

Received: 25 September 2025 • Accepted: 21 July 2026 • Published: 24 September 2026

Topic editor: Magalie Castelin • Section editor: Thierry Backeljau • Desk editor: Kristiaan Hoedemakers

Monograph

urn:lsid:zoobank.org:pub:8EB8471F-B5E1-4142-97FD-C569D2F26E5F

Molluscs associated with a cold seep on the Mtwara Mud Volcano off Tanzania (Mollusca: Gastropoda and Bivalvia)

Leon HOFFMAN^{1,*}  , André FREIWALD²  , Jara WESTBEEK³  ,
Kai PFENNINGS⁴  , Peter SHUNULA⁵  , Saleh YAHYA⁶   & Terue C. KIHARA⁷  

^{1,2,4} Marine Research Department, Senckenberg am Meer, Südstrand 40, Wilhelmshaven, Germany.

³ NBC Naturalis, Darwinweg 2, Leiden, the Netherlands.

^{5,6} Deep Sea Fishing Authority (DSFA), Fumba, Zanzibar, Tanzania.

⁷ Integrated Environmental Solutions (INES) UG, Südstrand 44, Wilhelmshaven, Germany.

* Corresponding author: Leon.Hoffman@Senckenberg.de

² Email: André.Freiwald@Senckenberg.de

³ Email: beyaflor2001@gmail.com

⁴ Email: Kai.Pfennings@Senckenberg.de

⁵ Email: pshunula20@gmail.com

⁶ Email: saleh_y@yahoo.com

⁷ Email: Terue.Kihara@ines-solutions.eu

Abstract. Molluscs living in cold seep habitats often exhibit adaptations to extreme environmental conditions like high concentrations of oil, methane, hydrogen sulphide, heavy metals, and high acidity. This paper reports on the mollusc fauna encountered on the Mtwara Mud Volcano (MV) with a crestal cold seep, which was discovered off Tanzania during the cruise SO306 by the German RV *Sonne* in 2024. Living specimens of the cold seep fauna include the bivalve *Gigantidas tanzaniensis* Hoffman, Westbeek & Kihara sp. nov., and the gastropods *Bathyacmaea nipponica* Okutani, Tsuchida & Fujikura, 1992, *Eatoniella kahawa* Hoffman sp. nov., *Provanna castanea* Hoffman & Kihara sp. nov., *Provanna mzunguko* Hoffman sp. nov., and *Enigmaticolus nipponensis* (Okutani & Fujiwara, 2000). Empty shells of species belonging to cold seep fauna include the bivalves *Gigantidas komekahawia* Hoffman, Pfennings & Freiwald sp. nov., *Lucinoma mviringo* Hoffman sp. nov., *Calyptogena pemba* Hoffman, Pfennings & Freiwald sp. nov., *Isorropodon mtwaraense* Hoffman sp. nov., and *Isorropodon cowioae* Hoffman sp. nov. A number of gastropods with, most likely, a large distribution along the east African margin were found as well: *Puncturella mrembo* Hoffman sp. nov., *P. alternata* Hoffman sp. nov., *Fissurisepta kilimanjaro* Hoffman sp. nov., *Cornisepta infundibulus* Hoffman sp. nov., *Anatoma agulhasensis* (Thiele, 1925), *A. japonica* (Adams, 1862), *A. chaki* Hoffman sp. nov., *Satondella goudi* Geiger, 2012, *Sinezona macleani* Geiger, 2006, *Toroidia marisindica* Hoffman sp. nov., *Skenea kitovu* Hoffman sp. nov., *Seamountiella laini* Hoffman sp. nov., *Cerithiella kupamba* Hoffman sp. nov., and *Pedicypraedia stylasteriophila* Hoffman, Pfennings & Freiwald sp. nov. At species level, most of the molluscan taxa at the Mtwara MV are different from those reported from other cold seep locations.

Two exceptions are the gastropods *Bathymacmaea nipponica* and *Enigmaticolus nipponensis*, both were originally described from cold seeps off Japan and their distributions are herein extended to the continental slope off Tanzania.

Keywords. South-West Indian Ocean, upper bathyal, Mollusca, taxonomy, new species.

Hoffman L., Freiwald A., Westbeek J., Pfennings K., Shunula P., Yahya S. & Kihara T.C. 2026. Molluscs associated with a cold seep on the Mtwara Mud Volcano off Tanzania (Mollusca: Gastropoda and Bivalvia). *European Journal of Taxonomy* 1099: 1–85. <https://doi.org/10.5852/ejt.2026.1099.3330>

Introduction

The sea floor on continental slopes around the world provides numerous habitats for marine life. Often these habitats are formed as a result of geological processes in the subsurface. For example, exposed rock formations on the sea floor provide substrates for sessile fauna like anthozoans and sponges, and diverging or submerging plate margins create hydrothermal vents with specific fauna that solely thrive in these hostile environments. Mud volcanos are also common geological structures that occur on land and on the sea floor as a result of upward forces in the subsurface. At the sea bottom, small hills of soft sediments and hard rocks are formed where the rock formations at the sea bottom are breached and subsequently pushed up; these are referred to as mud volcanos. When mud volcanos are formed in areas where hydrocarbons are being generated in the subsurface then these locations form a leak path for hydrocarbons (oil and hydrocarbon gases) to the sea (Judd & Hovland 2007). These natural hydrocarbon leaks are often referred to as cold seeps. Specialised bacteria, which are often present in the sea floor sediments, are able to convert oil and natural gases into energy and nutrients by alkane- and sulphide-oxidation processes (Judd & Hovland 2007). Some bacteria often occur as mats or thin foils on the sea floor and provide food for grazing gastropods. At seep settings, many invertebrates host sulphide and methane oxidising bacteria and the resulting chemosymbiosis is obligate in the siboglinid worms *Eteima* Jones, 1985 and *Lamellibrachia* Webb, 1969 (siboglinid worms). Similarly, some (sub)families of Bivalvia Linnaeus, 1758 are chemosymbiotic and are frequently represented in the fauna of cold seeps, for example Solemyidae Gray, 1840, Bathymodiolineae Kenk & Wilson, 1985, Lucinidae Fleming, 1828, Thyasiridae Dall, 1900 (1895), and Pliocardiinae Woodring, 1925. Some species of Bathymodiolineae and Pliocardiinae are known to harbour methane- as well as sulphide-oxidising bacteria (Olu *et al.* 1997, 2004; Laming *et al.* 2018).

Warén & Bouchet (1993, 2001, 2009) provided major overviews of gastropods from cold seeps from the Atlantic, Pacific and Arctic Oceans. An extensive record of live-collected macrofauna, including 81 named mollusc species, from cold seeps in the eastern Pacific Ocean at depths of 300–3600 m off western Costa Rica was given by Seid *et al.* (2025). Cordes *et al.* (2009) discuss the live-collected macrofauna of seeps in the northern Gulf of Mexico; their studies placed particular emphasis to bivalve species of the (sub)families Bathymodiolineae, Vesicomyidae Dall & Simpson, 1901 and Lucinidae. Little *et al.* (2025) described a complete inventory of a Late Pleistocene mollusc fauna from upper bathyal cold seep habitats off SE India (Bay of Bengal, northern Indian Ocean).

A cold seep was encountered at the crest of a mud volcano (Mtwara MV) off Tanzania during cruise SO306 by the German RV *Sonne* in August 2024 with a crestal depth of about 860 m (Hebbeln & Wienberg 2024). Dense populations of bivalves (subfamily Bathymodiolineae) were found during ROV surveys as well as other associated fauna like vesicomyids (Bivalvia), pectinodontids, provannids and eosiphonids (Gastropoda Cuvier, 1795). Increased concentrations of gases were found in the water column above the mud volcano (Hebbeln & Wienberg 2024). In this study we make an inventory of gastropods and bivalves found on the Mtwara MV off Tanzania and compare our cold seep species composition with those encountered with those in other cold seeps. The analytical methods include morphological studies and analyses of the mitochondrial DNA (*COI*).

Material and methods

Material and sampling methods

During SO306, three ROV dives and four box cores (area 0.25 m²) were completed on the Mtwara MV, offshore Tanzania, SW Indian Ocean at depths of 861–915 m; see Fig. 1 and Table 1.

Live specimens as well as empty shells were collected by ROV manipulators as well as in box cores. Soft tissues of live-collected specimens were preserved in 96% ethanol to enable molecular analyses. In addition, some live-collected specimens were preserved in 5% formalin, which was buffered with borax. These samples were used for morphological studies of the soft tissues. Specimens herein refer to live-collected individuals, shells refer to empty shells of dead gastropods or bivalves, valves refer to single valves of bivalves.

The sediments obtained by box core or ROV were sieved and fractions over 0.5 mm retained, whereas smaller sediment fractions were discarded. The sieved fractions were strained in fresh water to remove salt and dried in an oven at 50°C in excess of 24 hours. The dried fractions were hand sorted at Senckenberg am Meer in Wilhelmshaven (SaM), Germany.

Live specimens of large species (like *Gigantidas* Cosel & Marshall, 2003) were hand sorted on board. Due to shipping restrictions, hundreds of specimens of *Gigantidas* were cleaned on board, and their shells dried and packed for morphometric analyses at SaM. About 50 specimens were preserved in 96% ethanol for genetic analyses; about 50 specimens were shipped in a 5% formalin solution to enable study of soft parts. Some specimens of *Gigantidas* were dissected for genetic samples (from the posterior muscle stored in 96% ethanol) and morphological study of soft part (stored in a 5% formalin-seawater-

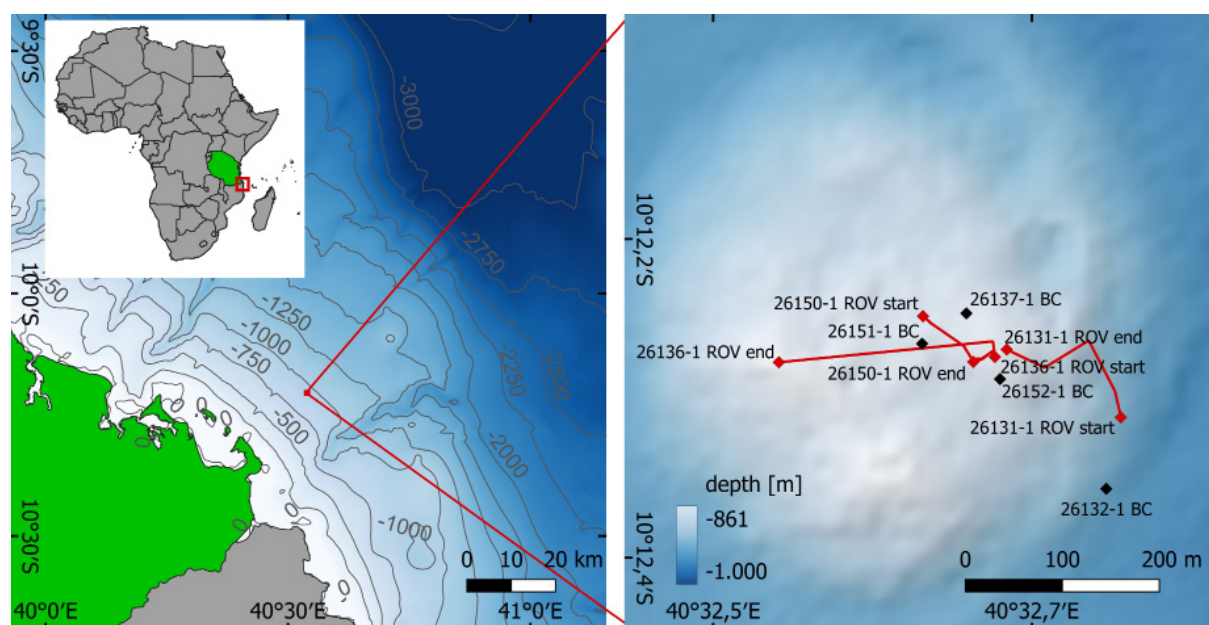


Fig. 1. Sampling locations on the Mtwara Mud Volcano off Tanzania during SO306 (August 2024). Bathymetry data by GEBCO (General Bathymetric Chart of the Oceans). Left, location of Mtwara MV off SE Tanzania. Right, bathymetry map of Mtwara MV with sampling locations as listed in Table 1; ROV cruises indicated with red lines, box cores indicated with black dots.

Table 1. Samples from the Mtwara Mud Volcano off Tanzania during SO306 (August 2024). Coordinates are given in degrees (South and East) and digital minutes. ROV samples were obtained by a manipulator arm, occasionally with the help of a scoop net. Box core (BC) recovery is indicated by the penetration depth in the sea bed, i.e., the height of the sample in the box core.

Station GeoB	Date	Latitude (S)	Longitude (E)	Water depth [m]	Recovery
26131-1 ROV start	19 Aug. 2024	10°12.485'	40°32.724'	906	17 samples
26131-1 ROV end	19 Aug. 2024	10°12.396'	40°32.816'	873	
26132-1 BC	19 Aug. 2024	10°12.321'	40°32.742'	915	28 cm
26136-1 ROV start	20 Aug. 2024	10°12.521'	40°32.747'	878	18 samples
26136-1 ROV end	20 Aug. 2024	10°12.478'	40°32.793'	863	
26137-1 BC	20 Aug. 2024	10°12.222'	40°32.663'	868	10–20 cm
26150-1 ROV start	23 Aug. 2024	10°12.521'	40°32.747'	873	4 samples
26150-1 ROV end	23 Aug. 2024	10°12.478'	40°32.793'	861	
26151-1 BC	23 Aug. 2024	10°12.239'	40°32.638'	866	9–26 cm
26152-1 BC	23 Aug. 2024	10°12.259'	40°32.682'	867	39 cm

borax solution). Large numbers of three small live-collected gastropods were taken in bulk samples of decaying byssus and periostracum and they were preserved in 96% ethanol.

Molecular methods

Sequences of a mitochondrial DNA marker (cytochrome c oxidase subunit 1, *COI*) were established at the German Centre for Biodiversity Research (DZMB) department at SaM. We selected *COI* because the specific analysis is facilitated by many accessible *COI* sequences of congeneric species in the public data bases BOLD (Barcode of Life Data systems) and GenBank.

DNA extraction was carried out using Chelex 100 (BIO-RAD: InstaGene Matrix 732-6030; Walsh *et al.* 2013), a resin-based medium. About 5 µl of soft tissue was immersed in 30 µl of Chelex and activated for 30 min at 56°C, followed by a chemical deactivation for 10 min at 99°C. PCR reactions were conducted using an Eppendorf Mastercycler Pro S (Eppendorf, Hamburg, Germany) and each PCR reaction contained: 13.0 µl of AccuStart II PCR ToughMix (2X) (QuantaBio, Beverly, MA, USA), 9.0 µl of highly purified water, 0.5 µl of each primer (10 pmol/µl) and 2.0 µl of DNA template in a mixture of total 25.0 µl. Primers designed to target *COI* sequences of marine invertebrates and Bathymodiolinae-specific primers were used and listed in Table 2.

The amplification conditions consisted of an initial denaturation step of 3 min at 94°C, followed by 40 cycles of 30 s denaturation at 94°C, 45 s annealing at 45°C, and 45 s elongation at 72°C, followed by a final extension step of 2 min at 72°C.

Two µl of the amplified products were visualised after electrophoresis on 1% agarose gels and the reactions which produced bands were sent to be sequenced in both directions by Macrogen (Amsterdam, Netherlands) using M13 sequence tails (Table 2).

Double stranded sequences were assembled and checked with Geneious Prime® 2025.1.3 (<http://www.geneious.com>; Kearse *et al.* 2012). *COI* sequences were aligned using MAFFT (Katoh *et al.* 2005) in Geneious Prime® 2025.1.3 (<http://www.geneious.com>; Kearse *et al.* 2012) and alignments were further edited manually. Sequences were translated into amino acids prior to any analysis, to ensure that no gaps or stop codons were present in the alignment. Species identification was performed using the BLAST search from Geneious Prime® 2025.1.3 (<http://www.geneious.com>; Camacho *et al.* 2009;

Table 2. List of primer pairs and tails used for amplification and sequencing *COI* from the 5' to 3' end, including related literature.

Primer name	Sequence	References
jgLCO	TITCIACIAAYCAYAARGAYATTGG	Geller <i>et al.</i> 2013
jgHCO	TAIACYTCIGGRTGICCRAARAAYCA	Geller <i>et al.</i> 2013
COIG	GTATTGAATTAGCACGTCCTGGAA	Génio <i>et al.</i> 2008
COIH	TACTATTCCAAACCCGGGTAAAT	Génio <i>et al.</i> 2008
M13FP	TGTAAAACGACGGCCAGT	Schuelke 2000
M13R-pUC	CAGGAAACAGCTATGAC	Messing 1983

Kearse *et al.* 2012) and BOLD system ver. 4 (<https://boldsystems.org/>; Ratnasingham *et al.* 2024) tree-based identification.

Based on the initial species identification through DNA barcoding, partial *COI* datasets of Bathymodiolinae sequences published by Oliver *et al.* (2024) and Pectinodontidae Pilsbry, 1891 sequences listed by Zhang & Zhang (2017) were downloaded from GenBank (Table 3). All sequences were aligned using MAFFT (Katoh *et al.* 2005) in Geneious Prime® 2025.1.3 (<http://www.geneious.com>; Kearse *et al.* 2012) and trimmed to match the start and length of the corresponding baseline barcode sequences from GenBank.

Maximum-likelihood (ML) analyses were performed to assess the phylogenetic relationship of our specimen with the rest of the congeners. The ML tree was obtained using IQ-TREE ver. 3.0.1 (Wong *et al.* 2025) based on the best substitution model determined by the ModelFinder module (Kalyaanamoorthy *et al.* 2017) under the BIC criterion. Node support was assessed with 1000 ultrafast bootstrapping replicates (uBS). IQ-TREE analyses were performed using R packages “ape” (Paradis & Schliep 2019), “seqinr” (Charif & Lobry 2007), “treeio” (Wang *et al.* 2020) and “ggtree” (Yu *et al.* 2017).

The genetic distance values were calculated using a neighbour-joining (NJ) analysis with the Kimura-2-parameter (K2P) evolutionary model (Kimura 1980) and *p*-distance using R packages “ape” (Paradis & Schliep 2019), “seqinr” (Charif & Lobry 2007), “phangorn” (Schliep 2011) and “ggtree” (Yu *et al.* 2017) with the pairwise deletion option. The topology of ML and NJ rooted trees were visualised and edited using FigTree ver. 1.4.4 (Rambaut & Drummond 2009) and ITOL: Interactive Tree of Life (<https://itol.embl.de/itol.cgi>; Letunic & Bork 2024).

Imaging methods

Selected specimens of small species were imaged in colour using a digital confocal microscope (Keyence VHX-2000, magnification 20–200×). Stacked images were combined using the Keyence software. Size measurements were done using the internally calibrated Keyence software. Alternatively, for specimens larger than 1 mm, stacked images were made using a conventional digital camera set up. High resolution images were taken using a scanning electron microscope (SEM; Vega3 Tescan) using high-vacuum and incident-electron energy of 10 keV. Both secondary electron- and back-scatter electron imaging were used. The SEM samples were coated with gold to improve imaging quality.

Data and sample retention

Sequences were deposited in GenBank (<https://www.ncbi.nlm.nih.gov/genbank/>; Sayers *et al.* 2025) under accession numbers: *COI* – PX935462 to PX935484. Additional relevant specimen information, taxonomic classifications, photos, DNA barcodes, used primer pairs and trace files were uploaded to BOLD system ver. 4 (<https://boldsystems.org/>; Ratnasingham *et al.* 2024), project “TANZ - Gastropods and Bivalves associated with cold seeps on the Mtwara mud volcano off Tanzania” in the public dataset

Table 3 (continued on next page). List of *COI* sequences from GenBank used for the molecular analyses in this study. Species name, GenBank accession number and reference are given.

Species	Authorship	Accession number	Reference
<i>Bathymodiolus septemdierum</i>	Hashimoto & Okutani, 1994	AP014562	Ozawa <i>et al.</i> 2017
<i>Bathymodiolus thermophilus</i>	Kenk & Wilson, 1985	KU597626	Assié <i>et al.</i> 2016
<i>Gigantidas childressi</i>	(Gustafson, Turner, Lutz & Vrijenhoek, 1998)	KU597636	Assié <i>et al.</i> 2016
<i>Gigantidas gladius</i>	Cosel & Marshall, 2003	AY608426	Smith <i>et al.</i> 2004
<i>Gigantidas haimaensis</i>	Xu, Feng, Tao & Qiu, 2019	MK534977	Xu <i>et al.</i> 2019
<i>Gigantidas horikoshii</i>	Hashimoto & Yamane, 2005	HF545113	Lorion <i>et al.</i> 2013
<i>Gigantidas mauritanicus</i>	(Cosel, 2002)	FJ890502	Lorion <i>et al.</i> 2010
<i>Gigantidas niobengalensis</i>	Oliver, Gonsalves, Samuel & Garzia, 2024	ON964868	Oliver <i>et al.</i> 2024
<i>Gigantidas platifrons</i>	(Hashimoto & Okutani, 1994)	KU975036	Xu <i>et al.</i> 2017
<i>Gigantidas taiwanensis</i>	(Cosel, 2008)	GU966638	Lorion <i>et al.</i> 2010
<i>Gigantidas tangaroa</i>	(Cosel & Marshall, 2003)	AY608439	Smith <i>et al.</i> 2004
<i>Gigantidas tanzaniensis</i>	Hoffman, Westbeek & Kihara sp. nov.	PX935462	Present study
<i>Gigantidas tanzaniensis</i>	Hoffman, Westbeek & Kihara sp. nov.	PX935463	Present study
<i>Gigantidas tanzaniensis</i>	Hoffman, Westbeek & Kihara sp. nov.	PX935464	Present study
<i>Gigantidas tanzaniensis</i>	Hoffman, Westbeek & Kihara sp. nov.	PX935465	Present study
<i>Gigantidas tanzaniensis</i>	Hoffman, Westbeek & Kihara sp. nov.	PX935466	Present study
<i>Gigantidas tanzaniensis</i>	Hoffman, Westbeek & Kihara sp. nov.	PX935467	Present study
<i>Gigantidas tanzaniensis</i>	Hoffman, Westbeek & Kihara sp. nov.	PX935468	Present study
<i>Gigantidas tanzaniensis</i>	Hoffman, Westbeek & Kihara sp. nov.	PX935469	Present study
<i>Gigantidas tanzaniensis</i>	Hoffman, Westbeek & Kihara sp. nov.	PX935470	Present study
<i>Gigantidas tanzaniensis</i>	Hoffman, Westbeek & Kihara sp. nov.	PX935471	Present study
<i>Gigantidas tanzaniensis</i>	Hoffman, Westbeek & Kihara sp. nov.	PX935472	Present study
<i>Gigantidas tanzaniensis</i>	Hoffman, Westbeek & Kihara sp. nov.	PX935473	Present study
<i>Gigantidas tanzaniensis</i>	Hoffman, Westbeek & Kihara sp. nov.	PX935474	Present study
<i>Gigantidas tanzaniensis</i>	Hoffman, Westbeek & Kihara sp. nov.	PX935475	Present study
<i>Gigantidas vrijenhoeki</i>	Jang, Ho, Jun, Kim & Won, 2020	MN136491	Jang <i>et al.</i> 2020
<i>Bathymacrea becki</i>	Zhang & Zhang, 2017	MG253685	Zhang & Zhang 2017
<i>Bathymacrea lactea</i>	Zhang, Zhang & Zhang, 2016	MG253686	Zhang & Zhang 2017
<i>Bathymacrea levinae</i>	Betters, Cortés & Cordes, 2024	OQ644584	Betters <i>et al.</i> 2024
<i>Bathymacrea nipponica</i>	Sasaki, Okutani & Fujikura, 1992	AB238588	Nakano & Ozawa 2007
<i>Bathymacrea nipponica</i>	Sasaki, Okutani & Fujikura, 1992	PX935476	Present study
<i>Bathymacrea nipponica</i>	Sasaki, Okutani & Fujikura, 1992	PX935477	Present study
<i>Bathymacrea nipponica</i>	Sasaki, Okutani & Fujikura, 1992	PX935478	Present study
<i>Bathymacrea nipponica</i>	Sasaki, Okutani & Fujikura, 1992	PX935479	Present study
<i>Bathymacrea nipponica</i>	Sasaki, Okutani & Fujikura, 1992	PX935480	Present study
<i>Bathymacrea nipponica</i>	Sasaki, Okutani & Fujikura, 1992	PX935481	Present study
<i>Pectinodonta aupouria</i>	Marshall, 1985	KC990591	Marshall <i>et al.</i> 2016
<i>Pectinodonta marinovichi</i>	Marshall, 1998	KC990594	Marshall <i>et al.</i> 2016
<i>Pectinodonta orientalis</i>	Schepman, 1908	KC970665	Marshall <i>et al.</i> 2016
<i>Pectinodonta rhyssa</i>	(Dall, 1925)	AB238589	Nakano & Ozawa 2007
<i>Paralepetopsis</i> sp. SWA-2009		FJ977752	Aktipis & Giribet 2010

Table 3 (continued). List of *COI* sequences from GenBank used for the molecular analyses in this study. Species name, GenBank accession number and reference are given.

Species	Authorship	Accession number	Reference
<i>Buccinum undatum</i>	Linnaeus, 1758	FN677402	Barco <i>et al.</i> 2010
<i>Calagrassor aldermenensis</i>	(Powell, 1971)	KC756035	Kantor <i>et al.</i> 2013
<i>Calagrassor hespericus</i>	Fraussen & Stahlschmidt, 2016	MW077007	Kantor <i>et al.</i> 2022
<i>Calagrassor tashiensis</i>	(Lee & Lan, 2002)	MW077011	Kantor <i>et al.</i> 2022
<i>Manaria brevicaudata</i>	(Schepman, 1911)	KC756050	Kantor <i>et al.</i> 2013
<i>Manaria kuroharai</i>	Azuma, 1960	MN752196	Kantor <i>et al.</i> 2020
<i>Manaria clandestina</i>	Bouchet & Warén, 1986	KC756056	Kantor <i>et al.</i> 2013
<i>Eclectofusus dedonderi</i>	(Fraussen & Hadorn, 2001)	MW076984	Kantor <i>et al.</i> 2022
<i>Eclectofusus fluentisonus</i>	(Fraussen & Stahlschmidt, 2016)	MW076991	Kantor <i>et al.</i> 2022
<i>Eosipho smithi</i>	(Schepman, 1911)	JQ950198	Kantor <i>et al.</i> 2012
<i>Enigmaticolus desbruyeresi</i>	(Okutani & Ohta, 1993)	MT894134	Chen <i>et al.</i> 2020
<i>Enigmaticolus nipponensis</i>	(Okutani & Fujiwara, 2000)	KC756033	Kantor <i>et al.</i> 2013
<i>Enigmaticolus nipponensis</i>	(Okutani & Fujiwara, 2000)	MN102347	Zhang <i>et al.</i> 2020
<i>Enigmaticolus nipponensis</i>	(Okutani & Fujiwara, 2000)	MT894131	Chen <i>et al.</i> 2020
<i>Enigmaticolus nipponensis</i>	(Okutani & Fujiwara, 2000)	PX935482	Present study
<i>Enigmaticolus nipponensis</i>	(Okutani & Fujiwara, 2000)	PX935483	Present study
<i>Enigmaticolus nipponensis</i>	(Okutani & Fujiwara, 2000)	PX935484	Present study
<i>Enigmaticolus nipponensis</i>	(Okutani & Fujiwara, 2000)	KC756034	Kantor <i>et al.</i> 2013
<i>Enigmaticolus nipponensis</i>	(Okutani & Fujiwara, 2000)	MT772320	Zhao <i>et al.</i> 2020
<i>Enigmaticolus nipponensis</i>	(Okutani & Fujiwara, 2000)	MT894133	Chen <i>et al.</i> 2020
<i>Enigmaticolus nipponensis</i>	(Okutani & Fujiwara, 2000)	MT894132	Chen <i>et al.</i> 2020
<i>Thermosipho auzendei</i>	(Warén & Bouchet, 2001)	KC687075	Kantor <i>et al.</i> 2013
<i>Gaillaea coriolis</i>	(Bouchet & Warén, 1986)	KC756066	Kantor <i>et al.</i> 2013

“<https://portal.boldsystems.org/recordset/DS-TANZ2025>”. Type materials (shells, ethanol samples) were stored in Senckenberg Naturmuseum, Frankfurt am Main, Germany. A subset of paratypes from location GeoB 26152-1 were stored in the Museum of New Zealand, Wellington, New Zealand; the associated specimens are indicated by museum codes starting with M.

Abbreviations

Institutional abbreviations

- GeoB = Geological sampling location in University of Bremen, Bremen, Germany
 DZMB = Deutsches Zentrum für Marine Biodiversitätsforschung, Wilhelmshaven, Germany
 M = Museum of New Zealand, Wellington, New Zealand
 SaM = Senckenberg am Meer, Wilhelmshaven, Germany
 SMF = Senckenberg Museum Frankfurt, Frankfurt am Main, Germany

Morphological abbreviations

- H = height of gastropod/bivalve shell
 L = length of bivalve shell (mm)
 T = tumidity of bivalve shell (mm)
 W = width of gastropod shell (mm)

Sampling abbreviations

BC = (video) box core (0.5 × 0.5 m)
COI = cytochrome c oxidase subunit 1, genetic marker in mitochondrial DNA
DNA = deoxyribonucleic acid, complex chemical compound with coded genetic sequences
ROV = remotely operated vehicle
stn = station

Results

Class Bivalvia Linnaeus, 1758
Order Mytilida Férussac, 1822
Superfamily Mytiloidea Rafinesque, 1815
Family Modiolidae Termier & Termier, 1950

Genus *Gigantidas* Cosel & Marshall, 2003

Type species

Gigantidas gladius Cosel & Marshall, 2003 by original designation. New Zealand, SW Pacific Ocean, Recent (Cosel & Marshall 2003: 37–45).

Gigantidas tanzaniensis Hoffman, Westbeek & Kihara sp. nov.
urn:lsid:zoobank.org:act:26C9FD7F-82C9-4A3A-B84A-DAAE58426641
Figs 2–6

Diagnosis

Large oblong, elongated, thin modioliform shell, wedge shaped, broadly rounded posterior, dorsal ligament margin long straight, ventral margin slightly concave, anterior narrowly rounded, subterminal umbos, shell colour light beige, exterior with dark brown periostracum. Maximum length 85 mm, maximum height 45 mm, maximum tumidity 38 mm. For adult specimens, height to length ratio 0.50, tumidity to length ratio 0.40 (Fig. 4).

Etymology

Named after Tanzania (*tanzaniensis* = feminine subjective; Latinised).

Type material

Holotype

SW INDIAN OCEAN – **Mtwara MV, off Tanzania** • live-collected specimen; 10°12.396' S, 40°32.816' E; 873 m depth; 19 Aug. 2024; stn SO306 / GeoB 26131-1-14; SMF 376545 (Fig. 2A–C).

Paratypes

SW INDIAN OCEAN – **Mtwara MV, off Tanzania** • 4 live-collected specimens; same data as for holotype; soft tissue in 5% formalin and DNA-grade samples in 96% ethanol; SMF 376548–376550, SMF 376617 • 5 live-collected specimens; stn SO306 / GeoB 26131-1-15; soft tissue in 5% formalin and DNA-grade samples in 96% ethanol; SMF 376551–376553 • 2 live-collected specimens; stn SO306 / GeoB 26137-1; SMF 376554 • 332 empty shells of live-collected specimens; stn SO306 / GeoB 26152-1; SMF 376546, SMF 376618 • 18 live-collected specimens; same locality data; juveniles in 96% ethanol; SMF 376547, SMF 376629 • 150 live-collected specimens; same locality data; M.342061.

Other material examined

SW INDIAN OCEAN – **Mtwara MV, off Tanzania** • 100+ valves; stn SO306 / GeoB 26152-1; SaM 87723 • 100+ valves; stn SO306 / GeoB 26137-1; SaM 87724.

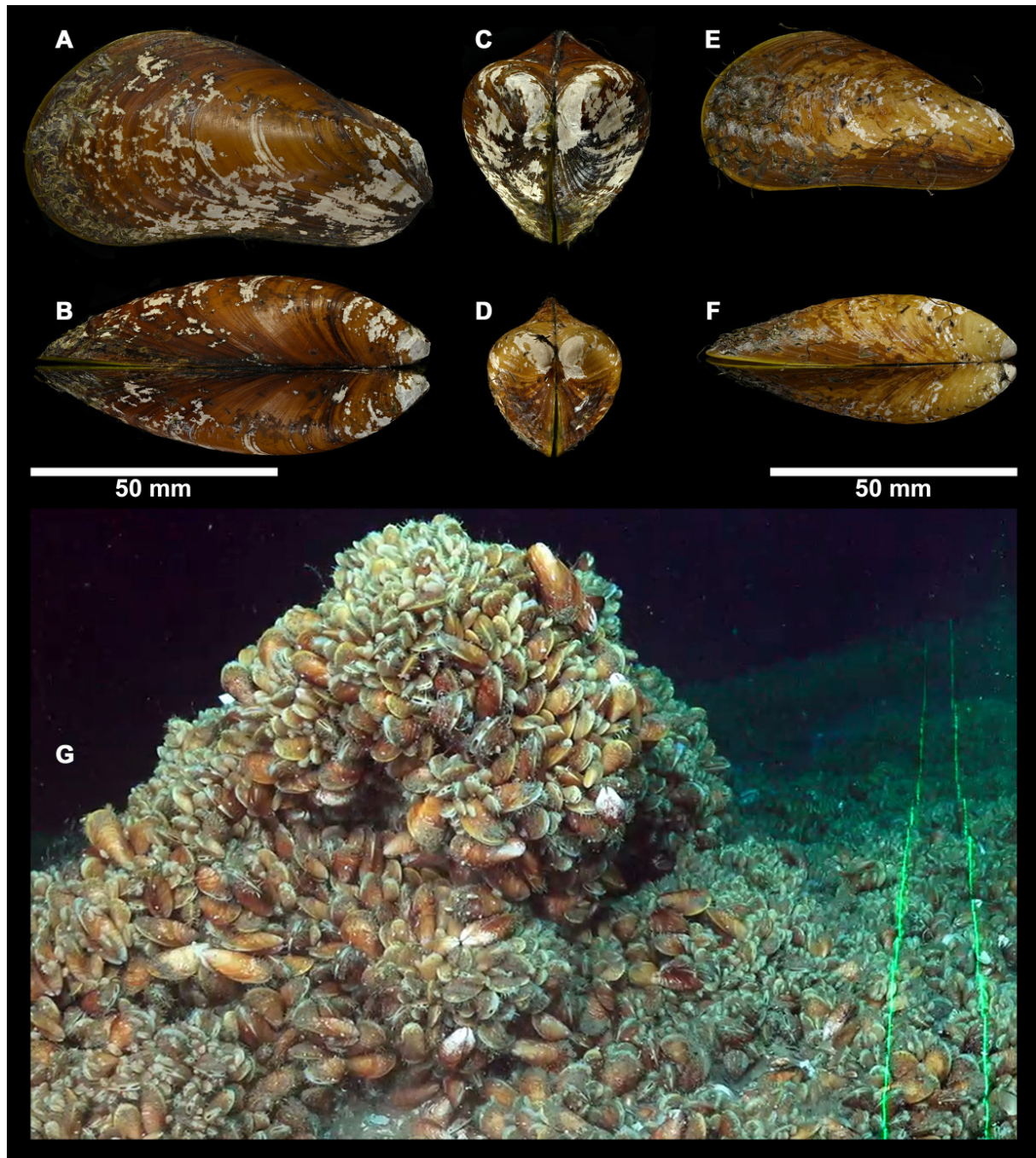


Fig. 2. *Gigantidas tanzaniensis* Hoffman, Westbeek & Kihara sp. nov., Tanzania, Mtwara Mud Volcano, SO306. **A–F.** GeoB26131-14 ROV. **A–C.** Holotype (SMF 376545), L=85 mm, H=44 mm, T=38 mm. **D–F.** Paratype (SMF 376548), same location, L=63 mm, H=33 mm, T=26 mm. **G.** GeoB26131 ROV, 885 m, dense population of *G. tanzaniensis* on an exposed rock and on the sea bottom. Laser guides at 10 cm width.

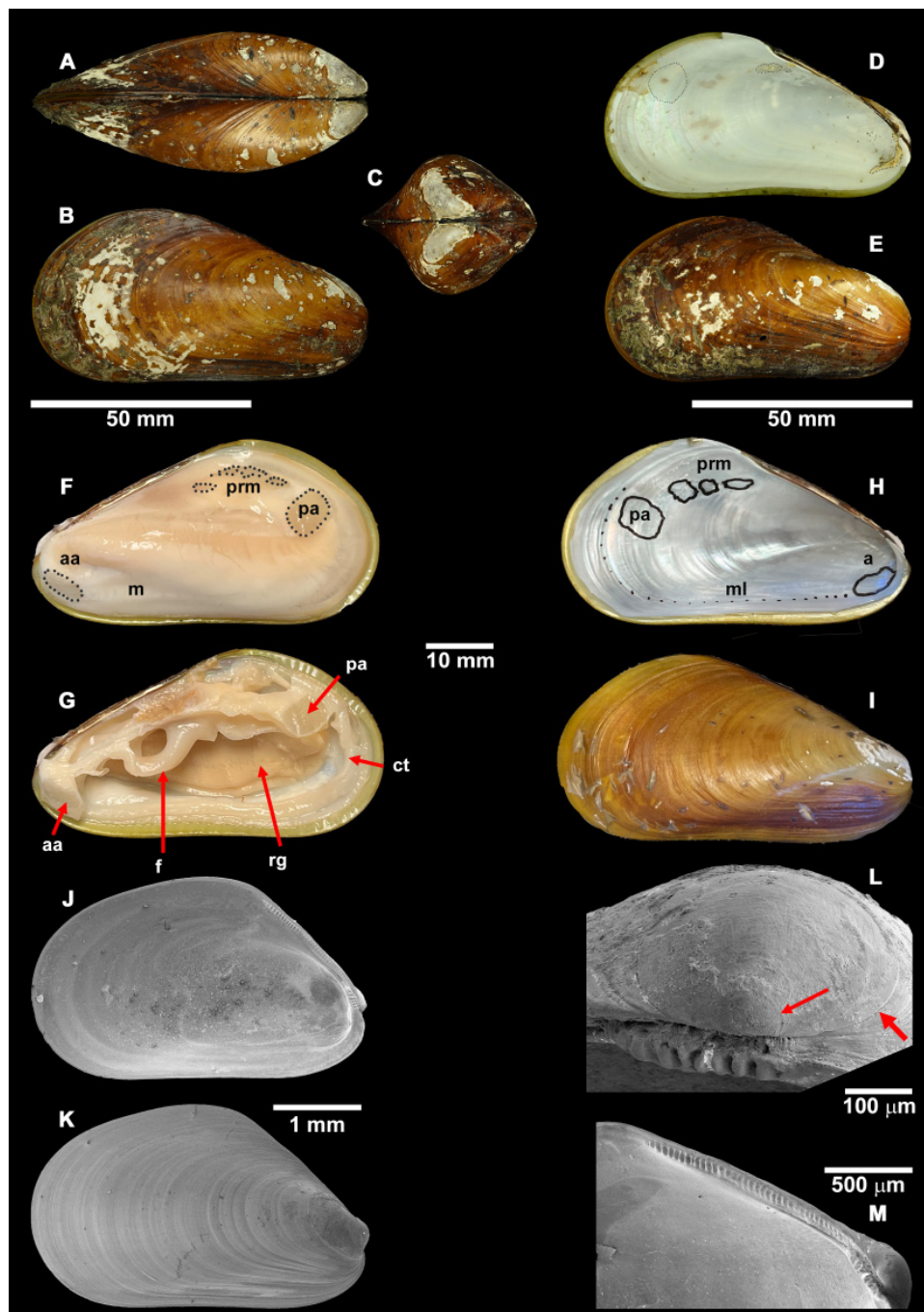


Fig. 3. *Gigantidas tanzaniensis* Hoffman, Westbeek & Kihara sp. nov., Tanzania, Mtwara Mud Volcano, SO306 A–C. Paratype (SMF 376618) GeoB26152-1. **A.** Dorsal view. **B.** Right view. **C.** Umbonal view, L=75 mm, H=40 mm, T=32 mm. **D–E.** Paratype, same locality, internal left valve, external right valve, L=70 mm, H=38 mm. **F–I.** Paratype (SMF 376550) GeoB26131-1-14 ROV. **F.** Soft parts with muscles penetrating mantle from left side. **G.** Left mantle and gill removed. **H.** Muscle imprints in left valve. **I.** External view right valve, L=53 mm, H=28 mm. **J–K.** Paratype (SMF 376629) GeoB26152-1, juvenile specimen, L=3.7 mm, H=2.3 mm. **L–M.** Paratype (SMF 376629) same locality. **L.** Prodissoconch-1 L=110 μ m (thin arrow), prodissoconch-2 L=400 μ m (thick arrow). **M.** Internal view of umbo and hinge line with dyssodont teeth. Abbreviations: aa=anterior adductor muscle; ct=ctenidium; f=foot with groove posteriorly; m=mantle; ml=mantle line; pa=posterior adductor muscle; prm=pedal retractory muscles; rg=right gill.

