*Ichthyology & Herpetology* 113, No. 3, 2025, 487–506

# Descriptions of Three Newly Discovered Abyssal Snailfishes (Liparidae) from the Eastern Pacific Ocean

Mackenzie E. Gerringer[1], Sarah Suplicz[1], Jessica L. Palmeri[1], Lydia Fregosi[1], Brett H. Woodworth[1], Emily McMahon[1], Samantha Shepard[1], Logan M. Peoples[2], and Jeffrey C. Drazen[3]

**Three species of snailfishes (family Liparidae) are described from single collections based on morphological and genetic evidence, from the eastern abyssal Pacific, depths 3,268–4,119 m. *Careproctus colliculi*, new species, the Bumpy Snailfish, can be identified by its pink color in life, 22 pectoral-fin rays (uppermost rays long), round head, eight caudal rays, large eye, and well-developed pterygiophores that form a large suction disk. *Careproctus yanceyi*, new species, the Dark Snailfish, bears a moderate ventral suction disk (<3% standard length), single nostrils, six branchiostegal rays, and is distinct from other eastern Pacific deepwater snailfishes in having a fully black body with a rounded head and horizontal mouth. Additional defining characters include a small gill opening located entirely above the pectoral fin, two pectoral radials, and 22 pectoral-fin rays. *Paraliparis em*, new species, the Sleek Snailfish, is distinguished from other snailfishes by its long, black, laterally compressed body, absence of a suction disk, prominently angled jaw, single pectoral-fin radial, anteriorly positioned anus, and five branchiostegal rays. Each of these three taxa has a distinct mitochondrial cytochrome *c* oxidase subunit I (COI) sequence compared to all other sequenced snailfishes. Genetically, *Paraliparis em*, new species, is most similar to *P. wolffi* from the Crozet Basin in the Indian Ocean, as well as bearing similarity to the northeastern Pacific snailfishes *P. megalopus* and *P. ulochir*, together known as *Paraliparis* Clade I. *Careproctus yanceyi*, new species, shows little similarity in COI sequences to other taxa and perhaps represents a distinct clade in the family. The COI sequence of *Careproctus colliculi*, new species, fits in the Osteocareprocta clade, most similar to *Careproctus continentalis*, *C. discoveryae*, *C. longipectoralis*, and *Osteodiscus cascadiae*. *Paraliparis em*, new species, and *Careproctus yanceyi*, new species, show significant morphological and genetic divergence from one another, despite both being black snailfishes collected on the same submersible dive. These findings reveal cryptic diversity in deep-sea snailfishes and highlight the necessity of combined imaging, morphological, and genetic approaches to studying fish biodiversity. These three newly discovered species begin to fill an important sampling gap for the family Liparidae and demonstrate the importance of snailfishes in communities of the abyssal seafloor.**

SNAILFISHES in the family Liparidae (Cottoidei) inhabit temperate to cold habitats across ocean basins (Burke, 1930; Chernova et al., 2004; Orr et al., 2019). In shallow waters, snailfishes use a specialized ventral suction disk to cling to rocks, forming a curled, snail-like posture that gives the group their English common name. The snailfishes play important roles in ecosystems from the intertidal zone to hadal trenches (>6,000 m), and these fishes are well adapted to a wide variety of habitats, likely due to rapid evolutionary rates (e.g., Orr et al., 2019; Gerringer et al., 2021).

The Liparidae include 31 accepted genera and 450 valid species, 43 of which have been described in the last ten years (Fricke et al., 2024). At the family level, the liparids are well distinguished by their scaleless bodies, ventral suction disk formed from modified pelvic fins in many genera, and elongated body forms compared to similar taxa such as the Cyclopteridae (e.g., Burke, 1930). However, the boundaries between snailfish genera are less clear. In particular, the species-rich genera *Paraliparis* and *Careproctus*—once distinguished by how reduced or fully formed the ventral suction disk appeared, respectively—have been shown by genetic evidence to be paraphyletic (Orr et al., 2019). With the ecological importance of the family, the high rate at which new snailfishes are being discovered (e.g., Orr and Maslenikov, 2007; Stein and Drazen, 2014; Orr, 2016, 2020, 2021; Matallanas and Piacentino, 2019; Orr et al., 2020; Chernova et al., 2021; Linley et al., 2022; Gardner et al., 2023; Mori et al., 2024), and the significant work needed in revising snailfish classifications (e.g., Orr et al., 2019), snailfish taxonomy remains an important undertaking to better understand marine biodiversity.

In addition to their broad distribution across cold, shallow seas, snailfishes inhabit multiple deep-sea habitats worldwide. Snailfishes are notably successful in deep-sea trenches, exceeding depths of 8,000 m (Nielsen, 1964; Fujii et al., 2010; Gerringer, 2019; Gerringer et al., 2021; Jamieson et al., 2021, 2023). Based on genetic evidence, snailfishes have independently evolved into hadal trenches at least twice: in the *Notoliparis/Pseudoliparis* clade and in one of the *Paraliparis* clades (Linley et al., 2022). Research on hadal snailfishes has increased in recent years and has shown these deepest living liparids to be incredibly well adapted to deep-sea trench habitats in diet, ability to live under high pressures, and life history (e.g., Gerringer et al., 2017a, 2017b, 2017c, 2018, 2020; Gerringer, 2019; Wang et al., 2019; Mu et al., 2021). However, very few studies have investigated other deep-living snailfishes that inhabit depths 1,000–5,000 m. In hadal trenches, snailfishes gather

---

[1] Biology Department, State University of New York at Geneseo, 1 College Circle, Geneseo, New York 14454; ORCID: (MEG) 0000-0002-2026-5829; and (JLP) 0009-0000-9636-3364; Email: (MEG) gerringer@geneseo.edu. Send correspondence to MEG.
[2] Flathead Lake Biological Station, University of Montana, 32125 Bio Station Ln., Polson, Montana 59860; ORCID: 0000-0002-0163-2769.
[3] Department of Oceanography, University of Hawaiʻi at Mānoa, 1000 Pope Rd., Honolulu, Hawaii 98622; ORCID: 0000-0001-9613-3833.
Submitted: 5 August 2024. Accepted: 11 April 2025. Associate Editor: K. L. Tang.
DOI: 10.1643/i2024069

**Table 1.** Collection information of three newly described species of abyssal snailfishes. One individual of each species was collected, now the holotypes.

| Species | Museum number | Collection number | Date | Latitude | Longitude | Depth (m) |
|---|---|---|---|---|---|---|
| *Careproctus colliculi*, new species | CAS-ICH 248611 | D1138-SS5 | 23 March 2019 | 36.38359°N | 122.66665°W | 3,268 |
| *Careproctus yanceyi*, new species | SIO 24-49 | AT4210-D5030-180 | 3 May 2019 | 34.67°N | 123.00°W | 4,119 |
| *Paraliparis em*, new species | SIO 24-50 | AT4210-D5030-181 | 3 May 2019 | 34.67°N | 123.00°W | 4,115 |

in large groups at bait falls, which sometimes even attract multiple species of liparids at the same time (Linley et al., 2016, 2022; Jamieson et al., 2021). At bathyal and abyssal depths, snailfishes are perhaps more difficult to find, with baited cameras and traps more commonly attracting other, larger fishes such as rattails (Macrouridae), cusk-eels (Ophidiidae), and cutthroat eels (Synaphobranchidae; e.g., Priede et al., 1990, 1991; Collins et al., 1998; Bailey et al., 2006). Although occasional records of snailfishes from bathyal depths have been found, typically in trawl samples (e.g., Chernova et al., 2004), there is a noticeable gap in snailfish collections from depths ~3,000 to 5,000 m. This gap has been hypothesized to reflect sampling bias, rather than a lack of abyssal snailfishes (Gerringer, 2019), but with few observations of abyssal and bathyal snailfishes, this hypothesis has not been tested.

In 2019, three snailfishes were collected by the human occupied vehicle (HOV) *Alvin* on the R/V *Atlantis* and the remotely operated vehicle (ROV) *Doc Ricketts* on the R/V *Western Flyer* from depths of 3,268–4,119 m in the eastern Pacific. Here, we describe these three new species of abyssal snailfishes using morphological and genetic evidence. These new collections demonstrate that snailfishes inhabit deep abyssal depths and call for further exploration of abyssal fish biodiversity.

## MATERIALS AND METHODS

***Collection.***—Specimens were collected on two expeditions in 2019, AT42-10 on the R/V *Atlantis* in May and a March expedition of the R/V *Western Flyer* (Table 1, Fig. 1). The AT42-10 expedition collected two black snailfishes from the abyssal study site Station M, located almost 300 km off the coast of Santa Barbara, California (e.g., Smith and Druffel, 1998). These snailfishes, described here as *Paraliparis em*, new species (collected as sample AT4210-D5030-181), and *Careproctus yanceyi*, new species (sample AT4210-D5030-180), were collected by suction sampler from ~4,100 m water depth, using the HOV *Alvin*. Both snailfishes were collected on the same dive, 5030, on 3 May 2019 (Table 1). The third specimen, described here as *Careproctus colliculi*, new species, was collected on 23 March 2019 by the ROV *Doc Ricketts* via suction sampler from 3,268 m water depth, less than 100 km offshore from Monterey Bay, California.

***Tissue collection.***—Fin clips were dissected from each snailfish shipboard. For the AT42-10 specimens, fin clips were stored in 95% ethanol and then frozen at –80°C. The fin clip of *C. colliculi*, new species, was frozen directly at –80°C prior to processing in the lab.

***DNA extraction.***—Fish tissue samples were digested with proteinase K at 56°C for one to two hours, then DNA was extracted using the Qiagen DNeasy® Blood & Tissue Kit according to the manufacturer's protocol (Qiagen, Hilden, Germany). Quantity of extracted DNA was determined using a Qubit 4 fluorometer (Invitrogen, Thermo Fischer Scientific Inc., Waltham, MA, USA), totaling 1.22 ng/μL for the holotypes of *Paraliparis em*, new species, AT4210-D5030-181; 25.3 ng/μL for *Careproctus yanceyi*, new species, AT4210-D5030-180; and 46 ng/μL for *Careproctus colliculi*, new species, D1138-SS5.

***DNA amplification and sequencing.***—To compare to previous studies and to gain sufficient context to position these fishes in a phylogenetic tree, primer sets targeting the mitochondrial cytochrome *c* oxidase subunit I (COI) and ribosomal 16S rRNA genes were used. First, following the methods of the largest sequencing effort for the snailfishes to date, conducted by Orr et al. (2019), the COI primers LCO1490: 5′–GGT CAA CAA ATC ATA AAG ATA TTG G–3′ and HCO2198: 5′–TAA ACT TCA GGG TGA CCA AAA AAT CA–3′ designed by Folmer et al. (1994) were used. PCR amplification for this gene included a 2-minute denaturation step at 95°C, followed by 35 cycles at 95°C for 1 minute, annealing at 40°C for 1 minute, and extension 72°C for 1.5 minutes, then a final annealing step at 72°C for 7 minutes, before being held at 4°C. Second, a

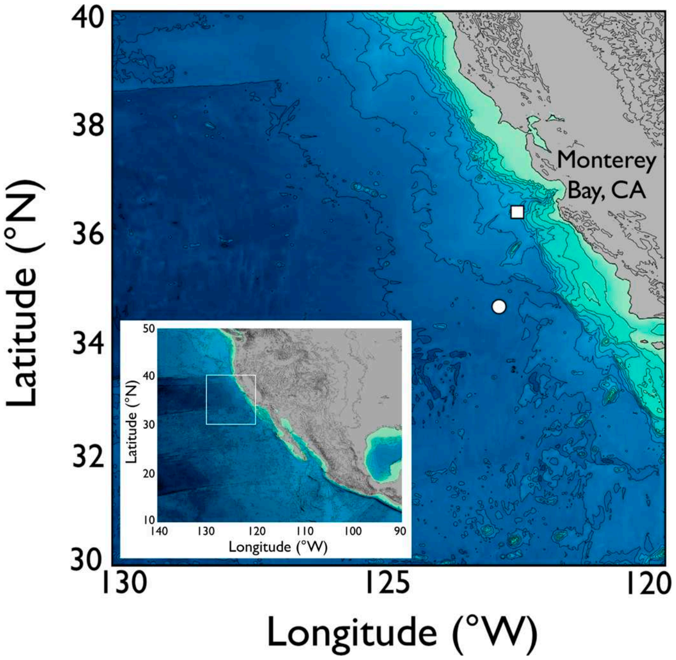

**Fig. 1.** Collection locations of three newly discovered abyssal snailfishes from deep waters off California, USA. The holotypes of both *Paraliparis em*, new species, and *Careproctus yanceyi*, new species, were collected at the same location (white circle). The collection location of the holotype of *Careproctus colliculi*, new species, is shown as a white square.

1,472 bp partial length fragment of the 16S rRNA gene for *Careproctus yanceyi*, new species, and *Paraliparis em*, new species, was amplified using the primers 16S_liparids_F (5′–CTA TTA ATA CCC CCA AAT ACC CC–3′) and 16S_liparids_R (5′–CGA TGT TTT TGG TAA ACA GGC G–3′; Gerringer et al., 2017b). For the 16S rRNA gene, PCR cycling included a 2-minute incubation at 95°C, 35 cycles of denaturation at 95°C for 30 seconds, annealing at 48°C for 30 seconds, and extension at 72°C for 1 minute, followed by 72°C for 5 minutes and a hold period at 4°C. PCR products were purified using a PureLink$^{TM}$ PCR Purification Kit (Thermo Fisher Scientific Inc.), according to the manufacturer's protocols. DNA concentrations were determined using a Qubit 4 fluorometer. Sanger sequencing for the forward and reverse directions (COI) and forward direction (16S rRNA) was performed for each gene by Retrogen, Inc. (San Diego, CA, USA). Sequence chromatograms were manually checked in FinchTV (Geospiza, Inc.) and assembled in Jalview v.2 (Waterhouse et al., 2009). N's were placed in positions of uncertainty. Sequence lengths for the COI gene are 379 bp for *Careproctus colliculi*, new species; 637 bp for *Careproctus yanceyi*, new species; and 641 bp for *Paraliparis em*, new species. Due to the lack of available comparative data for the 16S gene across the liparids, 16S trees were not used to position the taxa described here within the snailfish phylogeny; however, these sequences are being made available with this study for future comparison (545 bp for *Careproctus yanceyi*, new species; 450 bp for *Paraliparis em*, new species). All sequences are available through NCBI's GenBank (Benson et al., 2009), under the accession numbers: *Careproctus colliculi*, new species, PV300957 (COI); *Careproctus yanceyi*, new species, PV300956 (COI), PV298546 (16S); and *Paraliparis em*, new species PV300955 (COI), PV298545 (16S).

