careproctus shigemii	LC513147	Matsuzaki *et al*. (2020)
Careproctus simus	LC380005	Kai*; used in Orr *et al*. (2019)
Careproctus spinulosus	LC773203	Kai *et al*. (2024)

......continued on the next page

TABLE 2. (Continued)

Species	**GenBank Accession Number**	**References**
Careproctus surugaensis	LC797962	Kai *et al*. (2024)
Careproctus trachysoma	LC416714	Kai*; as *Careproctus rastrinus* in Orr *et al*. (2019)
Careproctus sp. (*georgianus*)	KX675934	Mabragaña *et al*. (2016)
Careproctus sp. (*georgianus*)	KX675935	Mabragaña *et al*. (2016)
Careproctus sp. (*georgianus*)	KX675936	Mabragaña *et al*. (2016)
Careproctus sp. (*georgianus*)	KX675937	Mabragaña *et al*. (2016)
Careproctus sp. (*georgianus*)	KX675938	Mabragaña *et al*. (2016)
Careproctus sp. (*georgianus*)	KX675939	Mabragaña *et al*. (2016)
Careproctus sp. (*georgianus*)	KX675940	Mabragaña *et al*. (2016)
Careproctus sp. JRAS06-305 (*georgianus*)	EU326326	Rock *et al*. (2008)
Careproctus zachirus	LC513151	Matsuzaki *et al*. (2020)
Elassodiscus sp. cf. *caudatus*	GU440308	Hastings & Burton*; used in Orr *et al*. (2019)
Liparis tanakae	JF952785	Zhang & Hanner (2011)
Paraliparis antarcticus	KX676116	Mabragaña *et al*. (2016)
Paraliparis bathybius	EU326411	Rock *et al*. (2008)
Paraliparis calidus	KY033936	Kenchington *et al*. (2017)
Paraliparis cephalus	KY570349	Elz *et al*.*
Paraliparis charcoti	HQ713138	Dettai *et al*. (2011)
Paraliparis copei	KY033937	Kenchington *et al*. (2017)
Paraliparis sp. (*dactylosus*)	FJ164953	Steinke *et al*. (2009)
Paraliparis leobergi	HQ713145	Dettai *et al*. (2011)
Paraliparis macropterus (*Careproctus* aff. *longipectoralis*)	JN641070	Smith *et al*.*
Paraliparis mawsoni	HQ713150	Dettai *et al*. (2011)
Paraliparis megalopus (*melanobranchus*)	FJ164959	Steinke *et al*. (2009)
Paraliparis neelovi	JN641069	Smith *et al*.*
Paraliparis paucidens	FJ164964	Steinke *et al*. (2009)
Paraliparis pectoralis	GU440448	Hastings & Burton*; used in Orr *et al*. (2019)
Paraliparis rosaceus	KY570351	Elz *et al*.*; used in Orr *et al*. (2019)
Paraliparis operculosus (*Paraliparis* sp.)	JN640730	Smith *et al*. (2012) supplementary material; used in Linley *et al*. (2022)
Paraliparis selti	MN422493	Linley *et al*. (2022)
Paraliparis thalassobathyalis	EU326328	Rock *et al*. (2008)
Paraliparis sp. cf. *rosaceus*	HQ713151	Dettai *et al*. (2011)
Paraliparis sp. cf. *rosaceus*	FJ164985	Steinke *et al*. (2009)
Paraliparis sp. MOP110189	MF956930	Robertson *et al*. (2017)
Paraliparis sp. JRAS06-106	EU326410	Rock *et al*. (2008)
Paraliparis sp. JRAS06-326 (*Careproctus georgianus*)	EU326329	Rock *et al*. (2008)
Nectoliparis pelagicus	FJ164909	Steinke *et al*. (2009)
Rhinoliparis attenuatus	FJ165100	Steinke *et al*. (2009)
Rhinoliparis attenuatus (*barbulifer*)	GU440505	Hastings & Burton*

Discussion

Liparidae is a taxon with few available reference genetic sequences from the Southern Hemisphere in public databases. Of >127 species analyzed with COI data by Orr *et al*. (2019), only 24% were from the Southern Hemisphere, representing 12% of species known from the area, indicating a lack of comparative material for analysis. This is particularly evident in the Patagonian-Falkland Islands region, where many species of *Careproctus* described by Andriashev (1991a, 1991b) have no barcode sequence or recent records.

Results showed that the COI sequence of *C. argosgeorgiae* **sp. nov.** is phylogenetically close to *C. ovigerus* Gilbert, 1896 and *C. surugaensis* Murasaki, Takami & Fukui 2018 sequences (Fig. 6). Morphologically, *Careproctus argosgeorgiae* **sp. nov.** differs from northeastern Pacific congeners, including *C. kamikawai* Orr 2012, *C. lycopersicus* Orr 2012, *C. ovigerus*, and *C. surugaensis*, in having three pairs of pleural ribs rather than two. It further differs in possessing simple teeth with low tooth counts per row (6–7), whereas the northern species have three-lobed teeth with higher counts, except for *C. ovigerus*. The gill slit extends anterior to the 18th pectoral-fin ray, compared with 4th-12th rays in the northeastern Pacific species. In addition, the new species has more pectoral-fin rays (P=37) and more caudal-fin rays (C=15) than *C. ovigerus* and *C. surugaensis*. The peritoneum is brown and the body coloration is uniformly light orange, in contrast to the darker peritoneum and pink to red coloration of the northern congeners (Orr 2012; Murasaki *et al*. 2018). The COI sequence of the new species was also closer to that of *C. georgianus*, for which a morphological comparison is provided below.