Description

PRODISSOCONCH. In two planktonic stages, only visible in juveniles (< 4 mm), eroded in larger specimens. Stage 1 with ovate, flattened valves, truncated dorsally, equivalve, equilateral; rough chaotic sculpture; length 110 μm , height 70 μm . Stage 2 more tumid, ovate, equivalve, equilateral; smooth with fine commarginal growth lines; length 400 μm (Fig. 3L).

DISSOCONCH. Externally smooth with fine commarginal growth lines. Outline modioliform; dorsal (ligament) margin straight along long, narrow external dark brown ligament inserted along the entire dorsal margin, weakly convex towards posterior; posterior broadly expanded, rounded; ventral margin slightly concave. Umbos subterminal, anterior area protruding slightly. Umbonal view with convex ridge from umbo to posterior-ventral margin, concave at anterior-ventral shell face. Periostracum and shell usually eroded at umbos. Interior shell, nacreous, smooth, with weak imprints of muscle scars. Posterior adductor muscle scar behind ligament, below margin, rounded. Anterior muscle scar placed on steep margin near umbonal cavity. Three separated pedal/byssus retractor muscle scars on posterior dorsal area. Anterior and dorsal margins thin, blunt. Posterior and ventral margins sharp. All margins excluding ligament covered by smooth, matt, dark brown periostracum, often covered with byssus threads. Juvenile specimens (< 4 mm) with higher posterior-dorsal outline; internally with a short set of dyssodont teeth below the umbo and a second set along the full posterior-dorsal margin (Fig. 3M).

SOFT PARTS. Light beige; gills and muscles slightly darker. Foot moderately developed, byssal gland small with about ten dark brown byssus threads. Mantle thin translucent, raised near margin, lined

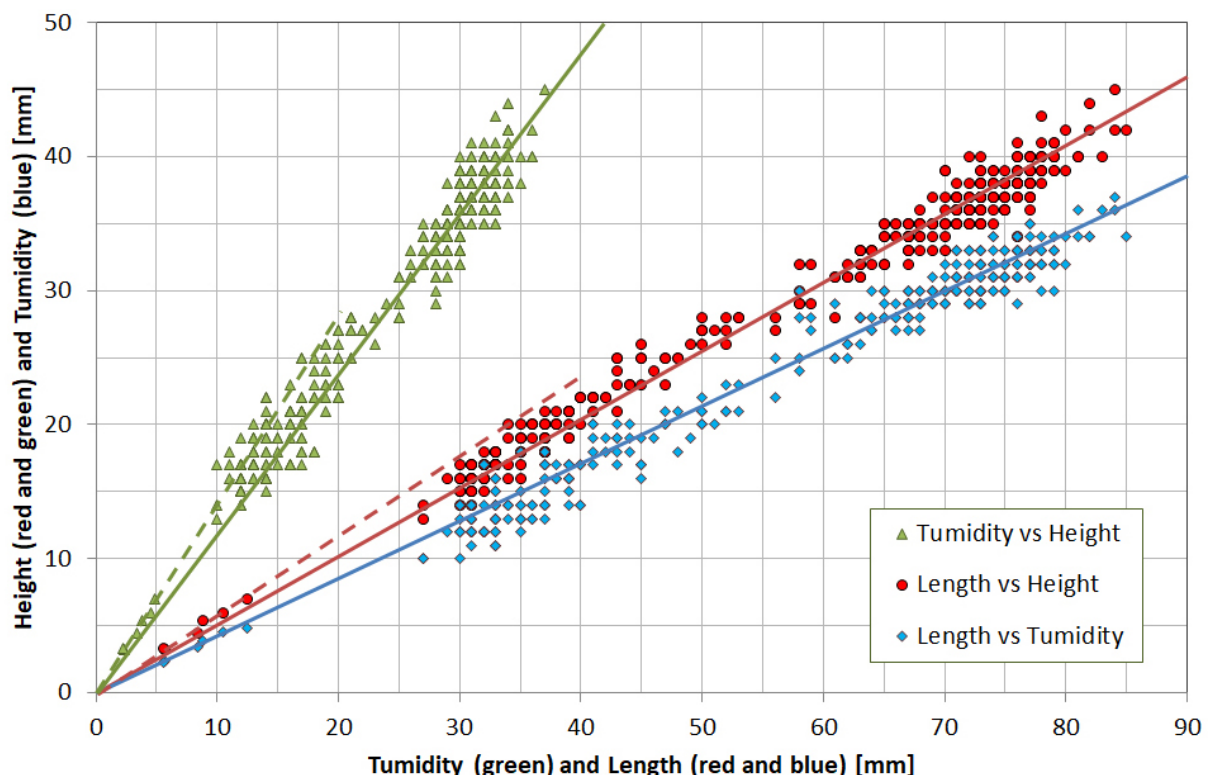


Fig. 4. *Gigantidas tanzaniensis* Hoffman, Westbeek & Kihara sp. nov., shell dimensions of live-collected specimens, SO306 / GeoB26152-1, off Tanzania. Shell length versus width indicated with red line and symbols; length versus tumidity in blue; tumidity versus height in green. Dashed lines refer to juvenile trends; solid lines to adult trends. Note that specimens with length less than 30 mm are poorly sampled. Number of specimens: 342.

with tentacles; separate posterior-ventral inhalant and posterior-dorsal exhalant openings. Large, oval, posterior adductor muscle behind ligament; smaller curved anterior adductor muscle near anterior margin opposite of umbo. Dorsally, a symmetrical network of thin muscles connecting to small scars on the valves on either end of the ligament. Posteriorly, a set of muscles connecting to the base of the byssal gland. Two posterior muscle sets link to a thickened node. Anteriorly, two thin muscles from each valve, opposite (dorsally) of the anterior muscle connect to the thickened node, which is connected with a muscle to the base of the foot (Fig. 3F–G).

VARIATION. Shell morphology is moderately variable (see Figs 2–3), a range in length to height ratio is 1.9–2.1 and length to tumidity ratio 2.2–2.9. Juvenile specimens (< 10 mm) appear to be less elongated with a significantly lower length to height ratio of 1.5–2.0 (Fig. 4).

Habitat

The species was found in dense populations (observed > 4000 specimens/m²) exposed near the crest of the mud volcano.

Molecular analyses

A total of 14 high-quality sequences of *COI* were obtained (Table 3) with a fragment size of 602 bp, no indels or stop codons were found. Overall mean nucleotide frequencies were G (21.4%), C (15.3%), A (21.8%) and T (41.5%) The ML analyses confirmed that the species here studied belongs to the genus *Gigantidas* (Fig. 5). Genetic distance values (Fig. 6) show 0% of intraspecific divergence and

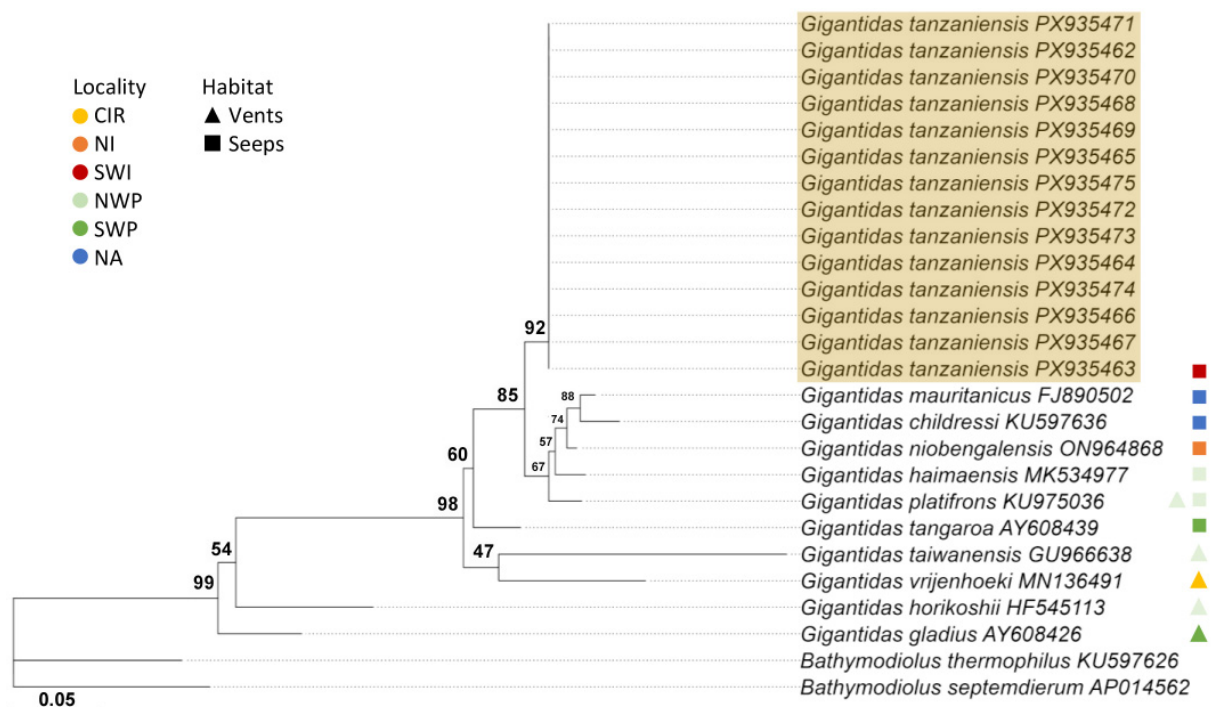


Fig. 5. Maximum-likelihood phylogenetic tree of *Gigantidas* Cosel & Marshall, 2003 based on *COI* sequences with *Bathymodiolus thermophilus* Kenk & Wilson, 1985 and *Bathymodiolus septemdierum* Hashimoto & Okutani, 1994 as outgroups. The GenBank accession numbers are added following species names. The new species is highlighted in dark yellow. Numbers at branches indicate ultrafast bootstrap support. The scale bar shows substitutions per site. Coloured circles indicate the locality: CIR=Central Indian Ridge; NA=Northern Atlantic; NI=Northern Indian Ocean; NW=Northwest Pacific; SW=Southwest Pacific; SWI=Southwest Indian Ocean. Habitat: vents represented by triangles and seeps by squares.

interspecific divergences ranging between 3.8 and 14.7% (K2P), and 3.7 and 13.0% (*p*-distance). The nearest known species is *Gigantidas platifrons* (Hashimoto & Okutani, 1994).

Differential diagnosis

The species is placed in the genus *Gigantidas* based on similarity of its mtDNA (*COI*) sequences with known congeners. The significant interspecific divergence of more than 3.5%, the morphological differences as well as their biogeographic isolation are considered adequate evidence to distinguish the present species from its nearest congeners *G. platifrons* from cold seeps in the NW Pacific Ocean and *G. mauritanicus* (Cosel, 2002) from the NE Atlantic Ocean. Both congeners have anterior umbos and have a length to height ratio of about 2, but they have a convex dorsal margin behind the umbo. *Gigantidas niobengalensis* Oliver, Gonsalves, Samuel & Garzia, 2024 from methane seeps in the Krishna-Godavari Basin, Bay of Bengal has a similar morphology but has a truncated posterior dorsal

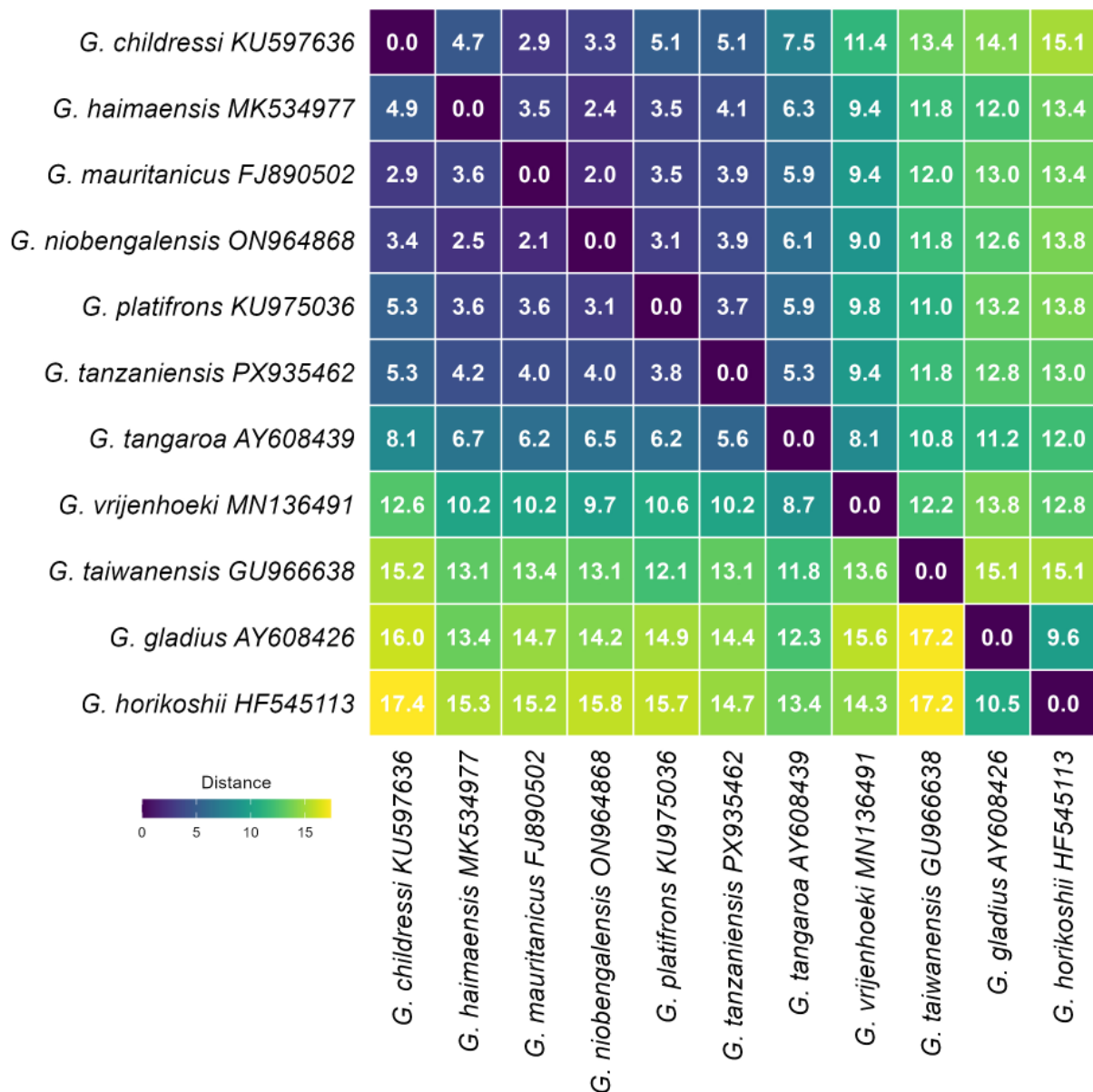


Fig. 6. Heatmap of interspecific genetic distance percentages between species of *Gigantidas* Cosel & Marshall, 2003 in *COI* (K2P: lower-left; *p*-distance: upper-right).

margin and is much larger (up to 161 mm) than *G. tanzaniensis* sp. nov. (up to 85 mm) which has a convex posterior dorsal margin; the divergence between the *COI* sequences of the species is 4.0%. *Gigantidas haimaensis* Xu, Feng, Tao & Qiu, 2019 from cold seeps in the South China Sea is also similar; again, the morphological differences to the present species are marginal, but the *COI* divergence is 4% and the biogeographic separation is large.

Gigantidas komekahawia Hoffman, Pfennings & Freiwald sp. nov.
urn:lsid:zoobank.org:act:94129408-8928-49A3-AE59-FFA128C94578

Fig. 7

Diagnosis

Large oblong, elongated, thin modioliform shell, most convex anteriorly; umbos on anterior-dorsal margin at about 20% of anterior margin, wide, flattened. Equivalve, inequilateral. Shell colour light beige, exteriorly covered in brown or dark brown periostracum. Maximum length 105 mm, maximum height 35 mm, length to height ratio 3.0.

Etymology

‘*Kome kahawia*’ (noun in apposition) means ‘brown mussel’ in Swahili.

Type material

Holotype

SW INDIAN OCEAN – **Mtwara MV, off Tanzania** • left valve; 10°12.321' S, 40°32.742' E; 915 m depth; 19 Aug. 2024; stn SO306 / GeoB 26132-1; video box core; SMF 376555 (Fig. 7A–B).

Paratypes

SW INDIAN OCEAN – **Mtwara MV, off Tanzania** • 6 valves (fragmentary, 4 RV, 2 LV); same data as for holotype; SMF 376556 (Fig. 7C–D) • 1 left valve; stn SO306 / GeoB 26136-1-10; SMF 376557.

Description

PRODISSOCONCH. Characteristics are unknown.

DISSOCONCH. Sculpture with fine commarginal growth lines. Outline in external side view; long posterior dorsal margin, weakly convex, straightened along ligament; anterior dorsal margin short and concave. Anterior end, subcircular, most convex; posterior end obliquely truncated at dorsal margin, widely convex towards ventral margin. Ventral margin long and concave. Face of valve flattened anteriorly and ventrally; long, broad, curved ridge from umbos towards posterior-ventral margin. Internally smooth with a commarginal, broad ventral line, large posterior and smaller anterior adductor muscle scars. Along internal dorsal margin inconspicuous small muscle scars.

VARIABILITY. Smaller valves have a thin shell with straightened ventral margin. Muscle scars are similar within the type set.

Differential diagnosis

Placement in the genus *Gigantidas* is based on the morphological similarity with the type species *G. gladius* Cosel & B.A. Marshall, 2003 from hydrothermal vents off New Zealand. The type species has both squat and elongate forms, which are genetically and anatomically similar and adult specimens are much larger (300 mm) with more extended anterior margin and more concave ventral margin; its habitat (hydrothermal vent) is different than that of the current species (cold seep). Other similar

species include *G. tangaroa* (Cosel & Marshall, 2003) from cold seeps off New Zealand, *G. vrijenhoeki* Jang, Ho, Jun, Kim & Won, 2020 from hydrothermal vents of the central Indian Ocean, *G. horikoshii* Hashimoto & Yamane, 2005 from hydrothermal vents off southern Japan, *G. samario* Cosel & Gracia, 2018 from hydrocarbon seeps off the Caribbean coast of Colombia. *Gigantidas komekahawia* sp. nov. has a distinctly separate biogeographical distribution from these known congeners. *Gigantidas tangaroa* has a similar outline with anterior bulge and concave ventral margin, brown to black colour of the periostracum and also lives in cold seeps, but its shells are thicker and the posterior-ventral margin is less convex when compared to the present species. *Gigantidas horikoshii* has a similar outline, but its shells are more tumid when compared to *G. komekahawia* and its habitat (hydrothermal vents) is different to the current species (cold seep). *Gigantidas samario* also lives in a cold seep habitat but it lacks the strong anterior bulge and has its umbo near the anterior end; the present species has the anterior bulge and its umbo is placed at 20% of the anterior margin. *Gigantidas vrijenhoeki* lives in hydrothermal vents and has its umbo placed at about 10% of the anterior margin and its ventral margin is strongly concave; the present species lives in cold seeps, and has its umbo more centrally and the concavity of the ventral margin is moderate. Other species of *Gigantidas* have an outline similar to species of *Bathymodiolus* Kenk & Wilson, 1985 with the umbo near the anterior end and a weakly concave or straight ventral margin.



Fig. 7. *Gigantidas komekahawia* Hoffman, Pfennings & Freiwald sp. nov., Tanzania, Mtwara Mud Volcano, SO306. **A–B.** Holotype (SMF 376555), GeoB26132-1, left valve, L=105 mm, H=33 mm. **C–D.** Paratype (SMF 376556), same locality, right valve, L=68 mm, H=23 mm. **E.** GeoB26136-1-10 ROV, left valve, L=95 mm, H=35 mm.

Order: Lucinida Gray, 1854
Superfamily Lucinoidea Fleming, 1828
Family Lucinidae Fleming, 1828

Genus *Lucinoma* Dall, 1901

Type species

Lucina filosa Stimpson, 1851, by original designation, Recent, NW Atlantic Ocean.

Lucinoma mviringo Hoffman sp. nov.

urn:lsid:zoobank.org:act:85434639-1B40-46AE-B1AB-DC5D635D02CA

Fig. 8

Diagnosis

Strong luciniform shell, subcircular, equivalve, subequilateral, flattened valves, most convex anteriorly; subtruncate posteriorly; umbos anterior of midline at about 40% from anterior margin, marginally protruding, pointed, beaks prosogyrate. Shell colour light beige, exteriorly covered with dark olive green periostracum. Observed maximum length 43 mm, maximum height 42 mm, tumidity 20 mm, length lunule 14 mm, length escutcheon 20 mm, length nymph 13 mm, length to height ratio 1.02, length to tumidity ratio 2.1.

Etymology

Circular shape or ‘*mviringo*’ (noun in apposition) in Swahili.

Type material

Holotype

SW INDIAN OCEAN – **Mtwara MV, off Tanzania** • shell; 10°12.222' S, 40°32.663' E; 868 m depth; 19 Aug. 2024; stn SO306 / GeoB 26137-1; video box core; SMF 376558 (Fig. 8).

Paratypes

SW INDIAN OCEAN – **Mtwara MV, off Tanzania** • 3 fragmentary valves; same data as for holotype; SMF 376559.

Description

PRODISSOCONCH. Characteristics are unknown.

DISSOCONCH. Sculpture with irregular, coarse, commarginal growth lines. Outline: protruding umbos ahead of midline, leaning forward; posterior dorsal margin weakly convex, curved along ligament with lanceolate escutcheon; anterior dorsal margin short, straightened lunular margin, lunule conspicuous; anterior end most convex; posterior end obliquely truncated at dorsal margin, widely convex towards ventral semicircular margin. Internally smooth with small umbonal pit, a thin hinge plate with marginal nymph, a narrow ridge at lunular margin. Two cardinal teeth in right valve, the anterior tooth (1) a thin ridge, the central tooth (3) strong and bifurcating, posteriorly a marginal knob on the hinge plate. Left valve with two teeth, one strong anterior tooth (2) and a smaller posterior one (4). Ventral margin smooth and sharp. Large posterior adductor muscle scar; small anterior muscle scar, with long straightened extension obliquely towards the centre of the ventral margin (elongated scar at 30° to midline, scar length/width ratio 5.0). Clear pallial line commarginal between adductor muscles. Aligned traces of the pallial blood vessel scars in the centre of the valve.

Differential diagnosis

Placement in the genus *Lucinoma* is based on the similarity with the type species *L. filosa* and by comparison of species in Taylor & Glover (2021). The type species is larger (60 mm) with more regular growth margins. *Lucinoma gagei* Oliver & Holmes, 2006 was described from an oxygen minimum zone off Ras Madrakah, Oman, at depths of 384–969 m, this species also shows regular commarginal margins but has an inequilateral outline, a weakly concave lunular margin, a protruding, truncated anterior margin, a depression on the posterior-ventral margin, and a single distinct tooth posteriorly above the posterior adductor muscle in both valves (Oliver & Holmes 2006: 65–66, figs 1–10). *Lucinoma mviringo* sp. nov. has a subequilateral outline, lacks the posterior-ventral depression, the lunular margin is straightened and teeth above the anterior teeth are very weak. The irregular commarginal sculpture is also present in *Lucinoma borealis* (Linnaeus, 1758) but that species is thicker and has more inflated valves. *Lucinoma kazani* Salas & Woodside, 2002 from the eastern Mediterranean Sea also has fine irregular commarginal growth margins but it has an angular outline and heavy hinge plates (Salas & Woodside 2002). *Lucinoma apocalyptic* Simone, 2024 was described from Brazil; it has a tumid shell (length to tumidity 1.7), numerous fine, somewhat irregular, commarginal margins, internally with radial markings and heavy hinge plates and teeth (Simone 2024: 86–87, fig. 57). *Lucinoma mviringo* has a similar outline and growth sculpture, but the shell is less tumid (length to tumidity ratio 2.1), it lacks internal radial markings and its hinge plates are thin. The South African *Lucinoma aequale* (Thiele, 1931) is a small (length 12 mm) congener with a similar sculpture and outline but its dorsal margin is obliquely truncated posteriorly and the lunular margin is concave (Thiele & Jaeckel 1931: 63, pl. 9 fig 93); the present species is rounded on the dorsal-posterior margin and its lunular margin is nearly straight.

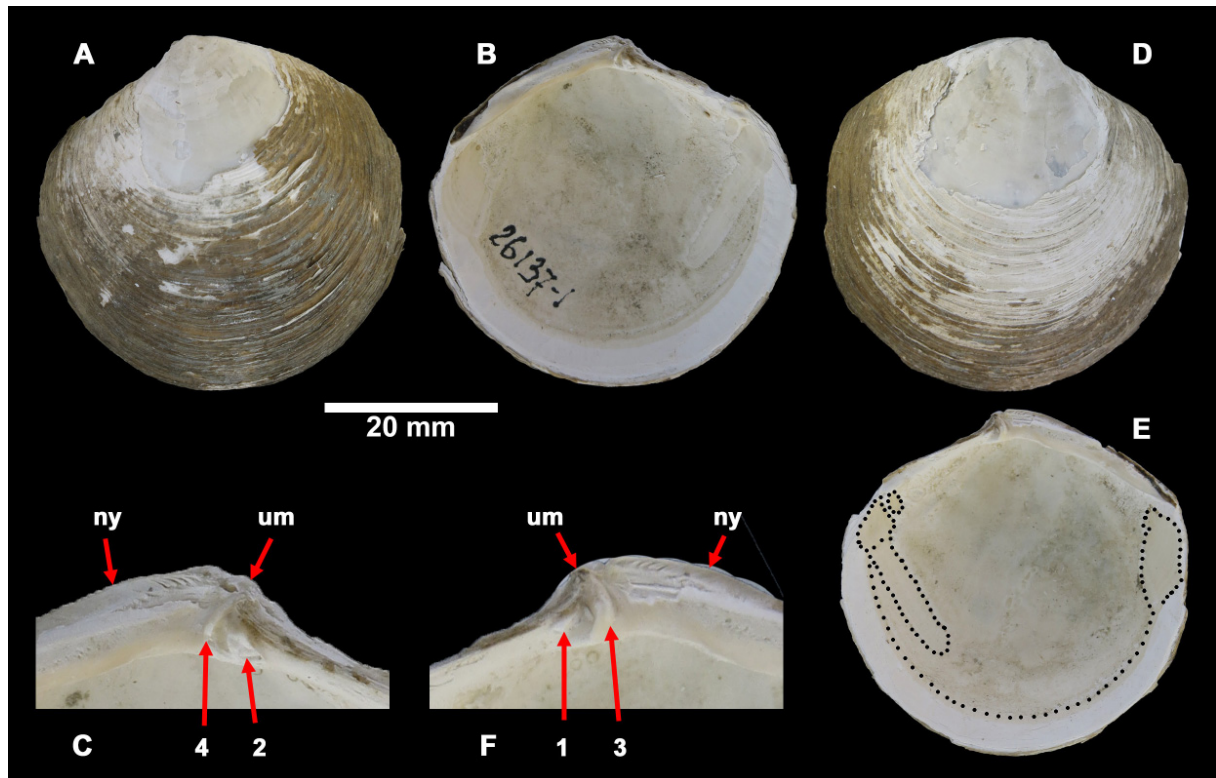


Fig. 8. *Lucinoma mviringo* Hoffman sp. nov., holotype (SMF 376558), Tanzania, Mtwara Mud Volcano, SO306 GeoB26137-1. **A–C.** Left valve. **A.** External view, L=43 mm, H=42 mm. **B.** Internal view. **C.** Hinge with cardinal teeth (2, 4), umbo (um) and nymph (ny). **D–F.** Right valve. **D.** External view. **E.** Internal view with muscle scars and mantle line. **F.** Hinge with cardinal teeth (1, 3), umbo (um) and nymph (ny). Scale bar for A–B, D–E.

Order Venerida Gray, 1854
Superfamily Glossoidea Gray, 1847 (1840)
Family Vesicomysidae Dall & Simpson, 1901

Genus *Calypptogena* Dall, 1891

Type species

Calypptogena pacifica Dall, 1891 by monotypy, Recent, off Alaska, NE Pacific Ocean (Dall 1891: 190).

Calypptogena pemba Hoffman, Pfennings & Freiwald sp. nov.
urn:lsid:zoobank.org:act:5E58434D-66E5-4E1E-B23A-F67D96665D3C
Fig. 9

Diagnosis

Oblong-oval, flattened, thick, strong, vesicomysiform valves; convex, broad weakly protruding umbos, leaning forward anterior of midline at about 25% of dorsal margin. Equivalve, inequilateral. Shell colour beige. Observed maximum length 170 mm, height 81 mm, tumidity 42 mm, escutcheon 77 mm, nymph 56 mm; length to height ratio about 2.1, length to tumidity ratio 4.0.

Etymology

The species is named after Pemba Island, off the Tanzanian mainland (*pemba* as a noun in apposition).

Type material

Holotype

SW INDIAN OCEAN – **Mtwara MV, off Tanzania** • right valve; 10°12.321' S, 40°32.742' E; 915 m depth; 19 Aug. 2024; stn SO306 / GeoB 26132-1; video box core; SMF 376560 (Fig. 9A–C).

Paratypes

SW INDIAN OCEAN – **Mtwara MV, off Tanzania** • 6 left valves; same data as for holotype; SMF 376561 (Fig. 9D–I) • 2 right valves (broken); stn SO306 / GeoB 26137-1; SMF 376562.

Description

PRODISSOCONCH. Characteristics are unknown

DISSOCONCH. Sculpture with irregular, fine, commarginal growth lines. Outline: posterior dorsal margin weakly convex, straightened across escutcheon and ligament; anterior dorsal margin convex; anterior and posterior ends widely convex; ventral margin straightened. Elongated narrow escutcheon, lanceolate; lunule not demarcated. Internally smooth, weak radial ridges from umbo to ventral margin; narrow dorsal ridge anteriorly; posteriorly narrow with strong ridge in left valve and thin margin in right valve. Small pit anterior of umbo with short radiating striae. Posterior of umbo, elongated nymph with ligament groove externally; elongated thin ridges on interior margin of nymph. Lateral teeth lacking. Right valve two elongated large teeth (1 and 3b) in V-shape below umbo, posterior one (3b) bifurcating; anteriorly, small, elongated tooth (3a) parallel to dorsal margin. Left valve three large, elongated teeth, two in V-shape below umbo (2a, 2b), third tooth (4) near posterior margin, long, straight. Ventral margin smooth, thin and blunt. Large, rounded, posterior adductor muscle scar, truncated towards umbo, pedal retractor muscle scar indistinct; smaller, deeply impressed, oval, anterior muscle scar, pedal retractor muscle scar indistinct. Thin ridge under anterior hinge plate demarcating a rough pit below umbo. Clear pallial line

between adductor muscles, commarginal but closer to margin posteriorly. Pallial sinus lacking. Radiating lines on posterior side.

VARIATION. Older specimens develop an anterior bulge, young specimens could be mistaken for species of *Venerupis* Lamarck, 1818 (Veneridae Rafinesque, 1815).

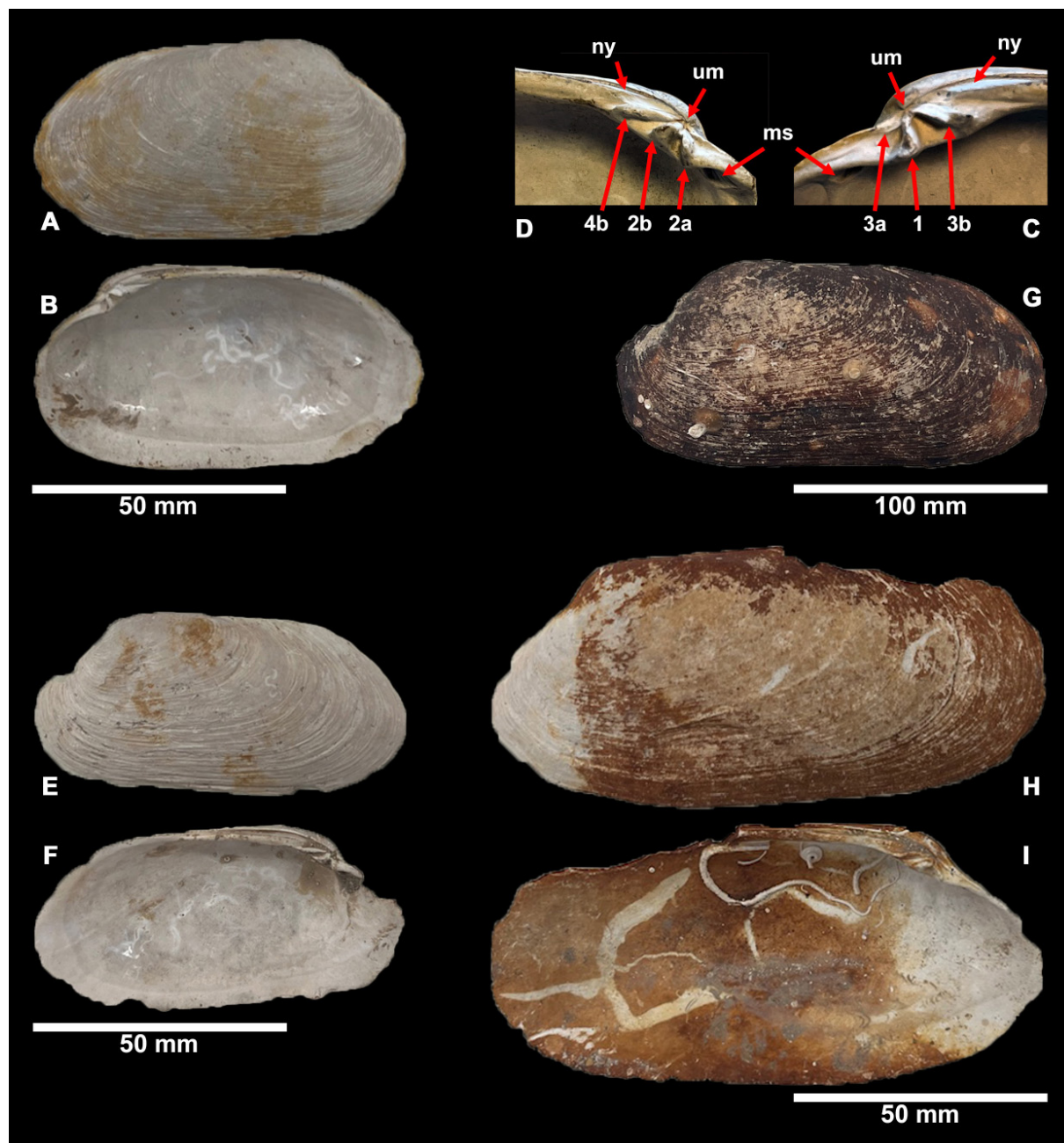


Fig. 9. *Calyptogena pemba* Hoffman, Pfennings & Freiwald sp. nov., Tanzania, Mtwara Mud Volcano, SO306 GeoB26132-1. **A–C.** Holotype (SMF 376560), right valve, L=77 mm, H=41 mm. **A.** External view. **B.** Internal view. **C.** Hinge with cardinal teeth 1, 3a, 3b, umbo (um), nymph (ny), muscle scar (ms). **D–I.** Paratypes (SMF 376561). **D–F.** Paratype, left valve, L=73 mm, H=36 mm. **D.** Hinge with cardinal teeth 2a, 2b and 4b. **E.** External view. **F.** Internal view. **G.** Paratype, left valve, L=170 mm, H=81 mm. **H–I.** Paratype, left valve, L=110 mm, H=52 mm..

Differential diagnosis

Placement in the genus *Calypptogena* Dall, 1891 is based on the similarity with the type species *C. pacifica*. The type species is smaller (40 mm) with a more convex posterior-dorsal margin, relatively thicker valves and stronger hinge plates. The present species is larger (maximum 170 mm), more oblong and less inflated and its hinge plates are thin. Many described species in *Calypptogena* are similar to the type species. The most characteristic differences with most species are thin hinge plates and more delicate teeth whereas most species in *Calypptogena* have stronger hinge plates and teeth (*C. pacifica*, *C. fausta* Okutani, Fujikura & Hashimoto, 1993a, *C. rectimargo* Scarlato, 1981, *C. valdiviae* (Thiele & Jaeckel, 1931), *C. gallardoi* Sellanes & Krylova, 2005, *C. starobogatovi* Krylova & Sahling, 2006). *Calypptogena goffrediae* Krylova & Sahling, 2006 and *C. costaricana* Krylova & Sahling, 2006 have thin hinge plates and weaker teeth but have an oval outline and more protruding umbos (Krylova & Sahling 2006) and *Calypptogena makranensis* Krylova & Sahling, 2006 has a more elongated outline, thin hinge plates and weak widely spreading teeth but has more protruding, pointed umbos (Krylova & Sahling 2006); *Calypptogena pemba* sp. nov. is more inflated and has a more oblong outline and weakly protruding umbos.

Genus *Isorropodon* Sturany, 1896

Type species

Isorropodon perplexus Sturany, 1896 by monotypy, Recent, Red Sea (Sturany 1896: 17), eastern Mediterranean Sea.

Isorropodon mtwaraense Hoffman sp. nov.

urn:lsid:zoobank.org:act:C620FE52-86F8-4190-99BB-C2F6E3BB4929

Fig. 10

Diagnosis

Fragile vesicomyiform shell, oblong-ovate, flattened, thin valves; convex, broadly protruding umbos, leaning forward anterior of midline at about 25% from anterior margin. Equivalve, inequilateral. Shell colour white with thin, light straw-coloured, periostracum. Maximum observed length 43 mm, height 30 mm, tumidity 22 mm; length to height ratio about 1.4.

Etymology

The species is named after the nearby city of Mtwara on the Tanzanian mainland (*mtwaraense* = neutral adjective; Latinised).

Type material

Holotype

SW INDIAN OCEAN – **Mtwara MV, off Tanzania** • shell; 10°12.259' S, 40°32.682' E; 867 m depth; 23 Aug. 2024; stn SO306 / GeoB 26152-1; video box core; SMF 376563 (Fig. 10).

Paratypes

SW INDIAN OCEAN – **Mtwara MV, off Tanzania** • 1 valve (juvenile right valve); same data as for holotype; SMF 376564 • 5 valves (2 LV, 3 RV); stn SO306 / GeoB 26132-1; SMF 376565 • 3 valves (2 LV, 1 RV); stn SO306 / GeoB 26137-1; SMF 376566.

Description

PRODISSOCONCH. Characteristics are unknown.