***Phylogenetic tree construction.***—Phylogenetic analyses were performed with a dataset modified from Orr et al. (2019) used to describe the family Liparidae. Sequences were accessed from GenBank (Benson et al., 2009) and the Barcode of Life Data (BOLD) Systems portal (Ratnasingham and Hebert, 2007) to create a dataset consisting of 273 sequences (Supplemental Table 1; see Data Accessibility). Sequences were aligned using multiple sequence comparison by log-expectation (MUSCLE; Edgar, 2004; McWilliam et al., 2013), and a handful of long sequences were trimmed to a final alignment length of 652 bp using Jalview v2 (Waterhouse et al., 2009). The average sequence length was 597 bp. Maximum-likelihood phylogenetic analyses were performed according to Orr et al. (2019) in R v4.4.1 (R Core Team, 2024) with the package phangorn v2.11 (Schliep, 2011). The optimal evolutionary model was identified as TIM1+G(4)+I using the command *modelTest*. A maximum-likelihood phylogenetic tree was inferred with nearest neighbor interchange (NNI) rearrangement using the command *pml_bb* (log likelihood, $\ln(L) = -12914.14$), and 1,000 bootstrap replicates were created using the command *bootstrap.pml*. Bootstrap support was mapped to the tree using the *plotBS* function, and the tree was rooted using ape v5.8 (Paradis and Schliep, 2019). The lumpfishes (family Cyclopteridae) *Cyclopterus lumpus* (BOLD Sequence ID: GBGC5052-08; Museum Catalog Number: ZMUB F1; NCBI GenBank: AM498313) and *Eumicrotremus orbis* (GBGCA12719-15, UW119780-1, AB917653) were used as outgroups to root the tree, using *ape* v5.8 (Paradis and Schliep, 2019). Trees were visualized using the Interactive Tree of Life v.5 (Letunic and Bork, 2021). Although our goal was not to reconstruct a complete phylogeny of the Liparidae, phylogenetic analyses are generally consistent with Orr et al. (2019). The sequence of *Careproctus bowersianus* (SGJWO046-18, UW 119291, MH630278) is highly dissimilar from other sequences in the tree and its position differs from that reported in Orr et al. (2019). Other clades resolve in a similar manner to that previously reported (Orr et al., 2019), whereas the relationships between clades remain unclear.

***Morphological descriptions.***—Definitions of measurements, counts, and characters follow established protocols for snailfishes (e.g., Stein et al., 2001; Andriashev, 2003; Stein, 2012), and museum abbreviations follow Sabaj (2020). All measurements and counts are based on specimens preserved in ethanol, which are typically ~10% smaller than fresh measurements for deep-water snailfishes (Gerringer et al., 2017b). Ratios for proportions are presented using both percent standard length (% SL) and percent head length (%HL). Pectoral girdles were dissected and stained using alizarin red S and alcian blue (Taylor, 1967a, 1967b). Radial counts are described according to the available information, but we note that these deep-water specimens have small and poorly ossified pectoral girdles. Distal radials were not examined due to damage and limited visibility. Sex was determined visually by abdominal cavity dissection, with females identified by the presence of eggs.

To determine counts of vertebrae, dorsal- and anal-fin rays, pre-dorsal-fin length, and branchiostegal ray counts, specimens were scanned using micro-computed tomography (micro-CT) at the Karel F. Liem Bioimaging Center at Friday Harbor Laboratories, University of Washington (Friday Harbor, WA, USA). Specimens were imaged using a Bruker SkyScan 1173 at 65 kV and 123 μA with a 1 mm aluminum filter. Scan resolution was 15.9 and 34.4 μm voxel size, sufficient for identifying taxonomically important characters such as tooth shape and ray counts, in addition to other characters such as otolith size. Each micro-CT scan was reconstructed using NRecon (Bruker, 2005–11), which included optimizing x-y alignment, reducing ring artifacts, correcting beam hardening artifacts, and post-aligning the segments of the scan. Scan segmentation was carried out in DataViewer (Bruker, 2004–11). Measurements and visualizations were conducted in 3D Slicer (Fedorov et al., 2012) and CT Vox (Bruker, 2004–11). Full micro-CT scans generated for this study are available via MorphoSource (Duke University) under the media ID numbers 000718441 (all three fishes, raw scan data), 000718935 (*Careproctus colliculi*, new species, and *Paraliparis em*, new species, high resolution raw scan data), 000718579 (*Careproctus colliculi*, new species, reconstructed and cropped scan), 000718591 (*Careproctus yanceyi*, new species, reconstructed and cropped scan), and 000719446 (*Paraliparis em*, new species, reconstructed and cropped scan). 3D models (STL, stereolithography files) are also provided on MorphoSource for each species (*Careproctus colliculi*, new species: full body 000744884, head 000744893, lower jaw 000744892, pharyngeal jaw 000744897, upper jaw 000744900; *Careproctus yanceyi*, new species: full body 000744854, head 000744858, lower jaw 000744861, pharyngeal jaw 000744872, upper jaw 000744874; *Paraliparis em*, new species: full body 000744827, head 000744830, lower jaw 000744838, pharyngeal jaw 000744843, upper jaw 000744849).

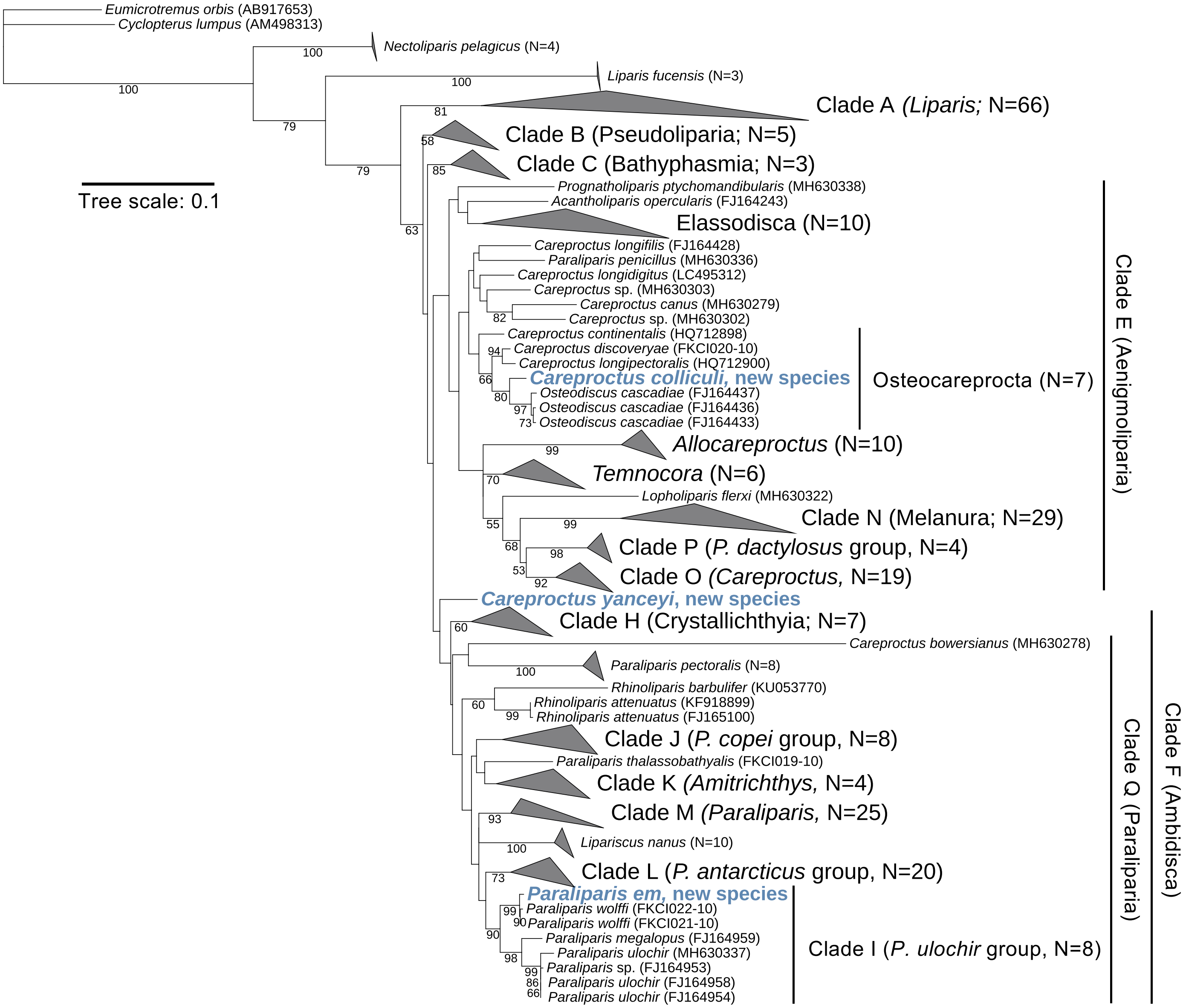

**Fig. 2.** Phylogenetic relationships of snailfishes, based on mitochondrial COI genes and maximum likelihood tree estimation (ln(L) = −12914.14). Taxa described here are shown in large blue type. Triangles represent collapsed clades, with the vertical size illustrating the number of sequences in the clade and the lateral shape illustrating branch length and diversity in the clade. The tree file and accession numbers for all sequences are provided in the supplementary information. Bootstrap values are shown for nodes with sufficient support (>50%). Informal clade names are based on Orr et al. (2019) classifications. All sequences are described in Supplementary Table 1, the full tree is presented in Supplementary Figure 1, and the tree file is available as supplemental material (see Data Accessibility).

***Data analysis and specimen availability.***—The collection map was created in the statistical programming platform R using the *marmap* package (Pante and Simon-Bouhet, 2013) using bathymetry data from the National Oceanic and Atmospheric Administration and National Centers for Environmental Information.

Specimens have been deposited at the Marine Vertebrate Collection at Scripps Institution of Oceanography (SIO; *Careproctus yanceyi*, new species, SIO 24-49; *Paraliparis em*, new species, SIO 24-50) and the California Academy of Sciences (CAS, *Careproctus colliculi*, new species, CAS-ICH 248611) and are available for future comparative study.

### *Careproctus colliculi* Gerringer, new species

urn:lsid:zoobank.org:act:761C95CC-F72C-4930-9AB4-EE5F60C52140
The Bumpy Snailfish
Figures 1, 2, 3, 4, 5; Tables 2, 3

***Holotype.***—CAS-ICH 248611 (collection number: D1138-SS5), 92.2 mm preserved total length (TL), 78.9 mm SL, mature female, Monterey Canyon, 36.38359°N, 122.66665°W, 3,268 m, R/V *Western Flyer*, 23 March 2019. Good condition.

***Diagnosis.***—*Careproctus colliculi* is distinguished from other eastern Pacific deep-water congeners by its well-developed

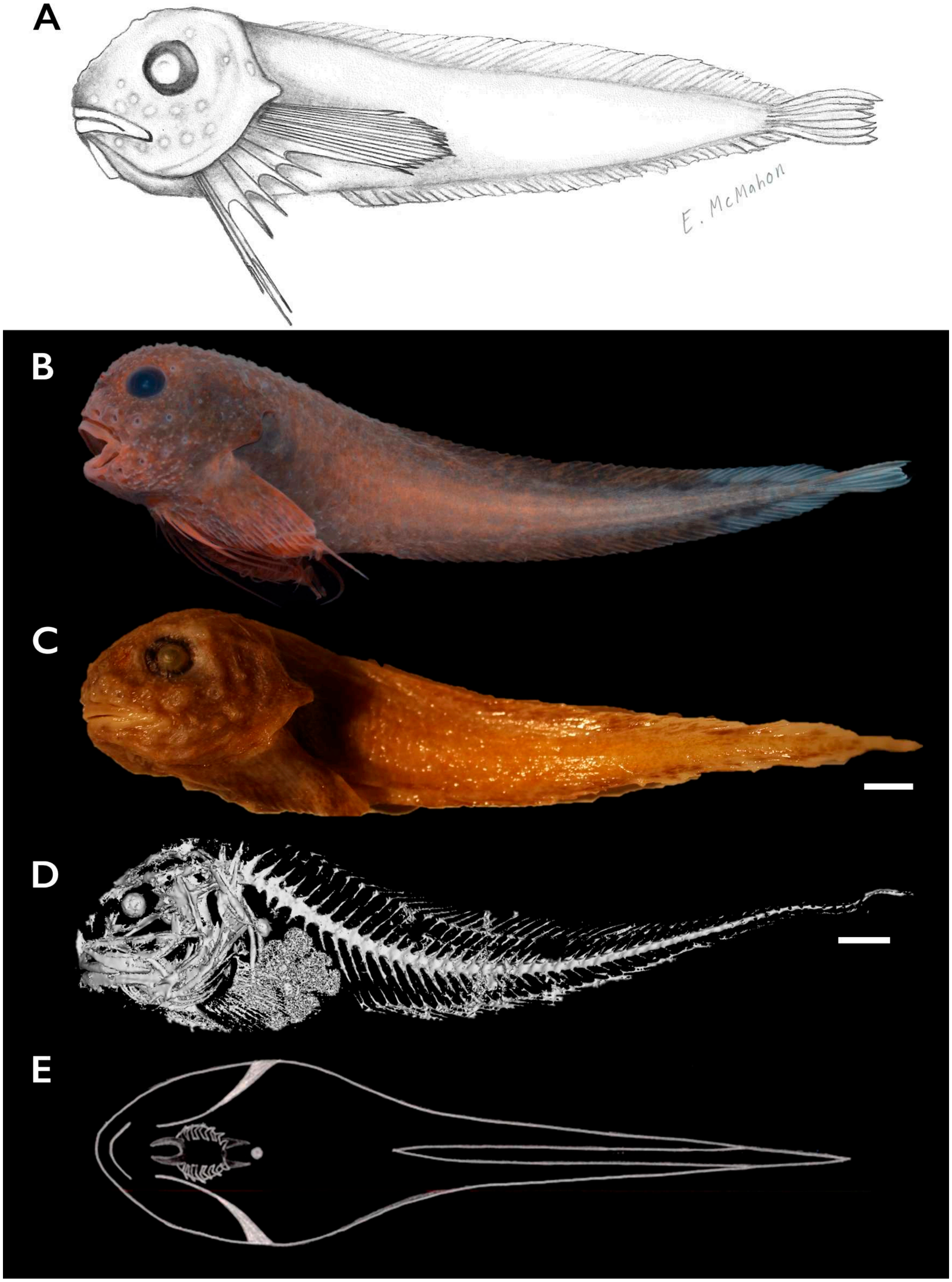

**Fig. 3.** Images of *Careproctus colliculi*, new species, the Bumpy Snailfish, based on the holotype CAS-ICH 248611. Standard length 78.9 mm. (A) Lateral view drawing. Artist: Emily McMahon. (B) Photograph of freshly collected specimen. Photo by Gustav Paulay (used with permission). (C) Photograph of specimen fixed in 4% formaldehyde, then stored in 70% ethanol. Photo by Mackenzie Gerringer. Scale bar 5 mm. (D) Lateral view of micro-computed tomography (micro-CT scan) of the holotype. Scale bar 5 mm. Scan by Mackenzie Gerringer. (E) Ventral view drawing. Artist: Emily McMahon.

suction disk, anteriorly positioned anus, simple canine teeth, 22 pectoral-fin rays, the upper ∼4 of which extend well beyond the other rays, round head, eight caudal-fin rays, large eye, and pink coloration with bumpy flesh, particularly anteriorly, in life.