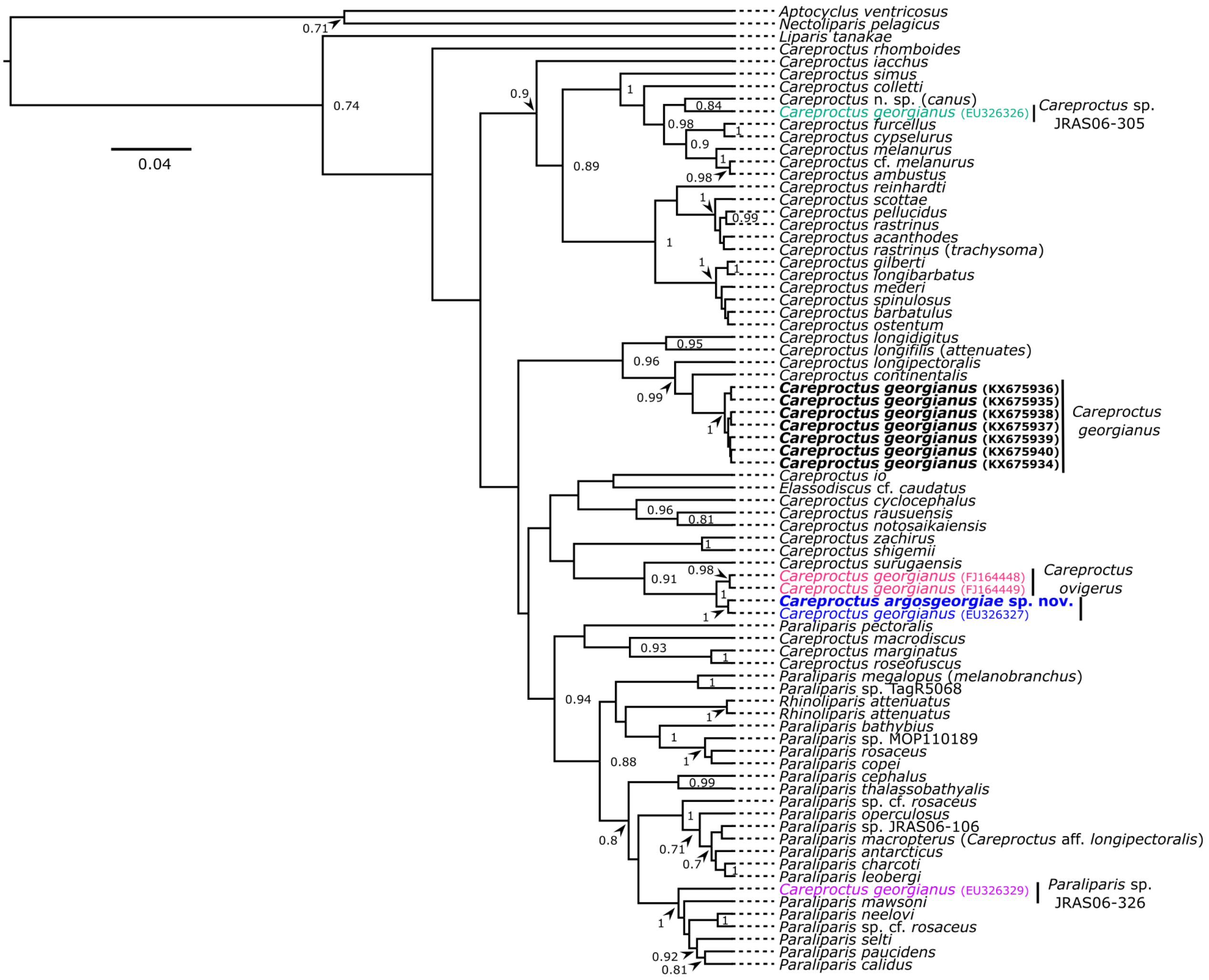

FIGURE 6. Bayesian-inferred phylogenetic tree of the Liparidae using COI barcode sequences showing *Careproctus argosgeorgiae* **sp. nov.** and *C. georgianus*. Bayesian posterior probabilities greater than 70% are shown at branch nodes. Five distinct clades labelled as *C. georgianus* are recovered; four (colored) represent misidentified sequences, whereas one clade (black, bold) is closest to *C. georgianus* sensu stricto.