DISSOCONCH. Sculpture with irregular, fine, commarginal growth lines. Outline: posterior dorsal margin straightened across narrow escutcheon and ligament; anterior dorsal margin and anterior end convex; posterior dorsal margin obliquely truncated; ventral margin widely convex. Elongated narrow escutcheon with dark brown, lanceolate, external ligament; lunule not demarcated. Internally smooth; small umbonal pit; large anterior adductor muscle scars merged with anterior pedal retractor scar in pointed end; posterior scars slightly larger with posterior pedal retractor scar in smaller rounded area above adductor scar; pallial line commarginal, pallial sinus absent. Margin blunt, thin, smooth. Hinge plates

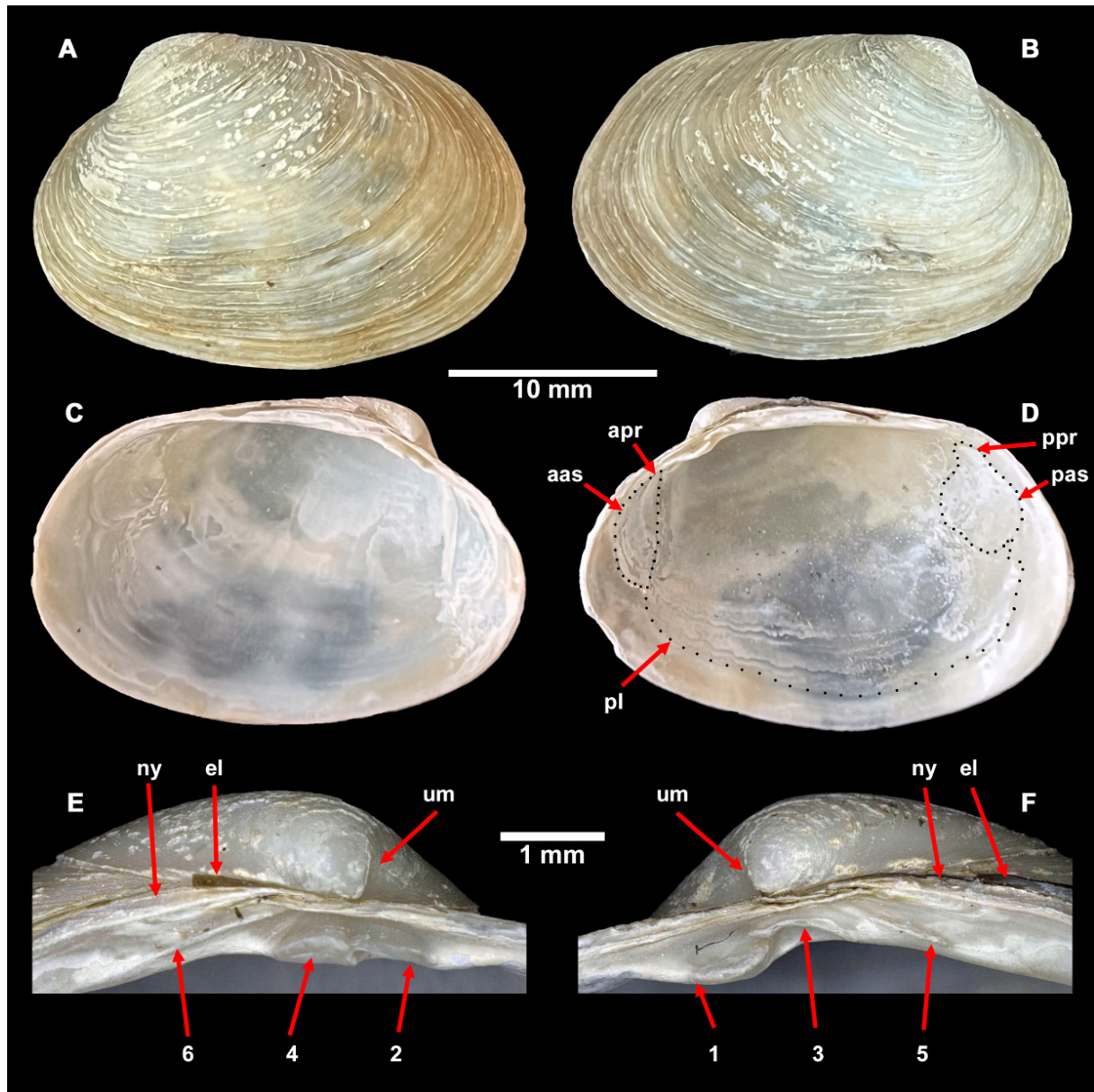


Fig. 10. *Isorropodon mtwaraense* Hoffman sp. nov., holotype (SMF 376563), Tanzania, Mtwara Mud Volcano, SO306 GeoB26152-1, L=25 mm, H=21 mm, T=11 mm. **A.** Left valve, external view. **B.** Right valve, external view. **C.** Left valve, internal view. **D.** Right valve, internal view, with pallial line (pl), anterior adductor scar (aas), posterior adductor scar (pas), anterior pedal retractor scar (apr), posterior pedal retractor scar (ppr). **E.** Hinge of left valve with cardinal teeth 2, 4, 6, nymph (ny), external ligament (el) and umbo (um). **F.** Hinge of right valve with cardinal teeth 1, 3, 5, nymph (ny), external ligament (el) and umbo (um).

thin with elongated nymph posteriorly. Right valve, anterior curved tooth (1), convex toward margin hinge plate; below umbo curved tooth (3) convex towards umbo, posteriorly elongated, straight, thin tooth (5); left valve anteriorly thick tooth (2), parallel to margin, below umbo curved tooth (4) convex towards umbo; posteriorly elongated straight thin tooth (6).

Differential diagnosis

Placement in the genus *Isorropodon* is based on the similarity with the type species *I. perplexum*. The type species has a more oval outline and stronger valves, hinge and teeth; its length to height ratio is larger (1.25–1.30). The present species has a more oblong outline and a lower length to height ratio (1.18). *Isorropodon bigoti* Cosel & Salas, 2001 from the Gulf of Guinea has its umbo placed more centrally. *Isorropodon curtum* Cosel & Salas, 2001 from Mauritania is less globose, more elongated (length to height ratio 1.43–1.50) and it has stronger valves. *Isorropodon striatum* (Jaekel & Thiele, 1931) from SW Africa has a different outline.

Remarks

Rodrigues *et al.* (2012) and Oliver & Drewery (2014) discussed chemoautotrophic bacteria in species of *Isorropodon*. It is likely that *Isorropodon mtwaraense* sp. nov. also shares this trait.

Isorropodon cowioae Hoffman sp. nov.

urn:lsid:zoobank.org:act:DCD86024-1DEF-46DA-B880-CBE2DC4C94C9

Fig. 11

Diagnosis

Angular-oval vesicomyliform shell, tumid, thick, strong valves; convex, broad weakly protruding umbos, leaning forward anterior of midline at about 40% of dorsal margin. Equivalve, inequilateral. Shell colour white. Observed maximum length 26 mm, width 19 mm, tumidity 19 mm; length to height ratio about 1.27, length to tumidity ratio about 1.27.

Etymology

‘*Cowioae*’ (feminine adjective) refers to the project name of the SO306 cruise: CoWIO (for Corals in the western Indian Ocean).

Type material

Holotype

SW INDIAN OCEAN – **Mtwara MV, off Tanzania** • right valve; 10°12.222' S, 40°32.663' E; 868 m depth; 20 Aug. 2024; SO306 / GeoB26137-1; video box core; SMF 376567 (Fig. 11A–B).

Paratypes

SW INDIAN OCEAN – **Mtwara MV, off Tanzania** • 9 valves (5 RV, 4 LV); same data as for the holotype; SMF 376568 (Fig. 11C–H) • 10 valves (5 RV, 5 LV); SO306 / GeoB26132-1; SMF 376569.

Description

PRODISSOCONCH. Characteristics are unknown

DISSOCONCH. Sculpture with irregular, fine, commarginal growth lines. Outline convex on all margins, posterior truncated and convexly pointed; narrow elongated escutcheon; lunule large, demarcated. Internally smooth; large umbonal pit. Strong central hinge plate. Right valve hinge with curved thin tooth (1) anterior of umbo near inside margin hinge; curved tooth (3a, 3b), convex towards umbo; posterior of umbo elongated straight tooth (5), parallel to posterior margin. Left valve hinge with small tooth (2a) anterior of umbo, parallel to margin; strong, large tooth (2b) convex towards umbo; posteriorly thin

elongated tooth (4) parallel to margin. Lateral teeth lacking; curved nymph posterior of umbo, externally of nymph, thin groove for curved ligament. Ventral margin smooth and blunt. Adductor muscles of comparable size. Ventral line commarginal; pallial sinus marginally developed.

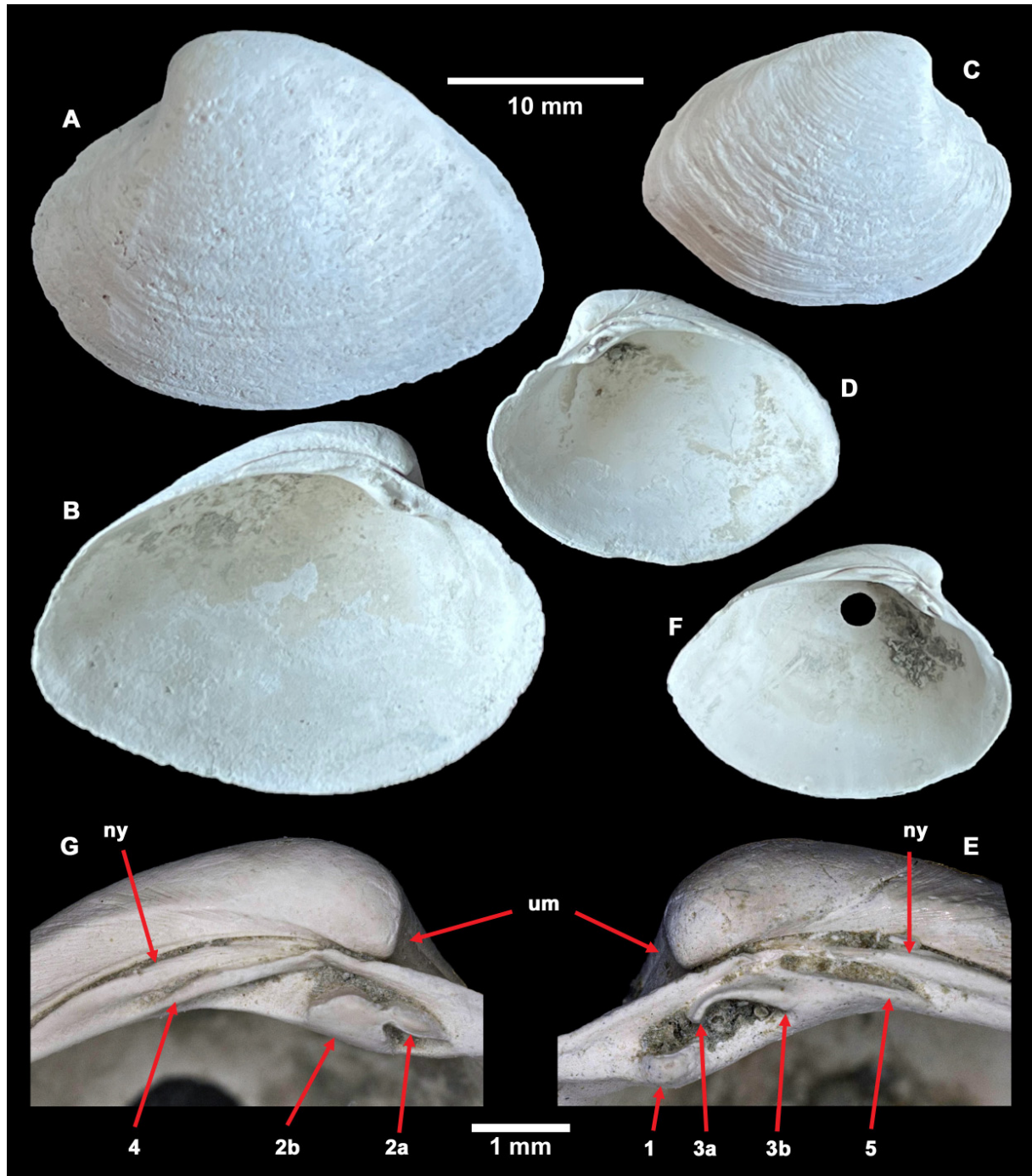


Fig. 11. *Isorropodon cowioae* Hoffman sp. nov., Mtwara Mud Volcano off Tanzania, SO306 GeoB26137-1. **A–B.** Holotype (SMF 376567), left valve, L=26 mm, H=19 mm. **C–H.** Paratypes (SMF 376568). **C–E.** Paratype (SMF 376568), right valve, L=20 mm, H=10 mm. **C.** External view. **D.** Internal view. **E** Hinge with cardinal teeth 1, 3a, 3b and 5, nymph (ny) and umbo (um). **F–H.** Paratype (SMF 376568), left valve with drill hole from predator, L=19 mm, H=13 mm. **F.** Internal view. **G.** Hinge with cardinal teeth 2a, 2b, 4, nymph (ny), umbo (um).

VARIATION. The length to height ratio is weakly variable with a range of 1.2–1.3.

Differential diagnosis

Congeneric species of *Isorropodon* have similar teeth and weak pallial sinus (Cosel & Salas 2001; Hoffman *et al.* 2019). Similar species are the eastern Mediterranean type species *I. perplexum* and the Mauritanian Atlantic *I. curtum* Cosel & Salas, 2001 and *I. bigoti* Cosel & Salas, 2001. The type species has rather fragile shells and has a more oblong outline; the present species has thick shells and is tapered at the posterior-ventral margin. *Isorropodon curtum* is oval, rounded posteriorly and its hinge is weaker; the current species is tapered posteriorly and has strong hinge plates. *Isorropodon bigoti* has a very similar outline with tapered posterior, but the posterior margin is obliquely truncated and its hinge is weaker than *I. cowioae* sp. nov.

Isorropodon sp.

Fig. 12

Material examined

SW INDIAN OCEAN – **Mtwara MV, off Tanzania** • 3 valves (2 LV, 1 RV); 10°12.222' S, 40°32.663' E; 868 m depth; 19 Aug. 2024; stn SO306 / GeoB 26137-1; video box core; SMF 376570 (Fig. 12).

Description

Oval vesicomyiform shell, flattened, thin, fragile valves, weakly convex; protruding pointed umbos, leaning forward anterior of midline at about 35% of dorsal margin. Equivalve, inequilateral. Shell colour white. Outline convex on all margins. Long narrow escutcheon; lunule not demarcated. Sculpture with irregular, fine, commarginal growth lines. Internally smooth; small umbonal pit; adductor muscle scars of equal strength; pallial line commarginal, pallial sinus uncertain. Margin sharp, smooth. Hinge thin; left valve three teeth parallel to margin, short elongated anterior tooth close to margin, posterior tooth longer, more distant from margin. Ventral margin smooth, thin and blunt. Length 30 mm, height 20 mm, tumidity 10 mm; length to height ratio 1.5, length to tumidity ratio 3.0.

Differential diagnosis

Placement in the genus *Isorropodon* is based on the similarity with the type species *I. perplexum*. The type species has stronger valves, hinge and teeth; its length to height ratio is slightly larger, about 1.25–1.30.



Fig. 12. *Isorropodon* sp. (SMF 376570), Mtwara Mud Volcano off Tanzania, SO306 GeoB26137-1, left valve, L=30 mm, H=20 mm, T=5 mm (1 valve). **A.** External view. **B.** Internal view.

The present species has a more elongated outline and a larger length to height ratio (1.50). *Isorropodon mtwaraense* sp. nov. from the same locality has an oblong outline and is more tumid. We refrain from describing a new species based on three fragmentary shells with hinge teeth in poor condition.

Class Gastropoda Cuvier, 1795
Subclass Patellogastropoda Lindberg, 1986
Superfamily Lepetoidea Gray, 1850
Family Lepetidae Gray, 1850

Genus *Propilidium* Forbes & Hanley, 1849

Type species

Patella ancyloides Forbes, 1840, type by subsequent designation, Recent, NE Atlantic and Mediterranean Sea.

Propilidium marisindicum Hoffman sp. nov.

urn:lsid:zoobank.org:act:A464AEAF-23A3-4FE6-9741-15F1787E7460

Fig. 13

Diagnosis

Small, elevated lepetiform shell, thin, fragile, conical, cap-shaped, fine granular sculpture. Apex posteriorly. Shell colour white. Observed maximum length 5.2 mm, height 2.6 mm, width 3.6 mm.

Etymology

Marisindicum (masculine adjective; from the Latin ‘*maris*’ - ‘off the sea’, and ‘*indicum*’ - ‘Indian’) is named after the Indian Ocean, the type locality.

Type material

Holotype

SW INDIAN OCEAN – **Mtwara MV, off Tanzania** • shell; 10°12.321' S, 40°32.742' E; 915 m depth; 19 Aug. 2024; stn SO306 / GeoB 26132-1; video box core; SMF 376571 (Fig. 13A–E).

Paratypes

SW INDIAN OCEAN – **Mtwara MV, off Tanzania** • 40 shells; same data as for holotype; SMF 376572 (Fig. 13F–K).

Description

PROTOCONCH. Characteristics are unknown.

TELEOCONCH. With curved apex, leaning posteriorly yet elevated, placed anteriorly; in side view posterior outline concave, anterior outline convex; apertural plane flat, ovate-oblong. Fine sculpture of weak radial ribs and irregular commarginal growth lines; tiny, elongated granules at crossings of ribs and major growth lines; external lip smooth, sharp. Internally smooth shallow apical pit; septum lacking; muscle scar inconspicuous.

Differential diagnosis

Placement in the genus *Propilidium* is uncertain but is based in the general outline and the fine granular sculpture. The type species has a similar shape and sculpture, and it has an apex that is rolled-over

towards the posterior, often retaining a protoconch. A differentiating characteristic of the present species is the elevated, eroded apex. Other congeners are very similar to the type species, like for example *P. lissocona* (Dall, 1927) and *P. curumim* Leal & Simone, 1998, and lack the elevated apex. *Propilidium tasmanicum* (Pilsbry, 1895) is smooth and elongated and also has a rolled-over apex. The elevated, curved, smooth apex is also found in the genera *Lepetella* Verrill, 1880 of the family Lepetellidae Dall, 1882 and *Bathyaltum* Haszprunar, 2011 in Hartmann *et al.*, 2011 of the family Bathysciadiidae Dautzenberg & Fischer, 1900. However, the sculptures of species in these genera are smooth in contrast to the present species.

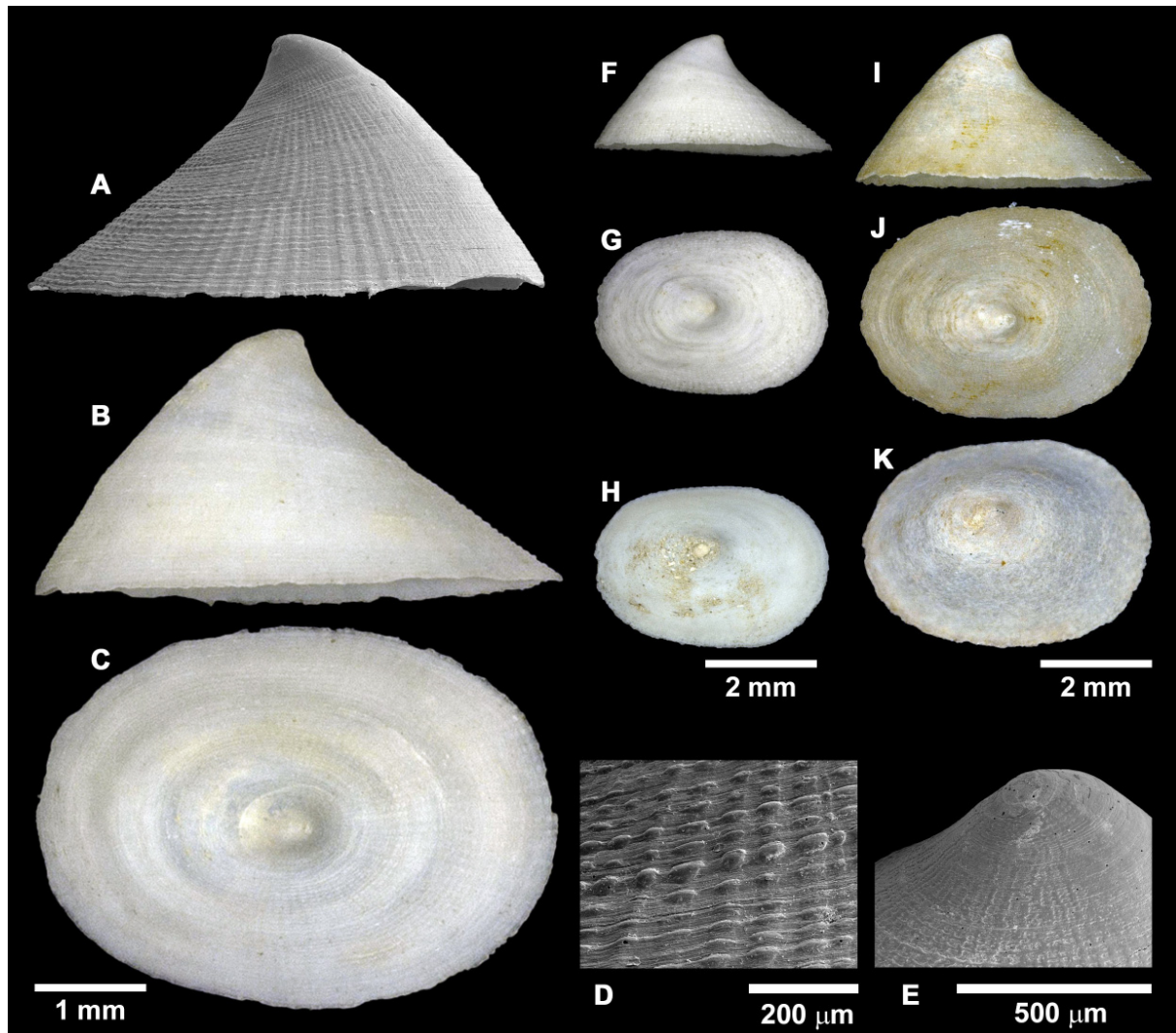


Fig. 13. *Propilidium marisindicum* Hoffman sp. nov., Tanzania, Mtwara Mud Volcano, GeoB26132-1. A–E. Holotype (SMF 376571), H=2.4 mm, L=4.7 mm, W=3.5 mm. A. Right side view (SEM). B. Left side view. C. Apical view. D. Sculpture near margin. E. Apex. F–K. Paratypes (SMF 376572). F–H. Paratype, H=2.0 mm, L=4.2 mm, W=2.9 mm. F. Left side view. G. Apical view. H. Internal view. I–K. Paratype, H=2.6 mm, L=5.2 mm, W=3.6 mm. I. Left side view. J. Apical view. K. Internal view.

Family Pectinodontidae Pilsbry, 1891

Genus *Bathyacmaea* Okutani, Tsuchida & Fujikura, 1992

Type species

Bathyacmaea nipponica Okutani, Tsuchida & Fujikura, 1992, type by original designation (Okutani *et al.* 1992: 140), Recent, off Japan, South China Sea (Chen & Sigwart 2023: 432), off Tanzania (this study).

Bathyacmaea nipponica Okutani, Tsuchida & Fujikura, 1992

Figs 14–17

Bathyacmaea nipponica Okutani, Tsuchida & Fujikura, 1992: 140–141, figs 7–11.

Serradonta vestimentifericola Okutani, Tsuchida & Fujikura, 1992: 139–140, figs 2–6.

Bathyacmaea secunda Okutani, Fujikura & Sasaki, 1993b: 130–131, figs 13–19.

Bathyacmaea tertia Sasaki, Okutani & Fujikura, 2003: 190–193, figs 3b, 4–5.

Bathyacmaea austrina Zhang & Zhang, 2020: 46, figs 1–9.

Bathyacmaea brevidentata Zhang & Zhang, 2020: 48, figs 10–17.

Diagnosis

Oblong-oval, elevated, thin, strong limpet, symmetrical along length axis; convex, broad strongly eroded apex, placed slightly anteriorly. Shell colour white. Observed maximum length 6.5 mm, width 4.6 mm, height 2.5 mm; length to width ratio about 1.4, length to height ratio about 2.6 (Fig. 15).

Material examined

SW INDIAN OCEAN – **Mtwara MV, off Tanzania** • 300+ live-collected specimens; stn SO306 / GeoB 26152-1; in 96% ethanol, SMF 376573 (Fig. 14A–D) • 100+ live-collected specimens; same locality data as for preceding; M.342063 • 3000+ empty shells; same locality data as for preceding; SMF 376574 • 93 shells; stn SO306 / GeoB 26132-1; SaM 87725 • 43 shells; stn SO306 / GeoB 26137-1; SaM 87727.

Description

PROTOCONCH. Characteristics are unknown.

TELEOCONCH. Outline in apical view: convex on all sides, most convex posteriorly, widely convex anteriorly, weakly convex on sides. Side view, steep slopes anteriorly and posteriorly, both at about 45° with flat aperture plane; apex strongly eroded. Sculpture with irregular, fine and coarse, commarginal growth lines; the side view shows a stronger growth at anterior end. Internally smooth, glossy, with thick opaque central area and translucent towards sharp margin.

SOFT PARTS. In apertural view: symmetrical along length axis; a large oblong-oval foot with central depression, margins smooth on all sides; head large and broad with two tentacles with thin blunt tips and thickened bases that are thinner at the joints on the side; no eyes discernible; oval mouth with thick oval labium, deep oral cavity. Mantle margin thick (likely shrunk by 96% ethanol), very thin translucent vellum inside.

VARIATION. Very little variability is shown in the population at the Mtwara MV in the straight and narrow growth curve (Fig. 15). A variable degree of apical erosions provides a larger spread in the length to height ratio. The species shows a wide morphological variety on a global scale as is suggested by the

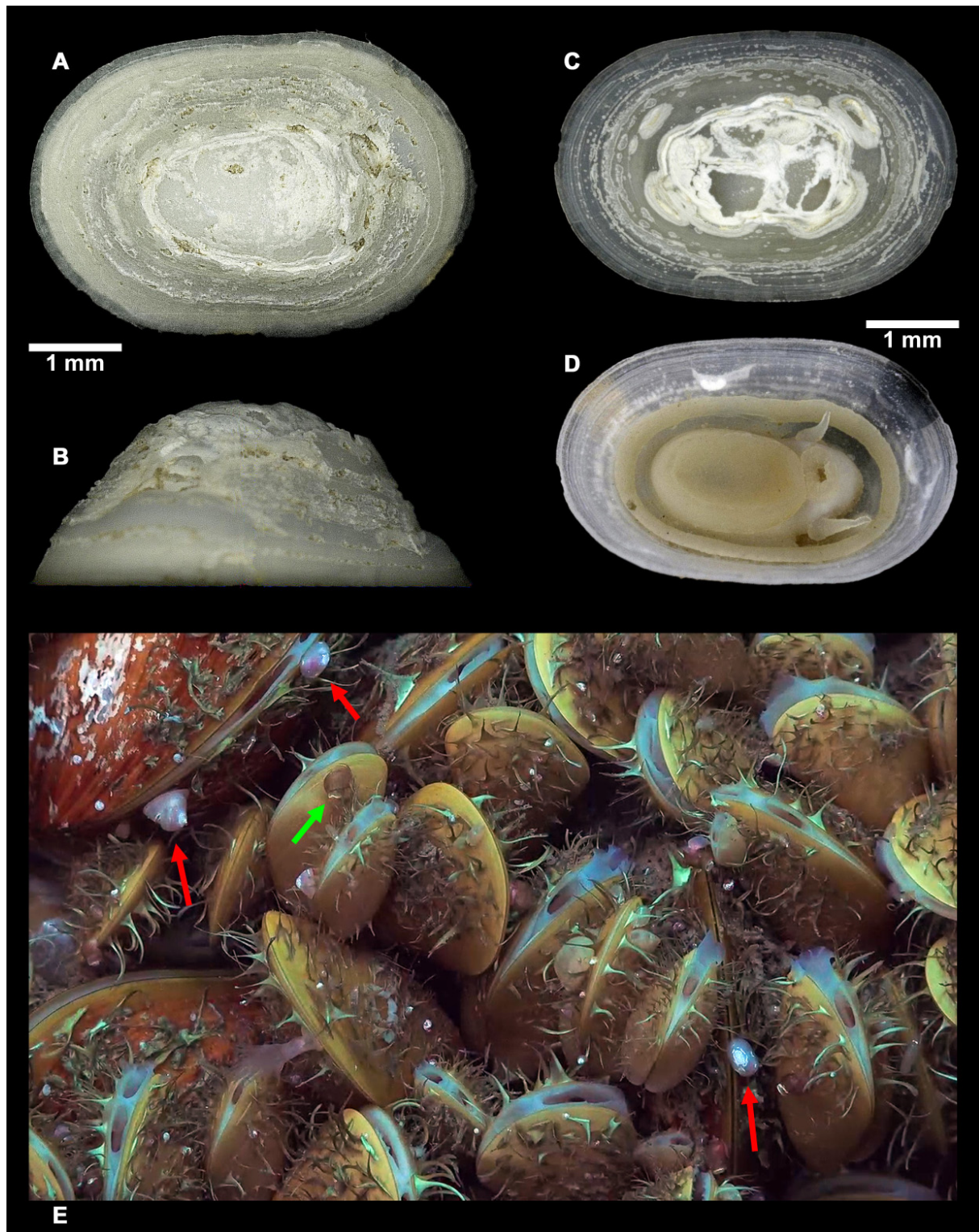


Fig. 14. *Bathymacrea nipponica* Okutani, Tsuchida & Fujikura, 1992 on *Gigantidas tanzaniensis* Hoffman, Westbeek & Kihara sp. nov., Tanzania, Mtwara Mud Volcano, SO306. **A–D.** GeoB26152-1 (SMF 376573). **A–B.** L=5.0 mm, W=3.4 mm, H=1.8 mm. **A.** Apical view. **B.** Side view. **C–D.** Same locality, L=4.5 mm, W=3.0 mm. **C.** Apical view. **D.** Apertural view with animal inside. **E.** ROV image, GeoB26136-1 ROV, 885 m depth, live *Bathymacrea nipponica* (red arrows) and *Provanna castanea* Hoffman & Kihara sp. nov. (green arrow) on *Gigantidas tanzaniensis*.

significant number of recent synonyms. Examples of morphological variety include the presence of radial riblets and a more oval apertural outline. The subsequent names from the cresonymy were synonymised based on DNA analyses (Chen & Sigwart 2023).

Molecular analyses

A total of six high-quality sequences of *COI* were obtained (Table 3) with fragment sizes ranging from 664 to 670 bp, no indels or stop codons were found. Overall mean nucleotide frequencies were G (20.9%), C (14.0%), A (24.3%) and T (40.9%). The ML analyses confirmed that the species here studied belongs to *Bathymacra nipponica* (Fig. 16). Genetic distance values (Fig. 17) show intraspecific divergences ranging between 0.5 and 0.9% for both K2P and *p*-distance, and interspecific divergences ranging between 6.2 and 12.0% (K2P), and 5.9 and 10.9% (*p*-distance), with the nearest known species *Bathymacra leviniae* Betters, Cortés & Cordes, 2024.

Habitat

The species were commonly associated with *Gigantidas tanzaniensis* sp. nov., *Provanna castanea* sp. nov., and *Enigmaticolus nipponensis* (Okutani & Fujiwara, 2000) in the mussel beds (Fig. 14E) as well as on the surrounding rocky sea bottom. It probably feeds by grazing.

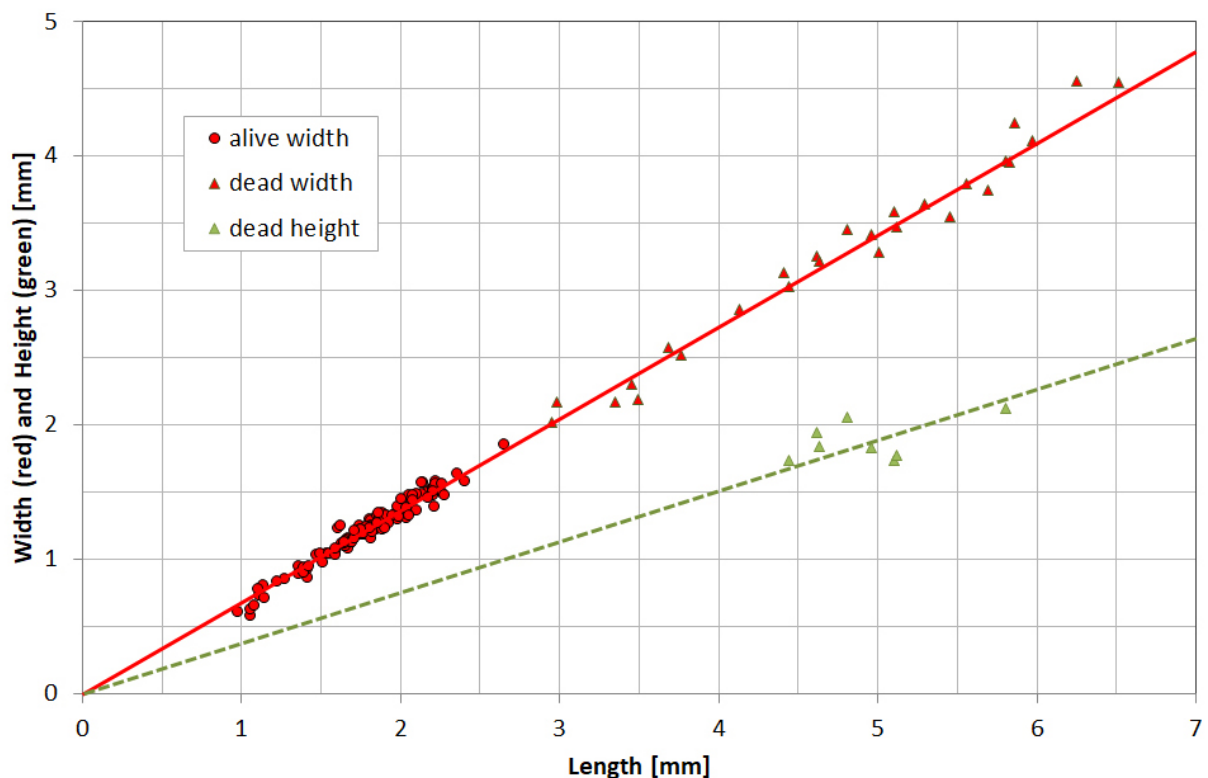


Fig. 15. *Bathymacra nipponica* Okutani, Tsuchida & Fujikura, 1992, shell dimensions of live-collected specimens and empty shells, SO306 / GeoB26152-1, off Tanzania. Shell length versus width indicated with red line and symbols; length versus height in green. Note that specimens with length less than 10 mm are poorly sampled. Number of individuals: 147 (120 live-collected specimens and 27 empty shells).

Distribution

The species is known from cold seep habitats off Japan and the South China Sea (Okutani *et al.* 1992; Chen & Sigwart 2023). The current find is the first in the western Indian Ocean.

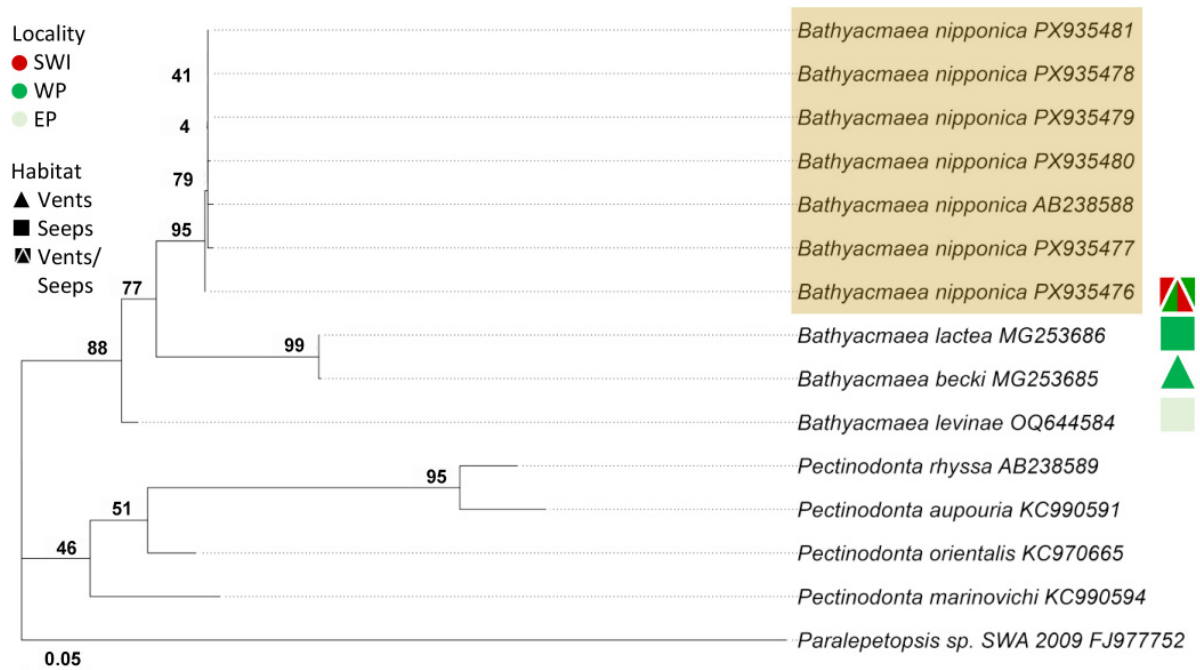


Fig. 16. Maximum-likelihood phylogenetic tree of *Bathyacmaea* Okutani, Tsuchida & Fujikura, 1992 based on *COI* sequences of selected species of Pectinodontidae Pilsbry, 1891 and with *Paralepetopsis* McLean, 1990 as outgroup. The GenBank accession numbers are added following species names. *Bathyacmaea nipponica* Okutani, Tsuchida & Fujikura, 1992 clade highlighted in dark yellow. Numbers at branches indicate ultrafast bootstrap support. The scale bar shows substitutions per site. Coloured circles indicate the locality: EP=East Pacific; SWI=Southwest Indian Ocean; WP=West Pacific. Habitat vents are represented by triangle, seeps by squares, both vent and seeps by triangle inside a square.

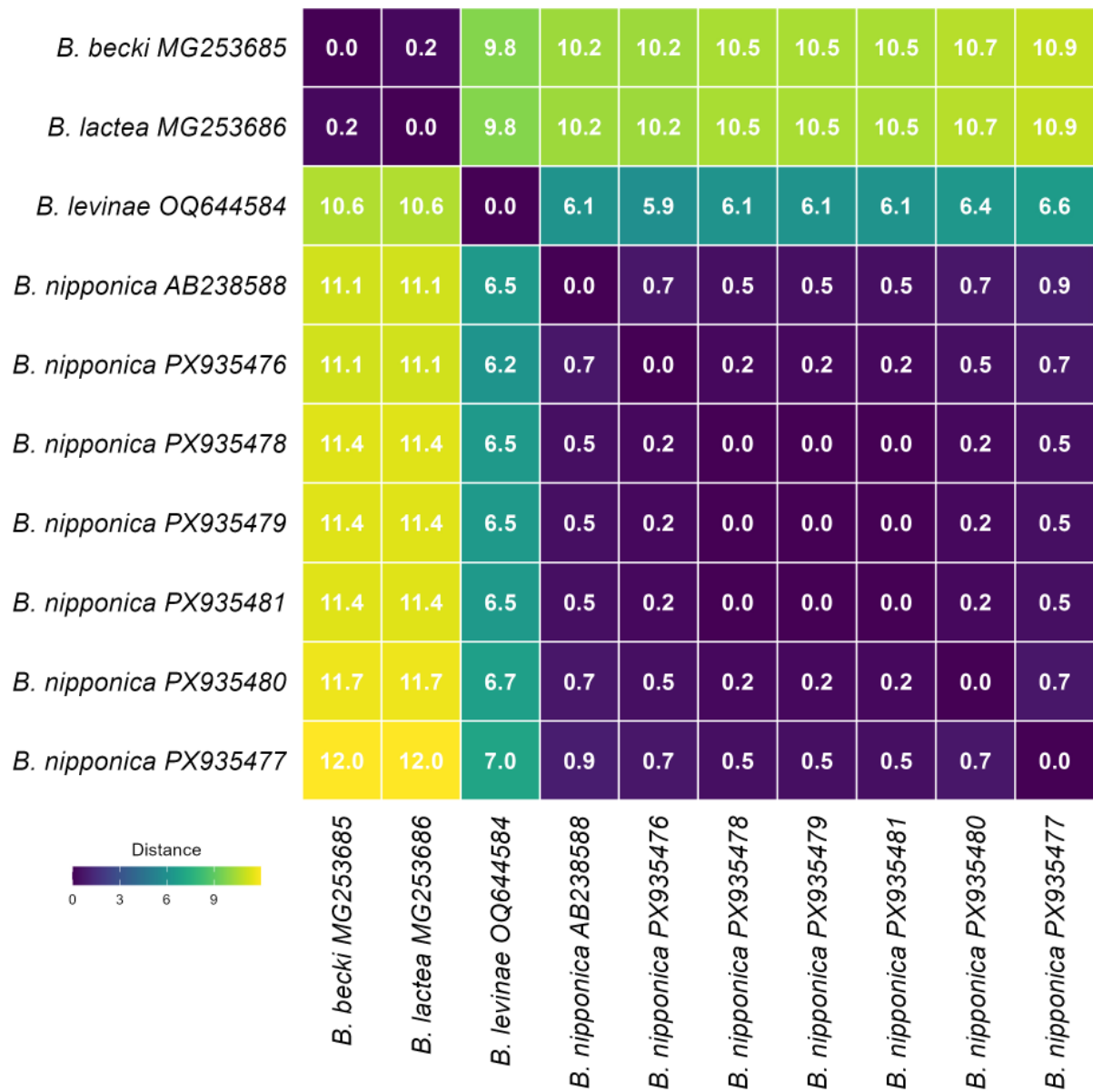


Fig. 17. Heatmap of inter- and intraspecific genetic distance percentages of *Bathyacmaea* Okutani, Tsuchida & Fujikura, 1992 in *COI* (K2P: lower; *p*-distance: upper).