***Description.***—Due to its genetic placement (Fig. 2), large ventral suction disk, single nostrils, and absence of pseudobranchs, we describe *Careproctus colliculi* in the genus *Careproctus* (Orr and Maslenikov, 2007; Orr, 2020). *Careproctus colliculi* has 53 total vertebrae, with 9 abdominal and 44

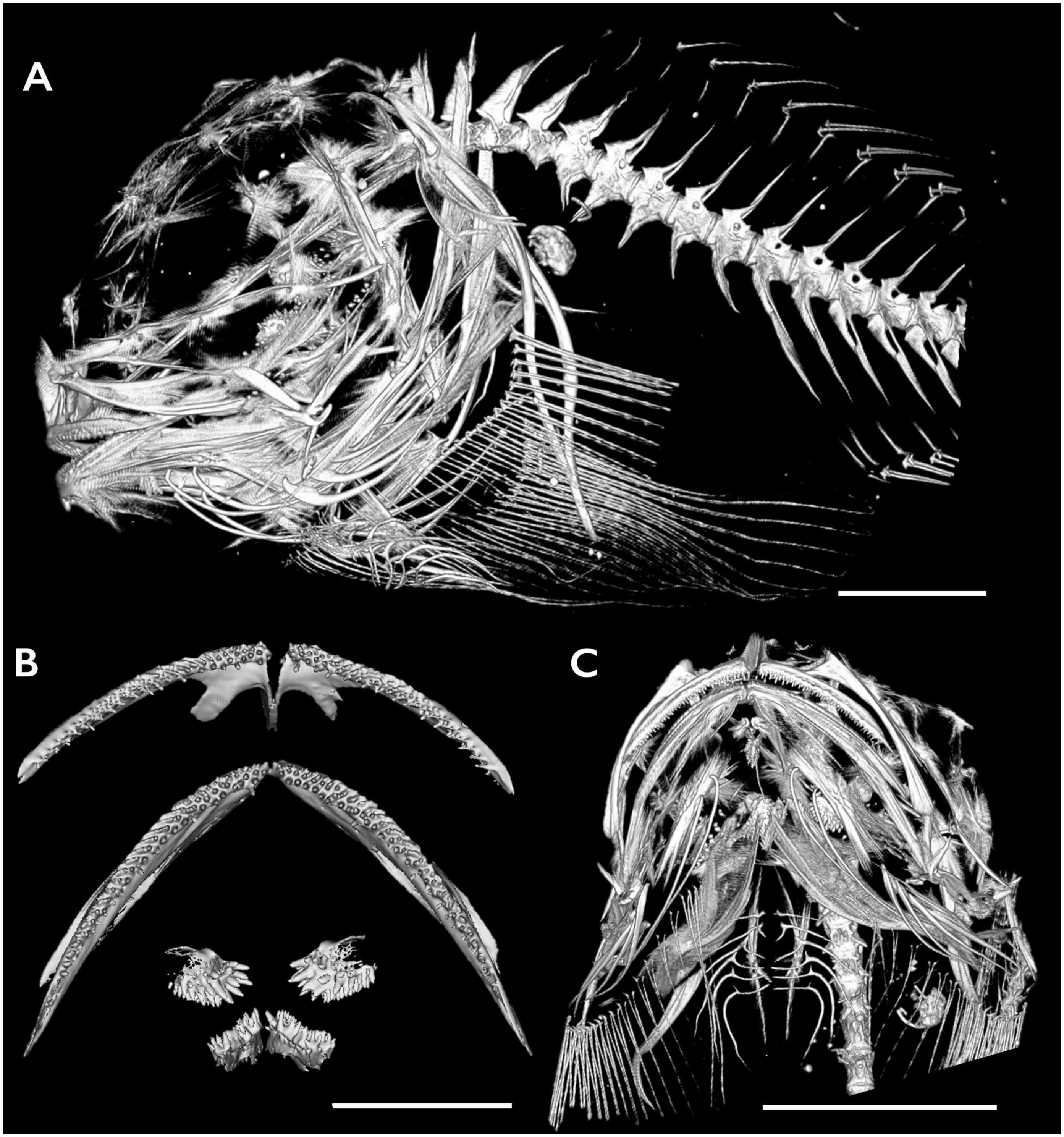

**Fig. 4.** Morphology of *Careproctus colliculi* from micro-CT scanning. (A) Lateral view micro-CT scan of *Careproctus colliculi*, head length 21.6 mm. (B) Jaw and tooth morphology: premaxilla (top), mandible (middle), pharyngeal jaws (bottom), micro-CT images. (C) Ventral view micro-CT, ventral suction disk. CT scans by Mackenzie Gerringer. Scale bars 5 mm.

caudal. Pleural ribs absent. Dorsal-fin rays 43, anal-fin rays 40, caudal-fin rays 8 (4 upper + 4 lower, no auxiliary rays), pectoral-fin rays 22 (15 upper lobe + 4 notch + 3 lower lobe), pectoral radials 2 visible, 6 branchiostegal rays. Measurements, counts, and ratios for *Careproctus colliculi* are shown in Tables 2 and 3.

Head rounded, snout deep and rounded, mouth horizontal (Fig. 3). Head length approximately 23% greater than head depth at occiput. Head depth similar to body depth. Opercular flap terminates in triangle with some fleshiness, two distinct opercular “spines” (meant here as the sharp edges of the opercle and subopercle supporting the opercular flap) below the thin

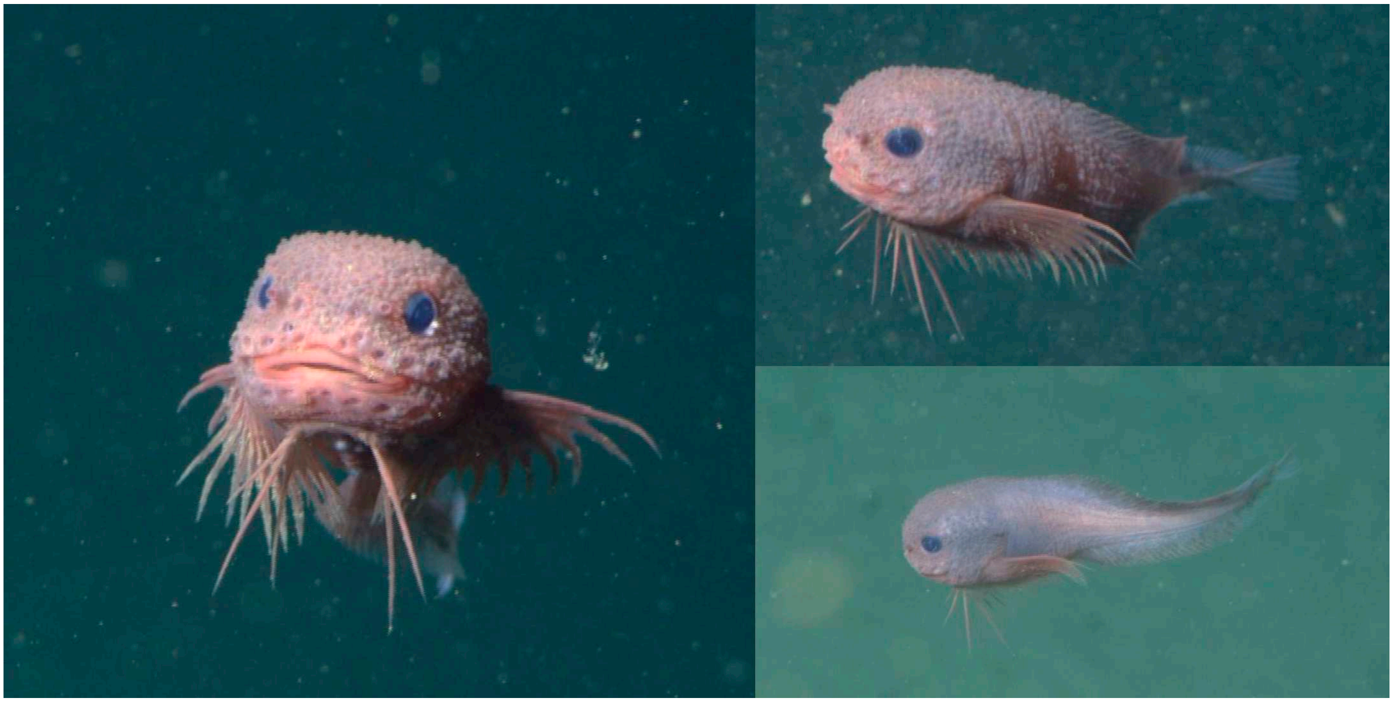

**Fig. 5.** *In situ* imagery of *Careproctus colliculi*, collected by the ROV *Doc Ricketts*, 3,263 m, Monterey Bay, California, USA. Copyright: MBARI (used with permission).

skin. Nostrils single, large, and protruding tubes. Teeth simple, sharp, long, and prominent (Fig. 4). Maxillary teeth present in 23 rows with a maximum of 7 teeth per row, forming a moderately wide band of 4 teeth across. Mandibular teeth arranged in 24 rows with a maximum of 6 teeth per row, forming a moderately wide band of 4 teeth across. Pharyngeal teeth well ossified, conical, and sharp, positioned on globular tooth plates. Eye moderate, 14.8% HL. Orbit moderately sized, 29.2% HL, dorsal margin below that of the head. Gill opening small, 8.7% SL, located mainly above the pectoral fin, but with a partial, ~2 mm overlap. Cephalic pores visible, often prominent. Nostril large in life, prominently raised. Nasal pores 2. Infraorbital pores 6, including 1 supraorbital pore. Preoperculomandibular pores 7. In the temporal pore series: postorbital pore 1, suprabranchial pore 1 (Fig. 3). Pore counts according to Burke (1930): 2-6-7-2. Some neuromasts present, difficult to identify.

Pectoral fin divided into upper and lower lobes with no rudimentary rays. Upper pectoral-fin lobe long, 28.9% SL and 105.6% HL, with lower pectoral-fin lobe slightly shorter than the upper, 26% SL, 94.9% HL. Upper pectoral rays tightly spaced, with widely spaced lower-lobe rays and moderately spaced notch rays, upper pectoral rays (~4) extending considerably beyond the length of the other upper lobe rays. Two pectoral radials visible, one in the center of the upper section of the pectoral girdle and the other in the lower section of the pectoral girdle. Pectoral girdle fragile, the lower radial is faint and poorly ossified.

Ventral suction disk present and large (Fig. 4), 5.8% SL and 21.3% HL in length, and 9.1% SL, 33.3% HL in width. Anus positioned anteriorly. Disk margin fragile, thin skin surrounding disk pterygiophores.

In life, skin pink, with most prominent coloration at the anterior of the body (Fig. 3, 5). In ethanol, body pale, slight duskiness. Peritoneum very dark in color. Holotype skin thin, in good condition. Head strikingly textured with small, soft, fleshy prickles giving skin a bumpy texture, covering the full body but especially prominent on the head of the fish (Fig. 5). Prickles round, relatively large (~1 mm) and variable in size, and irregularly distributed. Raised prickles appear well adhered, rather than deciduous. These bumps appear to be soft flesh, rather than ossified structures as found in other snailfishes such as *Liparis gibbus*. In some snailfishes, prickles can be sexually dimorphic traits, for example, found only in the males of *Liparis gibbus* (e.g., Able and McAllister, 1980). With only a single specimen from a single time point, it is not known whether these bumps are sexually dimorphic or ephemeral in *Careproctus colliculi*. Nostrils and pores prominent *in situ*. Pectoral fin webbed, with finger-like rays extending well beyond the connecting membrane between each ray. Lower pectoral fin with little webbing, rays extended in swimming, possibly to aid in sensing. In ethanol, skin smooth, prickles and skin texture are significantly less prominent after preservation but remain visible as small (<0.5 mm) bumps, particularly on the skin of the head. Subdermal extracellular matrix appearing partially lost in preservation, particularly around the head.