BLAST results indicate a close molecular affinity to *C. georgianus* from South Georgia (99.69% to EU326327). However, morphological data are inconsistent with this interpretation. *Careproctus georgianus* differs significantly from *C. argosgeorgiae* **sp. nov.** in lacking pleural ribs, having a higher number of vertebrae (56–60), fewer pectoral-fin rays (29–34) and fewer caudal-fin rays (10). In addition, the gill slit is short and positioned above the pectoral-fin, and the maximum recorded size is smaller, reaching only 105 mm TL (Lönnberg 1905; Andriashev & Stein 1998). These notable morphological differences, particularly in body form and skeletal features, are consistent with characters distinguishing other species of *Careproctus* (*see* Orr *et al*. 2019) and support the interpretation of *C. argosgeorgiae* **sp. nov.** as a distinct taxon despite its COI similarity to *C. georgianus*.

Analysis of the results (Fig. 6) shows that "*C. georgianus*" is represented in five distinct clades, which can be interpreted as indicating that the identification of voucher specimens in the database was incorrect in most, if not all, cases. The poor preservation quality of the specimens, which makes them difficult to identify, appears relevant. Additionally, COI sometimes fails to distinguish liparid species due to low sequence divergence, ranging from 0.2 to 9.1% in *Careproctus* (Orr *et al*. 2019), even when morphological differences are apparent, which can lead to misidentifications. This highlights the limitations of barcoding used alone for species delineation in liparids.

Contradictory genetic placements within Liparidae have been previously reported. For example, DNA barcoding results for Pacific Canadian fishes placed Antarctic *C. georgianus* basal to a clade containing species of *Paraliparis*, a position likely reflecting limited taxon sampling rather than close phylogenetic affinity (Steinke *et al*. 2009). Orr *et al*. (2019) placed *C. georgianus* within the Bathyphasmia informal clade C alongside *C. ovigerus*, highlighting its derived pectoral girdle (four equally spaced radials without fenestrae), high vertebral count, and small gill slit. These features contrast with the anatomy of *C. argosgeorgiae* **sp. nov.** as well, which exhibits a larger gill slit (reaching the 18th pectoral-fin ray), strong pleural ribs and pectoral girdle with at least two radials with fenestrae.

We agree with Orr *et al.* (2019) and assume voucher specimens TagR5832 and TagR5831 (FJ164448 & -49) from Steinke *et al*. (2009) represent *C. ovigerus*, as redescribed by Orr (2012), and based on the available photographs in BOLD (BIN: AAC6780). Additionally, the *C. georgianus* voucher JRAS06-350 (EU326327) of Rock *et al*. (2008) can tentatively be identified as *C. argosgeorgiae* **sp. nov.** (Fig. 6, Table 2). If so, Shag Rocks, South Georgia, probably should be considered part of its distribution. However, we were unable to analyze *C. georgianus* vouchers, and *C. georgianus* should remain uncertain until its identity is confirmed. Additionally, *C. georgianus* clade from Antarctic waters (KX675934–40) may represent the *C. georgianus sensu stricto*. However, this material could not be re-examined for this study, and future work on South Atlantic *Careproctus* diversity should aim to address this. In contrast, the Rock *et al*. (2008) *C. georgianus* voucher JRAS06-305 (EU326326) may be an unidentified *Careproctus* sp. that is grouped with a *Careproctus* sp. (Orr, unpublished) from British Columbia, while the *C. georgianus* voucher JRAS06-326 (EU326329) from Rock *et al*. (2008) is more likely a species of *Paraliparis* rather than *Careproctus*. However, in the absence of photographs or well-preserved specimens, this reassignment should be regarded as tentative.

Since its proposal by Balushkin (2012), *Volodichthys* has been applied only to the originally transferred species (e.g., Duhamel *et al*. 2014; Priede 2017; Koerber 2023). *Careproctus argosgeorgiae* **sp. nov.** is morphologically closest to *C. solovjevae*, a taxon originally assigned to *Volodichthys*. Orr *et al*. (2019) discussed *Bathyphasma* Gilbert, 1896 in the context of Southern and Northern Hemisphere clade relationships involving *C. ovigerus* and *C. georgianus*. Balushkin (2012) resurrected *Bathyphasma* and considered it closely related to *Volodichthys*. Although Orr *et al*. (2019) did not evaluate *Volodichthys* status, they placed *C. ovigerus* and *C. georgianus* together in clade C and retained both species in *Careproctus*. The placement of *C. argosgeorgiae* **sp. nov.** within clade C is consistent with this. However, a formal evaluation of the validity of *Bathyphasma* or *Volodichthys* lies beyond the scope of the present study.

In addition to its taxonomic distinctiveness, the capture circumstances and associated fauna provide insight into the ecological setting of *Careproctus argosgeorgiae* **sp. nov.** The new species is currently known from a single bathydemersal specimen collected on the Falkland Plateau at 1680 m, indicating an affinity with deep continental slope habitats. The species was taken as bycatch in longline gear targeting *Dissostichus eleginoides*, together with a fish assemblage dominated by deep-water rajids, macrourids and morids, consistent with the known ichthyofauna of the region at comparable depths. The holotype was a ripe female with large eggs collected in austral spring, suggesting seasonal reproductive activity. The presence of an ectoparasite further indicates a benthic-associated lifestyle typical of deepwater liparids.