Family Neolepetopsidae McLean, 1990

Genus *Paralepetopsis* McLean, 1990

Type species

Paralepetopsis floridensis McLean, 1990, type by original designation, Recent, Gulf of Mexico (McLean 1990: 510).

Paralepetopsis sahani Hoffman sp. nov.

urn:lsid:zoobank.org:act:B0541D2B-5774-4F91-93A2-FB19F67E49AD

Fig. 18

Diagnosis

Medium-sized, ovate, flattened, thick, conical, patelliform shell, radial and commarginal sculpture. Apex centrally, eroded. Shell colour white (holotype brown coating externally). Observed maximum length 16 mm, height 5 mm, width 13 mm.

Etymology

‘*Sahani*’ (noun in apposition) is a plate in Swahili.

Type material

Holotype

SW INDIAN OCEAN – **Mtwara MV, off Tanzania** • shell; 10°12.321' S, 40°32.742' E; 915 m depth; 19 Aug. 2024; stn SO306 / GeoB 26132-1; video box core; SMF 376575 (Fig. 18G–H).

Paratypes

SW INDIAN OCEAN – **Mtwara MV, off Tanzania** • 66 shells; same data as for holotype; SMF 376576, SMF 376619 (Fig. 18A–F, I–K) • 129 shells; stn SO306 / GeoB 26137-1; SaM 87726.

Description

PROTOCONCH. Characteristics are unknown.

TELEOCONCH. Weakly elevated conical shell with straight or weakly convex sides; sculpture of weak radial ribs and regular commarginal growth margins, weak nodules at crossings of ribs and growth margins; external lip with weak undulations following rib sculpture. Shell symmetrical across anterior-posterior midline and left-right midline. Internally smooth with weak imprint of horse-shoe shaped muscle scar, mantle line complete.

Differential diagnosis

Placement in the genus *Paralepetopsis* is uncertain because we only use the shell morphology. Congeners with a similar shape and radial sculpture are *P. ferruginosa* Warén & Bouchet, 2001, *P. lepichori* Warén & Bouchet, 2001, *P. tunnicliffae* McLean, 2008 and *P. variabilis* Betters, Cortés & Cordes, 2024. However, all these species lack a regular commarginal sculpture and have the apex placed posteriorly; the present species shows a dominant, regular, commarginal sculpture, a central apex and a larger maximum size. Some species in the genera *Neolepetopsis* McLean, 1990 of Neolepetopsidae McLean, 1990 and *Bathymacra* Okutani, Tsuchida & Fujikura, 1992 of Pectinodontidae are similar. For example, *Neolepetopsis gordensis* McLean, 2008 and *Neolepetopsis nicolasensis* McLean, 2008 from the eastern Pacific Ocean have their apex placed slightly posteriorly; *Neolepetopsis gordensis* has a concave

apertural plane and both have a thin shell with an internal imprint of the external sculpture. The present species has a central apex and a thicker shell with smooth interior. Okutani *et al.* (1993b) described shells of *B. nipponica* using a synonymous name (*Bathyacmaea* 'secunda'), these shells are similar in outline and show a radial rib sculpture. However, their sculpture is irregular and dominated by radial ribs, and its shell is smaller when compared to *P. sahani* sp. nov.

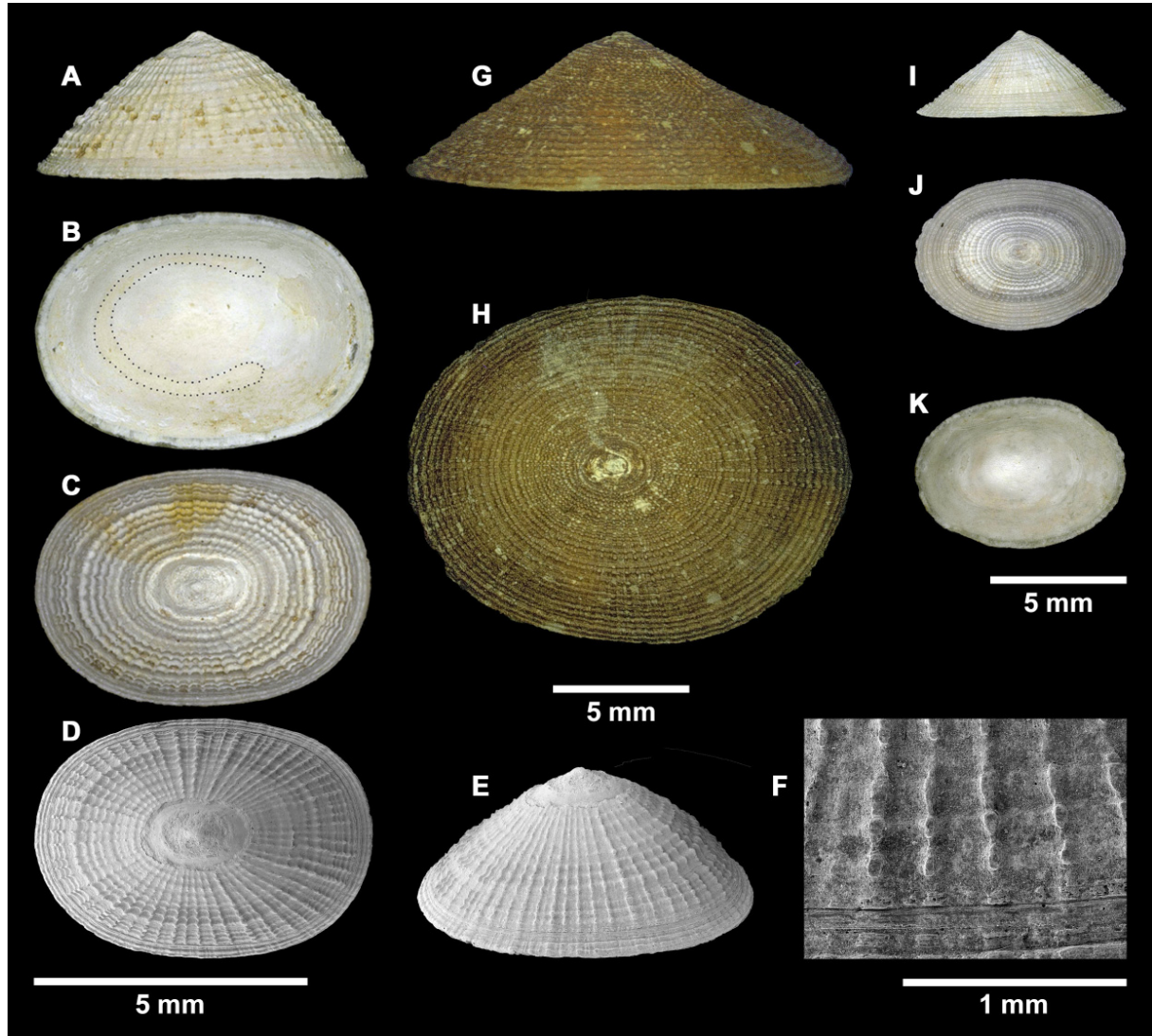


Fig. 18. *Paralepetopsis sahani* Hoffman sp. nov., Tanzania, Mtwara Mud Volcano, SO306 / GeoB26137-1. A–F. Paratype (SMF 376619), H=3 mm, L=7 mm, W=5 mm. A. Side view. B. Apertural view. C. Apical view. D. Apical view (SEM), sculpture near margin. E. Side view (SEM). F. Sculpture near margin (SEM). G–H. Holotype (SMF 376575), H=5 mm, L=16 mm, W=13 mm. G. Side view. H. Apical view. I–K. Paratype (SMF 376576), H=3 mm, L=8 mm, W=6 mm. I. Side view. J. Apical view. K. Apertural view.

Subclass Vetigastropoda Salvini-Plawen, 1980

Superfamily Fissurelloidea Fleming, 1822

Family Fissurellidae Fleming, 1822

Genus *Puncturella* Lowe, 1827

Type species

Puncturella (*Puncturella*) *noachina* Linnaeus, 1758, by monotypy, Recent, NE Atlantic, Mediterranean Sea.

Puncturella mrembo Hoffman sp. nov.

urn:lsid:zoobank.org:act:D98E1932-9D95-4D73-AF11-E5F1E3498BD0

Fig. 19

Diagnosis

Medium-sized, elevated, thin, fragile, conical, cap-shaped fissurelliform shell, apical foramen, radial sculpture. Apex posteriorly, nearly planispiral. Shell colour white; periostracum thin, colour light olive greenish. Observed maximum length 12 mm, height 7 mm, width 8 mm.

Etymology

‘*Mrembo*’ (noun in apposition) indicates a beauty in Swahili.

Type material

Holotype

SW INDIAN OCEAN – **Mtwara MV, off Tanzania** • shell (Fig. 19A–C); 10°12.321' S, 40°32.742' E; 915 m depth; 19 Aug. 2024; stn SO306 / GeoB 26132-1; video box core; SMF 376577 (Fig. 19A–C).

Paratypes

SW INDIAN OCEAN – **Mtwara MV, off Tanzania** • 66 shells; same data as for holotype; SMF 376578, SMF 376622 (Fig. 19D–N) • 1 shell with dried animal inside + 29 shells; stn SO306 / GeoB 26137-1; SMF 376579 • 2 shells; stn SO306 / GeoB 26152-1; SaM 87728.

Description

PROTOCONCH. Surface eroded, 1¼ whorls with demarcated margin, protruding nucleus, abapical side exposed (Fig. 19N).

TELEOCONCH. With ¼ convex quickly expanding whorl, oblong apertural cross-section; elongated pointed foramen anterior of apex; sculpture of strong radial ribs and strong, irregular, commarginal growth margins, rounded nodules at crossings of ribs and major growth margins; external lip with weak undulations following rib sculpture. Internally smooth with weak imprint of external sculpture, large triangular septum closed apically, flat rectangular foramen anteriorly; broad commarginal muscle scar; margin blunt, undulating, inside weakly scalloped.

Differential diagnosis

Placement in the genus *Puncturella* is based on the similarity with the type species, which is different by a stronger axial rib sculpture with ribs of equal strength. The present species has weaker ribs with stronger commarginal growth margins. *Puncturella capensis* Thiele, 1925 from southern Africa has a sculpture similar to that of the type species and is more elevated in side view (Herbert & Kilburn 1986:

16–18, figs 57–65). Other SE African species have a different shape and sculpture (Herbert & Kilburn 1986: 15–20).

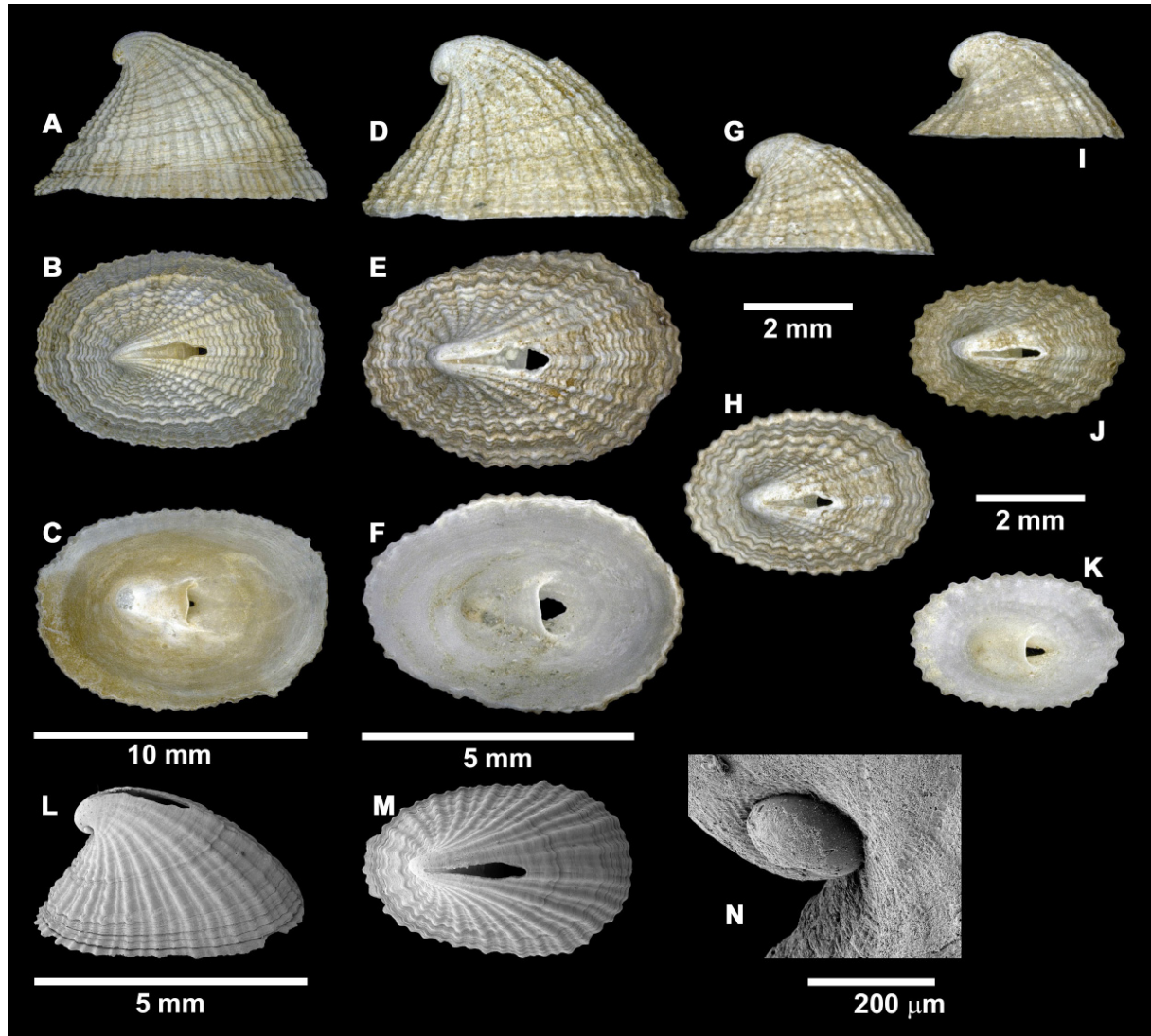


Fig. 19. *Puncturella mrembo* Hoffman sp. nov., Tanzania, Mtwara Mud Volcano. **A–C.** Holotype (SMF 376577), GeoB26132-1, H=6.0 mm, L=10.3 mm, W=7.2 mm. **A.** Side view. **B.** Apical view. **C.** Apertural view. **D–K.** Paratypes (SMF 376578), GeoB26137-1. **D–F.** Paratype, H=3.5 mm, L=6.0 mm, W=4.1 mm. **D.** Side view. **E.** Apical view. **F.** Apertural view. **G–H.** Paratype, H=2.1 mm, L=4.5 mm, W=3.0 mm. **G.** Side view. **H.** Apical view. **I–K.** Paratype, H=2.0 mm, L=4.0 mm, W=2.6 mm. **I.** Side view. **J.** Apical view. **K.** Apertural view. **L–N.** Paratype (SMF 376622), GeoB26132-1, H=2.6 mm, L=5.0 mm, W=3.3 mm. **L.** Side view. **M.** Apical view. **N.** Protoconch, apical view, W=200 µm.

***Puncturella alternata* Hoffman sp. nov.**

urn:lsid:zoobank.org:act:C7408D2F-1978-41B7-8734-1CDB652C7686

Fig. 20

Diagnosis

Medium-sized, elevated, thin, fragile, oblong, cap-shaped fissurelliform shell, posterior-dorsal foramen, radial sculpture. Apex protruding at posterior side, planispiral. Shell colour white. Maximum length 12 mm, height 7 mm, width 8 mm.

Etymology

Alternata (from the Latin adjective '*alternus*', meaning 'alternate' or 'by turns'), indicating the alternating strength of radial ribs.

Type material

Holotype

SW INDIAN OCEAN – **Mtwara MV, off Tanzania** • shell; 10°12.321' S, 40°32.742' E; 915 m depth; 19 Aug. 2024; stn SO306 / GeoB 26132-1; video box core; SMF 376580 (Fig. 20A–C).

Paratypes

SW INDIAN OCEAN – **Mtwara MV, off Tanzania** • 33 shells; same data as for holotype; SMF 376581 (Fig. 20D–F), SMF 376621 (Fig. 20J–M) • 1 shell; stn SO306 / GeoB 26137-1; SMF 76582 (Fig. 20G–I).

Description

PROTOCONCH. Surface eroded, $1\frac{1}{4}$ whorls with demarcated margin, weakly protruding nucleus, nearly planispiral, abapical side exposed (Fig. 20M).

TELEOCONCH. With $\frac{1}{4}$ convex quickly expanding whorl, well rounded on anterior-dorsal margin, concave posteriorly, oblong apertural cross-section; elongated rectangular foramen at mid-point between apex and anterior margin; reticulated sculpture of alternating weak and strong radial ribs and regular commarginal growth margins; external lip with weak undulations following sculpture. Internally smooth, short, curved septum at posterior side of foramen, broad callus along inner margins of foramen, converging in point towards the anterior lip margin; weak commarginal muscle scar; margin blunt, weakly undulating.

Differential diagnosis

The present species is a member of a cluster of morphologically similar species in *Puncturella* that have a foramen on the anterior dorsal margin and a reticulated sculpture. A similar species is *Puncturella fornicata* (Locard, 1898) from the NE Atlantic Ocean; this species has a coarser rib sculpture and a concave apertural plane in side view (Hoffman & Freiwald 2023). The present species has a fine sculpture and a flat apertural plane. *Puncturella asturiana* (Fischer, 1882) is another similar species from the NE Atlantic Ocean; this species has a finer rib sculpture and a concave apertural plane in side view, it has an oval outline (Hoffman & Freiwald 2023). The present species also has a fine sculpture but a flat apertural plane with an oblong outline. *Puncturella carinifera* (Schepman, 1908) and *Puncturella verrieri* (Crosse, 1871) from the western Pacific Ocean both have a stronger rib sculpture.

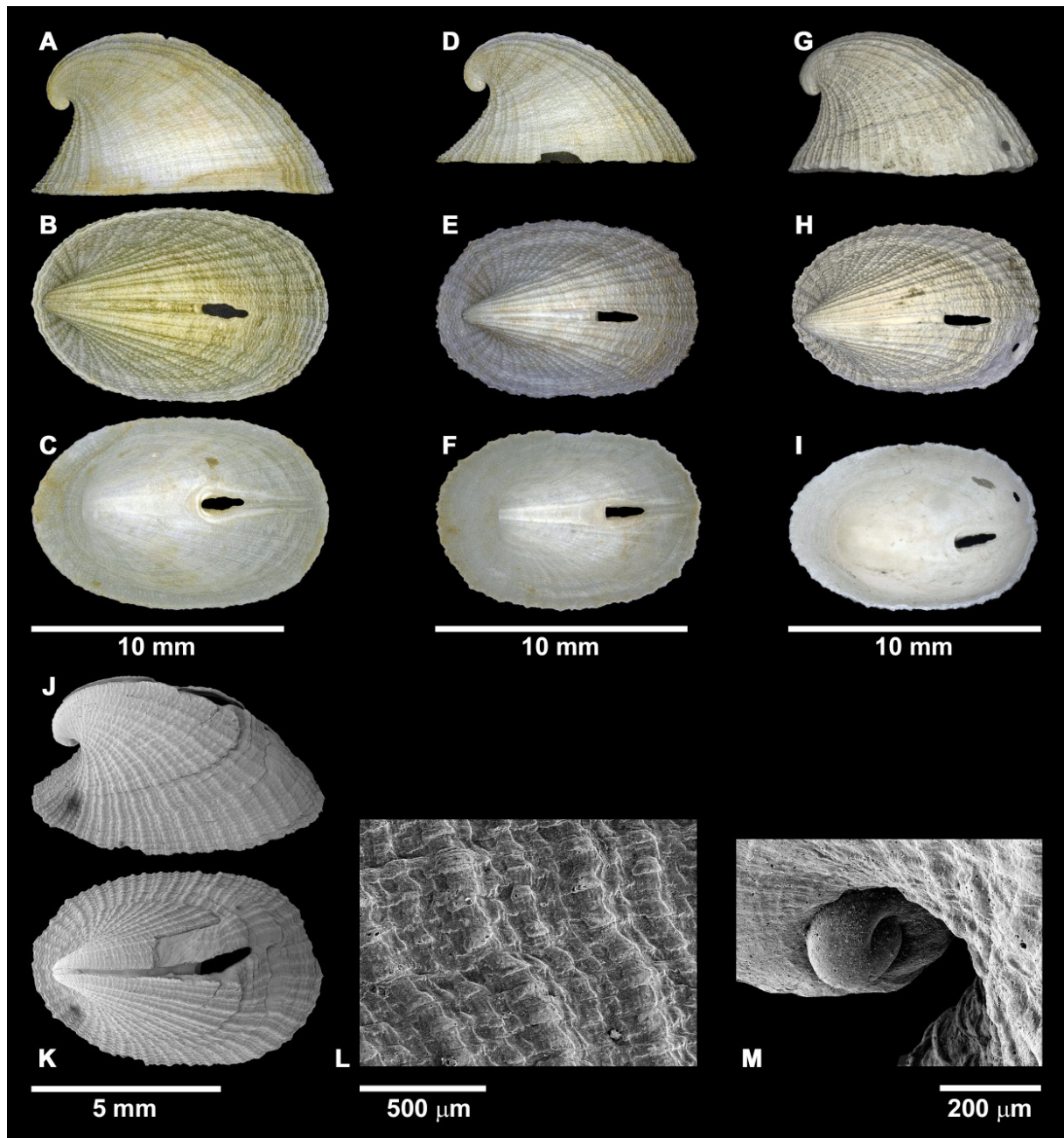


Fig. 20. *Puncturella alternata* Hoffman sp. nov., Tanzania, Mtwara Mud Volcano. **A–C.** Holotype (SMF 376580), GeoB26132-1, H=6.5 mm, L=12.0 mm, W=7.7 mm. **A.** Side view. **B.** Apical view. **C.** Apertural view. **D–F.** Paratype (SMF 376581), same location as for the holotype, H=5.2 mm, L=10.2 mm, W=7.1 mm. **D.** Side view. **E.** Apical view. **F.** Apertural view. **G–I.** Paratype (SMF 376582), GeoB26137-1, H=5.7 mm, L=11.0 mm, W=6.7 mm. **G.** Side view. **H.** Apical view. **I.** Apertural view. **J–M.** Paratype (SMF 376621) with large scar, GeoB26132-1, H=4.5 mm, L=7.8 mm, W=5.3 mm (SEM). **J.** Side view. **K.** Apical view. **L.** Sculpture near margin. **M.** Protoconch apical view. Diameter 280 μ m.

Genus *Fissurisepta* Seguenza, 1863

Type species

Fissurisepta papillosa Seguenza, 1863, type by subsequent designation. Described as a Miocene fossil from Italy (Seguenza 1863: 84); found alive off Mauritania (Hoffman & Freiwald 2018b).

Fissurisepta kilimanjaro Hoffman sp. nov.

urn:lsid:zoobank.org:act:58CA5100-C6F3-4677-9F32-72DEED25334E

Fig. 21

Diagnosis

Small, elevated, thin, fragile, conical, cap-shaped fissurelliform shell, apical foramen, sculpture with regular nodules. Apex centrally. Shell colour white. Observed maximum length 4.5 mm, height 2.6 mm, length 3.5 mm.

Etymology

‘*Kilimanjaro*’ (noun in apposition) suggests a morphological similarity with the volcano Kilimanjaro in northern Tanzania.

Type material

Holotype

SW INDIAN OCEAN – **Mtwara MV, off Tanzania** • shell; 10°12.321' S, 40°32.742' E; 915 m depth; 19 Aug. 2024; stn SO306 / GeoB 26132-1; video box core; SMF 376583 (Fig. 21A–C).

Paratypes

SW INDIAN OCEAN – **Mtwara MV, off Tanzania** • 13 shells; same data as for holotype; SMF 376584, SMF 376620 (Fig. 21D–H).

Description

PROTOCONCH. Absent, characteristics are unknown.

TELEOCONCH. Elevated conical shell with straight outlines in side view, oblong apertural cross-section; apical foramen with maximum convexity at the posterior end; sculpture of dense regular pattern of commarginally elongated nodules, placed in quincunx (crossing diagonals) alignment, apical sculpture with fine radiating flexuous lines with fine commarginally elongated nodules; major growth margins, abapical sculpture of downward pointing triangular nodules with vertical radial dashes between vertically aligned nodules; apertural plane slightly concave, margin blunt. Internally smooth; large triangular, slightly curved septum closed apically, round foramen anteriorly; broad commarginal muscle scar; margin blunt, smooth.

Differential diagnosis

Placement in the genus *Fissurisepta* is based on the similarity with the type species, which is different by fewer yet stronger nodules (Hoffman & Freiwald 2018b) when compared to the present species. Two similar species are *F. granulosa* Jeffreys, 1883 from the NE Atlantic Ocean and *F. manawatawhia* (Powell, 1937) from off New Zealand. *Fissurisepta granulosa* has fine aligned granules and lacks the quincunx arrangement (Hoffman *et al.* 2011a: 90, figs 36–38) and *F. manawatawhia* has a similar sculpture but with widely-spaced granules (Powell 1937: 177, pl. 48 fig. 8). The three remaining, known, congeneric species have a significantly different sculpture.

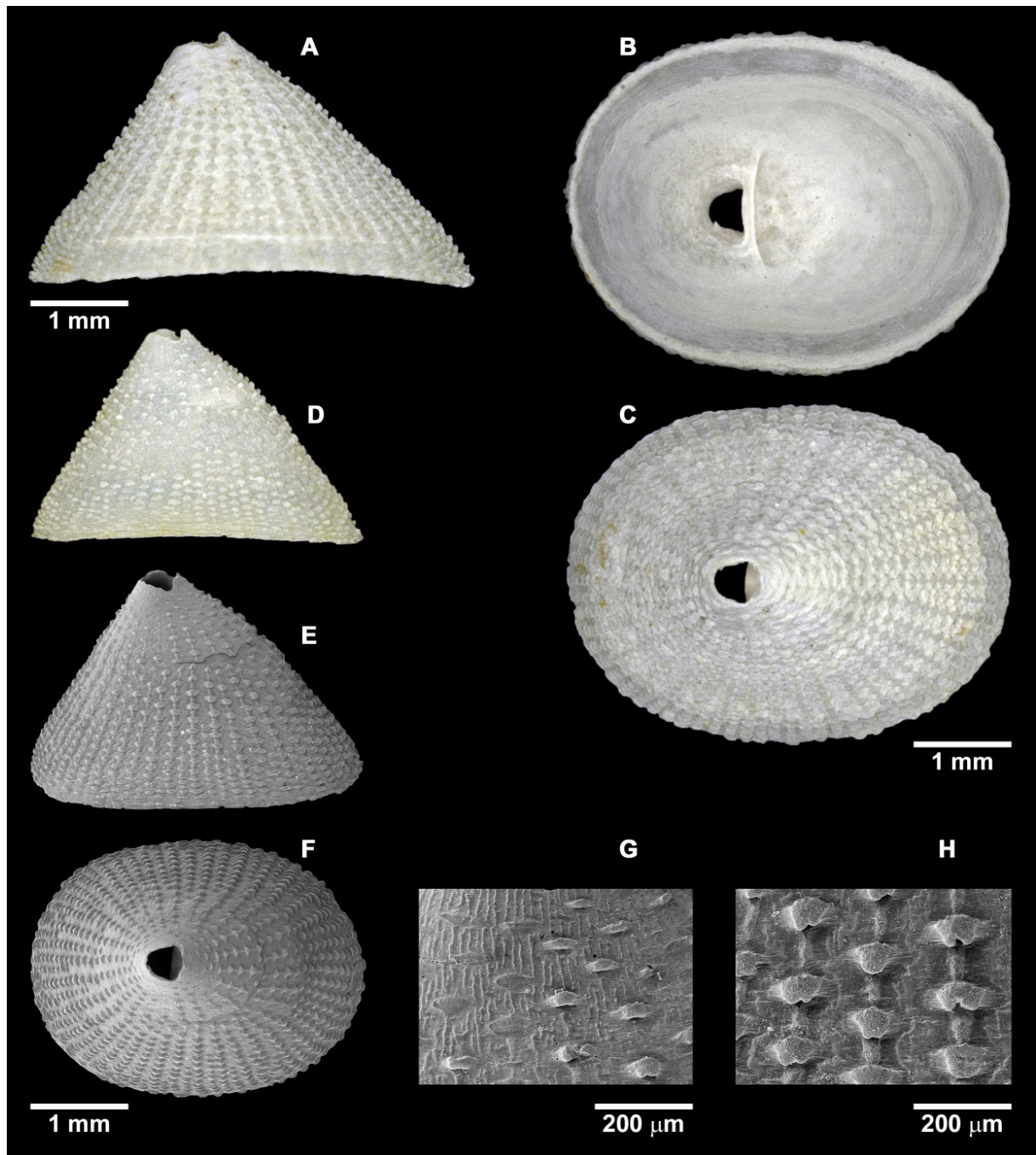


Fig. 21. *Fissurisepta kilimanjaro* Hoffman sp. nov., Tanzania, Mtwara Mud Volcano. **A–C.** Holotype (SMF 376583), GeoB 26132-1, H=2.6 mm, L=4.5 mm, W=3.5 mm. **A.** Side view. **B.** Apertural view. **C.** Apical view. **D–H.** Paratype (SMF 376620), same location, H=2.2 mm, L=3.3 mm, W=2.6 mm. **D.** Side view. **E.** Side view (SEM). **F.** Apical view. **G.** Adapical sculpture. **H.** Abapical sculpture near margin.

Genus *Cornisepta* McLean & Geiger, 1998

Type species

Fissurisepta antarctica Egorova, 1972, type by original designation, Recent, Antarctica (Egorova 1972: 383).

Cornisepta infundibulus Hoffman sp. nov.

urn:lsid:zoobank.org:act:A96E8B2D-000B-457B-ABE6-FD117FA29B82

Fig. 22

Diagnosis

Small, highly elevated, thin, fragile, conical fissurelliform shell; apical foramen, sculpture with tiny granules in a wavy pattern. Apex offset towards posterior. Shell colour translucent white. Observed maximum length 4 mm, height 4 mm, width 3 mm.

Etymology

Infundibulus (noun in apposition, from the Latin '*infundibulum*' for 'funnel'), referring to the funnel shape of the shell.

Type material

Holotype

SW INDIAN OCEAN – **Mtwara MV, off Tanzania** • shell; 10°12.321' S, 40°32.742' E; 915 m depth; 19 Aug. 2024; stn SO306 / GeoB 26132-1; video box core; SMF 376585 (Fig. 22C–D).

Paratypes

SW INDIAN OCEAN – **Mtwara MV, off Tanzania** • 4 shells; same data as for holotype; SMF 376586 (Fig. 22A–B, E–G, M–N), SMF 376623 (Fig. 22H–L).

Description

PROTOCONCH. Absent, characteristics are unknown.

TELEOCONCH. Funnel-shaped with slightly concave posterior outline and straight or slightly convex anterior outline in side view, oblong apertural cross-section; oblong, apical foramen, length about 15% of aperture; sculpture of obliquely aligned, flattened, minute granules, forming wavy patterns across shell face; occasionally linear, curved, bifurcate or forming quincunx alignments, adapical granules subcircular, abapically strongly elongate; growth margins absent; apertural plane flat. Internally smooth; large triangular, slightly curved septum, obliquely placed, covering about 60% of interior, foramen anteriorly; broad commarginal muscle scar; margin sharp, smooth.

VARIATION. The type set of five shells show a similar outline, but the sculpture is variable: in some the granules are more arranged in a quincunx pattern, in others they form wavy lines.

Differential diagnosis

Placement in the genus *Cornisepta* is based on the similarity with various congeneric species: *C. microphyma* Dautzenberg & Fischer, 1896 and *C. rostrata* (Seguenza, 1863) both from the NE Atlantic Ocean and *C. acuminata* (Watson, 1883) from the NW Atlantic Ocean. The apex of *C. rostrata* strongly leans to the posterior and its granules are finely aligned in oblique axial lines (Hoffman & Freiwald 2023); the present species has its apex placed more centrally and has a complex and more variable pattern. The apex of *C. microphyma* also strongly leans to the posterior and its granules are solely in a

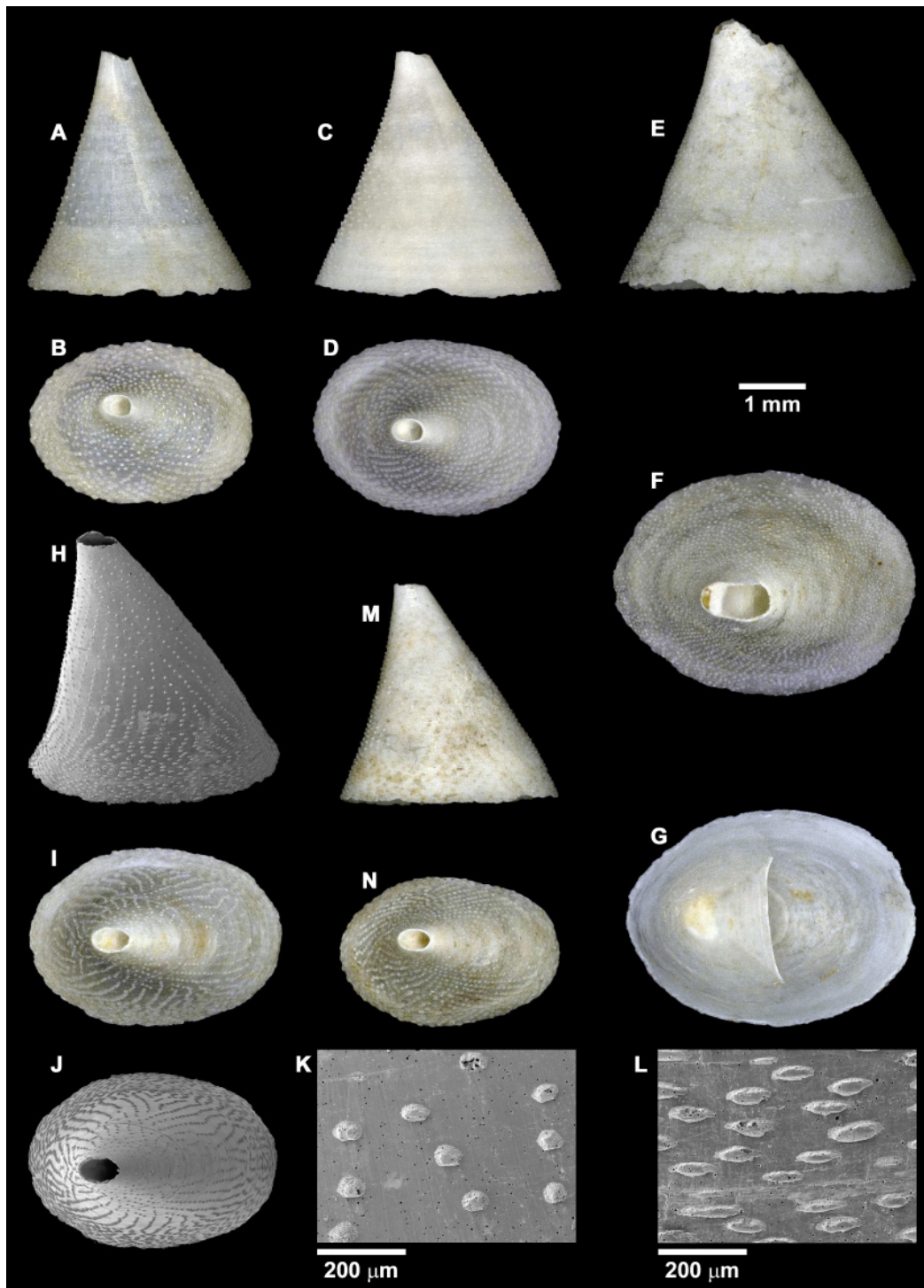


Fig. 22. *Cornisepta infundibulus* Hoffman sp. nov., Tanzania, Mtwara Mud Volcano, SO306 GeoB26137-1. **A–B.** Paratype (SMF 376586), H=3.7 mm, L=3.1 mm, W=2.5 mm. **A.** Side view. **B.** Apical view. **C–D.** Holotype (SMF 376585), H=3.7 mm, L=3.7, W=2.7 mm. **C.** Side view. **D.** Apical view. **E–G.** Paratype (SMF 376586), H=4.1 mm, L=4.5 mm, W=3.3 mm. **E.** Side view. **F.** Apical view. **G.** Apertural view with septum. **H–L.** Paratype (SMF 376623), H=4.0 mm, L=4.0 mm, W=2.9 mm. **H.** Side view. **I.** Apical view. **J.** Apical view (SEM). **K.** Adapical sculpture. **L.** Abapical sculpture near margin. **M–N.** Paratype (SMF 376586), H=3.3 mm, L=3.3 mm, W=2.3 mm. **M.** Side view. **N.** Apical view. Scale bars: A–J=1 mm; K–L = 200 μm.

quincunx arrangement; the present species has its apex placed more centrally and has a more variable pattern. *Cornisepta acuminata* has a similar outline but its granules are arranged solely in a quincunx arrangement and they are stronger and denser than in the present species. The remaining 15 known species of *Cornisepta* differ in having linear or pustular arrangements.

Genus *Zeidora* Adams, 1860

Type species

Zeidora calceolina Adams, 1860, type by monotypy (Adams 1860: 302), Recent, western Pacific, SW Indian Ocean.

Zeidora sp.

Fig. 23

Diagnosis

Small, flat, elongated, fragile fissurelliform shell; symmetric along length axis; apex at anterior end, planispiral. Shell colour white. Observed length 6.1 mm, height 2.5 mm, width 4.4 mm.

Material examined

SW INDIAN OCEAN – **Mtwara MV, off Tanzania** • 1 shell; 10°12.321' S, 40°32.742' E; 915 m depth; 19 Aug. 2024; stn SO306 / GeoB 26132-1; video box core; SMF 376587 (Fig. 23).

Description

PROTOCONCH. Broken, convolved, planispiral.

TELEOCONCH. With fast-expanding $\frac{1}{2}$ whorl with central selenizone and marginal slit. Outline ovate, convex with auricles on dorsal sides of apex/selenizone. Reticulate sculpture with regular commarginal lines, crossed by radial lines. Internally with large triangular flat septum with concave abapical margin. Imprint of selenizone and thin septum at adapical end of selenizone.