***Phylogenetic relationships.***—Mitochondrial COI sequencing reveals *Careproctus colliculi* belongs to the informal clade Osteocareprocta (Fig. 2), within the clade Aenigmoliparia (Clade E), as defined by Orr et al. (2019). The COI sequence of *C. colliculi* (379 bp) shares the most similarity with *Osteodiscus cascadiae* (97.36% to specimen TZFPA134-06, RBCM TagG5006, FJ164437; 97.10% to TZFPA133-06, RBCM TagG5005, FJ164436; and 97.10% to TZFPA101-06, RBCM 15941, FJ164433) previously identified as *Careproctus* cf. *cypselurus* (see Orr et al., 2019). The sequence also

**Table 2.** Measurements, counts, and ratios of three newly described snailfishes from the abyssal Pacific. Measurements taken from preserved specimens, given in mm. Dorsal-fin origin between vertebrae #, #. Values represent single collections, the holotypes of each species. Each species is known only from the holotype ($n = 1$). Disk length for *Careproctus colliculi* and *C. yanceyi* were measured from the micro-CT scan and represent the distance from the anterior-most portion of the first disk pterygiophores to the posterior-most portion of the last disk pterygiophores. *Paraliparis em* does not have a disk.

| | *Careproctus colliculi*, new species | *Careproctus yanceyi*, new species | *Paraliparis em*, new species |
|---|---|---|---|
| Measurements | | | |
| Standard length | 78.9 | 156.0 | 101.2 |
| Total length | 92.2 | 174.0 | 113.1 |
| Head length | 21.6 | 32.0 | 19.5 |
| Head depth at occiput | 17.1 | 26.7 | 16.9 |
| Head width | 16.9 | 22.7 | 10.9 |
| Snout length | 8.1 | 11.9 | 5.6 |
| Lower-lobe distance | 4.5 | 2.2 | 0.1 |
| Body depth | 19.9 | 34.2 | 15.1 |
| Orbit width | 6.3 | 7.0 | 7.2 |
| Disk length | 5.7 | 3.5 | — |
| Gill opening | 6.9 | 9.3 | 4.8 |
| Upper-jaw length | 9.3 | 6.8 | 8.1 |
| Lower-jaw length | 11.5 | 8.8 | 10.8 |
| Distance: mandible to disk | 11.3 | 13.4 | — |
| Distance: snout to anus | 19.0 | 36.7 | 17.3 |
| Distance: mandible to anus | 18.6 | 31.5 | 16.0 |
| Distance: disk to anus | 3.3 | 13.9 | — |
| Distance: anus to anal fin | 17.3 | 30.5 | 8.4 |
| Length upper-pectoral fin lobe | 22.8 | 22.1 | 17.9 |
| Length lower-pectoral fin lobe | 20.5 | 29.4 | 18.6 |
| Counts | | | |
| Total vertebrae | 53 | 63 | ~74 |
| Abdominal vertebrae | 9 | 11 | 10 |
| Caudal vertebrae | 44 | 52 | ~64 |
| Dorsal-fin origin | 4, 5 | 4, 5 | 5, 6 |
| Dorsal-fin rays | 43 | 57 | ~70 |
| Anal-fin rays | 40 | 53 | ~66 |
| Total pectoral rays | 22 | 22 | 17 |
| Pectoral-fin rays (upper lobe) | 15 | 13 | 10 |
| Pectoral-fin rays (notch) | 4 | 4 | 3 |
| Pectoral-fin rays (lower lobe) | 3 | 5 | 4 |
| Total caudal-fin rays | 8 | 10 | 4 |
| Caudal-fin rays (upper) | 4 | 5 | 3 |
| Caudal-fin rays (lower) | 4 | 5 | 1 |
| Caudal-fin rays (auxiliary) | 0 | 0 | 0 |

shares 97.10% similarity with *Careproctus discoveryae* (FKCI020-10, MNHN 2006-1232), 97.10% similarity with *Careproctus longipectoralis* (EATF504-10, MNHN 2008-2592, HQ712900), and 96.31% with *Careproctus longidigitus* (LC495312, Fig. 2).

***Reproduction.***—Holotype is a mature, gravid female. Eggs irregular in size, suggesting multiple developing cohorts, as found in other deep-water snailfishes such as *Pseudoliparis swirei* at hadal depths in the Mariana Trench (Gerringer et al., 2017b). Each ovary includes at least ten very large eggs, up to 4 mm in diameter, in addition to at least 20 small eggs that are less than 1 mm.

***Distribution.***—Known only from the holotype, eastern Pacific Ocean, abyssal depths off California, depth 3,268 m.

***Comparisons.***—*Careproctus colliculi*, the Bumpy Snailfish, is genetically and morphologically similar to *Osteodiscus cascadiae*. The genus *Osteodiscus* was originally distinguished from *Careproctus* in having a disk "covered only by thin skin, skeletal; fleshy margin absent; supporting rays of disk webbed between the tips, attenuate posteriorly, the most posterior extending almost to anus," along with other characteristics such as single nostrils and large cephalic pores that many snailfishes share (Stein, 1978). The position of the anus relative to the disk, thin skin between disk pterygiophores, and fragile disk margins of *C. colliculi* are similar, but this species does not display the webbing and absent margin or extended pterygiophores of *O. cascadiae*, the type species in this genus. Current morphological and genetic comparisons demonstrate similarities between *Osteodiscus* and the southern

**Table 3.** Ratios of the snailfishes *Careproctus colliculi*, *C. yanceyi*, and *Paraliparis em*. All measurements represent single holotypes and were taken on preserved specimens.

| | *Careproctus colliculi*, new species | | *Careproctus yanceyi*, new species | | *Paraliparis em*, new species | |
|---|---|---|---|---|---|---|
| Ratio (fixed specimen) | %SL | %HL | %SL | %HL | %SL | %HL |
| Head length | 27.4 | — | 20.5 | — | 19.3 | — |
| Head width | 21.4 | 78.2 | 14.6 | 70.9 | 10.8 | 55.9 |
| Snout length | 10.3 | 37.5 | 7.6 | 37.2 | 5.5 | 28.7 |
| Eye width | 4.1 | 14.8 | 2.1 | 10 | 3.4 | 17.4 |
| Orbit width | 8 | 29.2 | 4.5 | 21.9 | 7.1 | 36.9 |
| Upper-jaw length | 11.8 | 43.1 | 4.4 | 21.3 | 8 | 41.5 |
| Lower-jaw length | 14.6 | 53.2 | 5.6 | 27.5 | 10.7 | 55.4 |
| Body depth | 25.2 | 92.1 | 21.9 | 106.9 | 14.9 | 77.4 |
| Upper-pectoral fin length | 28.9 | 105.6 | 14.2 | 69.1 | 17.7 | 91.8 |
| Lower-pectoral fin length | 26 | 94.9 | 18.8 | 91.9 | 18.4 | 95.4 |
| Gill opening | 8.7 | 31.9 | 6 | 29.1 | 4.7 | 24.6 |
| Disk length | 5.8 | 21.3 | 2.7 | 13.1 | — | — |
| Distance: disk to anus | 4.2 | 15.3 | 8.9 | 43.4 | — | — |
| Distance: mandible to disk | 14.3 | 52.3 | 8.6 | 41.9 | — | — |
| Lower-lobe distance | 5.7 | 20.8 | 1.4 | 6.9 | 0.1 | 0.5 |
| Predorsal fin length | 40.9 | 149.5 | 23.8 | 116.3 | 17.5 | 90.8 |
| Preanal fin length | 44 | 160.6 | 41.1 | 200.3 | 24.8 | 128.7 |
| Distance: snout to anus | 24.1 | 87.9 | 23.5 | 114.7 | 17.1 | 88.7 |
| Distance: mandible to anus | 23.6 | 86.1 | 20.2 | 98.4 | 15.8 | 82.1 |
| Distance: anus to anal fin | 21.9 | 80.1 | 19.6 | 95.3 | 8.3 | 43.1 |

hemisphere species *C. continentalis*, *C. discoveryae*, and *C. longipectoralis*, which are now defined in the informal clade Osteocareprocta (Orr et al., 2019). *Careproctus colliculi* can be distinguished from *O. cascadiae* through the differences in disk morphology described above, also having eight, rather than seven, caudal-fin rays, a smaller gill opening extending no more than 2 mm or ~3 fin rays behind the pectoral fin, rather than up to seven fin rays behind the pectoral fin in *O. cascadiae* (Stein, 1978). Further, *O. cascadiae* is black or very dark brown, whereas *C. colliculi* is pink in life, fading to pale under preservation. *Careproctus discoveryae*, known only from the holotype in the Crozet Basin at 4,250 m, has ?5 caudal rays, whereas *C. colliculi* has 8, and although both have 22 pectoral-fin rays, the spacing differs considerably, with *C. colliculi* having 15 upper, 4 notch, and 3 lower lobe rays, whereas *C. discoveryae* has 12 upper, 5 notch, and 5 lower lobe rays. Although both are tadpole-shaped with round heads, *C. discoveryae* has a considerably more elongate tail, with a pre-anal-fin length of 37.8% vs. 44% SL in *C. colliculi* (Duhamel and King, 2007). *Careproctus colliculi* is also distinct from *C. longipectoralis* (2,025–2,037 m) and *C. continentalis* (425–600 m), found in the Weddell Sea in the Southern Ocean (Duhamel, 1992). *Careproctus continentalis* has 27 pectoral-fin rays and *C. longipectoralis* has 25, whereas *C. colliculi* has 22 (Andriashev and Prirodina, 1990; Duhamel, 1992). *Careproctus colliculi* lacks the dark coloration and distinctive long, black upper pectoral-fin rays of *C. longipectoralis* (Duhamel, 1992). Additional distinctions between *Careproctus colliculi* and other deep-water snailfishes of the North Pacific are described below in the comparisons for *C. yanceyi*.

***Etymology.***—*Careproctus colliculi* is named for the distinctive small bumps (from the Greek) that cover the skin, particularly the head and anterior portion of the fish in life (Fig. 5).

### *Careproctus yanceyi* Gerringer, new species

urn:lsid:zoobank.org:act:0236C0C1-BA79-4753-B2C4-4F156666C2F0
The Dark Snailfish
Figures 1, 2, 6, 7; Tables 2, 3

Priede et al., 2020, one of "two specimens of Liparidaev."

***Holotype.***—SIO 24-49 (collection number: AT4210-D5030-180), 197 mm TL upon collection, 189 mm SL, 74.4 g, 174.0 mm preserved TL, 156.0 mm preserved SL, mature female, Station M, 34.67°N, 123.00°W, 4,119 m, Cruise AT42-10, R/V *Atlantis*, 3 May 2019. Good condition.

***Diagnosis.***—*Careproctus yanceyi* is distinguished from other deep-water congeners in the eastern Pacific by the combination of the following characters: black body with rounded head and horizontal mouth, simple canine teeth, along with a moderate, but developed ventral suction disk (<3% SL), and small gill opening located entirely above the pectoral fin, which has 22 fin rays and two pectoral radials.

***Description.***—Based on the presence of a ventral suction disk, a single pair of nostrils, and the absence of pseudobranchs, we ascribe this fish to the paraphyletic genus *Careproctus* (e.g., Orr, 2020; Orr and Maslenikov, 2007). *Careproctus yanceyi* has 63 total vertebrae, with 11 abdominal and 52 caudal. Pleural ribs absent. Dorsal-fin rays 57, anal-fin rays 53, caudal-fin rays 10 (5 upper + 5 lower, no auxiliary rays), pectoral-fin rays 22 (13 upper lobe + 4 notch + 5 lower lobe), pectoral radials 2 visible, branchiostegal rays 6. Measurements, counts, and ratios for *C. yanceyi* are shown in Tables 2 and 3.

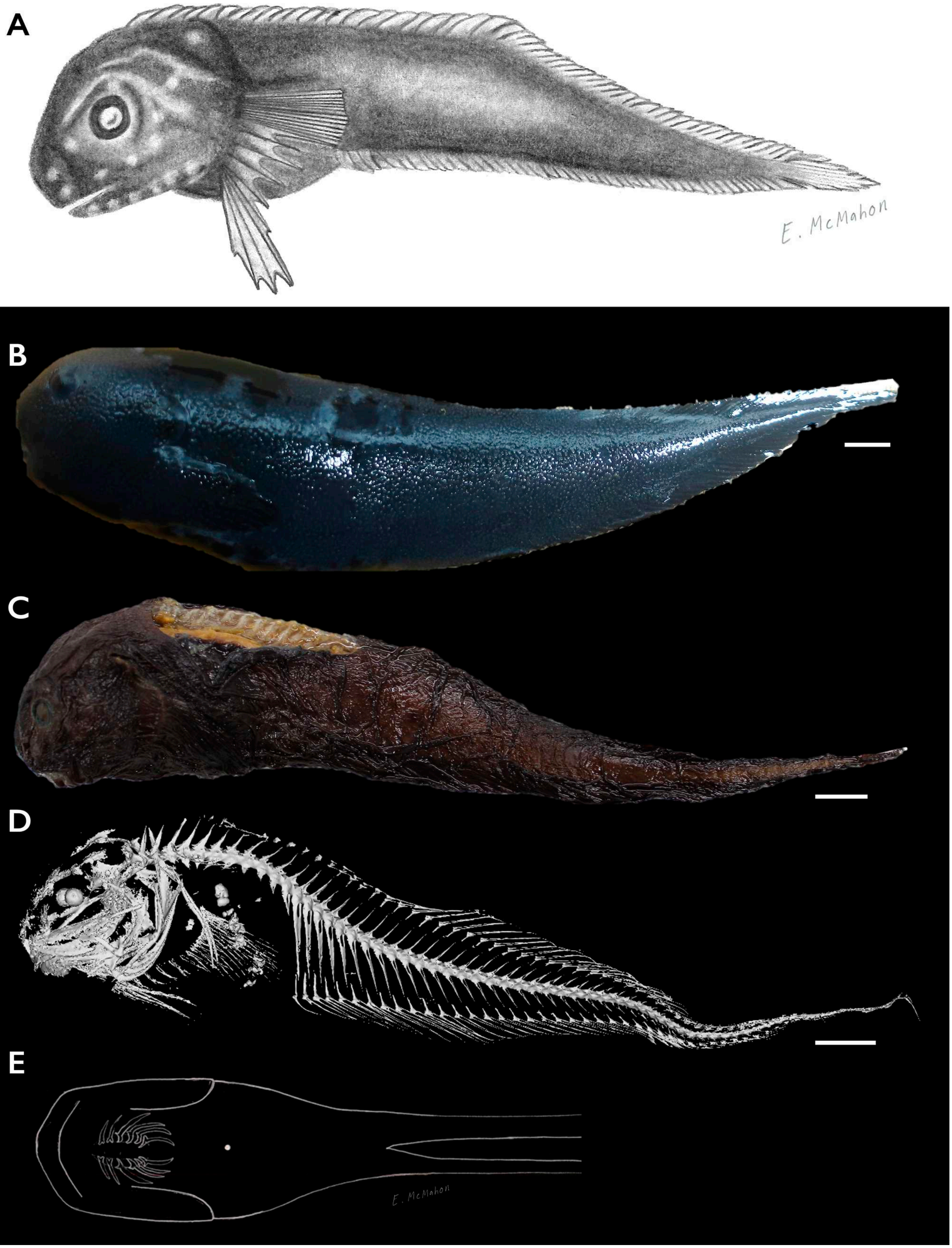

**Fig. 6.** *Careproctus yanceyi*, new species, the Dark Snailfish, based on the holotype, SIO 24-49. Standard length 156.0 mm. (A) Lateral view drawing. (B) Photograph of specimen upon collection. (C) Photograph of specimen fixed in 4% formaldehyde, then stored in 70% ethanol. (D) Lateral view of micro-computed tomography of the holotype. (E) Ventral view drawing, showing anterior portion of the fish. Artist (A, E): Emily McMahon. Photo (B) by Jeffrey Drazen. Photo (C) and CT scan (D) by Mackenzie Gerringer. Scale bars 10 mm.