Including more Southern Hemisphere liparid taxa in future phylogenetic analyses will provide key insights into historical biogeographic patterns and clarify the relationship of *C. argosgeorgiae* **sp. nov.** and other species with Northern Hemisphere congeners.

Acknowledgments

The authors express their gratitude to the factory crew of the F/V CFL Hunter for their careful handling of the specimen, and to MNHN curator Jhoann Canto Hernández for the holotype reception. The lead author thanks Capitán Fernando for his professionalism and support during the observer's stay and thanks the FIFD Observer Manager, Toni Trevizan, for the deployment. Special thanks to Dr. Zoe Fowler of the Veterinary section in the Department of Agriculture for the radiographic work. We also thank Daniela Álvarez Bravo for preparing the scientific illustration of *Careproctus argosgeorgiae* **sp. nov.** We thank the reviewers, including an anonymous reviewer, whose constructive comments helped improve the manuscript. The work of N.C. was conducted as part of the ZIN Research Theme No. 125012800885-4. The authors thank the Falkland Islands Government and FIFD for their financial support, which made this fisheries and taxonomic research possible.

References

Altschul, S.F., Gish, W., Miller, W., Myers, E.W. & Lipman, D.J. (1990) Basic local alignment search tool. *Journal of Molecular Biology*, 215 (3), 403–410.
https://doi.org/10.1016/S0022-2836(05)80360-2

Andriashev, A.P. (1977) On the method of studying the morphology and systematics of snailfishes (Liparidae). *Zoologicheskii Zhurnal*, 56 (1), 141–147. [in Russian, English summary]

Andriashev, A.P. (1990) Redescription of the syntypes of "*Liparis antarctica* Putnam n. subsp. (?) *falklandica* Lönnberg" with description of two new species of the genus *Careproctus* from the bathyal depths of Argentina and New Zealand. *Trudy Zoologicheskogo Instituta Akademia Nauk SSSR*, 222, 5–17. [in Russian, English summary]

Andriashev, A.P. (1991a) New species of Patagonian liparid fishes of the genus *Careproctus* (Scorpaeniformes, Liparididae). *Informational Bulletin of the Soviet Antarctic Expeditions*, 116, 10–24. [in Russian]

Andriashev, A.P. (1991b) New species of liparidid fishes of the genus *Careproctus* from Patagonia. Second Report. *Voprosy Ikhtiologii*, 31 (5), 707–716. [in Russian, English translation in *Journal of Ichthyology* 1992, 32 (1), 60–66]

Andriashev, A.P. (1998) A new deep-sea species of the genus *Careproctus* (Liparidae, Scorpaeniformes) from the equatorial part of the Atacama Trough. *Voprosy Ikhtiologii*, 38 (4), 548–549. [in Russian, English translation in *Journal of Ichthyology*, 38 (7), 541–542]

Andriashev, A.P. & Stein, D.L. (1998) Review of the snailfish genus *Careproctus* (Liparidae, Scorpaeniformes) in Antarctic and adjacent waters. *Contributions in Science*, 470, 1–63.
https://doi.org/10.5962/p.208099

Andriashev, A.P. (2003) *Liparid fishes (Liparidae, Scorpaeniformes) of the Southern Ocean and adjacent waters. Explorations of the Fauna of the Seas. 53 (61)*. Zoological Institute of the Russian Academy of Sciences, Sankt Petersburg, 475 pp. [in Russian, English diagnoses for species]

Bakun, A. (1993) The California Current, Benguela Current, and Southwestern Atlantic Shelf ecosystems: a comparative approach to identifying factors regulating biomass yields. *In*: Alexander, L.M., Sherman, K. & Gold, B.D. (Eds.), *Large Marine Ecosystems: Stress, Mitigation, and Sustainability*. American Association for the Advancement of Science, Washington, D.C., pp. 199–224.

Balushkin, A.V. (2012) *Volodichthys* gen. nov., a new genus of primitive snailfishes (Liparidae: Scorpaeniformes) of the Southern Hemisphere, with a description of a new species *V. solovjevae* sp. nov. (Cooperation Sea, the Antarctic). *Voprosy Ikhtiologii*, 52 (1), 5–14. [in Russian, English translation in *Journal of Ichthyology*, 52 (1), 1–10]
https://doi.org/10.1134/S0032945212010018

Barker, P.F., Dalziel, I.W.D. & Storey, B.C. (1983) Geologic framework of the Falkland Plateau. *Initial Reports of the Deep Sea Drilling Project*, 71, 107–121.
https://doi.org/10.2973/dsdp.proc.71.107.1983

Barnard, K.H. (1927) Diagnoses of new genera and species of South African marine fishes. *Annals and Magazine of Natural History*, Series 9, 20 (115), 66–79.
https://doi.org/10.1080/00222932708655566