Remarks

We refrain from naming the single fragmentary shell although we probably deal with an unnamed species. A similar species is *Z. pussa* Simone & Cunha, 2014 from off Brazil in the western Atlantic Ocean.



Fig. 23. *Zeidora* sp. (SMF 376587), Tanzania, Mtwara Mud Volcano, GeoB26137-1, H=2.5 mm, L=6.1 mm, W=4.4 mm. **A.** Side view. **B.** Dorsal view. **C.** Apertural view.

Superfamily Scissurelloidea Gray, 1847

Family Anatomidae McLean, 1989

Genus *Anatoma* Woodward, 1859

Type species

Scissurella crispata Fleming, 1828, Recent, NE Atlantic, by monotypy.

Anatoma agulhasensis (Thiele, 1925)

Fig. 24

Scissurella agulhasense Thiele, 1925: 41–42, pl. 13 fig. 2.

Anatoma agulhasensis – Herbert 1986: 611–613, figs 3, 11–14; 2015: 11. — Geiger 2012: 744–751, figs 597–603.

Diagnosis

Small, elevated, thin, fragile anatomid shell with reticulated sculpture on prosocline, globose whorls; strongly convex shoulder of whorls; selenizone with slit, deep open umbilicus. Shell colour white. Maximum height 3 mm, width 3 mm.

Material examined

SW INDIAN OCEAN – **Mtwara MV, off Tanzania** • 60 shells; stn SO306 / GeoB 26132-1; SaM 87729 (Fig. 24).

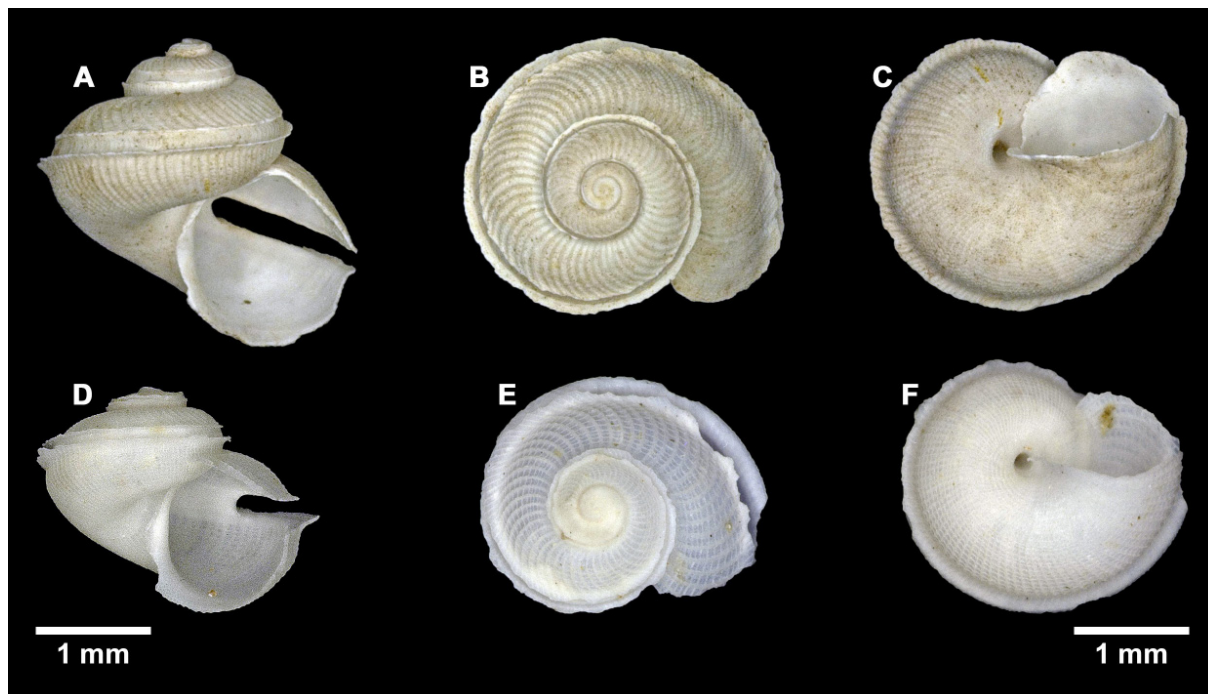


Fig. 24. *Anatoma agulhasense* (Thiele, 1925) (SaM 87729), Tanzania, Mtwara Mud Volcano, SO306 GeoB26132-1. **A–C.** H=2.7 mm, W=2.8 mm. **A.** Ventral view. **B.** Apical view. **C.** Abapical view. **D–F.** H=2.0 mm, W=2.5 mm. **D.** Ventral view. **E.** Apical view. **F.** Abapical view.

Description

PROTOCONCH. $\frac{3}{4}$ whorl with convex demarcated margin, weakly protruding nucleus.

TELEOCONCH. With 4 subcircular whorls: dome-shaped apex; selenizone slightly above periphery with sharp weakly protruding margin. Suture deep. Sculpture reticulated with strong prosocline ribs and weaker spiral. Umbilicus deep. Aperture sub-circular.

Remarks

The species is known from South Africa, Mozambique, Tanzania and the Comoros (Herbert 1986; Geiger 2012; own observations).

Anatoma japonica (Adams, 1862)

Fig. 25

Anatomus japonicus Adams, 1862: 347.

Anatoma ? *japonica* – Herbert 1986: 617-619, figs 5, 18–20; 2015: 11.

Anatoma japonica – Geiger 2012: 926-942, figs 749–760.

Diagnosis

Small, depressed, thin, fragile anatomid shell with fine reticulated sculpture on prosocline whorls; weakly convex sloping shoulder of whorls; selenizone with slit; deep narrow umbilicus. Shell colour white. Maximum height 4 mm, width 5 mm.

Material examined

SW INDIAN OCEAN – **Mtwara MV, off Tanzania** • 12 shells; 10°12.321' S, 40°32.742' E; 915 m depth; 19 Aug. 2024; stn SO306 / GeoB 26132-1; video box core; SaM 87730 (Fig. 25).

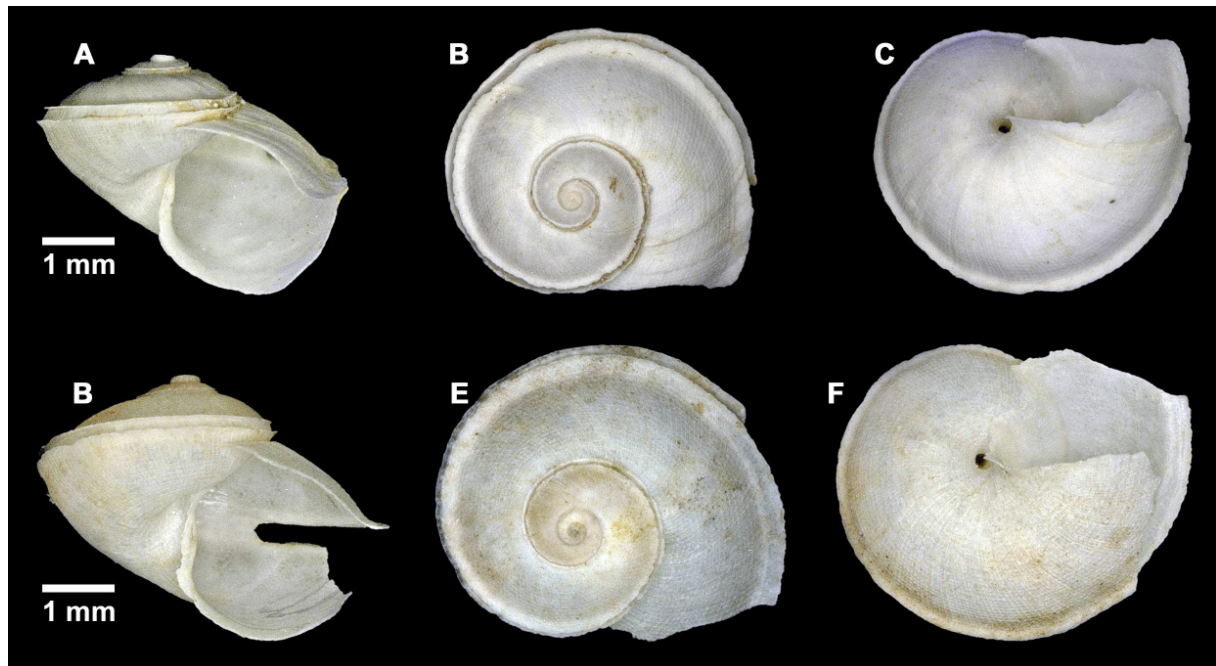


Fig. 25. *Anatoma japonica* (Adams, 1862) (SaM 87730), Tanzania, Mtwara Mud Volcano, SO306 GeoB26132-1. **A–C.** H=3.3 mm, W=4.3 mm. **A.** Ventral view. **B.** Apical view. **C.** Abapical view. **D–F.** H=3.7 mm, W=4.7 mm. **D.** Ventral view. **E.** Apical view. **F.** Abapical view.

Description

PROTOCONCH. $\frac{3}{4}$ whorl with convex demarcated margin, weakly protruding nucleus.

TELEOCONCH. With $3\frac{1}{2}$ angular whorls; flattened apex; sloping shoulders. Suture deep. Sculpture with fine flexuous riblets and spiral cords of equal strength. Aperture angular.

Remarks

The species is known from the Pacific Ocean and the western Indian Ocean (Adams 1862; Herbert 1986; Geiger 2012).

Anatoma chaki Hoffman sp. nov.

urn:lsid:zoobank.org:act:276F81CB-90BE-4D78-B120-0E72759C53AA

Fig. 26

Diagnosis

Small, elevated, thin, fragile anatomid shell with weak sculpture on globose whorls, selenizone with slit, deep open umbilicus. Shell colour white. Maximum height 2.6 mm, width 2.8 mm.

Etymology

‘*Chaki*’ is ‘chalk’ (noun in apposition) in Swahili, indicating the appearance of the external surface.

Type material

Holotype

SW INDIAN OCEAN – **Mtwara MV, off Tanzania** • shell; 10°12.321' S, 40°32.742' E; 915 m depth; 19 Aug. 2024; stn SO306 / GeoB 26132-1; video box core; SMF 376588 (Fig. 26E–G).

Paratypes

SW INDIAN OCEAN – **Mtwara MV, off Tanzania** • 16 shells; same data as for holotype; SMF 376589 (Fig. 26A–D), SMF 376624 (Fig. 26H–M) • 17 shells; stn SO306 / GeoB 26152-1; SMF 376590 • 1 shell; same locality; M.342065.

Description

PROTOCONCH. $\frac{3}{4}$ whorl with convex demarcated margin, weakly protruding nucleus; sculpture reticulated, nucleus hexagonal network; radially aligned cells towards margin; maximum diameter 180 μ m.

TELEOCONCH. With $3\frac{1}{2}$ subcircular whorls: first whorl quickly expanding, yielding dome-shaped apex; selenizone slightly above periphery with sharp weakly protruding margins; regularly spaced concave riblets. Suture deeply impressed slightly below periphery of preceding whorl. Sculpture fine, curved, axial riblets on first whorl, quickly fading in subsequent whorls, irregular convex axial margins on shoulder, fewer but stronger on ultimate whorl; weak spiral cordlets on globose shoulder; sculpture below selenizone with flexuous growth lines, few very weak spiral cordlets; weak spiral lines in umbilical area. Umbilicus deep, open with sharp, spiral keel which ends obliquely on columella. Aperture subcircular, pointed adapically; peristome complete, lip sharp, columellar lip wide at base, parietal lip demarcated, loosely connected to penultimate whorl; slit depth about 60° of last whorl; inside smooth.

Differential diagnosis

Placement in the genus *Anatoma* is based on the similarity with the type species, which is different by a strong reticulated sculpture. The present species only has weak sculpture. *Anatoma agulhasensis*

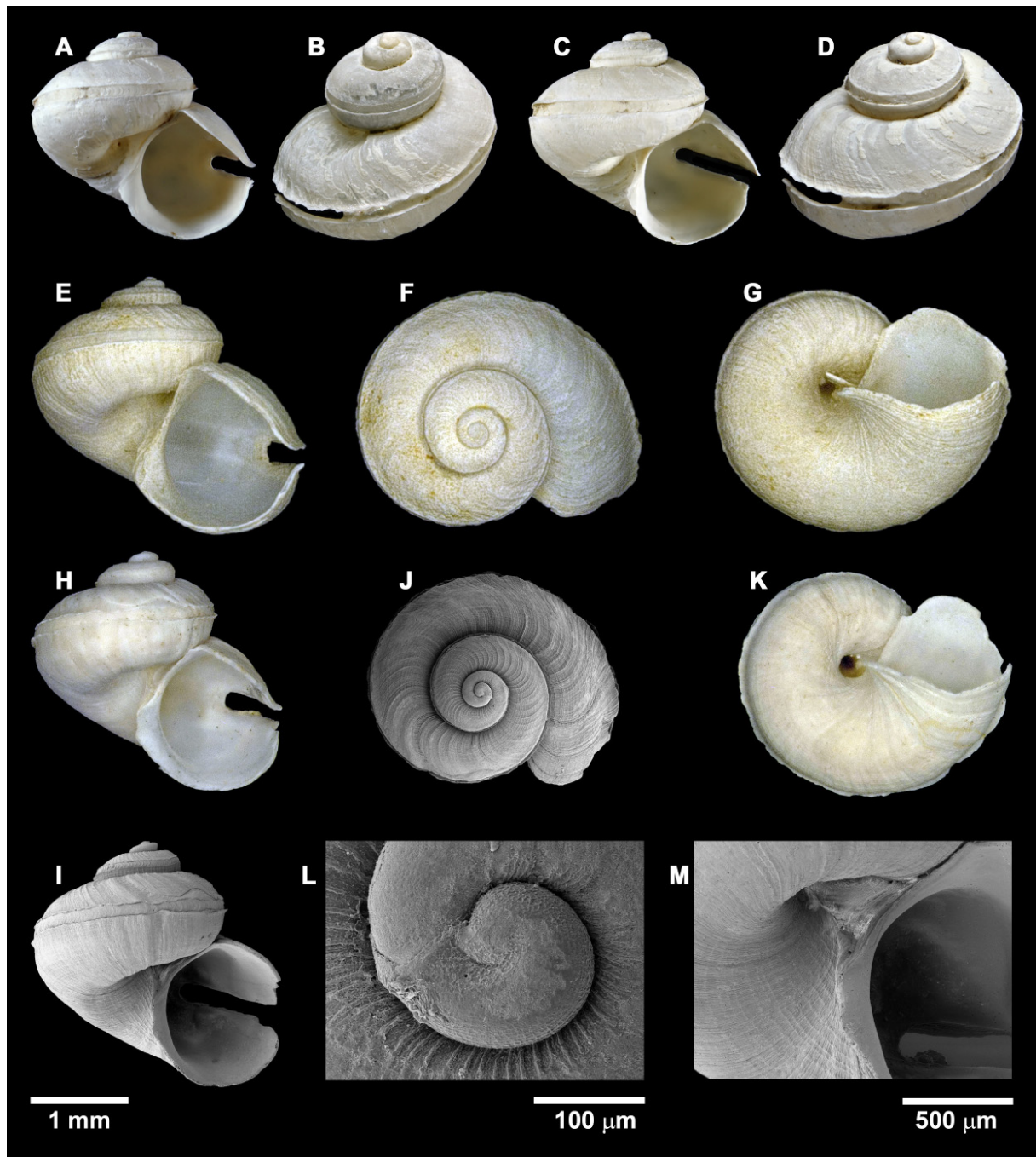


Fig. 26. *Anatoma chaki* Hoffman sp. nov., Tanzania, Mtwara Mud Volcano. **A–B.** Paratype (SMF 376589), GeoB 26132-1, H=2.1 mm, W=2.3 mm. **A.** Ventral view. **B.** External view. **C–D.** Paratype (SMF 376589), same locality, H=2.2 mm, W=2.3 mm. **C.** Ventral view. **D.** External view. **E–G.** Holotype (SMF 376588), GeoB 26132-1, H=2.6 mm, W=2.8 mm. **E.** Ventral view. **F.** Apical view. **G.** Abapical view. **H–M.** Paratype (SMF 376624), same locality, H=2.5 mm, W=2.5 mm. **H.** Ventral view. **I.** Ventral view (SEM). **J.** Apical view. **K.** Abapical view. **L.** Protoconch diameter 190 μ m. **M.** Umbilical view. Scale bar: A–K=1 mm; L–M=500 μ m.

(Thiele, 1925) from the SW Indian Ocean has a similar outline but has a strong reticulated sculpture covering the full shell (Geiger 2012: 744–751, figs 597–603). *Anatoma paucisculpta* Hoffman, Kniesz, Martínez Arbizu & Kihara, 2022 from hydrothermal vent habitats in the central Indian Ocean has few axial and little spiral sculpture and widely protruding margins of the selenizone (Hoffman *et al.* 2022: 155, fig. 11). The current species also has a weak sculpture, but it has weak margins on the selenizone and a different outline. All remaining known species have distinct reticulated sculptures (see for example Geiger 2012: vol. 2).

Family Scissurellidae Gray, 1847

Genus *Satondella* Bandel, 1998

Type species

Satondella minuta Bandel, 1998, type by original designation, Recent, western Pacific Ocean (Bandel 1998: 65; Geiger 2012: 682–684).

Satondella goudi Geiger, 2012

Fig. 27

Satondella goudi Geiger, 2012: 679–681, figs 639–640.

Diagnosis

Very small, weakly elevated, thin, fragile, scissurellid shell with convex, quickly expanding whorls; coarse, sharp axial sculpture; deep open umbilicus. Height 1.1 mm, width 1.6 mm. Shell colour white. Maximum height 2.0 mm, width 2.5 mm.

Material examined

SW INDIAN OCEAN – **Mtwara MV, off Tanzania** • 1 shell; 10°12.321' S, 40°32.742' E; 915 m depth; 19 Aug. 2024; stn SO306 / GeoB 26132-1; video box core; SMF 376591 (Fig. 27).

Description

PROTOCONCH. $\frac{3}{4}$ whorl with flexuous demarcated margin, weakly protruding nucleus.

TELEOCONCH. With $1\frac{1}{2}$ whorls with subcircular cross-section; flattened apex; sculpture of sharp prosocline ribs and weaker spiral lines. Foramen with sharp protruding margin, at about 30° from margin of lip;

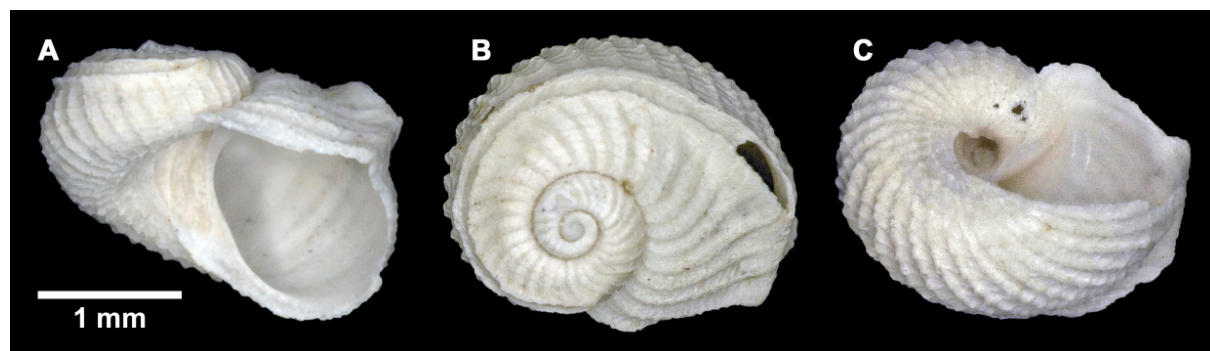


Fig. 27. *Satondella goudi* Geiger, 2012 (SMF 376591), Tanzania, Mtwara Mud Volcano, GeoB26132-1, H=2.0 mm, W=2.5 mm. **A.** Ventral view. **B.** Apical view. **C.** Abapical view.

selenizone length of about one whorl, with concave regular ribs. Umbilical area with sharp keel; parietal margin with strong curved rib; interior smooth with weak imprint of external sculpture.

Remarks

The species is known from three specimens, the holotype and one paratype from Indonesia and one specimen from southern Madagascar (Geiger 2012: 679–681). The distribution is hereby extended to off Tanzania.

Genus *Sinezona* Finlay, 1926

Type species

Schismope brevis Hedley, 1904, type by original designation, Recent, off New Zealand (Hedley 1904: 90).

Sinezona macleani Geiger, 2006
Fig. 28

Sinezona macleani Geiger, 2006: 16–19, figs 12–13.

Sinezona macleani – Geiger 2012: 495–500, figs 375–378.

Diagnosis

Very small, weakly elevated, thin, fragile, smooth scissurellid shell with convex, quickly expanding whorls; fine reticulate sculpture; deep open umbilicus. Shell colour white. Maximum height 2.6 mm, width 2.9 mm.

Material examined

SW INDIAN OCEAN – **Mtwara MV, off Tanzania** • 8 shells; 10°12.321' S, 40°32.742' E; 915 m depth; 19 Aug. 2024; stn SO306 / GeoB 26132-1; video box core; SMF 376592 (Fig. 28).

Description

PROTOCONCH. $\frac{3}{4}$ whorl with convex demarcated margin, weakly protruding nucleus.

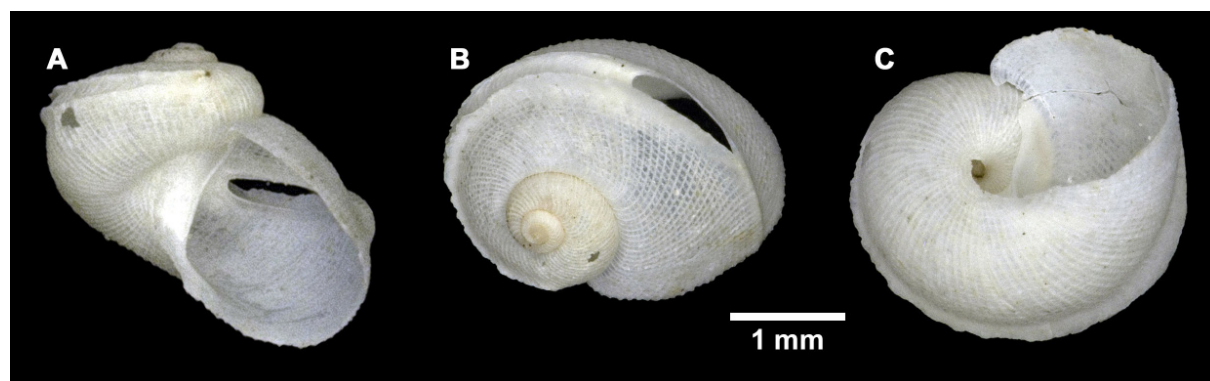


Fig. 28. *Sinezona macleani* Geiger, 2006 (SMF 376592), Tanzania, Mtwara Mud Volcano, GeoB26132-1, H=2.1 mm, W=2.3 mm. **A.** Ventral view. **B.** Apical view. **C.** Abapical view.

TELEOCONCH. With $2\frac{1}{4}$ whorls with subcircular cross-section, last whorl descending below periphery; flattened apex; sculpture reticulated by fine axial riblets and spiral cordlets of equal strength; umbilical area keeled, internally smooth; elongated, lanceolate, foramen with sharp margin at about 30° of margin of lip; length selenizone about one whorl.

Remarks

The species is known from the western Pacific Ocean to the western Indian Ocean off SE Africa (Geiger 2012).

Superfamily Trochoidea Rafinesque, 1815
Family Calliotropidae Hickman & McLean, 1990

Genus *Toroidia* Hoffman & Freiwald, 2018

Type species

Toroidia merianae Hoffman & Freiwald, 2018, type by original designation, Recent, off Mauritania, NE Atlantic (Hoffman & Freiwald 2018a: 90).

Toroidia marisindica Hoffman sp. nov.

urn:lsid:zoobank.org:act:0CFF40DE-985D-4AFF-B1EE-B56BDF85A852

Fig. 29

Diagnosis

Small, conoidal, elevated, fragile, calliotropid shell with weakly convex whorls, oblique axial ribs. Shell colour white. Maximum observed height 3 mm, width 2 mm.

Etymology

Marisindica (from the Latin ‘*maris*’ - ‘of the sea’, and ‘*indica*’ - ‘Indian’) refers to the Indian Ocean, the type locality.

Type material

Holotype

SW INDIAN OCEAN – **Mtwara MV, off Tanzania** • shell; $10^\circ 12.321' \text{ S}$, $40^\circ 32.742' \text{ E}$; 915 m depth; 19 Aug. 2024; stn SO306 / GeoB 26132-1; video box core; SMF 376613 (Fig. 29A–D).

Paratypes

SW INDIAN OCEAN – **Mtwara MV, off Tanzania** • 40 shells; same data as for holotype; SMF 376614 (Fig. 29E–H), SMF 376625.

Description

PROTOCONCH. Smooth, $\frac{3}{4}$ whorl with convex, weakly-demarcated margin, width 300 μm .

TELEOCONCH. With 4 whorls with subcircular cross-section; slightly cyrtconoidal outline, apical angle 58° . Suture deep. Sculpture on first whorl with orthocline or weakly prosocline axial riblets; the penultimate whorl with regular, sharp, axial ribs at about 30° with spire axis, strongest apically, fading abapically; the ultimate whorl with closely spaced riblets near margin of outer lip; ultimate and penultimate whorls with weak, broad spiral undulations. Umbilicus closed in mature specimens. Aperture sub-circular; outer lip prosocline, parietal lip absent, columellar lip well developed, sharply bent outward.

Differential diagnosis

Placement in the genus *Toroidia* is based on the morphological similarity with the type species. The type species has fine spiral cordlets and an open umbilicus; its protoconch has a diameter of 270 μm and the whorls are globose (Hoffman & Freiwald 2018a). The present species lacks an umbilicus and the spiral cordlets, its spire is more tightly coiled and its protoconch has a diameter of about 300 μm . *Toroidia toroides* (Hoffman, van Heugten & Lavaleye, 2011) from the Bay of Cadiz is very similar to *T. marisindica* Hoffman sp. nov., but it has spiral cordlets and a narrow open umbilicus (Hoffman *et al.* 2011b); *T. marisindica* sp. nov. has a closed umbilicus and weak spiral undulations. *Toroidia porcupinensis* Hoffman & Freiwald, 2018, from the Porcupine Basin off Ireland has strong spiral ribs and a first teleoconch whorl with opisthocline riblets; the present species only has a weak spiral sculpture and the riblets at the start of the teleoconch are orthocline or weakly prosocline (Hoffman & Freiwald 2018a). *Toroidia caboverdensis* Roosen & Trausel, 2025 from the Cape Verde Islands is similar to *T. toroides*, but it has a narrow open umbilicus and clear spiral cordlets. *Toroidia carolinensis* Roosen & Trausel, 2024, from off North Carolina, U.S.A. has a closed umbilicus but has sharp spiral cords and closely spaced axial ribs; the present species has a weak spiral sculpture and has less dense axial riblets.

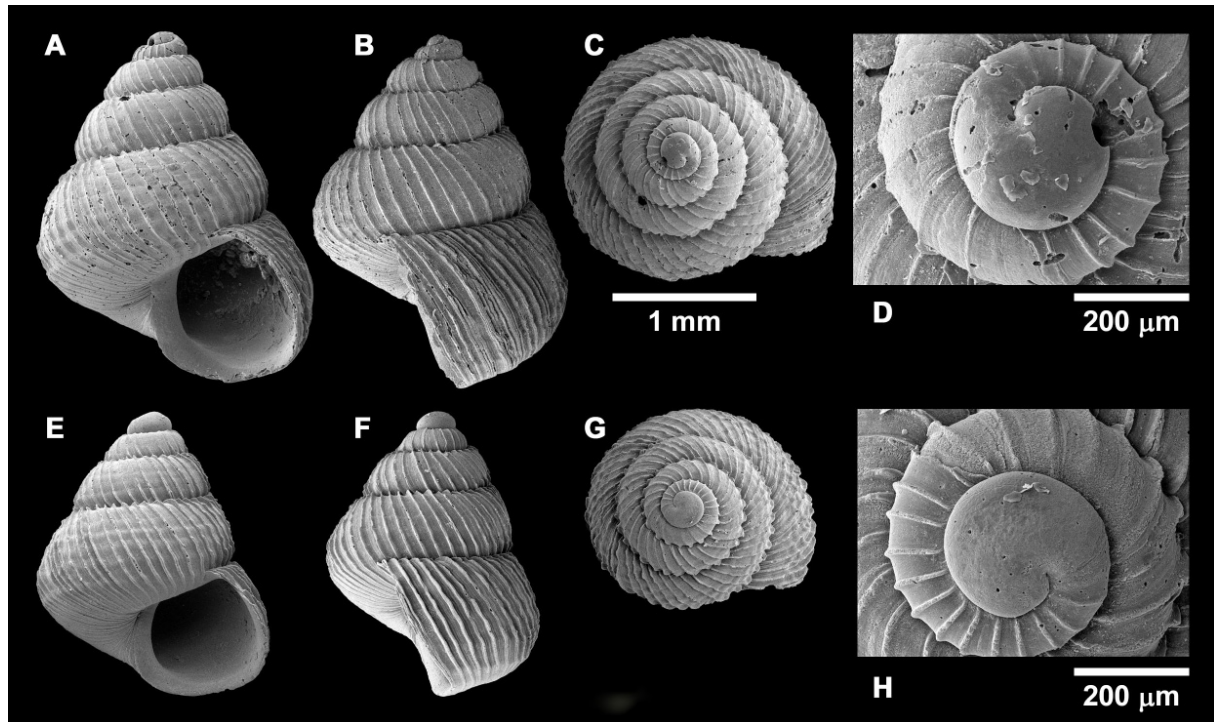


Fig. 29. *Toroidia marisindica* Hoffman sp. nov., Tanzania, Mtwara Mud Volcano, GeoB26132-1. **A–D.** Holotype (SMF 376613), H=2.5 mm, W=1.8 mm. **A.** Ventral view. **B.** Side view. **C.** Apical view. **D.** Protoconch diameter 310 μm . **E–H.** Paratype (SMF 376625), H=2.0 mm, W=1.6 mm. **E.** Ventral view. **F.** Side view. **G.** Apical view. **H.** Protoconch diameter 300 μm .

Family Skeneidae Clark, 1851

Genus *Skenea* Fleming, 1825

Type species

Helix serpuloides Montagu, 1808, by subsequent designation, Recent, NW Europe.

Skenea kitovu Hoffman sp. nov.

urn:lsid:zoobank.org:act:AD5E90CE-2CF6-49EE-96CA-0401419BDD47

Fig. 30

Diagnosis

Very small, weakly elevated, thin, fragile, smooth skeneiform shell with convex whorls, deep open umbilicus and smooth polished apex. Shell colour white. Maximum height 1.0 mm, width 1.2 mm.

Etymology

‘*Kitovu*’ is ‘umbilicus’ (noun in apposition) in Swahili, highlighting the deep open umbilicus.

Type material

Holotype

SW INDIAN OCEAN – **Mtwara MV, off Tanzania** • shell; 10°12.259' S, 40°32.682' E; 867 m depth; 23 Aug. 2024; stn SO306 / GeoB 26152-1; video box core; SMF 376593 (Fig. 30A–C).

Paratypes

SW INDIAN OCEAN – **Mtwara MV, off Tanzania** • 23 shells; same data as for holotype; SMF 376594 (Fig. 30D–I) • 10 specimens and shells; same location as for holotype; M.342066.

Description

PROTOCONCH. Smooth, glossy, $\frac{3}{4}$ whorls with convex demarcated margin, weakly protruding nucleus, diameter 280 μ m.

TELEOCONCH. With $1\frac{1}{2}$ whorls with subcircular cross-section; cyrtokonoidal apex. Base whorl with weak keel abapically. Suture deep at periphery on first whorl; descending in last $\frac{1}{2}$ whorl. Surface smooth, somewhat glossy, with very fine numerous prosocline growth lines. Aperture sub-circular, angular adapically, weakly angular abapically; peristome complete, lip sharp, prosocline, parietal lip demarcated, firmly connected to penultimate whorl.

Differential diagnosis

Placement in the genus *Skenea* is uncertain as the genus comprises a wide morphological variety. We are not aware of a similar skeneid with an elevated outline and without spiral sculpture on the shell face or umbilicus. The South African *Skenea fuscomaculata* (Sowerby III, 1892) lives in shallow water down to a depth of 32 metres. This species has a weakly elevated spire with pink blotches and regular cordlets (Herbert 2015: 43, figs 4n–p, 5m–o); the present species is more elevated, white and smooth. The South African *Dikoleps farica* (Bartsch, 1915) is translucent white but has a strong umbilical keel and fine cordlets (Herbert 2015: 42, fig. 5d–f); the keel in the umbilical area of the present species is weak and it lacks a spiral sculpture. A very similar species is *Skenea peterseni* (Friele, 1877) from the NE Atlantic: the species is small (width less than 2 mm), smooth with an umbilical keel with cordlets and narrow, tortuous umbilicus (Warén 1991: 60–61, figs 3f, 4a–b). In contrast, the present species has a weaker keel without cordlets and its umbilicus is wide open and deep.

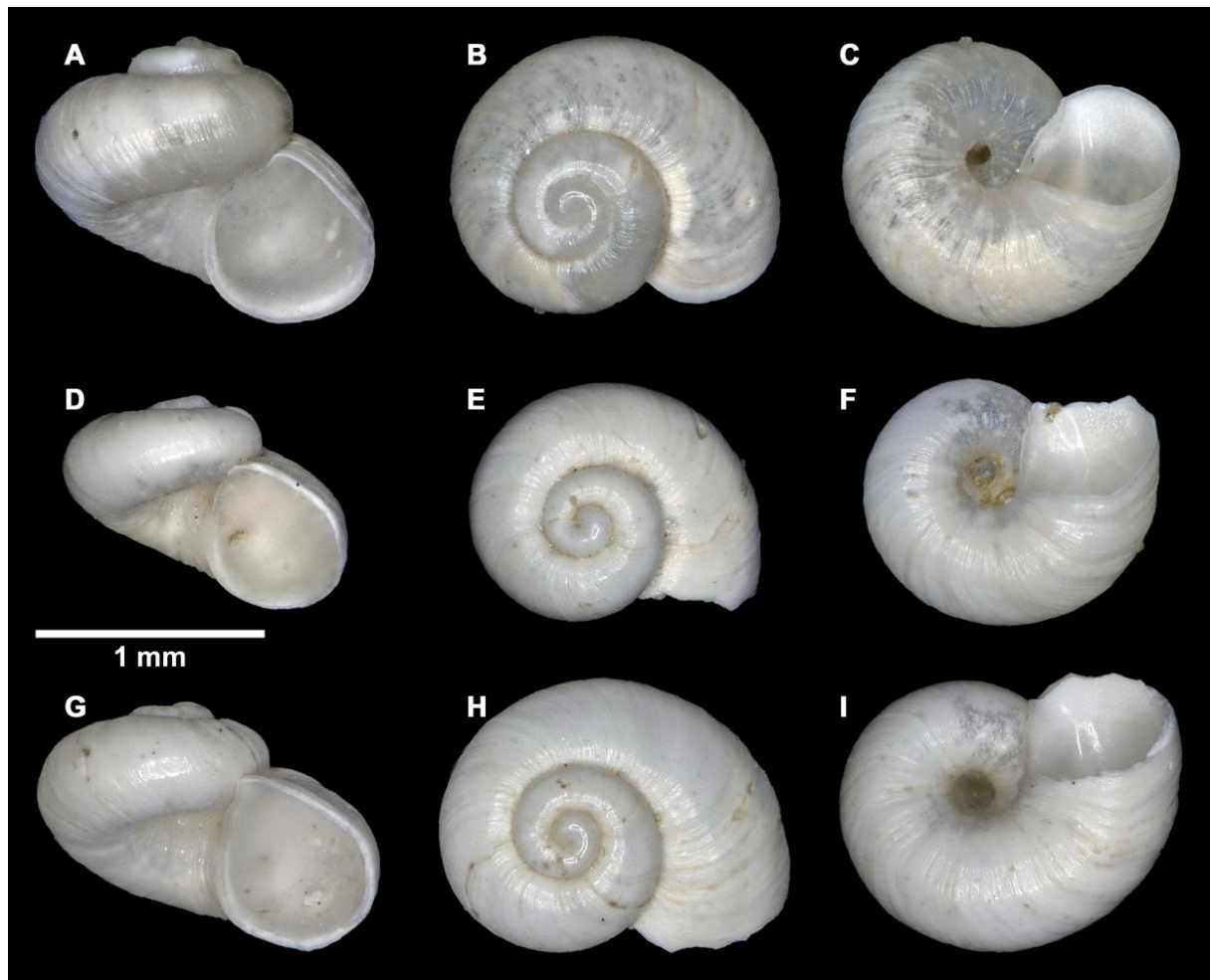


Fig. 30. *Skeneia kitovu* Hoffman sp. nov., Mtwara Mud Volcano off Tanzania, SO306 GeoB 26152-1. **A–C.** Holotype (SMF 376593), H=1.2 mm, W=1.3 mm. **A.** Ventral view. **B.** Apical view. **C.** Abapical view. **D–F.** Paratypes (SMF 376594). **D–F.** H=0.9 mm, W=1.2 mm. **D.** Ventral view. **E.** Apical view. **F.** Abapical view. **G–I.** H=1.2 mm, W=1.3 mm. **G.** Ventral view. **H.** Apical view. **I.** Abapical view.

Genus *Seamountiella* Rubio, Gofas & Rolán, 2019

Type species

Tinostoma azorica Dautzenberg & Fischer, 1896 accepted as *Seamountiella azorica* (Dautzenberg & Fischer, 1896) (Dautzenberg & Fischer 1896: 495; Rubio *et al.* 2019: 251), type by original designation, Recent, Azores, Atlantic Ocean.

Seamountiella laini Hoffman sp. nov.

urn:lsid:zoobank.org:act:D3C4F5D1-6AD3-42F4-AE46-23BCC66EEC0D

Fig. 31

Diagnosis

Small, flattened, strong, smooth skeneimorph shell with convex whorls, triangular hole in parietal callus. Shell colour white. Observed maximum height 3 mm, width 5 mm.

Etymology

‘*Laini*’ is ‘smooth’ (subjective) in Swahili, highlighting the glossy shell face.

Type material

Holotype

SW INDIAN OCEAN – **Mtwara MV, off Tanzania** • shell; 10°12.321' S, 40°32.742' E; 915 m depth; 19 Aug. 2024; stn SO306 / GeoB 26132-1; video box core; SMF 376615 (Fig. 31A–B).