Head rounded, snout deep, bluntly rounded, mouth horizontal (Fig. 6). Head length approximately 20% greater than head depth at occiput. Head depth similar to body depth. Opercular flap terminates in moderately fleshy, broad triangle with opercular "spines" identifiable below the skin. Nostrils single. All teeth simple, canine, and sharp, oriented interiorly (Fig. 7). Maxillary teeth present in 8 rows with a maximum of 12 teeth per row, forming a moderately wide band of 4 teeth across. Mandibular teeth arranged in 10 rows with a maximum of 15 teeth per row, forming a relatively wide band of 5 teeth across. Pharyngeal teeth well ossified, conical, and sharp, positioned on globular tooth plates. Eye small, 10% HL. Orbit moderately sized, 21.9% HL, dorsal margin well below that of the head. Gill opening small, 6% SL, located completely above pectoral fin. Cephalic pores visible, often prominent. Nostril moderate in size in preserved specimen. Nasal pores 2. Infraorbital pores 6, including 1 supraorbital pore. Preoperculomandibular pores 7. Suprabranchial pore 1 (Fig. 6). Pore counts according to Burke (1930): 2-6-7-1. Neuromasts present in 2 rows, along the body.

Pectoral fin divided into prominent upper and lower lobes with no rudimentary rays (Fig. 7). Upper pectoral-fin lobe moderate, 14.2% SL and 69.1% HL, with lower pectoral-fin lobe longer than the upper, 18.8% SL, 91.2% HL. Upper pectoral rays tightly spaced, with moderately spaced lower lobe and notch rays. Two pectoral radials visible, one in the upper section of the pectoral girdle and one in the lower section.

Ventral suction disk present (Fig. 7), moderate in size, length 2.7% SL, 13.1% HL, and width 4.0% SL, 19.4% HL. Disk margin moderately fleshy, disk small but robust. Pyloric caeca 12, digitate, thick, and short, relatively consistent in length.

In life, body completely black, skin textured with small moderately raised bumps covering the head and body. Bumps are densely packed, approximately 1 mm in diameter and 1 mm apart (Fig. 6). In ethanol, skin completely black. Skin texture does not remain after preservation. Skin smooth, loose, largely intact. Peritoneum very black. Subdermal extracellular matrix present, partially lost in preservation.

***Phylogenetic relationships.***—Based on the mitochondrial COI gene, *Careproctus yanceyi* is distinct from all other snailfish taxa that have been sequenced and does not cluster strongly into any of the defined snailfish clades (Fig. 2). Phylogenetic analysis shows that *C. yanceyi* may represent a monotypic branch sister to the informal Ambidisca (Clade F; composed of clades H and Q), although this relationship has low bootstrap support and reflects the low similarity of this fish to other sequenced snailfishes (Fig. 2). The COI sequence of *Careproctus yanceyi* (637 bp) is dissimilar to all other snailfishes. The most similar COI sequences identified included *Pseudoliparis swirei* (USNM 438982, KY659181) and *Notoliparis kermadecensis* (KY659176), both of which share 95.45% similarity with *C. yanceyi*. *Careproctus yanceyi* also shares 94.81% similarity with *C. longipectoralis* (MNHN 2008-2592, EATF504-10, HQ712900) and 94.78% with *C. ovigerus* (TZFPA097-06, RBCM TagR5831, FJ164449, previously identified as *C. georgianus*, see Orr et al., 2019 for clarifications on identifications). The COI sequence of *Careproctus yanceyi* is 93.14% similar to that of *C. colliculi*, described above. Due to morphology (described below) and genetic distance (94.97% similarity), this species is indeed distinct from *Paraliparis em*, new species, collected on the same dive from the same location.

***Reproduction.***—Holotype is a mature female with many small eggs up to 0.5 mm in diameter.

***Distribution.***—Known only from the holotype, eastern Pacific Ocean, abyssal depths off California, depth 4,119 m.

***Comparisons.***—*Careproctus yanceyi*, the Dark Snailfish, can be distinguished from other deep-water snailfishes in the region in the genus *Paraliparis* due to the presence of a developed ventral suction disk. Other deep-water snailfishes from the eastern Pacific include *C. filamentosus*, *C. longifilis*, *C. microstomus*, and *C. oregonensis*, which also have dark coloration, along with *C. atakamensis*, and *C. kamikawai* (Stein, 1978; Andriashev, 1998; Orr, 2012). *Careproctus yanceyi* is distinct from *P. selti* in having a ventral suction disk, dark coloration, and being known only from abyssal, rather than hadal or near-hadal depths, among other morphological differences (Linley et al., 2022). Although closer in habitat depth and disk morphology to *C. atakamensis*, which is known only from near the Atacama Trench in the Southeastern Pacific from depths of 2,710–3,080 m, *C. yanceyi* differs from *C. atakamensis* in having 63, rather than 59 vertebrae, a wider head (14.6% SL vs. 10.6% SL in *C. atakamensis*) and deeper body (21.9% SL vs. 14.0% SL) than in *C. atakamensis*, a smaller suction disk (2.7% SL in length vs. 6% SL in *C. atakamensis*), and a pigmented peritoneum (Andriashev, 1998). *Careproctus yanceyi* is easily distinguished from *C. microstomus* and *C. filamentosus* by fin-ray counts, having 57 rather than 61–67 and 58–63 dorsal-fin rays, respectively, and 10 rather than 8 and 7–8 caudal rays, respectively (Stein, 1978). *Careproctus yanceyi* differs from *C. oregonensis* and *C. kamikawai* in having simple, rather than lobed teeth (Stein, 1978; Orr, 2012). *Careproctus yanceyi* lacks the distinguishing long first pectoral-fin ray of *C. longifilis*, which in *C. longifilis* can extend to almost half the length of the fish's body (Stein et al., 2006).

*Careproctus yanceyi* is also distinct from other congeners in the broader northern Pacific. The following distinctions also apply to *C. colliculi*, described above. *Careproctus yanceyi* and *C. colliculi* have simple, rather than trilobed teeth, making these species different than *C. bromius* (Alaska, 80–232 m; Gardner et al., 2023), *C. iacchus* (Sea of Japan, Sea of Okhotsk, 152–313 m; Kai et al., 2018), *C. io* (Japan, ~400 m; Kai et al., 2024), *C. klisi* (Aleutian Islands, 134–280 m; Gardner et al., 2023), *C. longidigitus* (Hokkaido, Japan, 500–1,080 m; Kai and Matsuzaki, 2020), *C. lycopersicus* (Bering Sea, eastern Aleutian Islands, 304–1,096 m; Orr, 2012), *C. nelsoni* (Aleutian Islands, 220–329 m; Orr, 2016), *C. orri* (Japan, 640–808 m; Kai et al., 2021), *C. rausuensis* (Hokkaido, Japan, 356 m; Machi et al., 2012), *C. rhomboides* (Sea of Okhotsk, 570–825 m; Mori et al., 2024), *C. shigemii* (Sea of Okhotsk, 200–300 m; Matsuzaki et al., 2020), *C. staufferi* (Aleutian Islands, 205–366 m; Orr, 2016), *C. surugaensis* (Suruga Trough, Japan, 1,450–1,570 m; Murasaki et al., 2017), *C. tomiyamai* (Southern Japan, Pacific Coast, 600–808 m; Murasaki et al., 2022), and *C. zachirus* (Aleutian Islands to Hokkaido, 130–800 m; Matsuzaki et al., 2020). *Careproctus yanceyi* and *C. colliculi* differ from *C. candidus* (Alaska, 88–432 m) in that the new species both lack the distinctive dorsal-fin

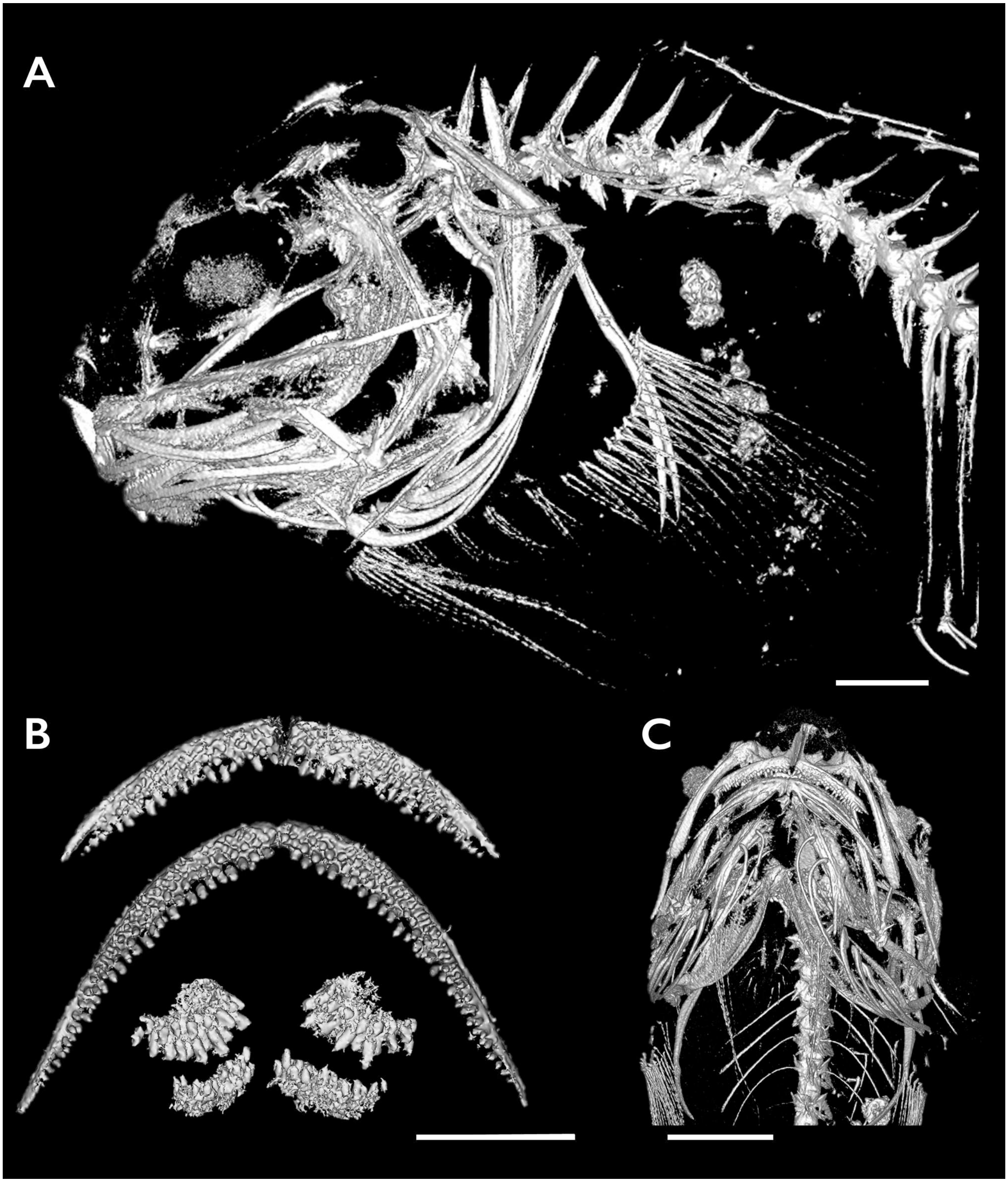

**Fig. 7.** Morphology of *Careproctus yanceyi* from micro-CT scanning. (A) Lateral view micro-CT. (B) Jaw and tooth morphology: premaxilla (top), mandible (middle), pharyngeal jaws (bottom), micro-CT images. (C) Ventral view micro-CT, ventral suction disk. Scale bars 5 mm. CT scans by Mackenzie Gerringer.

notch of *C. candidus* (Gardner et al., 2023). *Careproctus yanceyi* and *C. colliculi* have significantly fewer pectoral-fin rays (22 each) than *C. schmidti* (34 rays, Bering Sea, 852–862 m; Chernova et al., 2021) and *C. cyanogladius* (29–31 pectoral-fin rays, Japan, 2,698–3,223 m; Kai et al., 2021). Both new species lack the intense red coloration of *C. pulcher* (Bussol Strait, 2,350–2,358 m; Chernova et al., 2020), the globular head shape of *C. globulus* (Chernova et al., 2020) and have upper pectoral fins more than double the length (%SL) of *C. brevipectoralis* (Kuril Basin, Sea of Okhotsk, 3,301 m; Chernova et al., 2020). *Careproctus laperousei*, an abyssal snailfish known from depths of 4,796–4,803 m near the Kuril-

Kamchatka Trench, has a distinctly larger disk than either new species, 37% HL (Chernova et al., 2020), as compared to 13.1% in *C. yanceyi* and 21.3% in *C. colliculi*. *Careproctus yanceyi* is similar, but distinct from the recently redescribed *C. bathycoetus* from 3,292–3,305 m in the Kuril Basin in the Sea of Okhotsk, western North Pacific (Chernova and Thiel, 2024). *Careproctus yanceyi* can be distinguished from *C. bathycoetus* in having more caudal-fin rays (10 vs. 7 in *C. bathycoetus*), a longer pre-anal fin length (41.1% SL vs. 30% SL in *C. bathycoetus*), a smaller disk (13.1% HL vs. 27% HL), and more pyloric caeca (12 vs. 9 in *C. bathycoetus*; Chernova and Thiel, 2024). *Careproctus colliculi* differs from *C. bathycoetus* in many characters, most prominently color (*C. colliculi* is pink in life and pale preserved, rather than dark), but also in other characters including pre-anal fin length (44% SL in *C. colliculi* vs. 30% SL in *C. bathycoetus*), dorsal-fin rays (43 vs. 59–61 in *C. bathycoetus*), and anal-fin rays (40 vs. 53–55 in *C. bathycoetus*).

***Etymology.***—It is a privilege to name this species in recognition of Dr. Paul Yancey, Whitman College, USA, to honor his significant contributions to the field of deep-sea biology and fish physiology and in sincere gratitude for his generous mentorship and support.

### *Paraliparis em* Gerringer, new species

urn:lsid:zoobank.org:act:5EFC9303-006B-4A90-A53D-D7A890214ACE
The Sleek Snailfish
Figures 1, 2, 8, 9; Tables 2, 3

Priede et al., 2020, "*Paraliparis* sp. 1": figure 4A.

***Holotype.***—SIO 24-50 (collection number: AT4210-D5030-181), 119 mm TL upon collection, 111 mm SL, 7.35 g, 113.1 mm preserved TL, 101.2 mm preserved SL, mature female, Station M, 34.67°N, 123.00°W, 4,115 m, Cruise AT42-10, R/V *Atlantis*, 3 May 2019. Good condition.

***Diagnosis.***—*Paraliparis em* is distinguished from all other congeners by having five branchiostegal rays, one pectoral-fin radial, three widely spaced pectoral-notch rays (17 total), prominently angled jaw, narrow and elongate body, anteriorly positioned anus, and high number of vertebrae (about 74), dorsal-fin rays (about 70), and anal-fin rays (about 66).