Bonaparte, C.L. (1831) Saggio di una distribuzione metodica degli animali vertebrati. *Giornale Arcadico di Scienze Lettere ed Arti*, 52 (1831), 155–189.
https://doi.org/10.5962/bhl.title.48624

Brickle, P., Laptikhovsky, V. & Arkhipkin, A. (2005) Reproductive strategy of a primitive temperate notothenioid *Eleginops maclovinus*. *Journal of Fish Biology*, 66, 1044–1059.
https://doi.org/10.1111/j.0022-1112.2005.00663.x

Burke, C.V. (1930) Revision of the fishes of the family Liparidae. *Bulletin of the United States National Museum*, 150, 1–204.
https://doi.org/10.5479/si.03629236.150.1

Chernova, N.V. (2022) Amphiboreality and distribution of snailfishes (Cottiformes: Liparidae) in the Arctic and the North Atlantic. *Diversity*, 14, 1097.
https://doi.org/10.3390/d14121097

Chernova, N.V., Stein, D.L. & Andriashev, A.P. (2004) Family Liparidae Scopoli, 1777 – snailfishes. *California Academy of Sciences, Annotated Checklists of Fishes*, 31, 1–72.

Collett, R. (1879) Fiske fra Nordhavs-Expeditionens sidste Togt, Sommeren 1878. *Forhandlinger i Videnskabs-Selskabet i Christiania*, No. 14 (for 1878), 1–106. [in Norwegian]

Dettai, A., Lautredou, A.C., Bonillo, C., Goimbault, E., Busson, F., Causse, R., Couloux, A., Cruaud, C., Duhamel, G., Denys, G., Hautecoeur, M., Iglesias, S., Koubbi, P., Lecointre, G., Moteki, M., Pruvost, P., Tercerie, S. & Ozouf, C. (2011) The actinopterygian diversity of the CEAMARC cruises: barcoding and molecular taxonomy as a multi-level tool for new findings. *Deep Sea Research Part II: Topical Studies in Oceanography*, 58 (1–2), 250–263.
https://doi.org/10.1016/j.dsr2.2010.05.021

Drummond, A.J., Ho, S.Y.W., Phillips, M.J. & Rambaut, A. (2006) Relaxed phylogenetics and dating with confidence. *PLoS Biology*, 4 (5), e88.
https://doi.org/10.1371/journal.pbio.0040088

Duhamel, G., Hulley, P.-A., Causse, R., Koubbi, P., Vacchi, M., Pruvost, P., Vigetta, S., Irisson, J.-O.,Mormède, S., Belchier, M., Dettai, A., Detrich, H.W., Gutt, J., Jones, C.D., Kock, K.-H., Lopez Abellan, L.J. & Van de Putte, A.P. (2014) Biogeographic patterns of fish. *In*: De Broyer, C., Koubbi, P., Griffiths, H.J., Raymond, B., d'Udekem d'Acoz, C., Van de Putte, A.P., Danis, B., David, B., Grant, S., Gutt, J., Held, C., Hosie, G., Huettmann, F., Post, A. & Ropert-Coudert, Y. (Eds.), *Biogeographic Atlas of the Southern Ocean*. Scientific Committee on Antarctic Research, Cambridge, pp. 328–362.
https://doi.org/10.13140/2.1.1828.3203

Eastman, J.T., Hikida, R.S. & DeVries, A.L. (1994) Buoyancy studies and microscopy of skin and subdermal extracellular matrix of the Antarctic snailfish, *Paraliparis devriesi*. *Journal of Morphology*, 220, 85–101.
https://doi.org/10.1002/jmor.1052200108

Folmer, O., Black, M., Hoeh, W., Lutz, R. & Vrijenhoek, R. (1994) DNA primers for amplification of mitochondrial cytochrome c oxidase subunit I from diverse metazoan invertebrates. *Molecular Marine Biology and Biotechnology*, 3, 294–299.

Gatto, L., Catanzaro, D. & Milinkovitch, M.C. (2006) Assessing the applicability of the GTR nucleotide substitution model through simulations. *Evolutionary Bioinformatics Online*, 2, 145–155.
https://doi.org/10.1177/117693430600200020

Gerringer, M.E., Linley, T.D., Jamieson, A.J., Goetze, E. & Drazen, J.C. (2017) *Pseudoliparis swirei* sp. nov.: A newly discovered hadal snailfish (Scorpaeniformes: Liparidae) from the Mariana Trench. *Zootaxa*, 4358 (1), 161–177.
https://doi.org/10.11646/zootaxa.4358.1.7

Gilbert, C.H. (1896) The ichthyological collections of the steamer *Albatross* during the years 1890 and 1891. *Report of the United States Commission of Fish and Fisheries*, 19 (for 1893), Art. 6, 393–476, pls. 20–35.

Gilbert, C.H. & Burke, C.V. (1912a) Fishes from Bering Sea and Kamchatka. *Bulletin of the Bureau of Fisheries*, 30 (for 1910), 31–96.