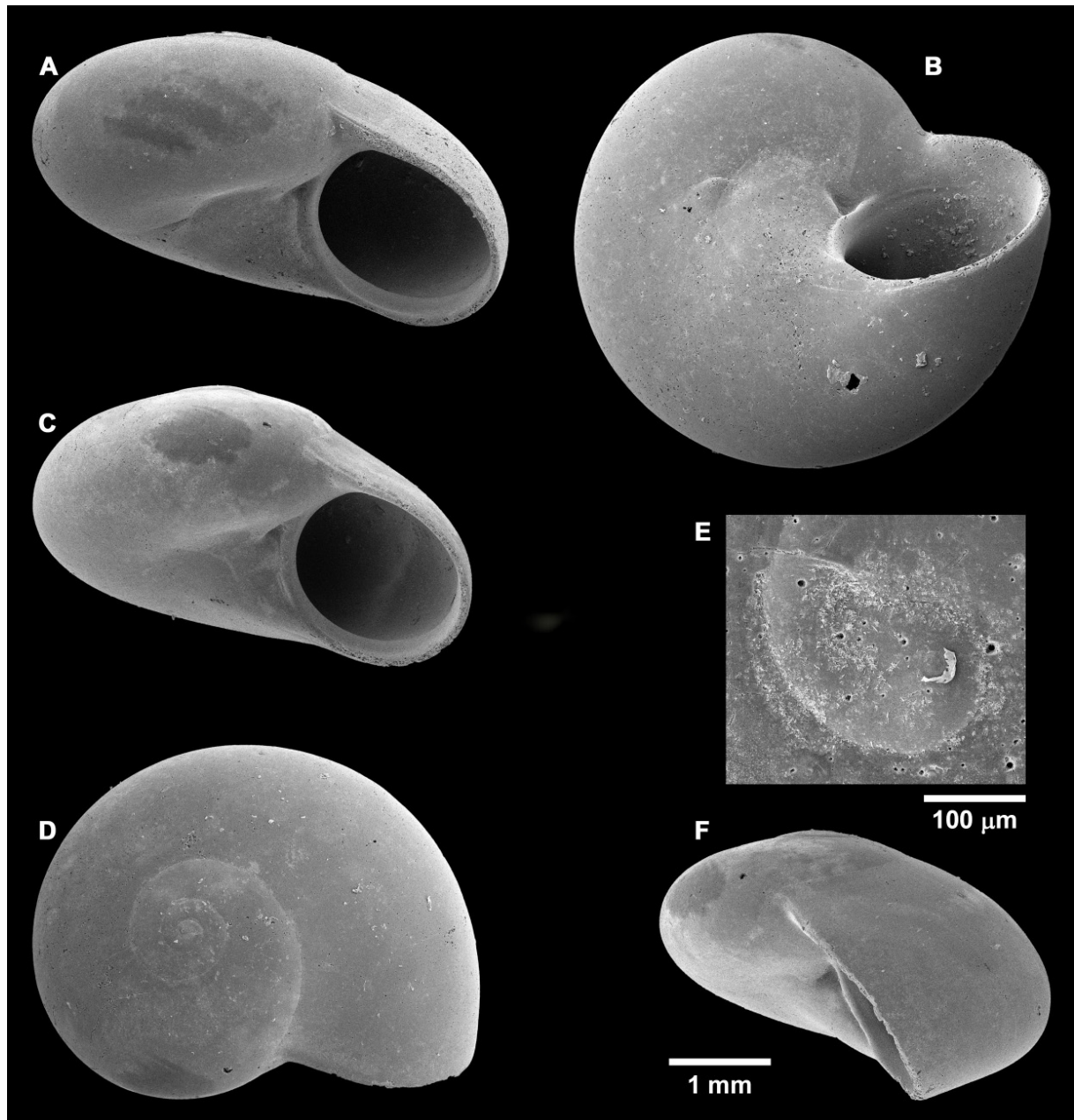


Fig. 31. *Seamountiella laini* Hoffman sp. nov., Tanzania, Mtwara Mud Volcano, GeoB26132-1. **A–B.** Holotype (SMF 376615), H=2.9 mm, W=4.7 mm. **A.** Ventral view. **B.** Abapical view. **C–F.** Paratype (SMF 376626), same location as for the holotype, H=2.8 mm, W=4.3 mm. **C.** Ventral view. **D.** Apical view. **E.** Protoconch diameter 250 µm. **F.** Side view. Scale bar: A–D, F=1 mm; E = 100 µm.

Paratypes

SW INDIAN OCEAN – **Mtwara MV, off Tanzania** • 11 shells; same data as for holotype; SMF 376616, SMF 376626 (Fig. 31C–F).

Description

PROTOCONCH. Smooth, $\frac{3}{4}$ flattened whorl with convex demarcated margin; flat nucleus, diameter 250 μm .

TELEOCONCH. With $2\frac{1}{2}$ whorls with ovate cross-section; cyrtconoidal apex; last whorl descending below penultimate whorl, glossy white, prosocline, growth margins absent, umbilicus absent, triangular hole at parietal lip. Suture smeared, very shallow. Aperture circular with internal rim; peristome complete, callus thick; pointed area filled by callus at joint with penultimate whorl.

Differential diagnosis

Placement in the genus *Seamountiella* is based on the strong similarity with the type species. The type species has a similar size, shape, and has a similar parietal perforation, but it has a slightly raised apex, a strongly prosocline lip and a protoconch of 260–290 μm (Rubio *et al.* 2019); the present species has a more flattened spire, its lip is somewhat less prosocline and the diameter of the protoconch is 250 μm . Three more named species are known within *Seamountiella*. *Seamountiella dimidia* Rubio, Gofas & Rolán, 2019 from the Azorean seamounts and *S. mayottensis* Rubio, Gofas & Rolán, 2019 from Mayotte have a width less than 3 mm and lack the parietal perforation. *Seamountiella caledonica* Rubio, Gofas & Rolán, 2019 from New Caledonia has a width less than 3.1 mm and an umbilical chink; the present species is larger (up to 5 mm) and it lacks the umbilical chink.

Subclass Caenogastropoda Cox, 1960
Superfamily Triphoroidea Gray, 1847
Family Newtoniellidae Korobkov, 1955

Genus *Cerithiella* Verrill, 1882

Type species

Cerithium metula Lovén, 1846; type by typification of replaced name, Recent, NE Atlantic Ocean.

Cerithiella kupamba Hoffman sp. nov.

urn:lsid:zoobank.org:act:7724B768-7A54-4692-9C9C-A97BEF061CB7

Fig. 32

Diagnosis

Small, highly elevated, cerithiopsiform shell with opisthocline axial ribs on upper face of whorl, crossed by two weakly keeled cords with pointed nodules at crossings. A third smooth subsutural cord and smooth base. Suture chanellised. Holotype height 6.0 mm, width 1.9 mm. Colour white, dull.

Etymology

‘*Kupamba*’ (feminine adjective) is ‘decorated’ in Swahili, highlighting the elegant, elevated shell with regular sculpture.

Type material

Holotype

SW INDIAN OCEAN – **Mtwara MV, off Tanzania** • shell; 10°12.259' S, 40°32.682' E; 867 m depth; 23 Aug. 2024; stn SO306 / GeoB 26152-1; video box core; SMF 376595 (Fig. 32).

Paratypes

SW INDIAN OCEAN – **Mtwara MV, off Tanzania** • 6 shells (fragmentary); stn SO306 / GeoB 26137-1; SMF 376596.

Description

PROTOCONCH. In two growth stages, highly raised, initial $1\frac{1}{4}$ convex whorls, quickly expanding, loosely coiled, smooth, nucleus pointed upwards, greyish white; transition to second stage unclear; next $1\frac{1}{2}$ whorls tightly coiled, flattened outline, sculpture with about 18 sharp opisthocline ribs; transition to teleoconch uncertain.

TELEOCONCH. With conoidal outline, 7 angular whorls, impressed suture. Sculpture with two spiral cords, upper cord demarcating the shoulder, lower cord at periphery; about 15 opisthocline ribs with broad nodules at the intersections with the cords. On base ultimate whorl, a smooth, strong, spiral cord below the suture; below the cord a flattened shell face, with fine growth lines. Outer lip sharp, columella curved, callus thin; curved fasciole and open siphonal canal.

VARIATION. The ribs, cords and nodules vary in strength.

Differential diagnosis

Placement in the genus *Cerithiella* is based on the morphological similarity with the type species *C. metula*. The type species has a tightly coiled protoconch with a swollen nucleus, its ribs are stronger and more numerous (Bouchet & Warén 1993: 590–597); the present species has a loosely coiled protoconch with a pointed tip and its ribs are weaker. Another similar species from the NE Atlantic

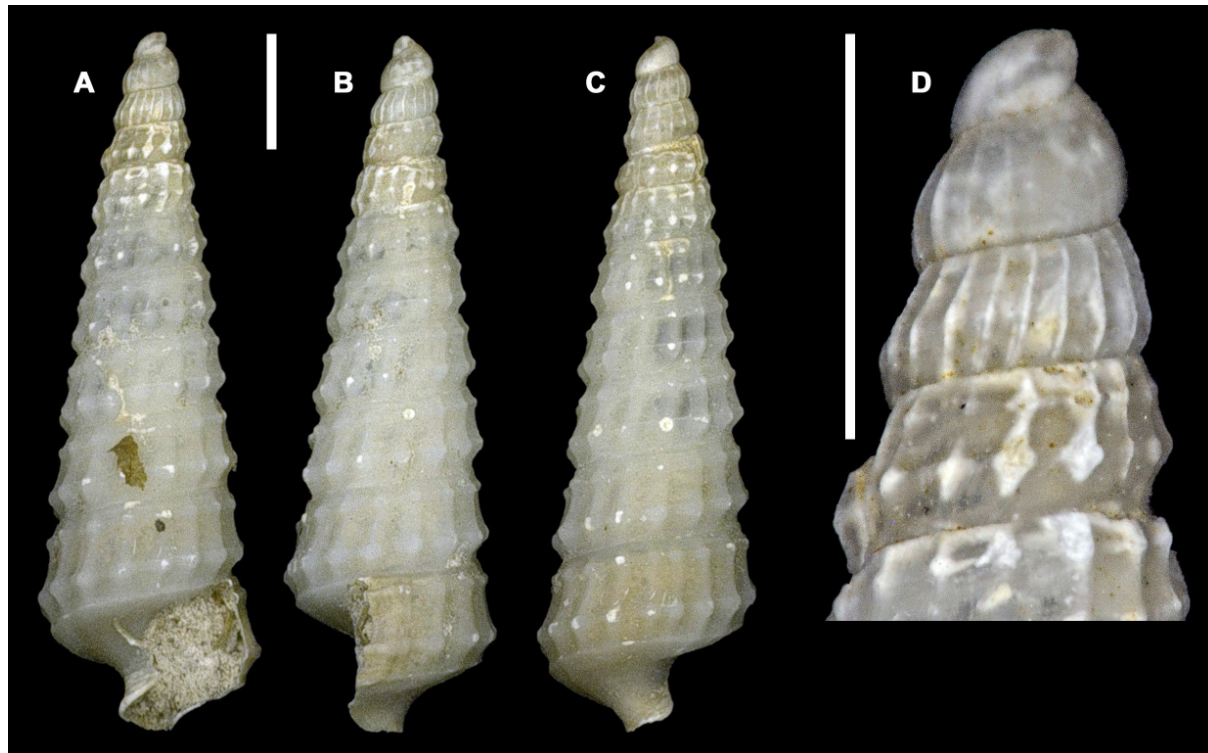


Fig. 32. *Cerithiella kupamba* Hoffman sp. nov., Tanzania, Mtwara Mud Volcano, SO306 GeoB26152-1. A–D. Holotype (SMF 376595), L=6.0 mm, W=1.9 mm. A. Ventral view. B. Side view. C. Dorsal view. D. Protoconch-1, L=550 µm; protoconch-2, L=950 µm. Scale bars: 1 mm.

is *C. amblytera* (Watson, 1880). This species has a raised cylindrical protoconch that is tightly coiled (Bouchet & Warén 1993: 597–599); the current species has a pointed, loosely coiled protoconch. *Cerithiella natalensis* Barnard, 1963 is also similar, but its protoconch has a blunt nucleus and bulbous second whorl and three cords on the upper face of the ultimate whorl (Barnard 1963: 126); the present species has only two cords and a different protoconch. The South African *C. argentea* Thiele, 1925 has a similar sculpture with two spiral cords but its protoconch has a bulbous nucleus (Thiele 1925: 122, pl. 9 fig. 22); the present species has an elevated semi-detached pointed nucleus. The eastern African *C. aethiopica* Thiele, 1925 has a similar raised nucleus of the protoconch as in the current species and its sculpture also has two spiral cords on the upper whorl face, but its upper cord is near the suture and the second cord is directly above the suture and close to the smooth subsutural cord (Thiele 1925: 122–123, pl. 9 fig. 23); the present species has its upper cord well below the suture and its second cord well above the suture. The Tanzanian *C. elata* Thiele, 1925 has a similar raised nucleus of the protoconch as in the current species, but its sculpture has one spiral cord on the upper whorl face below a long sloping shoulder (Thiele 1925: 123, pl. 10 fig. 1).

Superfamily Cingulopsoidea Fretter & Patil, 1958

Family Eatoniellidae Ponder, 1965

Genus *Eatoniella* Dall, 1876

Type species

Eatonia kerguelensis Smith, 1875, type by subsequent designation, Recent, off Kerguelen Island.

Eatoniella kahawa Hoffman sp. nov.

urn:lsid:zoobank.org:act:B910EB61-203D-43A5-BCC1-7CA28DEBB025

Fig. 33

Diagnosis

Small, elevated, strong, rissoiform shell. Observed maximum height 2 mm, width 1 mm. Colour dark brown with white blotches, fading to white in last whorl.

Etymology

‘*Kahawa*’ is ‘coffee’ (noun in apposition) in Swahili, highlighting the brown colour with white lip.

Type material

Holotype

SW INDIAN OCEAN – **Mtwara MV, off Tanzania** • specimen; 10°12.259' S, 40°32.682' E; 867 m depth; 23 Aug. 2024; stn SO306 / GeoB 26152-1; video box core; SMF 376597 (Fig. 33A–C).

Paratypes

SW INDIAN OCEAN – **Mtwara MV, off Tanzania** • 30 specimens + 300+ shells; same data as for holotype; SMF 376598–376599 (Fig. 33D–F), SMF 376628 (Fig. 33G–H) • 60 specimens; same data as for holotype; M.342064.

Description

PROTOCONCH. Eroded, about 1¼ weakly convex whorls with impressed suture, nucleus flattened, brown with white blotches.

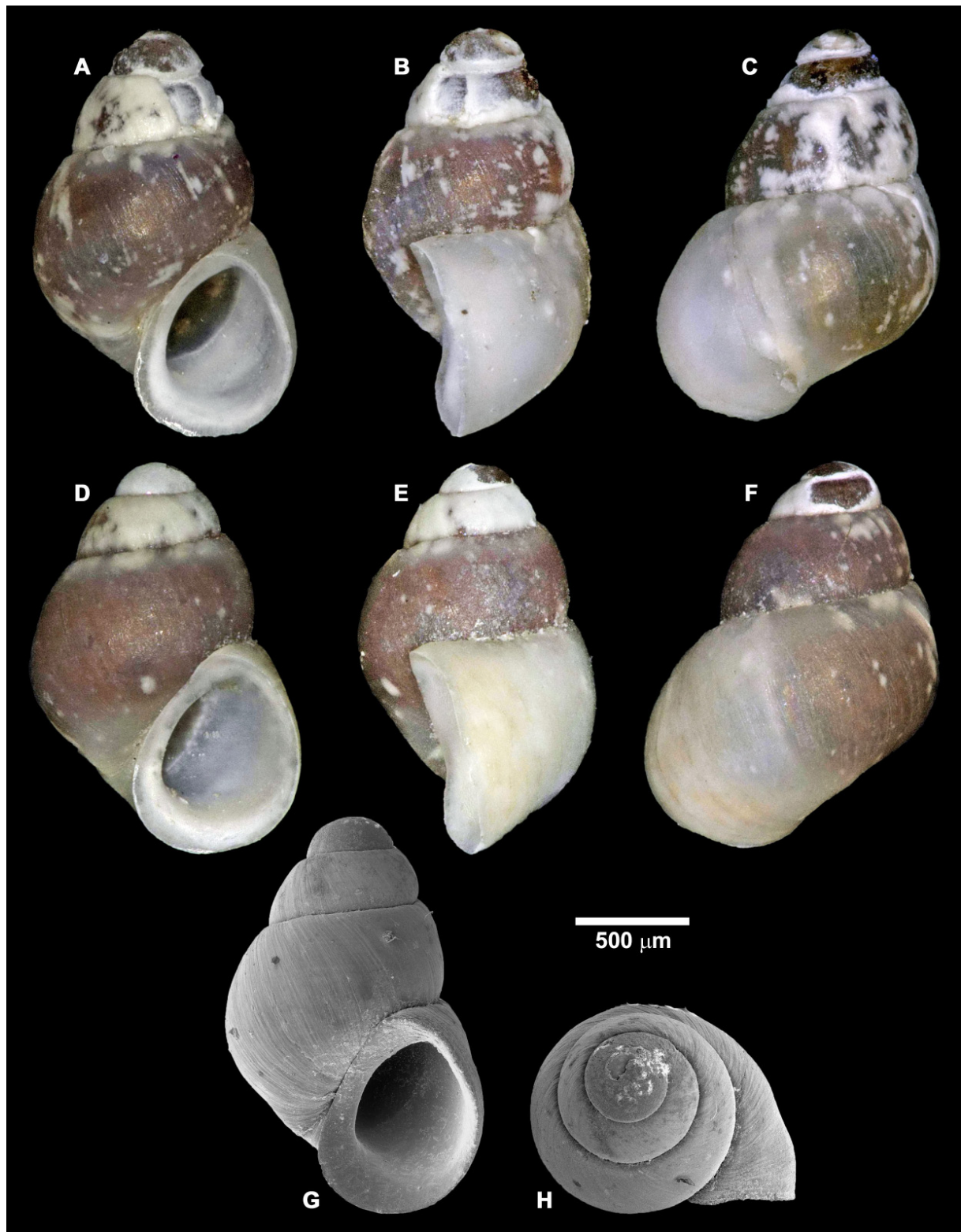


Fig. 33. *Eatoniella kahawa* Hoffman sp. nov., Tanzania, Mtwara Mud Volcano, SO306 GeoB 26152-1. A–C. Holotype (SMF 376597), L=1.6 mm, W=1.1 mm. A. Ventral view. B. Side view. C. Dorsal view. D–F. Paratype (SMF 376599), L=1.5 mm, W=1.1 mm. D. Ventral view. E. Side view. F. Dorsal view. G–H. Paratype (SMF 376628) (SEM), L=1.7 mm, W=1.1 mm. G. Ventral view. H. Apical view.

TELEOCONCH. Consists of $2\frac{1}{2}$ weakly convex whorls, cyrticonoid, deeply impressed suture, ultimate whorl descending. Sculpture smooth with many fine growth lines, prosocline, $15\text{--}20^\circ$ to spire axis. Aperture ovate, pointed adapically, peristome complete; blunt, bevelled lip, smooth; thick columellar and parietal callus with demarcated straight margin. Inside smooth, glossy. Periostracum absent. Operculum chitinous, brown, paucispiral, translucent.

SOFT PARTS. Not investigated.

VARIATION. Mainly in the colour pattern; frequently white blotches or smaller white or red spots on the shell face.

Differential diagnosis

Attempts to obtain mtDNA (*COI*) sequences failed. Placement in the genus *Eatoniella* is based on the morphological similarity with the type species. Species known from southern Africa include *E. thalia* (Bartsch, 1915), *E. capensis* (Thiele, 1912), *E. algoensis* (Thiele, 1912), and *E. afronigra* (Ponder & Worsfold, 1994). *Eatoniella thalia* is superficially similar, but it has a convex ultimate whorl that descends well below the periphery (Bartsch 1915) whereas the present species has a flattened whorl that aligns with the penultimate whorl. *Eatoniella capensis* is similar, but it has a more elevated spire with $4\frac{1}{2}$ whorls when adult and its aperture is more rounded (Thiele 1925); the present species is less elevated with $2\frac{1}{2}$ whorls and its aperture is slightly pointed adapically. *Eatoniella afronigra* is similar, but its whorls are more convex and the spire is more elevated; its shell is fragile, whitish (Ponder & Worsfold 1994). The present species has weakly convex whorls, and has a compact spire; its colour is predominantly brown. *Eatoniella algoensis* is similar but the spire is more elevated with almost 5 whorls; its shell is white-yellowish (Thiele 1925). The present species has a compact spire with fewer whorls, its colour is predominantly brown with white patches.

Habitat

The species was commonly associated with *Gigantidas tanzaniensis* sp. nov.; no specimens were found outside the mussel beds and it probably feeds by grazing; a possible food source could be bacteria. Most congeneric species live in shallow water and feed on algae. The presence of the present species on the deep Mtwara MV is unusual and unique.

Superfamily Abyssochrysoidea Tomlin, 1927

Family Provannidae Warén & Ponder, 1991

Genus *Provanna* Dall, 1918

Type species

Trichotropis (*Provanna*) *lomana* Dall, 1918, by monotypy, Recent, off California, USA, NE Pacific Ocean.

Provanna castanea Hoffman & Kihara sp. nov.

urn:lsid:zoobank.org:act:C07CAD7E-B31B-4E73-B275-A45B49DA9C1B

Figs 14E, 34

Diagnosis

Small, elevated, very fragile, rissoiform shell, decapitated and smooth. Observed maximum height 6 mm, width 5 mm. Colour white shell with chestnut-brown, somewhat glossy, periostracum. Young live-collected specimens with translucent shell and light brown or greenish periostracum.

Etymology

Castanea (from the Latin ‘*castanea*’ for ‘chestnut’) refers to the glossy chestnut brown surface.

Type material

Holotype

SW INDIAN OCEAN – **Mtwara MV, off Tanzania** • shell; 10°12.259' S, 40°32.682' E; 867 m depth; 23 Aug. 2024; stn SO306 / GeoB 26152-1; video box core; SMF 376600 (Fig. 34A–C).

Paratypes

SW INDIAN OCEAN – **Mtwara MV, off Tanzania** • 45 live-collected specimens + 3000+ shells; same data as for holotype; SMF 376601 (Fig. 34D–I) • 80 live-collected specimens and shells; same data as for holotype; M.342062.

Other material examined

SW INDIAN OCEAN – **Mtwara MV, off Tanzania** • 495 shells; stn SO306/GeoB 26132-1; SaM 87731 • 41 shells; stn SO306 / GeoB 26137-1; SaM 87732.

Description

PROTOCONCH. Missing or as partly dissolved internal cast, about 1 elevated whorl.

TELEOCONCH. Consists of two convex whorls, conoidal; shallow, impressed suture below periphery; shell surface frequently very thin, translucent. Sculpture smooth with many straightened, fine, growth lines, slightly prosocline. Aperture ovate, pointed adapically and abapically at joint of columella with outer lip, flattened abapically, lip sharp; thin columellar and parietal callus with concave margin. Inside smooth, very thin callus, matt.

OPERCULUM. Chitinous, translucent yellowish-brown, paucispiral.

SOFT PARTS. Not investigated.

VARIATION. Minor variations in width to length ratios are considered infra-specific. Live specimens have an olive green periostracum; empty shells are mostly covered with a chestnut-brown periostracum. The shells from the type locality are thin, fragile and translucent whereas those from GeoB 26132-1 and GeoB 26137-1 are strong and opaque.

Habitat

The species were commonly associated with *Gigantidas tanzaniensis* sp. nov., *Bathymacra nipponica* and *Enigmaticolus nipponensis* in the mussel beds (Fig. 14E) as well as on the surrounding rocky sea bottom. It probably feeds by grazing.

Molecular analyses

A single sequence of *COI* was obtained with fragment size of 500 bp, no indels or stop codons were found. Overall nucleotide frequencies were G (16.6%), C (20.6%), A (35.2%) and T (27.6%). While the sequence quality is not high enough for inclusion in our dataset, it was still sufficient for a successful BLAST search in GenBank, revealing a close relationship to *Provanna* sp. OM264355 with a pairwise identity of 94.1%.

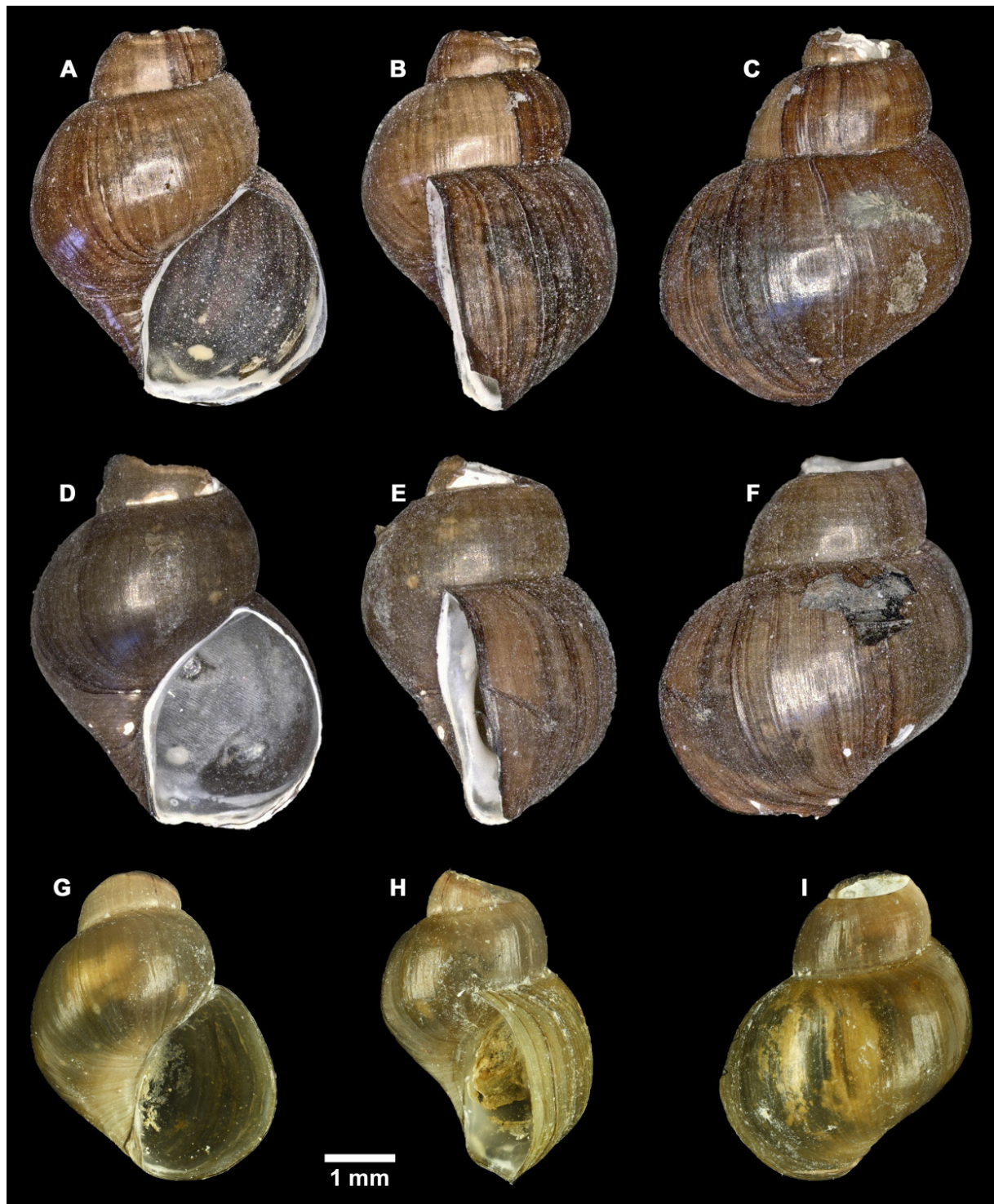


Fig. 34. *Provanna castanea* Hoffman & Kihara sp. nov., Tanzania, Mtwara Mud Volcano, SO306 GeoB 26152-1. **A–C.** Holotype (SMF 376600), L=5.3 mm, W=4.2 mm. **A.** Ventral view. **B.** Side view. **C.** Dorsal view. **D–F.** Paratypes (SMF 376601). **D–F.** L=5.3 mm, W=4.2 mm. **D.** Ventral view. **E.** Side view. **F.** Dorsal view. **G–I.** L=4.3 mm, W=3.5 mm. **G.** Ventral view. **H.** Side view. **I.** Dorsal view.

Differential diagnosis

Placement in the genus *Provanna* is based on morphological features such as the pointed lip at the base of the columella, the decapitated apex, and the strong periostracum (Better & Cordes 2023). The cold seep habitat is also typical for the genus. The external sculpture of congeneric species is very variable. *Provanna castanea* sp. nov. is a very smooth species similar to *P. laevis* Warén & Ponder, 1991, *P. glabrata* Sasaki, Ogura, Watanabe & Fujikura, 2016, *P. subglabra* Sasaki, Ogura, Watanabe & Fujikura, 2016, *P. kuroshimensis* Sasaki, Ogura, Watanabe & Fujikura, 2016, and *P. annae* Nekhaev, 2023. The northern Pacific species *P. laevis* has a more elongated shell with a matt periostracum (Warén & Ponder 1991: 53) whereas *P. castanea* is less elevated with a somewhat flattened abapical lip. *Provanna glabrata*, *P. subglabra* and *P. kuroshimensis* are northern Pacific species found off Japan and all possess a conical spire with flattened whorls (Sasaki *et al.* 2016), whereas the present species has more convex whorls. The northern Pacific *P. annae* has a similar thin shell, but whorls are less convex and the outer lip is rounded adapically (Nekhaev 2023: 5–10, fig. 2); *Provanna castanea* has a flattened base of the outer lip and its whorls are more convex.

***Provanna mzunguko* Hoffman sp. nov.**

urn:lsid:zoobank.org:act:5C388332-F0F4-4AFC-BD35-283FB18E846D

Fig. 35

Diagnosis

Small, elevated, fragile, buccinoiform shell, decapitated with strong spiral cords. Maximum height 6 mm, width 4 mm. Colour white shell with dark olive green, matt, periostracum.

Etymology

‘*Mzunguko*’ (noun in apposition) is Swahili for ‘spiral’ and refers to the spiral cords.

Type material**Holotype**

SW INDIAN OCEAN – **Mtwara MV, off Tanzania** • shell; 10°12.259' S, 40°32.682' E; 867 m depth; 23 Aug. 2024; stn SO306 / GeoB 26152-1; video box core; SMF 376602 (Fig. 35A–C).

Paratypes

SW INDIAN OCEAN – **Mtwara MV, off Tanzania** • 1 dried specimen + 19 shells; same data as for holotype; SMF 376603 (Fig. 35D–F).

Description

PROTOCONCH. Missing, characters are uncertain.

TELEOCONCH. Consists of 2½ convex whorls, conical; shallow, impressed suture well below periphery. Sculpture with 4–6 strongly protruding cords, one on the shoulder above the periphery, one below the periphery, one above the suture, 1–3 cords below the suture. Axial sculpture with nearly orthocline growth lines, slightly prosocline below suture. Aperture ovate, flared adapically and abapically, peristome complete, lip sharp; thin columellar and parietal lip with concave margin, indented by spiral cords; external lip with protrusions at spiral cords. Inside smooth, matt with strong imprint of external sculpture.

OPERCULUM. Translucent yellowish-brown, paucispiral.

SOFT PARTS. Not investigated.

VARIATION. Minor variations in width to length ratios are considered infra-specific. The number of cords varies from 4 to 6 cords; between shells, the strength of the cords is variable. Some colour variations in the periostracum are evident, some are olive green, others are reddish-brown.

Differential diagnosis

Placement in the genus *Provanna* is based on the similarity with congeners that have strong sculpture and the characteristic shape of the peristome (Betters & Cordes 2023: pl. 3). The generic placement is somewhat uncertain because we have been unable to obtain DNA sequences; this placement could be confirmed once suitable DNA samples become available in the future. The present species has a unique sculpture with solely spiral cords. Similar species are *Provanna cingulata* Chen, Watanabe & Ohara, 2018 from the Mariana Trough, *P. beebei* Linse, Nye, Copley & Chen, 2019 and *P. cooki* Linse, Nye, Copley & Chen, 2019 from the Caribbean Sea. *Provanna cingulata* has a similar outline, but its sculpture

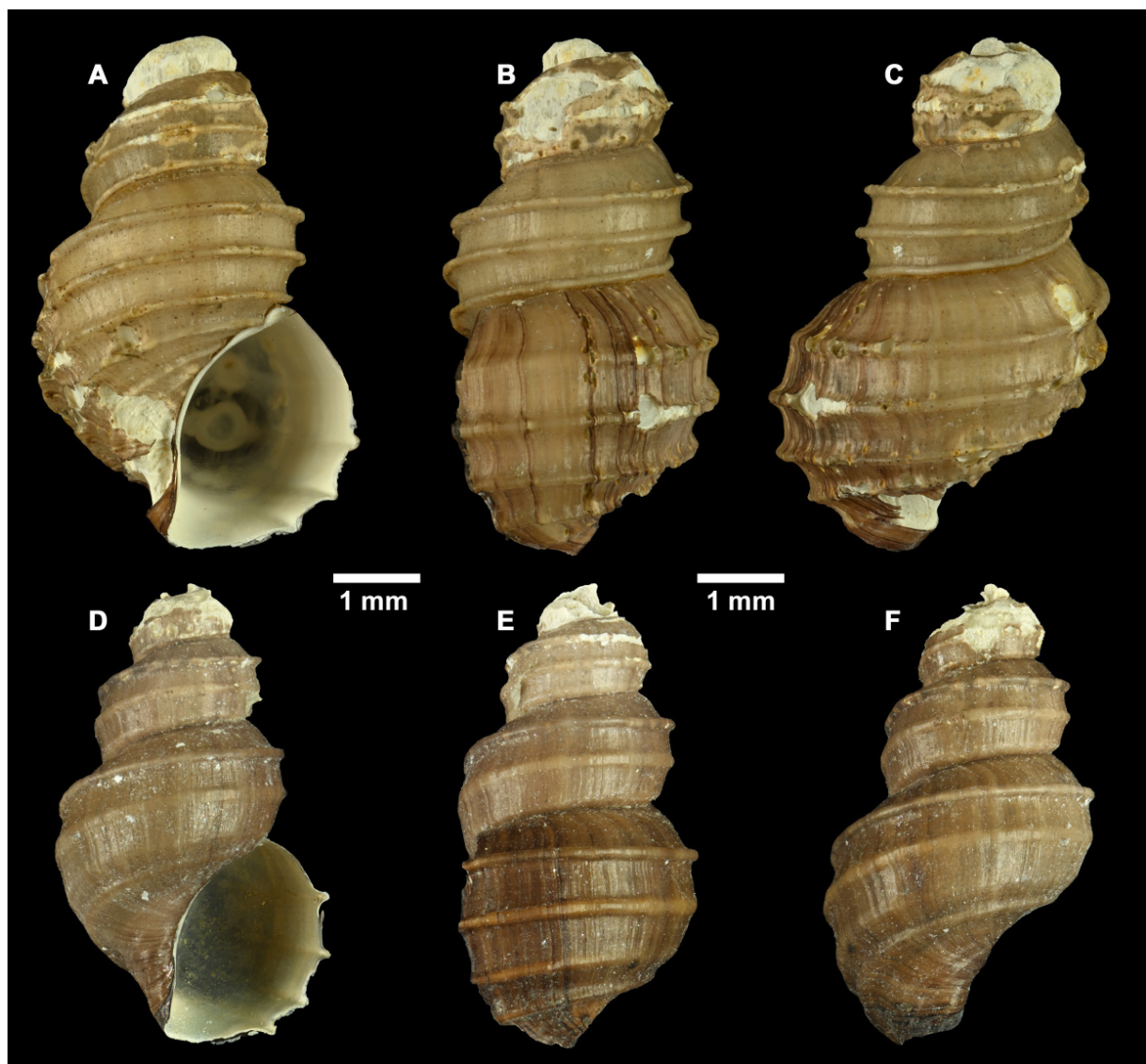


Fig. 35. *Provanna mzunguko* Hoffman sp. nov., Tanzania, Mtwara Mud Volcano, SO306 GeoB26152-1. A–C. Holotype (SMF 376602), L=6.0 mm, W=3.9 mm. A. Ventral view. B. Side view. C. Dorsal view. D–F. Paratype (SMF 376603), taken alive, L=5.6 mm, W=3.1 mm. D. Ventral view. E. Side view. F. Dorsal view.

has more and finer cords and its apex is complete or slightly damaged (Chen *et al.* 2018: 441–444, fig. 2); the current species has few stronger cords and lacks axial ribs. *Provanna beebei* has a similar outline and decapitated apex, but its sculpture has more and finer cords that are crossed by axial ribs on the upper whorl (Linse *et al.* 2019: 5–6, fig. 2); the current species has few stronger cords and lacks axial ribs. *Provanna cooki* has a similar outline and sculpture but has an undamaged apex with protoconch, it has an angular transition between the columella and the parietal area (Linse *et al.* 2019: 6–9, fig. 4); the current species has a smooth, flexuous columellar/parietal margin.

Superfamily Cypraeoidea Rafinesque, 1815

Family Ovulidae Fleming, 1822

Genus *Pedicypraedia* Lorenz, 2009

Type species

Pedicypraedia atlantica Lorenz, 2009 by original designation, Recent, Hyères Seamount, eastern Atlantic (Lorenz 2009: 88).

Pedicypraedia stylasteriophila Hoffman, Pfennings, Freiwald sp. nov.
urn:lsid:zoobank.org:act:BFFEC245-F39E-4EF2-A516-471DFE9724C8
Fig. 36

Diagnosis

Ovuliform shell, elongate, piriform, slightly depressed apically, exposed brown protoconch, sculpture with spiral cordlets, labium sharp. Maximum observed length 9 mm, width 4 mm.

Etymology

‘*Stylasteriophila*’ (Latinized concatenation of the hydroid genus *Stylaster* Gray, 1831 and ‘*phila*’, the feminine form of the Greek root meaning ‘loving’), referring to the food source.

Type material

Holotype

SW INDIAN OCEAN – **Mtwara MV, off Tanzania** • shell; 10°12.321' S, 40°32.742' E; 915 m depth; 19 Aug. 2024; stn SO306 / GeoB 26132-1; video box core; SMF 376604 (Fig. 36A–B).

Paratypes

SW INDIAN OCEAN – **Mtwara MV, off Tanzania** • 13 shells; same data as for holotype; SMF 376605, SMF 376628 (Fig. 36C–F).

Description

PROTOCONCH. Multispiral, 4 whorls, partially exposed, elevated conoidal spire, shell in 4 stages; stage 1: flattened nucleus, $\frac{3}{4}$ whorl, granulose sculpture, width 200 μ m; stage 2: $\frac{3}{4}$ whorl; sculpture with 2 exposed cords on smooth background; stage 3: more than one whorl, nodular sculpture spirally aligned; stage 4: more than one whorl, with three exposed spiral rows of pointed granules, interconnected by thin riblets with other granules in hexagonal pattern, width 650 μ m; colour brown.