***Description.***—*Paraliparis em* is placed in the genus *Paraliparis* due to its lack of a ventral suction disk and having a single pair of nostrils and single suprabranchial pore (e.g., Stein, 2012; Linley et al., 2022), along with mitochondrial COI sequences, which position *Paraliparis em* in *Paraliparis* Clade I (Fig. 2; Orr et al., 2019). *Paraliparis em* has about 74 total vertebrae, with 10 abdominal vertebrae and about 64 caudal vertebrae. Pleural ribs absent. Dorsal-fin rays about 70, anal-fin rays about 66, caudal-fin rays 4 (3 upper + 1 lower, no auxiliary rays), pectoral-fin rays 17 (10 upper lobe + 3 notch rays + 4 lower lobe), pectoral radial 1 visible, branchiostegal rays 5. Measurements, counts, and ratios for *Paraliparis em* are shown in Tables 2 and 3.

Head laterally compressed, abruptly angled snout, mouth slightly oblique (Fig. 8). Head length approximately 10% greater than head depth at occiput. Head depth greater than body depth. Opercular flap narrow, sharp triangle, terminating in two prominent "spines" below thin skin. Nostrils single. Teeth sharp, conical, angled interiorly (Fig. 9). Maxillary and mandibular teeth present in 19 rows each, with a maximum of 5 teeth per row, forming relatively narrow bands of three teeth across the maxilla and mandible. Pharyngeal jaws well ossified, pharyngeal teeth conical. Eye moderate, 17.4% HL. Orbit large, 36.9% HL. Dorsal margin of orbit located considerably below dorsal margin of head. Gill opening small, 4.7% SL, located completely above pectoral fin. Cephalic pores visible, often prominent. Nostril moderate in size in preserved specimen. Nasal pores 2. Infraorbital pores 6, including 1 supraorbital pore. Preoperculomandibular pores ?7, very large, skin damage may be altering this count. Suprabranchial pore 1 (Fig. 8). Pore counts according to Burke (1930): 2-6-?7-1. Neuromasts present in 2 rows along the body.

Pectoral fin divided into two lobes with a deep notch, rudimentary rays absent. Notch rays very widely spaced. Lower-lobe rays more widely spaced than upper-lobe rays (Fig. 9). Upper pectoral-fin lobe 17.7% SL, 91.8% HL, lower pectoral lobe 18.4% SL, 95.4% HL. Lower pectoral lobes nearly touching pelvic girdle. One pectoral radial visible, located centrally in the upper section of the pectoral fin. Pelvic suction disk absent. Holotype appears to lack pyloric caeca.

In life, body black, caudal fin and posterior-most section of body translucent. Skin very smooth. Subdermal extracellular matrix present, lost upon preservation. In ethanol, body black, peritoneum very black, tail less pigmented, partially translucent.

***Phylogenetic relationships.***—According to mitochondrial COI sequences, *Paraliparis em* is positioned in *Paraliparis* Clade I, within the larger Paraliparia Clade Q, as defined by Orr et al. (2019). This clade includes *P. megalopus*, *P. ulochir*, and *P. wolffi*. Phylogenetic relationships between this species and sequenced taxa are shown (Fig. 2). For this section of the COI gene (641 bp), *Paraliparis em* shares high similarity with *P. wolffi* (99.69% with specimen FKCI021-10, MNHN 2006-1233; 99.53% with FKCI022-10, MNHN 2006-1234). These differences reflect changes in 2 and 3 base pairs from the sequences of *P. wolffi*. *Paraliparis wolffi* is known only from abyssal depths in the Crozet Basin in the Indian Ocean (Duhamel and King, 2007), more than 18,000 km away from this collection of *P. em*. Given this great geographical distance, the lack of identical COI sequences, and the morphological differences (see Comparisons), *Paraliparis em* can confidently be called a distinct species. The COI sequence of *Paraliparis em* also shares 96.68% similarity with a *Paraliparis* sp. (TZFPA069-06, TagR5068, FJ164953), previously identified as *P. dactylosus*, 96.52% with *Paraliparis megalopus* (TZFPA130-06, TagG5002, FJ164959), previously identified as *Paraliparis melanobranchus*, and 96.52% with *Paraliparis ulochir* (TZFPA137-06, TagG5009, FJ164958), previously identified as *P. dactylosus*. See Orr et al. (2019) for clarifications on identifications. The COI sequence from *Paraliparis em* is 94.16% similar to the sequence from *Careproctus colliculi*, described above.

***Reproduction.***—Holotype is a mature, gravid female with multiple eggs of mixed sizes. The largest of these eggs are 1 mm in diameter.

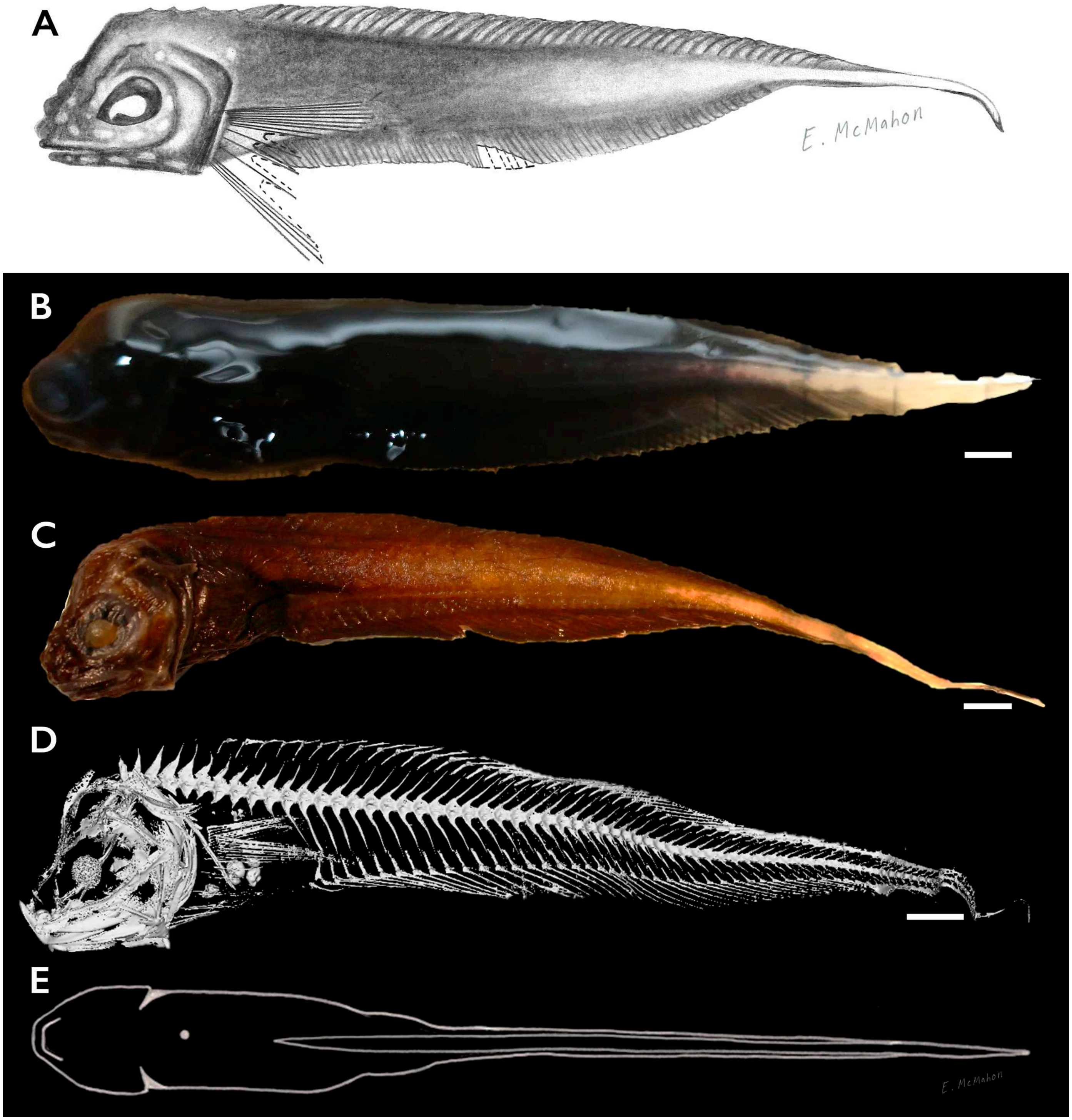

**Fig. 8.** *Paraliparis em*, new species, the Sleek Snailfish, based on the holotype SIO 24-50. Standard length 101.2 mm. (A) Lateral view drawing. (B) Photograph of specimen upon collection. (C) Photograph of specimen fixed in 4% formaldehyde, then stored in 70% ethanol. (D) Lateral view of micro-computed tomography (micro-CT scan) of the holotype. (E) Ventral view drawing. Artist (A, E): Emily McMahon. Photograph (C) and CT scan (D) by Mackenzie Gerringer. Photograph (B) by Jeffrey Drazen. Scale bars 5 mm.

***Distribution.***—Known only from the holotype, eastern Pacific Ocean, abyssal depths off California, depth 4,115 m. Although not confirmed by collections, Priede et al. (2020) note that a species called "*Paraliparis* sp. 1" appearing similar to *Paraliparis em*, with an elongate black body, translucent tail, and large eye, is regularly observed in ROV footage at Station M.

***Comparisons.***—*Paraliparis em*, the Sleek Snailfish, fits genetically into *Paraliparis* Clade I, as defined by Orr et al. (2019), related to *P. megalopus*, *P. ulochir*, and *P. wolffi*. *Paraliparis em* is genetically and morphologically most similar to *P. wolffi*, collected from the Crozet Islands from depths 4,182–4,195 m. In addition to slight differences in COI sequences, *Paraliparis*

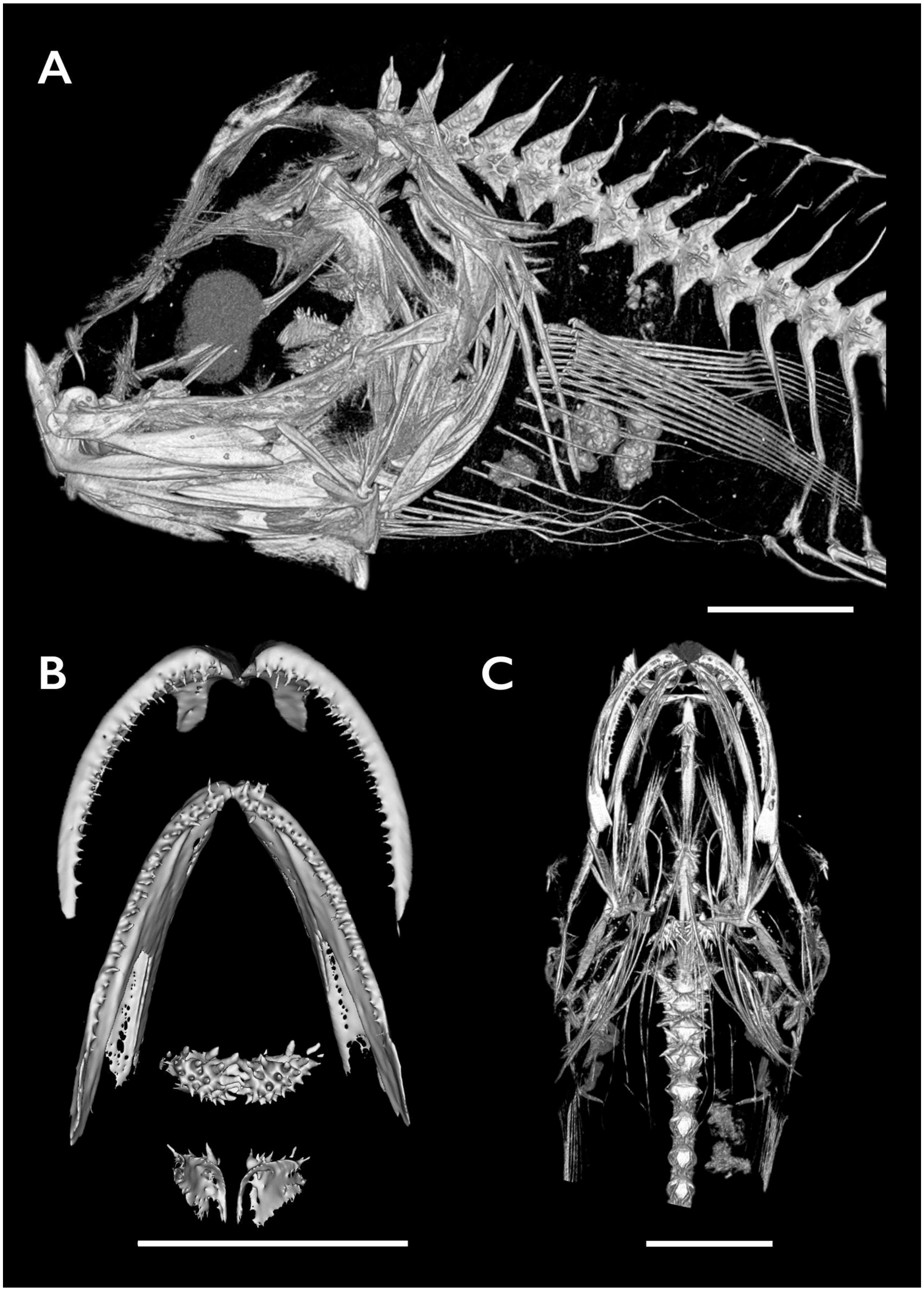

**Fig. 9.** Morphology of *Paraliparis em* from micro-CT scanning. (A) Lateral view micro-CT scan of *Paraliparis em*, head length 19.5 mm. (B) Jaw and tooth morphology, premaxilla (top), mandible (middle), pharyngeal jaws (bottom), micro-CT images. (C) Ventral view micro-CT, showing lack of suction disk in *Paraliparis em*. CT scans by Mackenzie Gerringer. Scale bars 5 mm.