Gilbert, C.H. & Burke, C.V. (1912b) New cyclogasterid fishes from Japan. *Proceedings of the United States National Museum*, 42 (1907), 351–380, pls. 41–48.
https://doi.org/10.5479/si.00963801.42-1907.351

Gill, T.N. (1861) Synopsis of the subfamily of Liparidae, with diagnoses of new genera. *Proceedings of the Academy of Natural Sciences of Philadelphia*, 13, 264–267.

Günther, A. (1878) Preliminary notices of deep-sea fishes collected during the voyage of *H.M.S. Challenger*. *Annals and Magazine of Natural History*, Series 5, 2 (7, 8 & 9), 17–28, 179–187 & 248–251.
https://doi.org/10.1080/00222937808682417

Huvenne, V.A.I., Tyler, P.A., Masson, D.G., Fisher, E.H., Hauton, C., Hühnerbach, V., Le Bas, T.P. & Wolff, G.A. (2011) A picture on the wall: innovative mapping reveals cold-water coral refuge in submarine canyon. *PLoS ONE*, 6 (12), e28755.
https://doi.org/10.1371/journal.pone.0028755

Kai, Y. & Matsuzaki, K. (2020) *Careproctus longidigitus*, a new snailfish (Liparidae) from the southern Sea of Okhotsk. *Ichthyological Research*, 67 (1), 133–138.
https://doi.org/10.1007/s10228-019-00711-y

Kai, Y., Tohkairin, A., Fujiwara, K. & Hamatsu, T. (2018) *Careproctus iacchus*, a new variegated snailfish (Liparidae) from the Seas of Japan and Okhotsk. *Ichthyological Research*, 65 (4), 417–422.
https://doi.org/10.1007/s10228-018-0626-7

Kai, Y., Morikawa, E. & Misawa, R. (2024) *Careproctus io* (Teleostei: Liparidae), a new snailfish from the western North Pacific, with comments on generic limits. *Species Diversity*, 29 (1), 111–117.
https://doi.org/10.12782/specdiv.29.111

Katoh, K., Rozewicki, J. & Yamada, K.D. (2019) MAFFT online service: multiple sequence alignment, interactive sequence choice and visualization. *Briefings in Bioinformatics*, 20 (4), 1160–1166.
https://doi.org/10.1093/bib/bbx108

Kenchington, E.L., Baillie, S.M., Kenchington, T.J. & Bentzen, P. (2017) Barcoding Atlantic Canada's mesopelagic and upper bathypelagic marine fishes. *PLoS ONE*, 12 (9), e0185173.
https://doi.org/10.1371/journal.pone.0185173

Koerber, S. (2023) On some marine fishes reported from Argentina and Uruguay, hitherto unnoticed or incorrectly included by the local ichthyological communities. *Historia Natural*, Tercera Serie, 13 (2), 25–51.

Krøyer, H.N. (1862) Nogle Bidrag til Nordisk ichthyologi. *Naturhistorisk Tidsskrift* (Kjøbenhavn), Series 3, 1, 233–310. [in Danish]

Kumar, S., Stecher, G., Li, M., Knyaz, C. & Tamura, K. (2018) MEGA X: molecular evolutionary genetics analysis across computing platforms. *Molecular Biology and Evolution*, 35 (6), 1547–1549.
https://doi.org/10.1093/molbev/msy096

Linley, T.D., Gerringer, M.E., Ritchie, H., Weston, J.N.J., Scott-Murray, A., Fernandez, V., Canto-Hernández, J., Wenzhöfer, F., Glud, R.N. & Jamieson, A.J. (2022) Independent radiation of snailfishes into the hadal zone confirmed by *Paraliparis selti* sp. nov. (Perciformes: Liparidae) from the Atacama Trench, SE Pacific. *Marine Biodiversity*, 52 (5), 56.
https://doi.org/10.1007/s12526-022-01294-0

Lönnberg, E. (1905) The fishes of the Swedish South Polar Expedition. *Wissenschaftliche Ergebnisse der Schwedischen Südpolar-Expedition*, 1901–1903, 5 (6), 1–72, pls. 1–5.

Mabragaña, E., Delpiani, S.M., Rosso, J.J., González-Castro, M., Deli Antoni, M., Hanner, R. & Díaz de Astarloa, J.M. (2016) Barcoding Antarctic fishes: species discrimination and contribution to elucidate ontogenetic changes in Nototheniidae. *In*: Trivedi, S., Ansari, A.A., Ghosh, S.K. & Rehman, H. (Eds.), *DNA Barcoding in Marine Perspectives: Assessment and Conservation of Biodiversity*. Springer International Publishing, Cham, pp. 213–242.
https://doi.org/10.1007/978-3-319-41840-7_14

Matallanas, J. & Pequeño, G. (2000) Description of *Careproctus patagonicus* sp. nov. and *C. magellanicus* sp. nov. (Pisces: Scorpaeniformes) from the lower slope of Drake Passage. *Journal of Fish Biology*, 56 (3), 519–527.
https://doi.org/10.1006/jfbi.1999.1173

Matallanas, J. & Piacentino, G. (2019) Description of *Careproctus fueguensis* sp. nov. (Teleostei: Liparidae) from Beagle Channel (Tierra del Fuego, Argentina). *Historia Natural*, Tercera Serie, 9 (2), 29–40.