TELEOCONCH. Convolved with 2 whorls, colour white. Outline most convex at periphery, well above midline, convex whorl adapically, straightened abapically. Sculpture with regular flattened nearly orthocline, axial growth stages, overlain by spiral, regular, rounded cordlets with fine spiral lines in

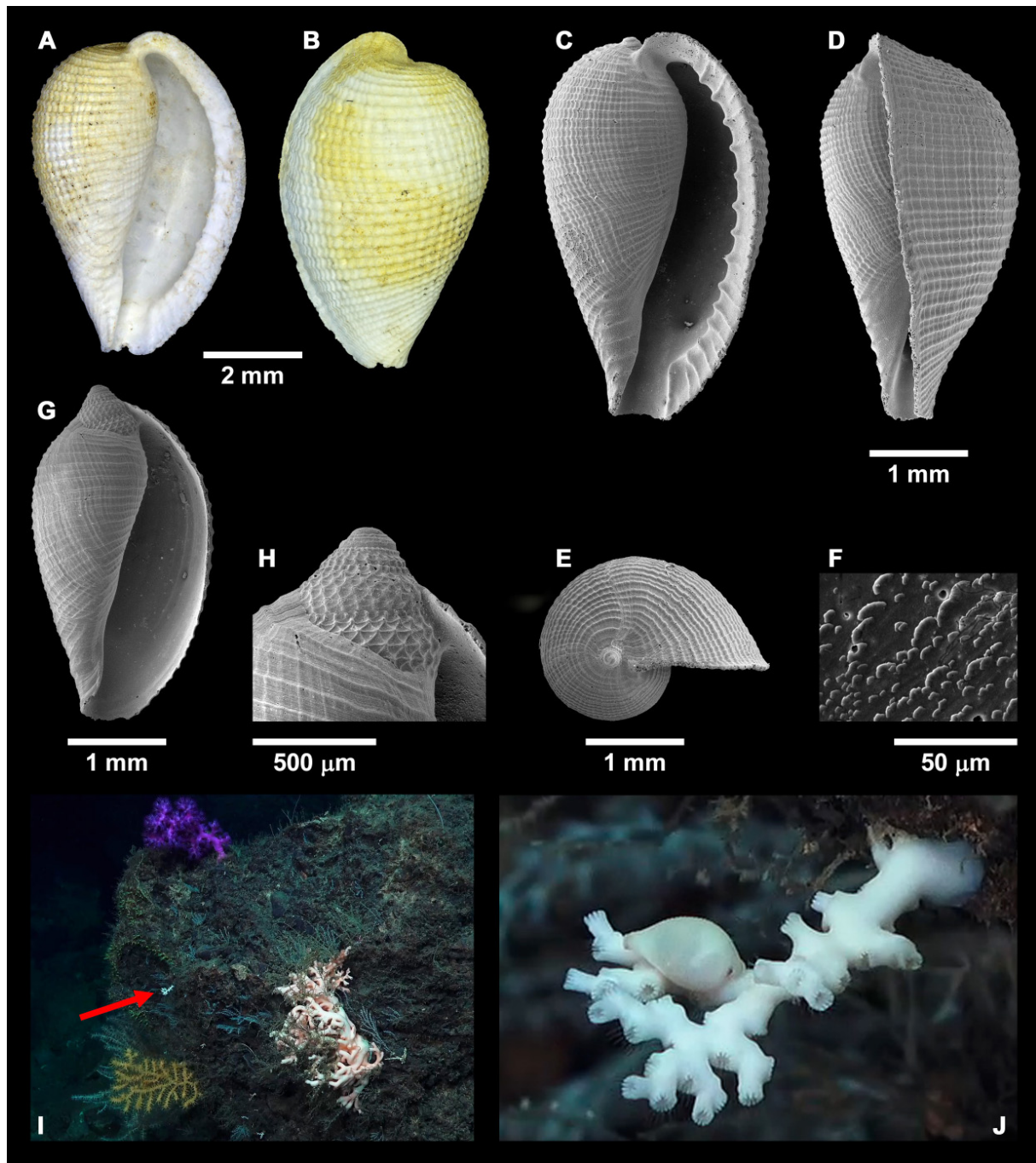


Fig. 36. *Pedicypraedia stylasteriophila* Hoffman, Pfennings & Freiwald sp. nov., Tanzania, Mtwara Mud Volcano. **A–H.** GeoB26132-1. **A–B.** Holotype (SMF 376604), H=6.5 mm, W=4.5 mm. **A.** Ventral view. **B.** Dorsal view. **C–F.** Paratype (SMF 376628), H=4.0 mm, W=2.3 mm. **C.** Ventral view. **D.** Side view. **E.** Apical view. **F.** Micro-sculpture at aperture. **G–H.** Paratype (SMF 376628), H=3.5 mm, W=1.9 mm. **G.** Ventral view. **H.** Exposed protoconch. **I–J.** SO306/GeoB26136-1. **I.** Deep-sea habitat with living scleractinians (white/orange), octocorals (purple and yellow-greenish), and hydrozoans (blueish-green), a small stylasterid is shown by the red arrow. **J.** Same location as in I, the stylasterid colony (possibly of the genus *Conopora* Moseley, 1879), with living *P. stylasteriophila*, the length of the shell is about 5 mm, the stylasterid colony is about 30 mm.

between; rectangular flattened nodules at crossings; small rectangular interspaces. Aperture elongated, curved, outer lip sharp with raised internal lip with rounded denticles, lirae between denticles and margin; columellar lip concave with long spiral ridges on exterior; parietal callus absent; siphonal canal narrow, open, with strong margins; internally smooth. Outer lip, parietal and columellar areas with minute, cemented scales, orientated towards exterior.

VARIATION. Exposure of protoconch may be the nucleus only or the top of the first two whorls. Juvenile specimens lack the denticulate lip but show a simple sharp labial edge. Adult lip has been observed on small species whereas the thin 'juvenile' lip has been observed in larger specimens.

Differential diagnosis

Placement in the genus *Pedicypraedia* is based on the similarity with the type species (the type species was the only taxon in the genus). The type species has a strong, straight callus along the columellar and parietal lip in an adult stage; its sculpture has dominant spiral cordlets with fine nodules and it lacks the axial ribs. The present species has axial ribs and spiral cords of equal strengths and it lacks the columellar / parietal callus. Species of the genus *Pedicularia* Swainson, 1840 adapt their external lips to the morphology of their hosts; the present species has a straight lip (in side view, Fig. 36D–E).

Habitat

One individual was observed on a stylasterid (possibly of the genus *Conopora* Moseley, 1879) from ROV images from GeoB 26136-1 in a rocky area with many cnidarians and hydroids (Fig. 36I–J).

Superfamily Buccinoidea Rafinesque, 1815

Family Eosiphonidae Kantor, Fedosov, Kosyan, Puillandre, Sorokin, Kano, Clark & Bouchet, 2021

Genus *Enigmaticolus* Fraussen, 2008

Type species

Eosipho desbruyeresi nipponensis Okutani & Fujiwara, 2000, by original designation, Recent, NW Pacific Ocean and SW Indian Ocean (off Madagascar) (Chen *et al.* 2020: 385); off Tanzania (this study).

Enigmaticolus nipponensis (Okutani & Fujiwara, 2000)

Figs 37–39

Eosipho desbruyeresi nipponensis Okutani & Fujiwara, 2000: 125–126, figs 6–10 (off Japan).

Enigmaticolus monnieri Fraussen, 2008: 77–78, figs 1–6 (off Madagascar).

Enigmaticolus nipponensis – Chen *et al.* 2020: 385, figs 1–2 (NW Pacific Ocean, Indian Ocean).

Diagnosis

Large, fragile, buccinoiform shell with elevated spire, weak sculpture and wide, oblique siphonal channel. Shell colour dark brown and white. Observed maximum length 100 mm, width 50 mm.

Material examined

SW INDIAN OCEAN – **Mtwara MV, off Tanzania** • 3 live-collected specimens; stn SO306 / GeoB 26131-1-16; SMF 376606–376607 (Fig. 39A–B) • 4 fragmentary shells; stn SO306 / GeoB 26137-1; SaM61352 • 1 live-collected specimen + 1 shell (broken); stn SO306 / GeoB 26150-1-4; SMF 376608 (Fig. 39C–D) • 1 live-collected specimen + 1 shell; stn SO306 / GeoB 26152-1; SMF 376609–376610 (Fig. 39E).

Habitat

At this location *Enigmaticolus nipponensis* was commonly associated with *Gigantidas tanzaniensis* sp. nov., *Bathymacra nipponica* and *Provanna castanea* sp. nov. in the mussel beds as well as on the surrounding rocky sea bottom (Fig. 39F). It probably is a scavenger or a carnivore of smaller molluscs.

Molecular analyses

A total of three high-quality sequences of *COI* were obtained (Table 3) with a fragment size of 669 bp, no indels or stop codons were found. Overall mean nucleotide frequencies were G (18.8%), C (17.0%), A (26.2%) and T (38.0%) The ML analyses confirmed that the specimens here studied belongs to the species *Enigmaticolus nipponensis* (Fig. 37). Genetic distance values (Fig. 38) show intraspecific

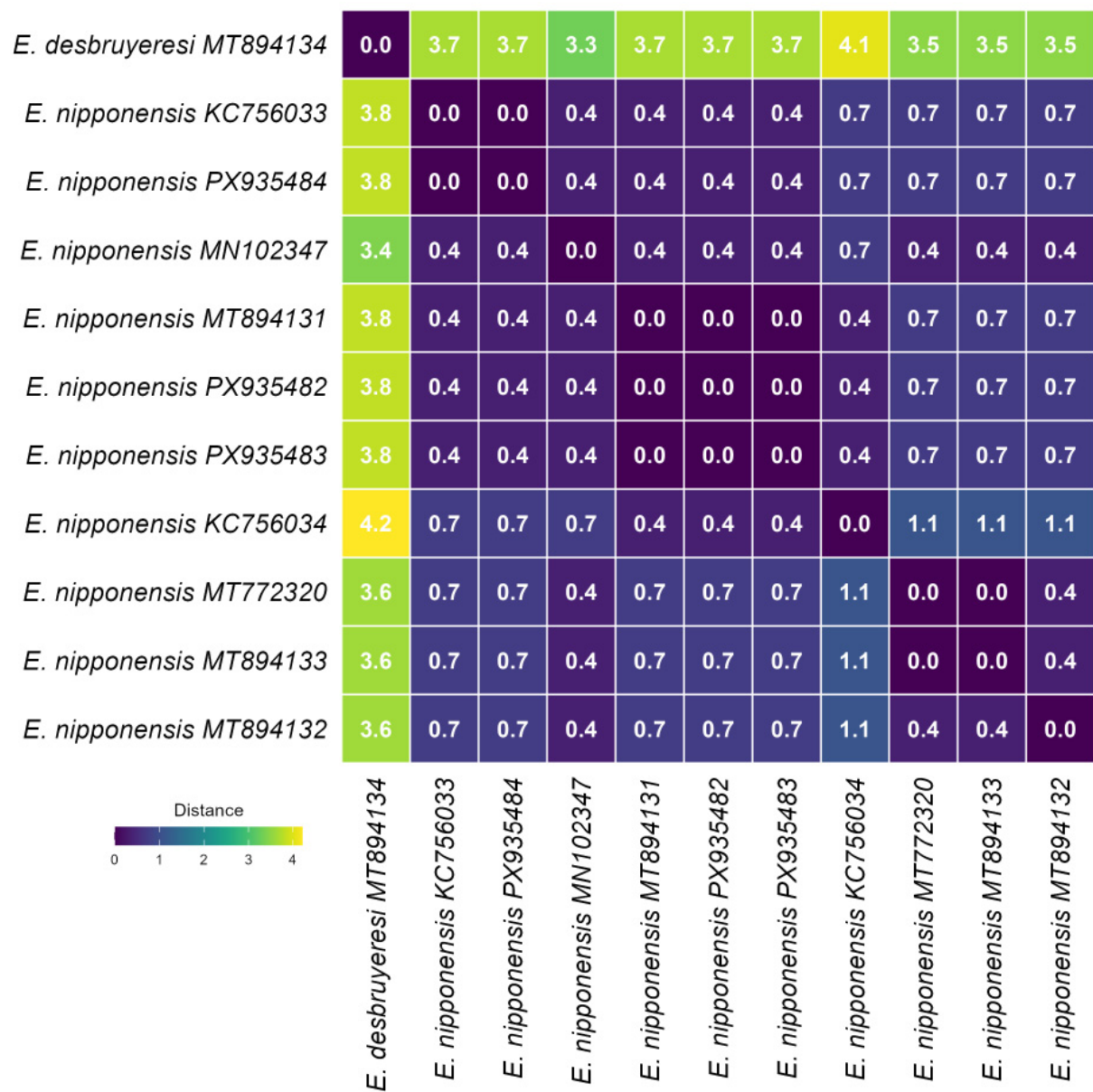


Fig. 38. Heatmap of interspecific genetic distance percentages of *Enigmaticolus* Fraussen, 2008 in *COI* (K2P: lower-left; *p*-distance: upper-right).

divergences ranging between 0.0 and 1.1% for both K2P and *p*-distance, and interspecific divergences ranging between 3.3 and 4.0% (K2P), and 3.4 and 4.2% (*p*-distance). Our specimens shared the same haplotype as *E. nipponensis* KC756033 sampled in Madagascar from seeps (Kantor *et al.* 2013) and *E. nipponensis* MT894131 collected in Okinawa Trough from vents, suggesting a high degree of genetic connectivity despite the vast distances and different habitats.

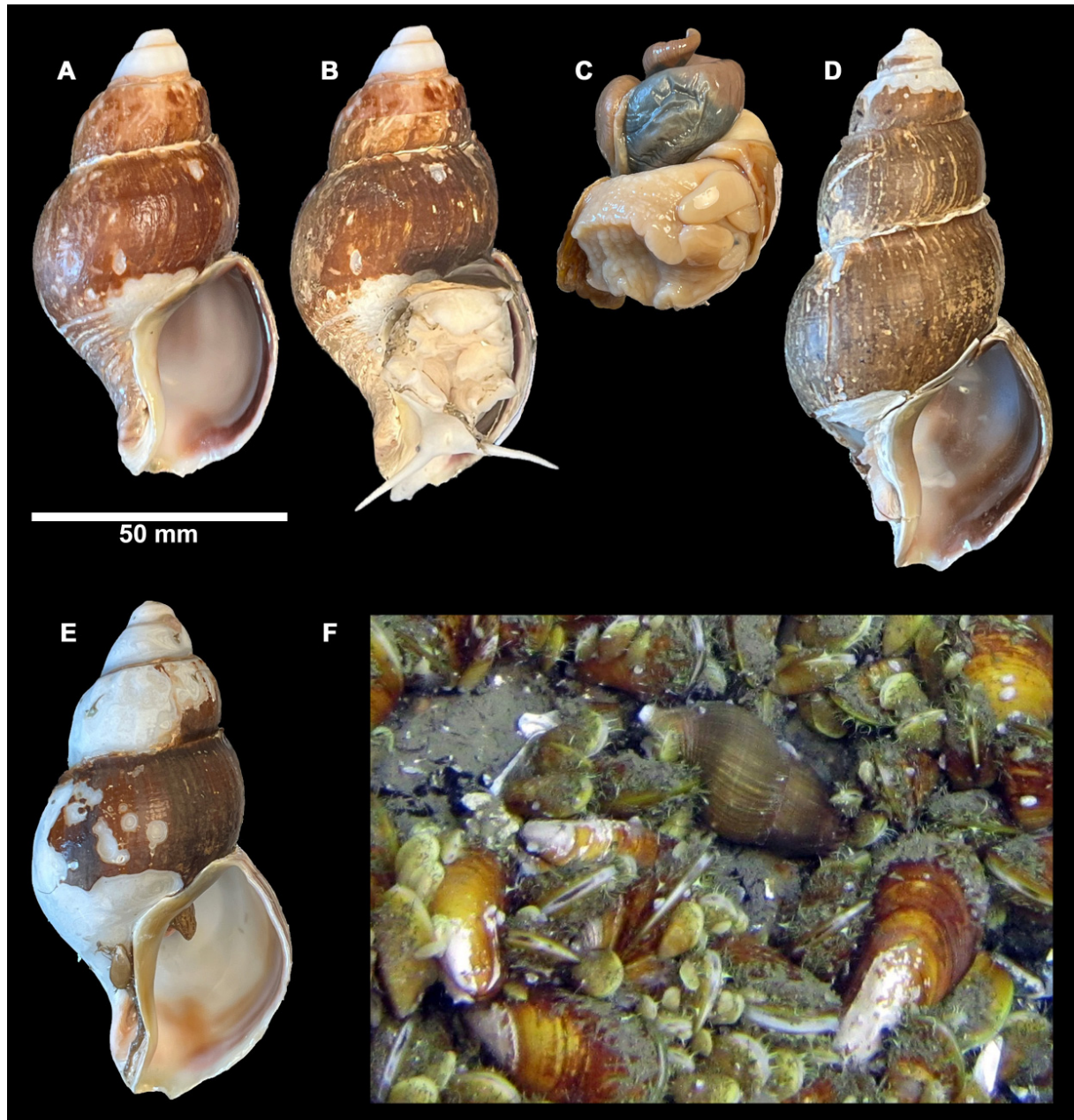


Fig. 39. *Enigmaticolus nipponensis* (Okutani & Fujiwara, 2000), Tanzania, Mtwara Mud Volcano, SO306. **A–B.** Specimen (SMF 376606), GeoB26131-1-16 ROV. **A.** Ventral view, L=91 mm, W=51 mm. **B.** Living animal. **C–D.** Specimen (SMF 376608), GeoB26150-1-4 ROV. **C.** Soft parts (formalin sample). **D.** Shell, ventral view, L=97 mm, W=50 mm. **E.** Specimen (SMF 376609), GeoB26152-1, ventral view, L=90 mm, W=50 mm. **F.** GeoB26136-1 ROV, 885 m, live *Enigmaticolus nipponensis* in bed of *Gigantidas tanzaniensis* Hoffman, Westbeek & Kihara sp. nov. on the sea bottom. Scale bar: A–E=50 mm.

Remarks

The species was originally described by Okutani & Fujiwara (2000) off Japan from hydrothermal vent habitats as a subspecies of *Enigmaticolus desbruyeresi* (Okutani & Ohta, 1993). Fraussen (2008) erected the new genus *Enigmaticolus* Fraussen, 2008 based on empty shells off Madagascar from an unknown habitat at about 800 m depth; his type species was named *Enigmaticolus monnieri* Fraussen, 2008. Chen *et al.* (2020) proved by mtDNA (*COI*) analyses that the subspecies of Okutani & Fujiwara (2000) and the topotypes of *E. monnieri* are synonyms. We assume that our specimens from Tanzania are *E. nipponensis*.

Subclass Heterobranchia Burmeister, 1837

Superfamily Orbitestelloidea Iredale, 1917

Family Xylodisculidae Warén, 1992

Genus *Xylodiscula* Marshall, 1988

Type species

Xylodiscula vitrea Marshall, 1988 by original designation, Recent, Australian part of Tasman Sea, SW Pacific Ocean (Marshall 1988: 989).

Xylodiscula sp.

Fig. 40

Diagnosis

Small, thin, fragile xylodisculiform shell with depressed spire, weak sculpture, weakly angular whorls. Shell colour white. Observed maximum height 1.7 mm, width 3.7 mm.

Material examined

SW INDIAN OCEAN – **Mtwara MV, off Tanzania** • 1 shell; 10°12.259' S, 40°32.682' E; 867 m depth; 23 Aug. 2024; stn SO306 / GeoB 26152-1; video box core; SMF 376611 (Fig. 40A–C) • 4 fragmentary shells; same location data as for preceding; SMF 376612.

Description

PROTOCONCH. Unknown characteristics.

TELEOCONCH. With 3 convex-triangular, loosely coiled whorls: cyrtconoidal outline. Suture deep at periphery; subsequent shoulder raised above suture, weak axial undulations near suture. Surface smooth, somewhat glossy, with numerous nearly orthocline growth lines. Umbilicus deep, wide. Aperture triangular-rounded with sharp lip; peristome complete; marginally connected to penultimate whorl on parietal margin; inside smooth.

Remarks

Placement in the genus *Xylodiscula* is uncertain and it is based on the morphological similarity with species described by Marshall (1988). Congeneric species are known from sunken wood. It is possible that the species feeds on other organic material, like for example the abundance of byssus fibres and periostracum from remains of individuals of *Gigantidas*. Similar species are the type species from off New South Wales, Australia, as well as *X. eximia* Marshall, 1988 and *X. librata* Marshall, 1988, both from off New Zealand. The type species shows a flat apical outline but its aperture is angular similar to the present species (which has a weakly raised spire). *Xylodiscula eximia* has a marginally protruding spire with a subcircular aperture; the present species is more elevated and shows an angular aperture.

Xylodiscula librata has a flattened spire (like the type species) but its whorls are more globose with a circular cross-section.

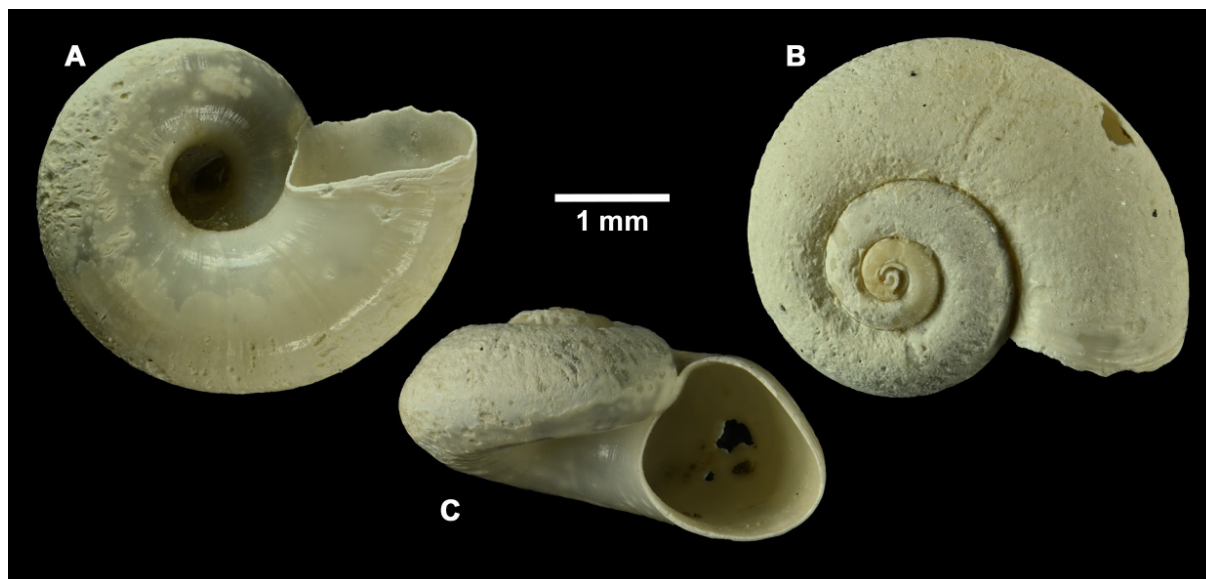


Fig. 40. *Xylodiscula* sp. (SMF 376611), Tanzania, Mtwara Mud Volcano, SO306 GeoB 26152-1, H=1.7 mm, W=3.7 mm. **A.** Abapical view. **B.** Apical view. **C.** Ventral view.

Discussion

Age has not been established for individuals of *Gigantidas tanzaniensis* sp. nov. herein, but we assume that large specimens (those over 80 mm in length) are over 10 years old as is common in large bathymodioline (Laming *et al.* 2018; Zhong *et al.* 2020). The size analysis (Fig. 4) shows a gap of specimens at about 55 mm in length. The gap could be caused by environmental conditions: (i) the population was not replenished by new settling individuals over a period of one or more years or (ii) no oocytes / gametes were formed over a time span or (iii) the food conditions at the habitat may have been unfavourable (changing or intermittent hydrocarbon supply). Note that the gap of specimens with a length less than 30 mm was caused by limited sampling of small specimens. It is possible that part of the variability in shell morphology is caused by sexual bimorphism. Another influencing factor will be the limited accommodation space during growth in a tightly set colony. Another cause could be access to food and mode of feeding. Old specimens likely feed exclusively in a chemosymbiotic manner (Duperron *et al.* 2007, 2009; Duperron 2010; Zhong *et al.* 2020) and they therefore depend on access to gases like methane or hydrogensulphide, which in turn will not be homogeneously distributed across the sea floor.

Based on mtDNA (*COI*) results, *G. tanzaniensis* sp. nov. forms a congeneric clade with representatives from the Atlantic, Pacific and Indian Ocean: *G. childressi* (Gustafson, Turner, Lutz & Vrijenhoek, 1998), *G. tangaroa*, *G. mauritanicus*, *G. haimaensis*, *G. platifrons*, and *G. niobengalensis*. All members of this clade are known from cold seeps. Most species of *Gigantidas* outside the cold seep clade are predominantly found in hydrothermal vent habitats (*G. gladius*, *G. horikoshii*, *G. taiwanensis* (Cosel, 2008), *G. vrijenhoeki*) and the *COI* divergences among those species are much larger than within the cold seep clade. *Gigantidas platifrons* has been encountered in both seeps and vents. Note that geographic distance does not seem to influence the mtDNA similarity between species in the clades.

Table 4. Bivalve and gastropod species found on Mtwara Mud Volcano, off Tanzania, SW Indian Ocean during cruise SO306. Species followed by an asterisk (*) were sampled alive and species followed by a cross (†) yielded *COI* sequences of the mitochondrial DNA.

Species	New to science	Cold seep fauna likely	General slope fauna likely
<i>Gigantidas tanzaniensis</i> *†	x	x	—
<i>Gigantidas komekahawia</i>	x	x	—
<i>Lucinoma mviringo</i>	x	x	—
<i>Calyptogena pemba</i>	x	x	—
<i>Isorropodon mtwaraense</i>	x	x	—
<i>Isorropodon cowioae</i>	x	x	—
<i>Isorropodon</i> sp.	—	x	—
<i>Propilidium marisindicum</i>	x	—	x
<i>Bathymacra nipponica</i> *†	—	x	—
<i>Paralepetopsis sahani</i>	x	x	—
<i>Puncturella mrembo</i> *	x	—	x
<i>Puncturella alternata</i>	x	—	x
<i>Fissurisepta kilimanjaro</i>	x	—	x
<i>Cornisepta infundibulus</i>	x	—	x
<i>Zeidora</i> sp.	—	—	x
<i>Anatoma agulhasensis</i>	—	—	x
<i>Anatoma japonica</i>	—	—	x
<i>Anatoma chaki</i>	x	—	x
<i>Satondella goudi</i>	—	—	x
<i>Sinezona macleani</i>	—	—	x
<i>Toroidia marisindica</i>	x	—	x
<i>Skenea kitovu</i>	x	—	x
<i>Seamountiella laini</i>	x	—	x
<i>Cerithiella kupamba</i>	x	—	x
<i>Eatoniella kahawa</i> *	x	—	x
<i>Provanna castanea</i> *†	x	x	—
<i>Provanna mzunguko</i> *	x	x	—
<i>Pedicypraedia stylasteriophila</i>	x	—	x
<i>Enigmaticolus nipponensis</i> *†	—	x	—
<i>Xylodiscula</i> sp.	—	—	x
Total 30 species	21	12	18

Table 4 summarises a set of taxa that probably live exclusively in the cold seep habitats and another set that probably belong to general habitats encountered on the continental slope. Typical seep fauna includes all bivalves of *Gigantidas*, *Lucinoma*, *Calyptogena*, and *Isorropodon* and five gastropod species of *Bathymacra*, *Paralepetopsis*, *Provanna*, and *Enigmaticolus*. All bivalves most likely depend on symbiotic chemosynthetic bacteria for energy and growth. The gastropods are grazers or carnivores.

Typical continental slope fauna are 18 gastropod species of *Propilidium*, *Puncturella*, *Fissurisepta*, *Cornisepta*, *Zeidora*, *Anatoma*, *Satondella*, *Sinezona*, *Toroidia*, *Skenea*, *Seamountiella*, *Cerithiella*, *Eatoniella*, *Pedicypraedia* and *Xylodiscula*. Most of these gastropod species are probably grazers, but some are carnivorous of invertebrates like sponges and hydrozoans.

Twenty-one species from the Mtwara MV are new to science; these include six bivalves and fifteen gastropods. Seven species were sampled alive; a DNA marker could be determined in four of these. It is most likely that many more mollusc species live on the Mtwara MV.

Distribution of cold seep fauna off eastern Africa

Hydrocarbons are generated in source rocks along the eastern African continent off Kenya, Tanzania and Mozambique (Davison & Steel 2017). It is most likely that many cold seeps are active along the East African margin and, hence, many similar habitats can be expected. Consequently, it is likely that the species related to the Mtwara MV could be found along the coast of Kenya, Tanzania and Mozambique. Lateral distribution of larvae would be facilitated by sea currents following the seashore.

Comparison with cold seeps from the northern Indian Ocean, the eastern Pacific and the Gulf of Mexico

Little *et al.* (2025) reported 12 species of Bivalvia and 15 of Gastropoda from a Late Pleistocene cold seep in the Krishna-Godavari Basin off SE India in about 1050 m water depth. Not a single species reported in their study was found at the Mtwara MV. Congeners shared with the Mtwara MV are species of *Gigantidas*, *Paralepetopsis* and *Anatoma*. They also concluded that a significant number of species were probably common on the continental slope outside the cold seep habitat. They found other genera that were classified as typical for cold seep fauna, which were absent at Mtwara MV, like for example bivalves of the genera *Acharax* Dall, 1908, *Conchocele* Gabb, 1866, *Pliocardia* Woodring, 1925 and *Archivesica* Dall, 1908. Taxa like *Acharax*, which live deeply buried in the sediments, were not easily picked up by ROV during our cruise. Vesicomys and bathymodiols, in contrast, occur in greater densities and with the shell partially protruding from the sediments such that they more easily observed, and collected by ROV. Our use of video-assisted box corers achieves a greater penetration of bottom sediments but hardly improves sampling of deeply buried taxa.

Seid *et al.* (2025) reported on 11 cold seep locations in the eastern Pacific Ocean at depths of 300–3600 m off western Costa Rica. They reported 81 live-collected bivalve and gastropod species of which 50 are obligate to seep habitats. These seep related fauna included one solemyid species (*Acharax*), five bathymolid species (*Bathymodiolus* and *Idas* Jeffreys, 1876), two thyasirids (*Thyasira* Lamarck, 1818), 12 vesicomys species (*Archivesica*, *Calypotgena*, *Phreagena* Woodring, 1938 and *Pliocardia* Woodring, 1925), three neolepetopsid species (*Eulepetopsis* McLean, 1990, *Neolepetopsidae* sp., *Paralepetopsis*), one pectinodontid (*Bathymacmaea*), one abyssochrysid (*Abyssochrysis* Tomlin, 1927), three provannids (*Provanna*), one each of Aeolidioidea Gray, 1827, Fionioidea Gray, 1857, Goniodorididae H. Adams & A. Adams, 1854, Aplustridae Gray, 1847 (*Parvaplustrum* Powell, 1951), Orbitestellidae Iredale, 1917 (*Lurifax* Warén & Bouchet, 2001), two species of Hyalogyrinidae Warén & Bouchet, 1993 (*Hyalogyra* Marshall, 1988, *Hyalogyrina* Marshall, 1988), one of Caymanabyssiidae Marshall, 1986 (*Colotrachelus* Marshall, 1986), three of Pyropeltidae McLean & Haszprunar, 1987 (*Pyropelta* McLean & Haszprunar, 1987), three of Lepetodrilidae McLean, 1988 (*Lepetodrilus* McLean, 1988), one of Larocheidae Finlay, 1927 (*Bathyxyllophila* Marshall, 1988), three of Cataegidae McLean & Quinn, 1987 (*Kanoia* Warén & Rouse, 2016, *Fucaria* Warén & Bouchet, 1993), one of Melanodrymiidae Salvini-Plawen & G. Steiner, 1995 (*Leptogyropsis* Marshall, 1988), two of Neomphalidae McLean, 1981 (*Helicrenion* Warén & Bouchet, 1993), one of Peltospiridae McLean, 1989. All species are distinct from the species from the Mtwara MV. Congeners of *Paralepetopsis*, *Bathymacmaea* and *Provanna* are shared between the two seep areas. The high number of live-collected species off Costa Rica (81) suggests greater biodiversity in terms of species when compared with the Mtwara MV (7 live-collected species). A high number of species (31) were not obligate to cold seep habitats.

Cordes *et al.* (2009) reviewed the macrofauna of cold seeps off the Mississippi Delta in the northern Gulf of Mexico. They reported at least five bathymodiolin species including three of *Bathymodiolus*, one of *Temu* Gustafson, Turner, Lutz & Vrijenhoek, 1998 and *Idas* each, two vesicomys with one of *Vesicomys* Dall, 1886 and *Calypotgena* each, one thyasirid (of *Thyasira*).

Conclusions

Thirty gastropod and bivalve species were found on the Mtwara MV off Tanzania; 21 species are new to science. More than half of all species probably have a wide distribution along the eastern African continental slope.

Cold seep fauna from different locations do share few congeners. At species level, most of the molluscan fauna at the Mtwara MV is different from those reported in other cold seep basins. Two exceptions are the gastropods *Bathyacmaea nipponica* and *Enigmaticolus nipponensis*, both were originally described from cold seeps off Japan.

Acknowledgements

We acknowledge the scientific staff, captain and crew involved in the cruise SO306 (CoWIO) executed by the German vessel RV *Sonne*. Special thanks go to Dierk Hebbeln, Claudia Wienberg and AF for the planning and execution plan of the cruise. The cruise was funded by the Bundesministerium für Forschung, Technologie und Raumfahrt (BMFTR) under the grant #03G0306B to AF. Nicol Mahnken at SaM prepared colour images used in this paper. We thank Pedro Martínez Arbizu for the use of the molecular laboratory facilities at the German Centre for Biodiversity Research at SaM. Sahar Khodami provided guidance during the activities in the molecular laboratory. This publication has the number 116 of the SaM Metabarcoding and Molecular Laboratory. The manuscript greatly improved from many comments by the reviewers David Herbert, Kerry Walton, and Elena Krylova as well as by the editor Thierry Backeljau.

Author contributions

LH, JW, AF, KP, PS and SY executed the sample gathering on board, including location planning, washing box core sediments, preliminary sorting of sediments, preservation of soft tissue materials on ethanol and formaldehyde, and confocal imaging of selected specimens. PS and SY arranged licensing of sampling off Tanzania and enabled the use of genetic sequences following the Nagoya protocol. JW and LH did the molecular laboratory work, and TK executed the genetic analyses. LH drafted the initial manuscript and executed the taxonomic studies; TK drafted all sections concerning genetics; JW, AF, KP, PS and SY added components to later versions. AF and KP selected the best images from ROV dives. All agreed to the submitted manuscript.

References

- Adams A. 1860. On some new genera and species of Mollusca from Japan. *Annals and Magazine of Natural History* (3) 5: 299–303 <https://doi.org/10.1080/00222936008697220>
- Adams A. 1862. On some new species of Scissurellidae from the Seas of China and Japan. *Annals and Magazine of Natural History* (3) 10: 346–348. <https://doi.org/10.1080/00222936208681336>
- Aktipis S.W. & Giribet G. 2010. A phylogeny of Vetigastropoda and other “archaeogastropods”: re-organizing old gastropod clades. *Invertebrate Biology* 129 (3): 220–240. <https://doi.org/10.1111/j.1744-7410.2010.00198.x>
- Assié A., Borowski C., van der Heijden K., Raggi L., Geier B., Leisch N., Schimak M.P., Dubilier N. & Petersen J.M. 2016. A specific and widespread association between deep-sea *Bathymodiolus* mussels and a novel family of Epsilonproteobacteria. *Environmental Microbiology Reports* 8 (5): 805–813. <https://doi.org/10.1111/1758-2229.12442>

Bandel K. 1998. Scissurellidae als Modell für die Variationsbreite einer natürlichen Einheit der Schlitzbandschnecken (Mollusca, Archaeogastropoda). *Mitteilungen des Geologisch-Paläontologischen Instituts der Universität Hamburg* 81: 1–120.

Barco A., Claremont M., Reid D.G., Houart R., Bouchet P., Williams S.T., Cruaud C., Couloux A. & Oliverio M. 2010. A molecular phylogenetic framework for the Muricidae, a diverse family of carnivorous gastropods. *Molecular Phylogenetics and Evolution* 56 (3): 1025–1039. <https://doi.org/10.1016/j.ympev.2010.03.008>

Barnard K.H. 1963. Contributions to the knowledge of South African marine Mollusca. Part III. Gastropoda: Prosobranchiata: Taenioglossa. *Annals of the South African Museum* 47 (1): 1–199.

Bartsch P. 1915. Report on the Turton Collection of South African marine mollusks, with additional notes on other South African shells contained in the United States National Museum. *Bulletin of the United States National Museum* 91: 1–305. <https://doi.org/10.5479/si.03629236.91.i>

Bettters M.J. & Cordes E.E. 2023. New records of *Provanna* (Gastropoda, Provannidae) from the Costa Rica Margin and an identification key for the genus. *ZooKeys* 1189: 1–32. <https://doi.org/10.3897/zookeys.1189.109734>

Bettters M.J., Cortés J. & Cordes E.E. 2024. New species and records of limpets (Mollusca, Gastropoda) from the Pacific Costa Rica Margin. *ZooKeys* 1214: 281–324. <https://doi.org/10.3897/zookeys.1214.128594>

Bouchet P. & Warén A. 1986. Mollusca Gastropoda: Taxonomical notes on tropical deep water Buccinidae with descriptions of new taxa. in: Forest, J. (Ed.) Résultats des Campagnes MUSORSTOM I et II Philippines (1976, 1980). Tome 2. *Mémoires du Muséum national d'Histoire naturelle, Série A, Zoologie* 133: 457–499.

Bouchet P. & Warén A. 1993. Revision of the Northeast Atlantic bathyal and abyssal Mesogastropoda. *Bollettino Malacologico* supplemento 3: 579–840. <https://doi.org/10.5962/bhl.title.140732>

Camacho C., Coulouris G., Avagyan V., Ma N., Papadopoulos J., Bealer K. & Madden T.L. 2009. BLAST+: architecture and applications. *BMC Bioinformatics* 10: 421. <https://doi.org/10.1186/1471-2105-10-421>

Charif D. & Lobry J.R. 2007. SeqinR 1.0-2: A contributed package to the R project for statistical computing devoted to biological sequences retrieval and analysis. In: Bastolla U., Porto M., Roman H.E. & Vendruscolo M. (eds) *Structural Approaches to Sequence Evolution: Molecules, Networks, Populations*. Biological and Medical Physics, Biomedical Engineering, Springer, Berlin, Heidelberg. https://doi.org/10.1007/978-3-540-35306-5_10

Chen C. & Sigwart J.D. 2023. The lost vent gastropod species of Lothar A. Beck. *Zootaxa* 5270 (3): 401–436. <https://doi.org/10.11646/zootaxa.5270.3.2>

Chen C., Watanabe H.K. & Ohara Y. 2018 [2016]. A very deep *Provanna* (Gastropoda: Abysochrysoidea) discovered from the Shinkai Seep Field, Southern Mariana Forearc. *Journal of the Marine Biological Association of the United Kingdom* 98 (3): 439–447. <https://doi.org/10.1017/S0025315416001648>

- Chen C., Xu T., Fraussen K. & Qiu J.-W. 2020. Integrative taxonomy of enigmatic deep-sea true whelks in the sister-genera *Enigmaticolus* and *Thermosipho* (Gastropoda: Buccinidae). *Zoological Journal of the Linnean Society* 193: 230–240. <https://doi.org/10.1093/zoolinnean/zlaa134>
- Cordes E.E., Bergquist D.C. & Fisher C.R. 2009. Macro-ecology of Gulf of Mexico cold seeps. *Annual Review of Marine Science* 1: 143–168. <https://doi.org/10.1146/annurev.marine.010908.163912>
- Cosel R. von 2002. A new species of bathymodioline mussel (Mollusca, Bivalvia, Mytilidae) from Mauritania (West Africa), with comments on the genus *Bathymodiolus* Kenk & Wilson, 1985. *Zoosystema* 24 (2): 259–271.
- Cosel R. von 2008. A new bathymodioline mussel (Bivalvia: Mytiloidea: Mytilidae) from vent sites near Kueishan Island, north east Taiwan. *The Raffles Bulletin of Zoology Supplement* 19: 105–114.
- Cosel R. von & Gracia A. 2018. A new mussel species, *Gigantidas samario* (Bivalvia: Mytilidae: Bathymodiolinae), from hydrocarbon seep communities off the Caribbean coast of Colombia. *Archiv für Molluskenkunde* 147 (2): 173–179. <https://doi.org/10.1127/arch.moll/147/173-179>
- Cosel R. von & Marshall B.A. 2003. Two new species of large mussels (Bivalvia: Mytilidae) from active submarine volcanoes and a cold seep off the eastern North Island of New Zealand, with description of a new genus. *The Nautilus* 117 (2): 31–46.
- Cosel R. von & Salas C. 2001. Vesicomidae (Mollusca: Bivalvia) of the genera *Vesicomya*, *Waisiuconcha*, *Isorropodon* and *Callogonia* in the eastern Atlantic and Mediterranean. *Sarsia* 86 (4–5): 333–366. <https://doi.org/10.1080/00364827.2001.10425523>
- Dall W.H. 1876. Mollusks. In: J.H. Kidder (ed.) Contributions to the natural history of Kerguelen Island, made in connection with the United States "Transit-of-Venus" Expedition, 1874–1875, II. *Bulletin of the United States National Museum* 3: 42–48.
- Dall W.H. 1891. On some new or interesting west American shells obtained from the dredgings of the U.S. Fish Commission steamer Albatross in 1888, and from other sources. *Proceedings of the US National Museum* 14: 173–191. <https://doi.org/10.5479/si.00963801.14-849.173>
- Dall W. H. 1901. Synopsis of the Lucinacea and of the American species. *Proceedings of the United States National Museum* 23 (1237): 779–833.
- Dall W.H. 1918. Description of new species of shells, chiefly from Magdalena Bay, Lower California. *Proceedings of the Biological Society of Washington* 31: 5–8.
- Dall W.H. 1925. Illustrations of unfigured types of shells in the collections of the United States National Museum. *Proceedings of the United States National Museum* 66, art. 17, no. 2554: 1–41. <https://doi.org/10.5479/si.00963801.66-2554.1>
- Dall W.H. 1927. Small shells from dredgings off the southeast coast of the United States by the United States Fisheries Steamer "Albatross", in 1885 and 1886. *Proceedings of the United States National Museum* 70 (2667): 1–134. <https://doi.org/10.5479/si.00963801.70-2667.1>
- Dautzenberg P. & Fischer H. 1896. Dragages effectués par l'*Hirondelle* et par la *Princesse Alice* 1888–1895. 1. Mollusques Gastéropodes. *Mémoires de la Société zoologique de France* 9: 395–498.