*em* is distinguished from *P. wolffi* in having only one pectoral radial instead of two, having a small instead of large gill slit, a slightly longer HL (19.3% SL vs. 16.4–18.4% SL for *P. wolffi*), and three notch rays in the pectoral fin instead of two in *P. wolffi* (Duhamel and King, 2007). *Paraliparis em* is distinct from the morphologically similar *P. kreffti* in having one pectoral radial instead of two, along with a far deeper habitat depth (4,000 vs. 2,000 m) and distant distribution (Scotia Sea; Andriashev, 1998). *Paraliparis em* differs from other congeners in this clade in multiple ways. Unlike *P. megalopus*, which is known from depths 2,830–3,585 m off Oregon, USA, *P. em* has two opercular "spines" instead of one and much smaller eyes, 17.4% HL in *P. em* vs. 22.6–34.8% HL in *P. megalopus* (Stein, 1978). Although *P. ulochir* and *P. em* bear some genetic and morphological similarities, they are distinct in habitat depth (700–1,900 m for *P. ulochir*; Stein, 1978; 4,000 m for *P. em*). *Paraliparis ulochir* has significantly more pectoral-fin rays, 24 with nine closely spaced lower-lobe rays (Stein, 1978), as compared to 17 total pectoral rays and 4 lower-lobe rays in *P. em*. *Paraliparis dactylosus*, a species that has sometimes been misidentified as a member of this clade in the literature (see full explanation in Orr et al., 2019), lives at significantly shallower depths of 541–960 m and is morphologically distinct in having more pectoral-fin rays (26–30 vs. 17 in *P. em*), fewer vertebrae (59–61 vs. about 74 in *P. em*), and paler body coloration than the black *P. em* (Stein, 1978). *Paraliparis em* is distinct from other recently described snailfishes from the western Pacific Ocean in location, but also by the presence of five branchiostegal rays instead of six (*P. flammeus*: Kai et al., 2020; *P. hokuto* and *P. atramentatus*: Murasaki et al., 2020; *P. ruficometes*: Murasaki et al., 2018; *P. variabilidens*: Murasaki et al., 2019).

***Etymology.***—*Paraliparis em* is named after its collection site, Station M, where it has been regularly observed. The name honors the invaluable contribution of time series data, such as those from Station M, and the many people who make long-term monitoring of biological communities possible.

## DISCUSSION

The finding of three new species of abyssal snailfishes suggests that the family Liparidae contributes even more to the diversity of abyssal ichthyofauna than previously recognized. Snailfishes are known to inhabit the full depth range for bony fishes, to depths exceeding 8,000 m (Nielsen, 1964; Jamieson and Yancey, 2012; Yancey et al., 2014; Gerringer et al., 2021; Jamieson et al., 2023). Although snailfishes are dominant at hadal depths and are known from bathyal depths (e.g., Stein et al., 2006), there is a noticeable gap in snailfish collections at abyssal depths, with few, single observations near 4,000 m and very few between 3,000 and 5,300 m (Gerringer, 2019; Priede et al., 2020). This study supports the previously proposed hypothesis (e.g., Gerringer, 2019) that this lack of observations is due to sampling and not a true bathymetric gap in the *in situ* distribution of snailfishes. The present finding of three new abyssal snailfishes lends further credence to calls for additional abyssal sampling efforts and alternative sampling methods that target non-bait attending fauna and fishes that are less likely to enter an enclosed trap structure.

These newly discovered snailfishes also inform our understanding of snailfish evolution. The genetic and morphological similarity between *Careproctus colliculi* and other members of the informal clade Osteocareprocta that are known only from the Southern Ocean supports the hypothesis that some deep-water snailfishes may have evolved from polar relatives (e.g., Linley et al., 2022). This hypothesis is further supported by the close morphological and genetic similarity between *Paraliparis em* and the Crozet Basin species *P. wolffi* (Duhamel and King, 2007). Though there was high similarity in this portion of the COI gene, short COI sequences like this are known to have limitations in resolving taxonomic relationships between liparid species (e.g., Orr et al., 2019). Additional sequencing would also allow better understanding of how similar these taxa are. It is possible that both taxa evolved from a deep polar ancestor and have dispersed to these distant locations. Future efforts to sequence larger portions of snailfish genomes and to build sampling resolution across the family would allow these hypotheses to be tested. A similar evolution from polar waters to the eastern Pacific has been suggested for the hadal snailfish species *P. selti* in the Atacama Trench, positioned within a different group, Clade M (Linley et al., 2022). The present findings suggest that evolution from shallower, cold-adapted species in the Southern Ocean may be relatively common and could have occurred across multiple clades. The rattails, family Macrouridae, seem to display a similar evolutionary pattern (Gaither et al., 2016). Genera that have historically been divided in classification by hemisphere, such as the Pacific hadal snailfish genera *Notoliparis* and *Pseudoliparis*, have been shown to represent closely related taxa based on genetic, morphological, and behavioral evidence (Gerringer et al., 2017b; Orr et al., 2019). Trends of evolution across habitat depth and temperature, in addition to region, should be considered in future revisions of the family.

The five branchiostegal rays of *Paraliparis em*, which are clearly visible in the micro-CT scan of the specimen (scan data and 3D models available on MorphoSource), distinguish this species from others in the paraphyletic *Paraliparis* "genus." This characteristic is shared by *Nectoliparis pelagicus* Gilbert and Burke 1912, the monotypic genus that was originally distinguished from the genus *Paraliparis* due to this feature (Gilbert and Burke, 1912). The phylogenetic positioning and generic assignment of *Nectoliparis pelagicus* has been well supported by genetic and morphological evidence, which show this genus to be sister to all other snailfishes (Orr et al., 2019). Despite the fishes sharing the same number of branchiostegal rays, we are confident that *Paraliparis em* is distinct from *Nectoliparis pelagicus* due to the COI sequence of *P. em*, elongate body, sloped head, sharply angled jaw structure, one rather than three pectoral radials, and the position of the small gill slit above, rather than in front of the pectoral fin (Gilbert and Burke, 1912; Orr et al., 2019). Five branchiostegal rays are also known from *Lipariscus nanus*, which is positioned in the Clade Q Paraliparia by Orr et al. (2019). In addition to having a distinctly different COI sequence, *Paraliparis em* is distinguished from *L. nanus* by color, with *L. nanus* being pale or reddish, having longer lower pectoral rays, considerably more dorsal-fin rays (∼70 in *P. em* vs. 53 in *L. nanus*), and more anal-fin rays (about 66 in *P. em* vs. 50 in *L. nanus*), and living at 4,000 m instead of 300–600 m (Gilbert, 1915). Our finding of five branchiostegal rays in *Paraliparis em* suggests that the sixth branchiostegal ray most commonly found in snailfishes might have been lost three times: in the *N. pelagicus* clade and multiple times within Clade Q Paraliparia, including *L. nanus* and *P. em* (Clade I). With increasing accessibility of non-destructive techniques such as CT scanning, future work should examine branchiostegal ray counts across snailfishes and investigate ties between this morphology and respiratory or suction feeding function.

Morphological and genetic evidence demonstrate that the two black snailfishes from Station M—*Careproctus yanceyi* and *Paraliparis em*—are indeed distinct taxa, revealing cryptic diversity in abyssal snailfishes. *Paraliparis em* has been identified as one of the most abundant fishes at Station M in video surveys, after the rattails *Coryphaenoides armatus* and *Coryphaenoides yaquinae* (Priede et al., 2020). Because *P. em* and *C. yanceyi* are both black abyssal snailfishes, it would be easy to mistake these for larger and smaller individuals of the same species in videos or photographs, so it is possible that previous abundance estimates represent a combined total of both snailfishes. The present finding of these distinct species that appear similar at first glance serves as another reminder of the importance of physical collections and taxonomic analyses of deep-living fishes. This finding also suggests strong potential for additional cryptic diversity within the family Liparidae, particularly in deepwater groups where observations and collections remain challenging. Without physical collections and confident identification, the true diversity of deep-water demersal fish communities could be greatly underestimated. Only by integrating multiple methods of investigation—including videography, morphology, genetics, genomics, physiology, and ecology—will it be possible to understand the biodiversity and function of deep-sea ecosystems.

## DATA ACCESSIBILITY

Specimens are deposited at the Scripps Institution of Oceanography Marine Vertebrate Collection (*Careproctus yanceyi*: SIO 24-49; *Paraliparis em*: SIO 24-50) and California Academy of Sciences (*Careproctus colliculi*: CAS-ICH 248611) and are available for future comparative study. Full CT scans generated for this study are available open access via MorphoSource (Duke University) at the Media ID numbers: *Careproctus colliculi* 000718579, *Careproctus yanceyi* 000718591, *Paraliparis em* 000719446 (reconstructed, cropped files), 000718441 (raw scan data, all three species, 34.4 μm voxel size), and 000718935 (raw scan data, *Careproctus colliculi* and *Paraliparis em*, 15.9 μm voxel size). 3D models (STL, stereolithography files) are provided on MorphoSource for each species (*Careproctus colliculi*: full body 000744884, head 000744893, lower jaw 000744892, pharyngeal jaw 000744897, upper jaw 000744900; *Careproctus yanceyi*: full body 000744854, head 000744858, lower jaw 000744861, pharyngeal jaw 000744872, upper jaw 000744874; *Paraliparis em*: full body 000744827, head 000744830, lower jaw 000744838, pharyngeal jaw 000744843, upper jaw 000744849). Additional images of *in situ* observations and photographs of freshly collected specimens are provided in the supplementary information. Supplemental material is available at https://www.ichthyologyandherpetology.org/i2024069. Genetic sequences have been deposited in NCBI's GenBank, accession numbers PV300957 (COI, *Careproctus colliculi*), PV300956 (COI, *Careproctus yanceyi*), PV298546 (16S, *Careproctus yanceyi*), PV300955 (COI, *Paraliparis em*), and PV298545 (16S, *Paraliparis em*). Unless an alternative copyright statement noting that a figure is reprinted from a previous source appears in a figure caption, the published images and illustrations in this article are licensed by the American Society of Ichthyologists and Herpetologists for use if the use includes a citation to the original source (American Society of Ichthyologists and Herpetologists, the DOI of the *Ichthyology & Herpetology* article, and any individual image credits listed in the figure caption) in accordance with the Creative Commons Attribution CC BY License. ZooBank publication urn:lsid:zoobank.org:pub:F16D4DB1-C6BA-4EFA-8287-B6DDC13B57F2.

## AI STATEMENT

The authors declare that no AI-assisted technologies were used in the design and generation of this article and its figures.

## ACKNOWLEDGMENTS

We thank the captains, crews, and science parties of the R/V *Atlantis* expedition AT42-10, the HOV *Alvin* Team, pilot Danik Forsman, science observers Jesse A. Black and Claudia Benitez-Nelson, the R/V *Western Flyer* expedition, chief scientist Steve Haddock (MBARI), Gustav Paulay (Florida Museum of Natural History), and the pilots of the R/V *Doc Ricketts*, who collected these specimens. Thanks to Gustav Paulay and Steve Haddock for providing additional metadata and context on collections. Funding for these expeditions was provided by the National Science Foundation Division of Ocean Sciences (Grant OCE-1829612 to J. Drazen) and by the Monterey Bay Aquarium Research Institute (MBARI) and the David and Lucile Packard Foundation. We are grateful to Matthew Church (University of Montana) and the Flathead Lake Biological Station for use of lab facilities to complete genetic analyses and Josephine Reinhardt (State University of New York at Geneseo) for time and assistance with DNA extraction protocols. We thank Alejandro Damian-Serrano (University of Oregon), Casey Dunn, and Kirstin Dion (Yale University) for extraction and shipping of DNA from *Careproctus colliculi*. The authors extend their sincere gratitude to the Geneseo Research Foundation and the Sorrell Chesin research awards at SUNY Geneseo for further support of this work and to Anne Baldwin, Betsy Colón, and Sheila McCart (SUNY Geneseo) for award administration and support of student research. We thank the museum collections teams that curate and care for fish specimens for all their time and support, including Jon Fong (California Academy of Sciences), Benjamin Frable, and Dahiana Arcila (Scripps Institution of Oceanography), essential work for understanding biodiversity on our planet.

## LITERATURE CITED

**Able, K. W., and D. E. McAllister.** 1980. Revision of the snailfish genus *Liparis* from Arctic Canada. Canadian Journal of Fisheries and Aquatic Sciences 208:1–52.

**Andriashev, A. P.** 1998. A new deep-sea species of the *Careproctus* genus (Liparidae, Scorpaeniformes) from the equatorial region of the Atakama Trench (Chile). Journal of Ichthyology 38:541–542.

**Andriashev, A. P.** 2003. Snailfishes (Liparidae, Scorpaeniformes) from the Southern Ocean and adjacent waters. Issledovaniya fauny morei (Study of Marine Fauna), St. Petersburg.

**Andriashev, A. P., and V. P. Prirodina.** 1990. Notes on the first occurrence of liparid fishes of the genus *Careproctus* (Lipariididae) from the coasts of the Antarctic Continent with description of three new species. Uo [Japanese Society of Ichthyology] 39:1–4.

**Bailey, D. M., H. A. Ruhl, and K. L. Smith, Jr.** 2006. Long-term change in benthopelagic fish abundance in the abyssal northeast Pacific Ocean. Ecology 87:549–555.

**Benson, D. A., I. Karsch-Mizrachi, D. J. Lipman, J. Ostell, and E. W. Sayers.** 2009. GenBank. Nucleic Acids Research 37:D26–D31.

**Burke, V.** 1930. Revision of the fishes of the family Liparidae. Bulletin of the United States National Museum 150:i–xii, 1–204.

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

**Chernova, N. V., and R. Thiel.** 2024. First capture of the deep-sea *Careproctus bathycoetus* (Liparidae) a century after the fish was described (North Pacific)—revised diagnosis and notes on ecology. Taxonomy 4:748–760.

**Chernova, N., R. Thiel, and I. Eidus.** 2020. Four new species of *Careproctus* (Cottoidei: Liparidae) from the deep-water vicinity of the southern Kuril Islands (Western North Pacific). Zootaxa 4821:71–87.

**Chernova, N. V., E. V. Vedischeva, and A. V. Datskii.** 2021. A new species of snailfishes (Liparidae) of the genus *Careproctus* from the Northern Slope of the Aleutin [sic] Basin (Bering Sea). Journal of Ichthyology 61:487–495.

**Collins, M. A., I. G. Priede, S. Addison, A. Smith, and P. M. Bagley.** 1998. Acoustic tracking of the dispersal of organic matter by scavenging fishes in the deep-sea. Hydrobiologia 371:181–186.

**Duhamel, G.** 1992. Descriptions d'espèces nouvelles de *Careproctus* et *Paraliparis* et données nouvelles sur ces genres et le genre *Edentoliparis* de l'océan Austral (Cyclopteridae, Liparinae). Cybium 16:183–207.

**Duhamel, G., and N. King.** 2007. Deep-sea snailfish (Scorpaeniformes: Liparidae) of genera *Careproctus* and *Paraliparis* from the Crozet Basin (Southern Ocean). Cybium 31:379–387.

**Edgar, R. C.** 2004. MUSCLE: multiple sequence alignment with high accuracy and high throughput. Nucleic Acids Research 32:1792–1797.

**Fedorov, A., R. Beichel, J. Kalpathy-Cramer, J. Finet, J.-C. Fillion-Robin, S. Pujol, C. Bauer, D. Jennings, F. Fennessy, M. Sonka, J. Buatti, S. Aylward, J. V. Miller, S. Pieper, and R. Kikinis.** 2012. 3D Slicer as an image computing platform for the quantitative imaging network. Magnetic Resonance Imaging 30:1323–1341.