Matsuzaki, K., Kamiunten, M. & Yanagimoto, T. (2020) The eggs of two snailfish species in gill cavity of golden king crab *Lithodes aequispinus* from the Nemuro Strait, southwestern Sea of Okhotsk, Japan. *Aquaculture Science*, 68 (1), 25–32. [in Japanese]
https://doi.org/10.11233/aquaculturesci.68.25

Mecklenburg, C.W., Møller, P.R. & Steinke, D. (2011) Biodiversity of arctic marine fishes: taxonomy and zoogeography. *Marine Biodiversity*, 41 (1), 109–140.
https://doi.org/10.1007/s12526-010-0070-z

Miya, M., Takeshima, H., Endo, H., Ishiguro, N.B., Inoue, J.G., Mukai, T., Satoh, T.P., Yamaguchi, M., Kawaguchi, A., Mabuchi, K. & Shirai, S.M. (2003) Major patterns of higher teleostean phylogenies: a new perspective based on 100 complete mitochondrial DNA sequences. *Molecular Phylogenetics and Evolution*, 26 (1), 121–138.
https://doi.org/10.1016/S1055-7903(02)00332-9

Mori, T., Matsuzaki, K., Kai, Y. & Tashiro, F. (2025) *Careproctus rhomboides*, a new snailfish (Cottoidei: Liparidae) from the western North Pacific. *Ichthyological Research*, 72 (1), 29–37.
https://doi.org/10.1007/s10228-024-00953-5

Murasaki, K., Takami, M. & Fukui, A. (2018) *Careproctus surugaensis* sp. nov. (Liparidae), a new snailfish from Suruga Trough, Japan. *Ichthyological Research*, 65 (2), 237–244.
https://doi.org/10.1007/s10228-017-0608-1

Nikolsky, G.V. (1963) *The ecology of fishes*. Academic Press, London, 352 pp.

Norman, J.R. (1938) Coast fishes. Part III. The Antarctic zone. *Discovery Reports*, 18, 1–105, pl. 1.
https://doi.org/10.5962/bhl.part.19412

Orr, J.W. (2012) Two new species of snailfishes of the genus *Careproctus* (Scorpaeniformes: Liparidae) from the Bering Sea and eastern North Pacific Ocean, with a redescription of *Careproctus ovigerus*. *Copeia*, 2012 (2), 257–265.
https://doi.org/10.1643/CI-11-006

Orr, J.W. & Maslenikov, K.P. (2007) Two new variegated snailfishes of the genus *Careproctus* (Teleostei: Scorpaeniformes: Liparidae) from the Aleutian Islands, Alaska. *Copeia*, 2007 (3), 699–710.
https://doi.org/10.1643/0045-8511(2007)2007[699:TNVSOT]2.0.CO;2

Orr, J.W., Spies, I., Stevenson, D.E., Longo, G.C., Kai, Y., Ghods, S.H. & Hollowed, A.B. (2019) Molecular phylogenetics of snailfishes (Cottiformes: Liparidae) based on mtDNA and RADseq genomic analyses, with comments on selected morphological characters. *Zootaxa*, 4642 (1), 1–79.
https://doi.org/10.11646/zootaxa.4642.1.1

Orr, J.W., Pitruk, D.L., Manning, R., Stevenson, D.E., Gardner, J.R. & Spies, I. (2020) A new species of snailfish (Cottiformes: Liparidae) closely related to *Careproctus melanurus* of the eastern North Pacific. *Copeia*, 108 (4), 711–726.

https://doi.org/10.1643/CI2020008

Orr, J.W. (2025) Resurrection of the snailfish genus *Allinectes* (Teleostei: Cottiformes: Liparidae) for seven North Pacific species, including descriptions of three new species from Alaska. *Zootaxa*, 5609 (3), 301–334. https://doi.org/10.11646/zootaxa.5609.3.1

Pallas, P.S. (1769) *Spicilegia Zoologica quibus novae imprimis et obscurae animalium species iconibus, descriptionibus atque commentariis illustrantur. Vol. 1. Fasciculus 7.* Gottlieb August Lange, Berolini, 42 pp., pls. 1–6.