- Davison I. & Steel I. 2017. Geology and hydrocarbon potential of the East African continental margin: A review. *Petroleum Geoscience* 24 (1): 57–91. <https://doi.org/10.1144/petgeo2017-028>
- Duperron S. 2010. The diversity of deep-sea mussels and their bacterial symbioses. In: Kiel S. (ed.) *The Vent and Seep Biota*: 137–167. Springer, Basingstoke, UK. https://doi.org/10.1007/978-90-481-9572-5_6
- Duperron S., Sibuet M., MacGregor B.J., Kuypers M.M.M., Fisher C.R. & Dubilier N. 2007. Diversity, relative abundance, and metabolic potential of bacterial endosymbionts in three *Bathymodiolus* mussels (Bivalvia: Mytilidae) from cold seeps in the Gulf of Mexico. *Environmental Microbiology* 9: 1423–1438. <https://doi.org/10.1111/j.1462-2920.2007.01259.x>
- Duperron S., Lorion J., Samadi S., Gros O. & Gaill F. 2009. Symbioses between deep-sea mussels (Mytilidae: Bathymodiolinae) and chemosynthetic bacteria: diversity, function and evolution. *Comptes Rendus Biologies* 332: 298–310. <https://doi.org/10.1016/j.crv.2008.08.003>
- Egorova E.I. 1972. New species of prosobranch gastropods (Gastropoda, Prosobranchia) of the Davis Sea. *Issledovaniya Fauny Morey* 11 (19): 383–394. [In Russian.]
- Finlay H.J. 1926. A further commentary on New Zealand molluscan systematics. *Transactions of the New Zealand Institute* 57: 320–485.
- Fleming J. 1828. *A History of British Animals, Exhibiting the Descriptive Characters and Systematical Arrangement of the Genera and Species of Quadrupeds, Birds, Reptiles, Fishes, Mollusca, and Radiata of the United Kingdom; Including the Indigenous, Extirpated, and Extinct Kinds, together with Periodical and Occasional Visitants*. Edinburgh, Bell & Bradfute / London, James Duncan. <https://doi.org/10.5962/bhl.title.12859>
- Forbes E. 1840. On some new and rare British mollusca. *Annals and Magazine of Natural History* 5 (29): 102–108. <https://doi.org/10.1080/00222934009496773>
- Forbes E. & Hanley S.C.T. 1848–1853. *A History of British Mollusca and Their Shells*. 4 Volumes. van Voorst, London. <https://doi.org/10.5962/bhl.title.16341>
- Fraussen K. 2008. *Enigmaticolus*, a new genus of deep water buccinids (Gastropoda: Buccinidae) with description of a new species from Madagascar. *Gloria Maris* 46 (4–5): 74–82.
- Fraussen K. & Stahlschmidt P. 2016. The extensive Indo-Pacific deep-water radiation of *Manaria* E.A. Smith, 1906 (Gastropoda: Buccinidae) and related genera, with descriptions of 21 new species. in: Héros V., Strong E.E. & Bouchet P.(eds) *Tropical Deep-Sea Benthos*, volume 29. *Mémoires du Muséum national d'Histoire naturelle* 208: 363–456.
- Friele H. 1877. Preliminary report on the Mollusca from the Norwegian North Atlantic Expedition in 1876. *Nyt Magazin for Naturvidenskaberne* 23: 1–10.
- Geiger D.L. 2006. Eight new species of Scissurellidae and Anatomidae (Mollusca: Gastropoda: Vetigastropoda) from around the world, with discussion of two senior synonyms. *Zootaxa* 1128 (1): 1–33. <https://doi.org/10.11646/zootaxa.1128.1.1>
- Geiger D.L. 2012. *Monograph of the Little Slit Shells. Volume 1. Introduction, Scissurellidae*: 1–728. *Volume 2. Anatomidae, Larocheidae, Depressizonidae, Sutilizonidae, Temnocinclidae*: 729–1291. Santa Barbara Museum of Natural History Monographs 7.

- Geller J., Meyer C., Parker M. & Hawk H. 2013. Redesign of PCR primers for mitochondrial cytochrome c oxidase subunit I for marine invertebrates and application in all-taxa biotic surveys. *Molecular Ecology Resources* 13 (5): 851–861. <https://doi.org/10.1111/1755-0998.12138>
- Génio L., Johnson S., Vrijenhoek R., Cunha M., Tyler P., Kiel S. & Little C. 2008. New record of “*Bathymodiolus*” *mauritanicus* Cosel, 2002 from the Gulf of Cadiz (NE Atlantic) Mud Volcanoes. *Journal of Shellfish Research* 27: 53–61. [https://doi.org/10.2983/0730-8000\(2008\)27\[53:NROBMC\]2.0.CO;2](https://doi.org/10.2983/0730-8000(2008)27[53:NROBMC]2.0.CO;2)
- Gustafson R.G., Turner R.D., Lutz R.A. & Vrijenhoek R.C. 1998. A new genus and five new species of mussels (Bivalvia: Mytilidae) from deep-sea sulfide/hydrocarbon seeps in the Gulf of Mexico. *Malacologia* 40 (1–2): 63–112.
- Hartmann H., Hess M. & Haszprunar G. 2011. Interactive 3D anatomy and affinities of Bathysciadiidae (Gastropoda, Coccilinoidea): Deep-sea limpets feeding on decaying cephalopod beaks. *Journal of Morphology* 272: 259–279. [online 22 December 2010, but Code-compliant date of publication 2011.]
- Hashimoto J. & Okutani T. 1994. Four new mytilid mussels associated with deep-sea chemosynthetic communities around Japan. *Venus* 53 (2): 61–83. https://doi.org/10.18941/venusjjm.53.2_61
- Hashimoto J. & Yamane T. 2005. A new species of *Gigantidas* (Bivalvia: Mytilidae) from a vent site on the Kaikata Seamount Southwest of the Ogasawara (Bonin) Islands, Southern Japan. *Venus* 64 (1–2): 1–10. https://doi.org/10.18941/venus.64.1-2_1
- Hebbeln D. & Wienberg C. (eds) 2024. *Cold-Water Corals in the West Indian Ocean, Cruise No. SO306, August 8–September 9, 2024, Port Louis (Mauritius) – Durban (South Africa), CoWIO*. Sonne Berichte, MARUM, University of Bremen. https://doi.org/10.48433/cr_so306
- Hedley C. 1904. Additions to the marine molluscan fauna of New Zealand. *Records of the Australian Museum* 5 (2): 86–97. <https://doi.org/10.3853/j.0067-1975.5.1904.1040>
- Herbert D.G. 1986. A revision of the southern African Scissurellidae (Mollusca: Gastropoda: Prosobranchia). *Annals of the Natal Museum* 27 (2): 601–632.
- Herbert D.G. 2015. An annotated catalogue and bibliography of the taxonomy, synonymy and distribution of the Recent Vetigastropoda of South Africa (Mollusca). *Zootaxa* 4049 (1): 1–98. <https://doi.org/10.11646/zootaxa.4049.1.1>
- Herbert D.G. & Kilburn R.N. 1986. Taxonomic studies on the Emarginulinae (Mollusca: Gastropoda: Fissurellidae) of southern Africa and Mozambique. *Emarginula, Emarginella, Puncturella, Fissurisepta, and Rimula*. *South African Journal of Zoology* 21 (1): 1–27. <https://doi.org/10.1080/02541858.1986.11447951>
- Hoffman L. & Freiwald A. 2018a. A new genus and two new species in Calliotropidae (Mollusca: Gastropoda) from NE Atlantic cold-water coral habitats. *Miscellanea Malacologica* 7 (5): 89–96.
- Hoffman L. & Freiwald A. 2018b. Last snails standing: a tale of Fissurellidae (Gastropoda) from deep-water coral habitats off Mauritania since the Pleistocene. *Miscellanea Malacologica* 7 (6): 115–126.
- Hoffman L. & Freiwald A. 2023. Species in Fissurellidae (Gastropoda) from the North Atlantic with a focus on the Azorean seamounts. *Basteria* 87 (1): 77–96.

- Hoffman L., Heugten B. van & Lavaleye M.S.S. 2011a. Gastropoda (Mollusca) from the Rockall and Hatton Banks, northeastern Atlantic Ocean. Part 2. *Miscellanea Malacologica* 4 (6): 85–118.
- Hoffman L., Heugten B. van & Lavaleye M.S.S. 2011b. *Margarites toroides* n.sp. (Turbinidae, Gastropoda) off the northwestern Moroccan Coast, northeastern Atlantic Ocean. *Miscellanea Malacologica* 5 (3): 57–60.
- Hoffman L., Cosel R. von & Freiwald A. 2019. New and little-known Pliocardiinae (Bivalvia, Vesicomyidae) from the continental slope off Mauritania. *Basteria* 83 (4–6): 151–157.
- Hoffman L., Kniesz K., Martínez Arbizu P. & Kihara T.C. 2022. Abyssal vent field habitats along plate margins in the Central Indian Ocean yield new species in the genus *Anatoma* (Vetigastropoda: Anatomidae). *European Journal of Taxonomy* 826: 135–162. <https://doi.org/10.5852/ejt.2022.826.1841>
- Jang S.J., Ho P.T., Jun S.Y., Kim D. & Won Y.J. 2020. A newly discovered *Gigantidas* bivalve mussel from the Onnuri Vent Field in the northern Central Indian Ridge. *Deep Sea Research Part I: Oceanographic Research Papers* 161: e103299. <https://doi.org/10.1016/j.dsr.2020.103299>
- Jeffreys J.G. 1883. On the Mollusca procured during the ‘Lightning’ and ‘Porcupine’ Expeditions 1868–70. (Part V). *Proceedings of the Zoological Society of London* 1882: 656–687.
- Judd A. & Hovland M. 2007. Seabed fluid flow and biology. In: *Seabed Fluid Flow: The Impact on Geology, Biology and the Marine Environment*: 248–289. Cambridge University Press, Cambridge. <https://doi.org/10.1017/CBO9780511535918>
- Kalyanamoorthy S., Minh B.Q., Wong T.K., Von Haeseler A. & Jermin L.S. 2017. ModelFinder: fast model selection for accurate phylogenetic estimates. *Nature methods* 14 (6): 587–589. <https://doi.org/10.1038/nmeth.4285>
- Kantor Y.I., Puillandre N., Rivasseau A. & Bouchet P. 2012. Neither a buccinid nor a turrid: a new family of deep-sea snails for *Belomitra* P. Fischer, 1883 (Mollusca, Neogastropoda), with a review of Recent Indo-Pacific species. *Zootaxa* 3496 (1): 1–64. <https://doi.org/10.11646/zootaxa.3496.1.1>
- Kantor Y.I., Puillandre N., Fraussen K., Fedosov A.E. & Bouchet P. 2013. Deep-water Buccinidae (Gastropoda: Neogastropoda) from sunken wood, vents and seeps: molecular phylogeny and taxonomy. *Journal of the Marine Biological Association of the United Kingdom* 93 (8): 2177–2195. <https://doi.org/10.1017/S0025315413000672>
- Kantor Y.I., Kosyan A., Sorokin P., Herbert D.G. & Fedosov A. 2020. Review of the abyssal-hadal genus *Bayerius* (Gastropoda: Neogastropoda: Buccinidae) from the North-West Pacific, with description of two new species. *Deep Sea Research Part I: Oceanographic Research Papers* 160: e103256. <https://doi.org/10.1016/j.dsr.2020.103256>
- Kantor Y.I., Fedosov A.E., Kosyan A.R., Puillandre N., Sorokin P.A., Kano Y., Clark A. & Bouchet P. 2022. Molecular phylogeny and revised classification of the Buccinoidea (Neogastropoda). *Zoological Journal of the Linnean Society* 194 (3): 789–857. <https://doi.org/10.1093/zoolinnean/zlab031>
- Katoh K., Kuma K.I., Toh H. & Miyata T. 2005. MAFFT version 5: improvement in accuracy of multiple sequence alignment. *Nucleic Acids Research* 33 (2): 511–518. <https://doi.org/10.1093/nar/gki198>
- Kearse M., Moir R., Wilson A., Stones-Havas S., Cheung M., Sturrock, S., Buxton S., Cooper A., Markowitz S., Duran C., Thierer T., Ashton B., Meintjes P. & Drummond A. 2012. Geneious Basic:

an integrated and extendable desktop software platform for the organization and analysis of sequence data. *Bioinformatics* 28 (12): 1647–1649. <https://doi.org/10.1093/bioinformatics/bts199>

Kenk V.C. & Wilson B.R. 1985. A new mussel (Bivalvia: Mytilidae) from hydrothermal vents in the Galapagos Rift zone. *Malacologia* 26: 253–271.

Kimura M. 1980. A simple method for estimating evolutionary rates of base substitutions through comparative studies of nucleotide sequences. *Journal of Molecular Evolution* 16 (2): 111–120. <https://doi.org/10.1007/BF01731581>

Krylova E.M. & Sahling H. 2006. Recent bivalve molluscs of the genus *Calypptogena* (Vesicomidae). *Journal of Molluscan Studies* 72: 359–395.

Laming S.R., Gaudron S.M. & Duperron S. 2018. Lifecycle ecology of deep-sea chemosymbiotic mussels: a review. *Frontiers of Marine Science* 5: e282. <https://doi.org/10.3389/fmars.2018.00282>

Leal J.H. & Simone L.R.L. 1998. *Propilidium curumim*, a new species of Lepetidae (Gastropoda, Patellogastropoda) from off Southern and Southeastern Brazil. *Bulletin of Marine Science* 63 (1): 157–165.

Letunic I. & Bork P. 2024. Interactive Tree of Life (iTOL) v6: recent updates to the phylogenetic tree display and annotation tool. *Nucleic Acids Research* 52 (W1): W78–W82. <https://doi.org/10.1093/nar/gkae268>

Linnaeus C. 1758. *Systema Naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis*. [The System of Nature Through the Three Kingdoms of Nature, According to Classes, Orders, Genera, Species, with Characters, Differences, Synonyms, Places.]. Impensis Direct. Laurentii Salvii. Holmiae [Stockholm]. <https://doi.org/10.5962/bhl.title.68927>

Linse K., Nye V., Copley J.T. & Chen C. 2019. On the systematics and ecology of two new species of *Provanna* (Abyssochrysoidea: Provannidae) from deep-sea hydrothermal vents in the Caribbean Sea and Southern Ocean. *Journal of Molluscan Studies* 85 (4): 426–439. <https://doi.org/10.1093/mollus/eyz024>

Little C.T.S., Kumar R., Johnson J.E. & Hoffman L. 2025. Bathyal molluscs from Upper Pleistocene methane seeps, Krishna-Godavari Basin, offshore eastern India. *Acta Palaeontologica Polonica* 70 (3): 443–477. <https://doi.org/10.4202/app.01179.2024>

Lorenz F. 2009. Two new Pediculariidae from Hyères Seamount, eastern central Atlantic (Gastropoda: Cypraeoidea). *Acta Conchyliorum* 10: 87–94.

Lorion J., Buge B., Cruaud C. & Samadi S. 2010. New insights into diversity and evolution of deep-sea Mytilidae (Mollusca: Bivalvia). *Molecular Phylogenetics and Evolution* 57 (1): 71–83. <https://doi.org/10.1016/j.ympev.2010.05.027>

Lorion J., Kiel S., Faure B., Kawato M., Ho S.Y., Marshall B., Shinji Tsuchida, Miyazaki J.-I. & Fujiwara Y. 2013. Adaptive radiation of chemosymbiotic deep-sea mussels. *Proceedings of the Royal Society B* 280: e20131243. <https://doi.org/10.1098/rspb.2013.1243>

Lovén S.L. 1846. Index Molluscorum litora Scandinaviae occidentalia habitantium. *Öfversigt af Kongliga Vetenskaps Akademiens Förhandlingar* 1846: 134–160, 182–204. <https://doi.org/10.5962/bhl.title.59081>

- Lowe R.T. 1827. On *Balanus punctatus*, *Puncturella flemingii*, together with some corrections relative to *Turbo carneus*, and some of the *Chiton* before described. *Zoological Journal* 3: 76–80.
- Marshall B.A. 1985. Recent and Tertiary deep-sea limpets of the genus *Pectinodonta* Dall (Mollusca: Gastropoda) from New Zealand and New South Wales. *New Zealand Journal of Zoology* 12(2): 273–282. <https://doi.org/10.1080/03014223.1985.10428281>
- Marshall B.A. 1988. Skeneidae, Vitrinellidae and Orbitestellidae (Mollusca: Gastropoda) associated with biogenic substrata from bathyal depths off New Zealand and New South Wales. *Journal of Natural History* 22 (4): 949–1004. <https://doi.org/10.1080/00222938800770631>
- Marshall B.A. 1998. A new deep-sea limpet of the genus *Pectinodonta* Dall, 1882 from New Zealand, and new distribution records for for *P. aupaupurua* and *P. morioria* Marshall, 1985 (Gastropoda: Acmaeidae). *The Nautilus* 112 (2): 52–57.
- Marshall B.A., Puillandre N., Lambourdière J., Coulou A. & Samadi S. 2016. Deep-sea wood-eating limpets of the genus *Pectinodonta* Dall, 1882 (Mollusca: Gastropoda: Patellogastropoda: Pectinodontidae) from the tropical West Pacific. In: Héros V., Strong E.E. & Bouchet P. (eds) *Tropical Deep-Sea Benthos* 29. Mémoires du Muséum national d'Histoire naturelle 208: 235–265. Muséum national d'Histoire naturelle, Paris
- McLean J.H. 1990. Neolepetopsidae, a new docoglossate limpet family from hydrothermal vents and its relevance to patellogastropod evolution. *Journal of Zoology* 222 (3): 485–528. <https://doi.org/10.1111/j.1469-7998.1990.tb04047.x>
- McLean J.H. 2008. Three new species of the family Neolepetopsidae (Patellogastropoda) from hydrothermal vents and whale falls in the Northeastern Pacific. *Journal of Shellfish Research* 27 (1): 15–20. [https://doi.org/10.2983/0730-8000\(2008\)27\[15:tnsotf\]2.0.co;2](https://doi.org/10.2983/0730-8000(2008)27[15:tnsotf]2.0.co;2)
- McLean J.H. & Geiger D.L. 1998. New genera and species having the *Fissurisepta* shell form, with a generic-level phylogenetic analysis (Gastropoda: Fissurellidae). *Contributions in Science, Natural History Museum of Los Angeles County* 475: 1–32. <https://doi.org/10.5962/p.208103>
- Messing J. 1983. [2] New M13 vectors for cloning. *Methods in Enzymology* 101: 20–78. [https://doi.org/10.1016/0076-6879\(83\)01005-8](https://doi.org/10.1016/0076-6879(83)01005-8)
- Montagu G. 1808. *Supplement to Testacea Britannica with Additional Plates*. Woolmer, Exeter.
- Nakano T. & Ozawa T. 2007. Worldwide phylogeography of limpets of the order Patellogastropoda: molecular, morphological and palaeontological evidence. *Journal of Molluscan Studies* 73 (1): 79–99. <https://doi.org/10.1093/mollus/eym001>
- Nekhaev I.O. 2023. Who lives in the hot heart of the cold sea? A new species of *Provanna* (Caenogastropoda: Provannidae) from the hydrothermal zone of Piip Volcano, northwestern Pacific. *Diversity* 15 (4): e581. <https://doi.org/10.3390/d15040581>
- Okutani T. & Fujiwara Y. 2000. Gastropod fauna of a thermal vent site on the North Knoll of Iheya Ridge, Okinawa Trough. *Venus* 59 (2): 123–128. https://doi.org/10.18941/venusjjm.59.2_123
- Okutani T. & Ohta S. 1993 New buccinid and turrid gastropods from North Fiji and Lau Basins. *Venus* 52 (3): 217–221. https://doi.org/10.18941/venusjjm.52.3_217

- Okutani T., Tsuchida E. & Fujikura K. 1992. Five bathyal gastropods living within or near the *Calyplogena*-community of the Hatsushima islet, Sagami Bay. *Venus* 51 (3): 137–148. https://doi.org/10.18941/venusijm.51.3_137
- Okutani T., Fujikura K. & Hashimoto J. 1993a. Another new species of *Calyplogena* (Bivalvia: Vesicomyidae) from bathyal depth in Suruga Bay, Japan. *Venus* 52 (2): 121–126. https://doi.org/10.18941/venusijm.52.2_121
- Okutani T., Fujikura K. & Sasaki T. 1993b. New taxa and new distribution records of deepsea gastropods collected from or near the chemosynthetic communities in the Japanese waters. *Bulletin of the National Science Museum, Series A (Zoology)* 19: 123–143.
- Oliver P.G. & Drewery J. 2014. New species of chemosymbiotic clams (Bivalvia: Vesicomyidae and Thyasiridae) from a putative ‘seep’ in the Hatton–Rockall Basin, north-east Atlantic. *Journal of the Marine Biological Association of the United Kingdom* 94 (2): 389–403. <https://doi.org/10.1017/S0025315413001136>
- Oliver P.G. & Holmes A.M. 2006. A new species of *Lucinoma* (Bivalvia: Lucinoidea) from the Oxygen Minimum Zone of the Oman Margin, Arabian Sea. *Journal of Conchology* 39 (1): 63–77.
- Oliver P.G., Gonsalves M.J.B.D., Samuel D. & Garzia M. 2024. *Gigantidas niobengalensis* sp. nov. (Bivalvia: Mytiloidea) from a methane seep in the Krishna-Godavari Basin, Bay of Bengal. *Journal of Conchology* 45 (2): 221–233. <https://doi.org/10.61733/jconch/4521>
- Olu K., Lance S., Sibuet M., Henry P., Fiala-Médioni A. & Diné A. 1997. Cold seep communities as indicators of fluid expulsion patterns through mud volcanoes seaward of the Barbados accretionary prism. *Deep Sea Research Part I: Oceanographic Research Papers* 44: 811–841. [https://doi.org/10.1016/S0967-0637\(96\)00123-9](https://doi.org/10.1016/S0967-0637(96)00123-9)
- Olu K., Sibuet M., Fiala-Médioni A., Gofas S., Salas C., Mariotti A., Foucher J.-P. & Woodside J. 2004. Cold seep communities in the deep eastern Mediterranean Sea: Composition, symbiosis and spatial distribution on mud volcanoes. *Deep Sea Research Part I: Oceanographic Research Papers* 51: 1915–1936. <https://doi.org/10.1016/j.dsr.2004.07.004>
- Ozawa G., Shimamura S., Takaki Y., Yokobori S.I., Ohara Y., Takishita K., Maruyama T., Fujikura K. & Yoshida T. 2017. Updated mitochondrial phylogeny of pteriomorph and heterodont Bivalvia, including deep-sea chemosymbiotic *Bathymodiolus* mussels, vesicomyid clams and the thyasirid clam *Conchocele* cf. *bisecta*. *Marine Genomics* 31: 43–52. <https://doi.org/10.1016/j.margen.2016.09.003>
- Paradis E. & Schliep K. 2019. ape 5.0: an environment for modern phylogenetics and evolutionary analyses in R. *Bioinformatics* 35 (3): 526–528. <https://doi.org/10.1093/bioinformatics/bty633>
- Pilsbry H.A. 1895. Note on Tasmanian *Acmaea* and *Ischnochiton*. *The Nautilus* 8 (11): 127–129.
- Ponder W.F. 1965. The family Eatoniellidae in New Zealand. *Records of the Auckland Institute and Museum* 6 (2): 47–100.
- Ponder W.F. & Worsfold T.M. 1994. A review of the rissoiform gastropods of southwestern South America (Mollusca, Gastropoda). *Contributions in Science* 445: 1–63. <https://doi.org/10.5962/p.208081>
- Powell A.W.B. 1937. New species of marine Mollusca from New Zealand. *Discovery Reports* 15: 153–222.

Rambaut A. & Drummond A. 2009. December. *FigTree v1 4.4: Tree figure drawing tool*. Available from <https://tree.bio.ed.ac.uk/software/figtree/> [accessed 1 Sep. 2026].

Ratnasingham S., Wei C., Chan D., Agda J., Agda J., Ballesteros-Mejia L., Boutou H.A., El Bastami Z.M., Ma E., Manjunath R., Rea D., Ho C., Telfer A., McKeowan J., Rahulan M., Steinke C., Dorsheimer J., Milton M. & Hebert P.D. 2024. BOLD v4: A centralized bioinformatics platform for DNA-based biodiversity data. In: DeSalle R. (ed.) *DNA Barcoding: Methods and Protocols*: 403–441. Humana Press, Springer Protocols, New York. https://doi.org/10.1007/978-1-0716-3581-0_26

Rodrigues C.F., Cunha M.R., Olu K. & Duperron S. 2012. The smaller vesicomysid bivalves in the genus *Isorropodon* (Bivalvia, Vesicomysidae, Pliocardiinae) also harbour chemoautotrophic symbionts. *Symbiosis* 56 (3): 129–137. <https://doi.org/10.1007/s13199-012-0168-0>

Roosen M.T. & Trausel J. 2024. A new species of *Toroidia* Hoffman & Freiwald, 2018 (Gastropoda, Calliotropidae) from the NW Atlantic, of the coast of North Carolina (USA). *Gloria Maris* 62 (3): 116–118.

Roosen M.T. & Trausel J. 2025. Description of *Toroidia caboverdensis* spec. nov. (Gastropoda: Calliotropidae) from the Cabo Verde archipelago. *Basteria* 89 (1): 43–45.

Rubio F., Gofas S. & Rolán E. 2019. A new genus of small Vetigastropoda from eastern Atlantic Ocean and Indo-Pacific islands and seamounts. *Iberus* 37 (2): 249–265.

Salas C. & Woodside J. 2002. *Lucinoma kazani* n. sp. (Mollusca, Bivalvia): evidence of a living community associated with a cold seep in the Eastern Mediterranean Sea. *Deep-Sea Research I* 49: 991–1005. [https://doi.org/10.1016/S0967-0637\(02\)00010-9](https://doi.org/10.1016/S0967-0637(02)00010-9)

Sasaki T., Okutani T. & Fujikura K. 2003. New taxa and new records of patelliform gastropods associated with chemoautosynthesis-based communities in Japanese waters. *The Veliger* 46 (3): 189–210.

Sasaki T., Ogura T., Watanabe H.K. & Fujikura K. 2016. Four new species of *Provanna* (Gastropoda: Provannidae) from vents and a seep off Nansei-shoto area, southwestern Japan. *Venus* 74 (1–2): 1–17. https://doi.org/10.18941/venus.74.1-2_1

Sayers E.W., Beck J., Bolton E.E., Brister J.R., Chan J., Connor R., Feldgarden M., Fine A.M., Funk K., Hoffman J., Kannan S., Kelly C., Klimke W., Kim S., Lathrop S., Marchler-Bauer A., Murphy T.D., O’Sullivan C., Schmieder E., Skripchenko Y., Stine A., Thibaud-Nissen F., Wang J., Ye J., Zellers E., Schneider V.A. & Pruitt K.D. 2025. Database resources of the National Center for Biotechnology Information in 2025. *Nucleic Acids Research* 53 (D1): D20–D29. <https://doi.org/10.1093/nar/gkae979>

Scarlato O.A. 1981. *Bivalve Molluscs of the Temperate Latitudes of the Western Part of the Pacific Ocean*. Guides to the fauna of the USSR 126; Nauka, Leningrad.

Schepman M.M. 1908. The Prosobranchia of the Siboga Expedition. Part I. Rhipidoglossa and Docoglossa with an appendix by Prof. R. Bergh. *Siboga-Expeditie* 49a: 1–107. <https://doi.org/10.5962/bhl.title.50521>

Schepman M.M. 1911. The Prosobranchia of the Siboga Expedition. Part IV. Rachiglossa. *Siboga-Expeditie* 49d: 247–363. Leiden, E.J. Brill. <https://doi.org/10.5962/bhl.title.50521>

Schliep K.P. 2011. phangorn: phylogenetic analysis in R. *Bioinformatics* 27 (4): 592–593. <https://doi.org/10.1093/bioinformatics/btq706>

- Schuelke M. 2000. An economic method for the fluorescent labelling of PCR fragments. *Nature Biotechnology* 18 (2): 233–234. <https://doi.org/10.1038/72708>
- Seguenza G. 1863. Paleontologia malacologica delle rocce terziarie del distretto di Messina studiata nei suoi rapporti zoologici e geognostici. Fissurellidi. *Annali dell'Accademia degli Aspiranti Naturalisti, Napoli* (3) 2: 77–95.
- Seid C.A., Hiley A.S., McCowin M.F., Carvajal J.I., Cha H., Ahyong S.T., Ashford O.S., Breedy O., Eernisse D.J., Goffredi S.K., Hendrickx M.E., ... & Rouse G.W. 2025. A faunal inventory of methane seeps on the Pacific margin of Costa Rica. *ZooKeys* 1222: 1–250. <https://doi.org/10.3897/zookeys.1222.134385>
- Sellanes J. & Krylova E. 2005. A new species of *Calypptogena* (Bivalvia: Vesicomysidae) from a recently discovered methane seepage area off Concepción Bay, Chile (~36°S). *Journal of the Marine Biological Association of the United Kingdom* 85 (4): 969–976. <https://doi.org/10.1017/s0025315405011963>
- Simone L.R.L. & Cunha C.M. 2014. Taxonomical study on the mollusks collected in Marion-Dufresne (MD55) and other expeditions to SE Brazil: the Fissurellidae (Mollusca, Vetigastropoda). *Zoosystema* 3835 (4): 437–468. <https://doi.org/10.11646/zootaxa.3835.4.2>
- Simone L.R.L. 2024. New species, misidentifications and problematic taxonomy of some Atlantic South American marine mollusks: a review. *Papeis Avulsos de Zoologia* 64: e202464031: 1–104. <https://doi.org/10.11606/1807-0205/2024.64.031>
- Smith E.A. 1875. Descriptions of some new shells from Kerguelen's Island. *Annals and Magazine of Natural History* ser. 4 16 (91): 67–73. <https://doi.org/10.1080/00222937508681123>
- Smith P.J., McVeagh S.M., Won Y. & Vrijenhoek R.C. 2004. Genetic heterogeneity among New Zealand species of hydrothermal vent mussels (Mytilidae: *Bathymodiolus*). *Marine Biology* 144 (3): 537–545. <https://doi.org/10.1007/s00227-003-1207-4>
- Sowerby G.B. III. 1892. *Marine Shells of South Africa. A Catalogue of all the Known Species with References to Figures in Various Works, Descriptions of New Species, and Figures of Such as are New, Little Known, or Hitherto Unfigured*. G.B. Sowerby, London.
- Stimpson W. 1851. *Shells of New England; a Revision of the Synonymy of the Testaceous Mollusks of New England, with Notes on their Structure and their Geographical and Bathymetrical Distribution, with Figures of New Species*. Phillips, Sampson and Company, Boston. <https://doi.org/10.5962/bhl.title.13123>
- Sturany R. 1896. Zoologische Ergebnisse VII. Mollusken I (Prosobranchier und Opisthobranchier; Scaphopoden; Lamellibranchier) gesammelt von S.M. Schiff “Pola” 1890–1894. *Denkschriften der Kaiserlichen Akademie der Wissenschaften, Mathematisch-Naturwissenschaftliche Classe* 63: 1–36.
- Swainson W. 1840. *A Treatise on Malacology; or the Natural Classification of Shells and Shell-fish*. Longman, London.
- Taylor J. & Glover E. 2021. *Biology, Evolution and Generic Review of the Chemosymbiotic Bivalve Family Lucinidae*. Publication 182. The Ray Society, London.
- Thiele J. 1912. Die antarktischen Schnecken und Muscheln. *Deutsche Südpolar-Expedition, 1901–1903, im Auftrage des Reichsamtes des Innern. Wissenschaftliche Ergebnisse* 13, Zoologie 5 (2): 185–285. <https://doi.org/10.5962/bhl.title.11185>

Thiele J. 1925. Gastropoden der Deutschen Tiefsee-Expedition. II Teil. *Wissenschaftliche Ergebnisse der Deutschen Tiefsee-Expedition auf dem Dampfer "Valdivia", 1898–1899* 17 (2): 35–382 [reprints paginated 1–348].

Thiele J. & Jaeckel S. 1931. Muscheln der Deutschen Tiefsee Expedition. *Wissenschaftliche Ergebnisse der Deutschen Tiefsee-Expedition auf dem Dampfer "Valdivia", 1898–1899* 21: 159–268.

Verrill A.E. 1880. Notice of the remarkable marine fauna occupying the outer banks off the southern coast of New England. *American Journal of Science* 3 (20): 390–403.

Verrill A.E. 1882. Catalogue of marine Mollusca added to the fauna of the New England region, during the past ten years. *Transactions of the Connecticut Academy of Arts and Sciences* 5 (2): 447–587.

Walsh P.S., Metzger D.A. & Higuchi R. 2013. Chelex 100 as a medium for simple extraction of DNA for PCR-based typing from forensic material. *BioTechniques* 54 (3): 134–139.
<https://doi.org/10.2144/000114018>

Wang L.G., Lam T.T.Y., Xu S., Dai Z., Zhou L., Feng T., Guo P., Dunn C.W., Jones B.R., Tyler B., Zhu H., Guan Y., Yong J. & Yu G. 2020. Treeio: an R package for phylogenetic tree input and output with richly annotated and associated data. *Molecular Biology and Evolution* 37 (2): 599–603.
<https://doi.org/10.1093/molbev/msz240>

Warén A. 1991. New and little-known Mollusca from Iceland and Scandinavia. *Sarsia*. 76 (1–2): 53–124.
<https://doi.org/10.1080/00364827.1991.10413466>

Warén A. 1992. New and little known “Skeneimorph” gastropods from the Mediterranean Sea and the adjacent Atlantic Ocean. *Bollettino Malacologico* 27 (10–12): 149–248.

Warén A. & Bouchet P. 1993. New records, species, genera, and a new family of gastropods from hydrothermal vents and hydrocarbon seeps. *Zoologica Scripta* 22: 1–90.
<https://doi.org/10.1111/j.1463-6409.1993.tb00342.x>

Warén A. & Bouchet P. 2001. Gastropoda and Monoplacophora from hydrothermal vents and seeps new taxa and records. *The Veliger* 44 (2): 116–231.

Warén A. & Bouchet P. 2009. New gastropods from deep-sea hydrocarbon seeps off West Africa. *Deep Sea Research Part II: Topical Studies in Oceanography* 56 (23): 2326–2349.
<https://doi.org/10.1016/j.dsr2.2009.04.013>

Warén A. & Ponder W.F. 1991. New species, anatomy, and systematic position of the hydrothermal vent and hydrocarbon seep gastropod family Provannidae fam.n. (Caenogastropoda). *Zoologica Scripta* 20 (1): 27–56. <https://doi.org/10.1111/j.1463-6409.1991.tb00273.x>

Watson R.B. 1879–1883. Mollusca of H.M.S. 'Challenger' Expedition. *Journal of the Linnean Society of London* 14: 506–529, 586–605, 692–716 [1879]; 15: 87–126, 217–230 [1880], 245–274, 388–412, 413–455, 457–475 [1881]; 16: 247–254, 324–343, 358–372, 373–392 [1882], 594–611 [1883]; 17: 26–40, 112–130, 284–293, 319–340, 341–346 [1883].

Woodward S.P. 1859. On a new species of mollusk of the genus *Scissurella* D'Orbigny. *Proceedings of the Zoological Society of London* 27 (392–405): 202–204

Wong T.K., Ly-Trong N., Ren H., Baños H., Roger A.J., Susko E., Bielow C., Nicola De Maio N., Goldman N., Hahn M.W., Huttley G., Robert Lanfear, R. & Minh B.Q. 2025. IQ-TREE 3: Phylogenomic

Inference Software using Complex Evolutionary Models. *Molecular Biology and Evolution* 43: 1–6. <https://doi.org/10.32942/X2P62N>

Xu T., Sun J., Lv J., Watanabe H.K., Li T., Zou W., Rouse G.W., Wang S., Qian P.-Y., Bao Z. & Qiu J.-W. 2017. Genome-wide discovery of single nucleotide polymorphisms (SNPs) and single nucleotide variants (SNVs) in deep-sea mussels: Potential use in population genomics and cross-species application. *Deep Sea Research Part II: Topical Studies in Oceanography* 137: 318–326. <https://doi.org/10.1016/j.dsr2.2016.03.011>

Xu T., Feng D., Tao J. & Qiu J.W. 2019. A new species of deep-sea mussel (Bivalvia: Mytilidae: *Gigantidas*) from the South China Sea: morphology, phylogenetic position, and gill-associated microbes. *Deep Sea Research Part I: Oceanographic Research Papers* 146: 79–90. <https://doi.org/10.1016/j.dsr.2019.03.001>

Yu G., Smith D.K., Zhu H., Guan Y. & Lam T.T.-Y. 2017. ggtree: an R package for visualization and annotation of phylogenetic trees with their covariates and other associated data. *Methods in Ecology and Evolution* 8 (1): 28–36. <https://doi.org/10.1111/2041-210X.12628>

Zhang S.-Q. & Zhang S.-P. 2017. *Bathymacra becki*, a new species of pectinodontid limpet (Gastropoda: Pectinodontidae) from a hydrothermal vent of the Manus Back-Arc Basin. *The Nautilus* 131 (4): 217–225.

Zhang S.-Q. & Zhang S.-P. 2020. Two new species of genus *Bathymacra* from deep-sea chemosynthetic areas in the western Pacific (Gastropoda: Pectinodontidae). *The Nautilus* 134 (1): 45–50.

Zhang S.-Q., Zhang J.-L. & Zhang S.-P. 2016. A new species of *Bathymacra* (Gastropoda: Pectinodontidae) from a methane seep area in the South China Sea. *The Nautilus* 130 (1): 1–4.

Zhang S.-Q., Zhang S.-P. & Chen H. 2020. *Enigmaticolus inflatus* sp. nov., a new buccinid species from a methane seep area in the South China Sea (Gastropoda: Neogastropoda). *Zootaxa* 4728 (3): 385–389. <https://doi.org/10.11646/zootaxa.4728.3.8>

Zhao Y., Xu T., Law Y. S., Feng D., Li N., Xin R., Wang H., Ji F., Zhou H. & Qiu J.-W. 2020. Ecological characterization of cold-seep epifauna in the South China Sea. *Deep Sea Research Part I: Oceanographic Research Papers* 163: e103361. <https://doi.org/10.1016/j.dsr.2020.103361>

Zhong Z., Wang M., Chen H., Zheng P. & Li C. 2020. Gametogenesis and reproductive traits of the cold-seep mussel *Gigantidas platifrons* in the South China Sea. *Journal of Oceanology and Limnology* 38: 1304–1318. <https://doi.org/10.1007/s00343-020-0027-4>

Printed versions of all papers are deposited in the libraries of two of the institutes that are members of the *EJT* consortium: Muséum national d'Histoire naturelle, Paris, France and Royal Museum for Central Africa, Tervuren, Belgium. The other members of the consortium are: Royal Belgian Institute of Natural Sciences, Brussels, Belgium; Meise Botanic Garden, Meise, Belgium; Natural History Museum of Denmark, Copenhagen, Denmark; Naturalis Biodiversity Center, Leiden, the Netherlands; Museo Nacional de Ciencias Naturales-CSIC, Madrid, Spain; Leibniz Institute for the Analysis of Biodiversity Change, Bonn – Hamburg, Germany; National Museum of the Czech Republic, Prague, Czech Republic; The Steinhardt Museum of Natural History, Tel Aviv, Israël.