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

**Fricke, R., W. N. Eschmeyer, and R. Van der Laan (Eds.).** 2024. Eschmeyer's Catalog of Fishes: Genera, Species, References. https://researcharchive.calacademy.org/research/ichthyology/catalog/fishcatmain.asp (Electronic version accessed 1 August 2024).

**Fujii, T., A. J. Jamieson, M. Solan, P. M. Bagley, and I. G. Priede.** 2010. A large aggregation of liparids at 7703 meters and a reappraisal of the abundance and diversity of hadal fish. BioScience 60:506–515.

**Gaither, M. R., B. Violi, H. W. I. Gray, F. Neat, J. C. Drazen, R. D. Grubbs, A. Roa-Varón, T. Sutton, and A. R. Hoelzel.** 2016. Depth as a driver of evolution in the deep sea: insights from grenadiers (Gadiformes: Macrouridae) of the genus *Coryphaenoides*. Molecular Phylogenetics and Evolution 104:73–82.

**Gardner, J. R., J. W. Orr, and L. Tornabene.** 2023. Two new species of snailfishes (Cottiformes: Liparidae) from the Aleutian Islands, Alaska, and a redescription of the closely related *Careproctus candidus*. Ichthyology & Herpetology 111:54–71.

**Gerringer, M. E.** 2019. On the success of the hadal snailfishes. Integrative Organismal Biology 1:obz004.

**Gerringer, M. E., A. H. Andrews, G. R. Huss, K. Nagashima, B. N. Popp, T. D. Linley, N. D. Gallo, M. R. Clark, A. J. Jamieson, and J. C. Drazen.** 2018. Life history of abyssal and hadal fishes from otolith growth zones and oxygen isotopic compositions. Deep Sea Research Part I: Oceanographic Research Papers 132:37–50.

**Gerringer, M. E., J. C. Drazen, and P. H. Yancey.** 2017a. Metabolic enzyme activities of abyssal and hadal fishes: pressure effects and a re-evaluation of depth-related changes. Deep Sea Research Part I: Oceanographic Research Papers 125:135–146.

**Gerringer, M. E., T. D. Linley, A. J. Jamieson, E. Goetze, and J. C. Drazen.** 2017b. *Pseudoliparis swirei* sp. nov.: a newly-discovered hadal snailfish (Scorpaeniformes: Liparidae) from the Mariana Trench. Zootaxa 4358:161–177.

**Gerringer, M. E., T. D. Linley, and J. G. Nielsen.** 2021. Revision of the depth record of bony fishes with notes on hadal snailfishes (Liparidae, Scorpaeniformes) and cusk eels (Ophidiidae, Ophidiiformes). Marine Biology 168:167.

**Gerringer, M. E., B. N. Popp, T. D. Linley, A. J. Jamieson, and J. C. Drazen.** 2017c. Comparative feeding ecology of abyssal and hadal fishes through stomach content and amino acid isotope analysis. Deep Sea Research Part I: Oceanographic Research Papers 121:110–120.

**Gerringer, M. E., P. H. Yancey, O. V. Tikhonova, N. E. Vavilov, V. G. Zgoda, and D. R. Davydov.** 2020. Pressure tolerance of deep-sea enzymes can be evolved through increasing volume changes in protein transitions: a study with lactate dehydrogenases from abyssal and hadal fishes. The FEBS Journal 287:5394–5410.

**Gilbert, C. H.** 1915. Fishes collected by the United States fisheries steamer "Albatross" in Southern California in 1904. Proceedings of the U.S. National Museum 48:305–380.

**Gilbert, C. H., and C. V. Burke.** 1912. Fishes from Bering Sea and Kamchatka. Bulletin of the Bureau of Fisheries 30:31–96.

**Jamieson, A. J., T. D. Linley, S. Eigler, and T. Macdonald.** 2021. A global assessment of fishes at lower abyssal and upper hadal depths (5000 to 8000 m). Deep Sea Research Part I: Oceanographic Research Papers 178:103642.

**Jamieson, A. J., P. J. Maroni, T. Bond, Y. Niyazi, J. Kolbusz, P. Arasu, and H. Kitazato.** 2023. New maximum depth record for bony fish: Teleostei, Scorpaeniformes, Liparidae (8336 m, Izu-Ogasawara Trench). Deep Sea Research Part I: Oceanographic Research Papers 199:104132.

**Jamieson, A. J., and P. H. Yancey.** 2012. On the validity of the Trieste flatfish: dispelling the myth. Biological Bulletin 222:171–175.

**Kai, Y., H. Endo, F. Tashiro, and N. Nakayama.** 2021. Two new species of snailfishes of the genus *Careproctus* (Cottoidei: Liparidae) from the western North Pacific Ocean with a range extension of *Careproctus brevipectoralis*. Zootaxa 4951:361–371.

**Kai, Y., and K. Matsuzaki.** 2020. *Careproctus longidigitus*, a new snailfish (Liparidae) from the southern Sea of Okhotsk. Ichthyological Research 67:133–138.

**Kai, Y., E. Morikawa, and R. Misawa.** 2024. *Careproctus io* (Teleostei: Liparidae), a new snailfish from the western North Pacific, with comments on generic limits. Species Diversity 29:111–117.

**Kai, Y., K. Murasaki, R. Misawa, A. Fukui, E. Morikawa, and Y. Narimatsu.** 2020. A new species of snailfish of the genus *Paraliparis* (Liparidae) from the western North Pacific, with redescriptions of the poorly known species *Paraliparis mandibularis*. ZooKeys 968:143–159.

**Kai, Y., A. Tohkairin, K. Fujiwara, and T. Hamatsu.** 2018. *Careproctus iacchus*, a new variegated snailfish (Liparidae) from the Seas of Japan and Okhotsk. Ichthyological Research 65:417–422.

**Letunic, I., and P. Bork.** 2021. Interactive Tree of Life (iTOL) v5: an online tool for phylogenetic tree display and annotation. Nucleic Acids Research 49:W293–W296.

**Linley, T. D., M. E. Gerringer, H. Ritchie, J. N. J. Weston, A. Scott-Murray, V. Fernandez, J. Canto-Hernández, F. Wenzhöfer, R. N. Glud, and A. J. Jamieson.** 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 52:56.

**Linley, T. D., M. E. Gerringer, P. H. Yancey, J. C. Drazen, C. L. Weinstock, and A. J. Jamieson.** 2016. Fishes of the hadal zone including new species, *in situ* observations and depth records of Liparidae. Deep Sea Research Part I: Oceanographic Research Papers 114:99–110.

**Machi, K., T. Nobetsu, and M. Yabe.** 2012. *Careproctus rausuensis*, a new liparid fish (Percomorphacea: Cottiformes), collected from Hokkaido, Japan. Bulletin of the National Museum of Nature and Science Series A Zoology, Suppl. 6:33–40.

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

**Matsuzaki, K., T. Mori, M. Kamiunten, T. Yanagimoto, and Y. Kai.** 2020. A new species of *Careproctus* (Cottoidei: Liparidae) from the Sea of Okhotsk and a redescription of the blacktip snailfish *Careproctus zachirus*. Ichthyological Research 67:399–407.

**McWilliam, H., W. Li, M. Uludag, S. Squizzato, Y. M. Park, N. Buso, A. P. Cowley, and R. Lopez.** 2013. Analysis tool web services from the EMBL-EBI. Nucleic Acids Research 41:597–600.

**Mori, T., K. Matsuzaki, Y. Kai, and F. Tashiro.** 2024. *Careproctus rhomboides*, a new snailfish (Cottoidei: Liparidae) from the western North Pacific. Ichthyological Research 72:29–37.

**Mu, Y., C. Bian, R. Liu, Y. Wang, G. Shao, J. Li, Y. Qiu, T. He, W. Li, J. Ao, Q. Shi, and X. Chen.** 2021. Whole genome sequencing of a snailfish from the Yap Trench (~7,000 m) clarifies the molecular mechanisms underlying adaptation to the deep sea. PLoS Genetics 17:1–25.

**Murasaki, K., Y. Kai, H. Endo, and A. Fukui.** 2022. A new snailfish of the genus *Careproctus* (Cottoidei: Liparidae) from the Pacific coast of southern Japan. Ichthyological Research 70:225–232.

**Murasaki, K., M. Takami, and A. Fukui.** 2017. *Careproctus surugaensis* sp. nov. (Liparidae), a new snailfish from Suruga Trough, Japan. Ichthyological Research 65:237–244.

**Murasaki, K., M. Takami, and A. Fukui.** 2018. *Paraliparis ruficometes* sp. nov. (Liparidae), a new snailfish from Suruga Trough, Japan. Ichthyological Research 66:88–96.

**Murasaki, K., M. Takami, and A. Fukui.** 2019. *Paraliparis variabilidens*, a new snailfish (Liparidae) from the Suruga Trough, Japan. Ichthyological Research 66:509–514.

**Murasaki, K., M. Takami, and A. Fukui.** 2020. *Paraliparis hokuto*, a new snailfish (Cottoidei: Liparidae) from Suruga Bay, Japan, and a new record of the rare species *Paraliparis atramentatus* Gilbert and Burke 1912. Ichthyological Research 67:167–175.

**Nielsen, J. G.** 1964. Fishes from depths exceeding 6000 meters. Galathea Report 7:113–124.

**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 2012:257–265.

**Orr, J. W.** 2016. Two new species of snailfishes of the genus *Careproctus* (Liparidae) from the Aleutian Islands, Alaska. Copeia 104:890–896.

**Orr, J. W.** 2020. A new snailfish of the genus *Careproctus* (Cottiformes: Liparidae) from the Beaufort Sea. Copeia 108:815–819.

**Orr, J. W.** 2021. Three new small snailfishes of the genus *Careproctus* (Teleostei: Cottiformes: Liparidae) from the Aleutian Islands, Alaska. Ichthyology & Herpetology 109:456–466.

**Orr, J. W., and K. P. Maslenikov.** 2007. Two new variegated snailfishes of the genus *Careproctus* (Teleostei: Scorpaeniformes: Liparidae) from the Aleutian Islands, Alaska. Copeia 2007:699–710.

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

**Orr, J. W., I. Spies, D. E. Stevenson, G. C. Longo, Y. Kai, S. Ghods, and M. Hollowed.** 2019. Molecular phylogenetics of snailfishes (Cottoidei: Liparidae) based on MtDNA and RADseq genomic analyses, with comments on selected morphological characters. Zootaxa 4642:1–79.

**Pante, E., and B. Simon-Bouhet.** 2013. marmap: a package for importing, plotting and analyzing bathymetric and topographic data in R. PLoS ONE 8:e73051.

**Paradis, E., and K. Schliep.** 2019. ape 5.0: an environment for modern phylogenetics and evolutionary analyses in R. Bioinformatics 35:526–528.

**Priede, I. G., P. M. Bagley, J. D. Armstrong, K. L. Smith Jr., and N. R. Merrett.** 1991. Direct measurement of active dispersal of food-falls by deep-sea demersal fishes. Nature 351:647–649.

**Priede, I. G., J. C. Drazen, D. M. Bailey, L. A. Kuhnz, and D. Fabian.** 2020. Abyssal demersal fishes recorded at station M (34°50′N, 123°00′W, 4100 m depth) in the northeast Pacific Ocean: an annotated check list and synthesis. Deep Sea Research Part II: Topical Studies in Oceanography 173:104648.

**Priede, I. G., K. L. Smith Jr., and J. D. Armstrong.** 1990. Foraging behaviour of abyssal grenadier fish: inferences from acoustic tagging and tracking in the North Pacific Ocean. Deep Sea Research Part A. Oceanographic Research Papers 37:81–101.

**R Core Team.** 2024. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/

**Ratnasingham, S., and P. D. N. Hebert.** 2007. BOLD: The Barcode of Life Data System (www.barcodinglife.org). Molecular Ecology Notes 7:355–364.

**Sabaj, M. H.** 2020. Codes for natural history collections in ichthyology and herpetology. Copeia 108:593–669.

**Schliep, K. P.** 2011. phangorn: phylogenetic analysis in R. Bioinformatics 27:592–593.

**Smith, K. L., Jr., and E. R. M. Druffel.** 1998. Long time-series monitoring of an abyssal site in the NE Pacific. Deep Sea Research Part II: Topical Studies in Oceanography 45:573–586.

**Stein, D. L.** 1978. A review of the deepwater Liparidae (Pisces) from the coast of Oregon and adjacent waters. Occasional Papers of the California Academy of Sciences 127:1–55.

**Stein, D. L.** 2012. A review of the snailfishes (Liparidae, Scorpaeniformes) of New Zealand, including descriptions of a new genus and sixteen new species. Zootaxa 54:1–54.

**Stein, D. L., N. Chernova, and A. P. Andriashev.** 2001. Snailfishes (Pisces: Liparidae) of Australia, including descriptions of thirty new species. Records of the Australian Museum 53:341–406.

**Stein, D. L., and J. C. Drazen.** 2014. *Paraliparis hawaiiensis*, a new species of snailfish (Scorpaeniformes: Liparidae) and the first described from the Hawaiian Archipelago. Journal of Fish Biology 84:1519–1526.

**Stein, D. L., J. C. Drazen, K. L. Schlining, J. P. Barry, and L. Kuhnz.** 2006. Snailfishes of the central California coast: video, photographic and morphological observations. Journal of Fish Biology 69:970–986.

**Taylor, W. R.** 1967a. An enzyme method of clearing and staining small vertebrates. Proceedings of the United States National Museum 122:1–17.

**Taylor, W. R.** 1967b. Outline of a method of clearing and staining tissues with pancreatic enzymes and staining bones of small vertebrates. Turtox News 45:308–309.

**Wang, K., Y. Shen, Y. Yang, X. Gan, G. Liu, K. Hu, Y. Li, Z. Gao, L. Zhu, G. Yan, L. He, X. Shan, L. Yang, S. Lu … S. He.** 2019. Morphology and genome of a snailfish from the Mariana Trench provide insights into deep-sea adaptation. Nature Ecology & Evolution 3:823–833.

**Waterhouse, A. M., J. B. Procter, D. M. A. Martin, M. Clamp, and G. J. Barton.** 2009. Jalview Version 2—a multiple sequence alignment editor and analysis workbench. Bioinformatics 25:1189–1191.

**Yancey, P. H., M. E. Gerringer, J. C. Drazen, A. A. Rowden, and A. J. Jamieson.** 2014. Marine fish may be biochemically constrained from inhabiting the deepest ocean depths. Proceedings of the National Academy of Sciences of the United States of America 111:4461–4465.