Pearman, T., Brewin, P., Baylis, A. & Brickle, P. (2022) Deep-sea epibenthic megafaunal assemblages of the Falkland Islands, Southwest Atlantic. *Diversity*, 14 (8), 637. https://doi.org/10.3390/d14080637

Priede, I.G. (2017) Systematic description of deep-sea fishes. *In:* Priede, I.G. (Ed.), *Deep-Sea Fishes: Biology, Diversity, Ecology and Fisheries*. Cambridge University Press, Cambridge, pp. 139–316. https://doi.org/10.1017/9781316018330.005

Rambaut, A. (2012) FigTree*. Version 1.4.3*. Institute of Evolutionary Biology, University of Edinburgh, Edinburgh. [software pagckage]

Robert, K., Jones, D.O.B., Georgiopoulou, A. & Huvenne, V.A.I. (2020) Cold-water coral assemblages on vertical walls from the Northeast Atlantic. *Diversity and Distributions*, 26 (3), 284–300. https://doi.org/10.1111/ddi.13011

Robertson, D.R., Angulo, A., Baldwin, C.C., Pitassy, D., Driskell, A., Weigt, L. & Navarro, I.J. (2017) Deep-water bony fishes collected by the B/O *Miguel Oliver* on the shelf edge of Pacific Central America: an annotated, illustrated and DNA-barcoded checklist. *Zootaxa*, 4348 (1), 1–125. https://doi.org/10.11646/zootaxa.4348.1.1

Rock, J., Costa, F.O., Walker, D.I., North, A.W., Hutchinson, W.F. & Carvalho, G.R. (2008) DNA barcodes of fish of the Scotia Sea, Antarctica indicate priority groups for taxonomic and systematics focus. *Antarctic Science*, 20 (3), 253–262. https://doi.org/10.1017/S0954102008001120

Scopoli, G.A. (1777) *Introductio ad historiam naturalem, sistens genera lapidum, plantarum et animalium hactenus detecta, caracteribus essentialibus donata, in tribus divisa, subinde ad leges naturae*. Apud Wolfgangum Gerle, Pragae, x + 506 pp. https://doi.org/10.5962/bhl.title.10827

Smith, P.J., Steinke, D., Dettai, A., McMillan, P., Welsford, D., Stewart, A. & Ward, R.D. (2012) DNA barcodes and species identifications in Ross Sea and Southern Ocean fishes. *Polar Biology*, 35, 1297–1310. https://doi.org/10.1007/s00300-012-1173-8

Smitt, F.A. (1898) Poissons de l'expédition scientifique à la Terre de Feu. II. *Bihang till Kongliga Svenska Vetenskaps-Akademiens Handlingar*, 24 (4), No. 5, 1–80, pls. 1–6.

Stehmann, M.F.W. (1985) Ergebnisse der Forschungsreisen des FFS *Walther Herwig* nach Südamerika. LXIV. *Bathyraja papilionifera* sp. n. (Pisces: Batoidea: Rajidae), eine weitere neue Rochenart aus dem Südwestatlantik vom nordargentinischen Kontinentalabhang. *Archiv für Fischereiwissenschaft*, 36 (1/2), 195–211.

Stein, D.L. & Andriashev, A.P. (1990) Liparididae. *In:* Gon, O. & Heemstra, P.C. (Eds.), *Fishes of the Southern Ocean*. J.L.B. Smith Institute of Ichthyology, Grahamstown, pp. 231–255.

Stein, D.L., Chernova, N.V. & Andriashev, A.P. (2001) Snailfishes (Pisces: Liparidae) of Australia, including descriptions of thirty new species. *Records of the Australian Museum*, 53 (3), 341–406. https://doi.org/10.3853/j.0067-1975.53.2001.1351

Stein, D.L. (2006) New and rare species of snailfishes (Scorpaeniformes: Liparidae) collected during the ICEFISH cruise of 2004. *Polar Biology*, 29 (7), 705–712. https://doi.org/10.1007/s00300-006-0108-7

Steinke, D., Zemlak, T.S., Boutillier, J.A. & Hebert, P.D.N. (2009) DNA barcoding of Pacific Canada's fishes. *Marine Biology*, 156, 2641–2647. https://doi.org/10.1007/s00227-009-1284-0

Suchard, M.A., Lemey, P., Baele, G., Ayres, D.L., Drummond, A.J. & Rambaut, A. (2018) Bayesian phylogenetic and phylodynamic data integration using BEAST 1.10. *Virus Evolution*, 4 (1), vey016. https://doi.org/10.1093/ve/vey016

Vaillant, L.L. (1888) Poissons. *In*: Mission scientifique du Cap Horn, 1882–1883. Tome VI. Zoologie. *Poisson.* Part 1, Article C. Gauthier-Villars et Fils, Imprimeurs-Libraires, Paris, pp. C1–C35, pls. 1–4.

Ward, R.D., Zemlak, T.S., Innes, B.H., Last, P.R. & Hebert, P.D.N. (2005) DNA barcoding Australia's fish species. *Philosophical Transactions of the Royal Society B*, 360, 1847–1857. https://doi.org/10.1098/rstb.2005.1716

Whitley, G.P. (1939) Taxonomic notes on sharks and rays. *Australian Zoologist*, 9 (3), 227–262, pls. 20–22.

Zhang, J.-B. & Hanner, R. (2011) DNA barcoding is a useful tool for the identification of marine fishes from Japan. *Biochemical Systematics and Ecology*, 39 (1), 31–42. https://doi.org/10.1016/j.bse.2010.12.017