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Melanodrymia biconica sp. nov. (Gastropoda, Melanodrymiidae) from hydrothermal vents in the Indian Ocean

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Abstract. The gastropod *Melanodrymia biconica* sp. nov. (Melanodrymiidae) is described as a new species from abyssal hydrothermal vent habitats on the Central and Southeast Indian Ridge (Indian Ocean). It is a small species that is characterised by its biconical outline with a rounded peripheral keel and a large spiral chord at the base of the shell. The new species is the sixth taxon of the genus *Melanodrymia* and the first congener known from the Indian Ocean. The five previously described congeners live in the eastern Pacific Ocean. A minimum divergence of 7% exists between the mitochondrial DNA sequence (*COI*) of *M. biconica* and other congeners. The simple protoconchs of species in *Melanodrymia* suggest a non-planktonic larval stage.

Keywords. Mollusca, Neomphaloidea, Central Indian Ridge, Southeast Indian Ridge, deep sea.

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Introduction

During the research conducted by the German Federal Institute for Geosciences and Natural Resources (Bundesanstalt für Geowissenschaften und Rohstoffe) to identify polymetallic massive sulphide deposits in the Indian Ocean, the INDEX project provided detailed baseline studies in the German license area.

As part of the environmental program carried by this project, recent studies revealed that Mollusca account for a considerable number of benthic taxa in the hydrothermal vents along the Central (CIR) and the Southeast Indian Ridges (SEIR) (Gerdes *et al.* 2019a, 2019b, 2021). Similar observations were reported from other vents of the Carlsberg Ridge (Zhou *et al.* 2022; Jang *et al.* 2023), CIR (Hashimoto *et al.* 2001; Van Dover *et al.* 2001, 2002; Nakamura *et al.* 2012; Watanabe & Beedessee 2015; Kim *et al.* 2020),

Southwest Indian Ridge (Tao *et al.* 2012; Copley *et al.* 2016; Zhou *et al.* 2018; Sun *et al.* 2020) and studies on Indian Ocean vent biodiversity, connectivity, and conservation (Perez *et al.* 2021; Zhou *et al.* 2022).

The molluscan fauna along the ridges is composed almost exclusively of endemic gastropods. Notable occurrences in this environment include some representatives of the families Cancellariidae Forbes & Hanley, 1851; Skeneidae W. Clark, 1851 (Okutani *et al.* 2004); and Provannidae Warén & Ponder, 1991 (Okutani *et al.* 2004, Johnson *et al.* 2014). Okutani *et al.* (2004) described the endemic *Desbruyeresia marisindica* Okutani, Hashimoto & Sasaki, 2004; *Bruceiella wareni* Okutani, Hashimoto & T. Sasaki, 2004; and *Iphinopsis boucheti* Okutani, Hashimoto & Sasaki, 2004 and later, Okutani (in Johnson *et al.* 2014) described *Alviniconcha marisindica* following extensive DNA sequencing within the genus *Alviniconcha* Okutani & Ohta, 1988. A recent study has discussed the geographical subdivision of *Alviniconcha* across Indian Ocean vents (Jang *et al.* 2023).

During the last years, special attention was paid to Peltospiridae J.H. McLean, 1989 with the description of the iconic "scaly-foot gastropod" *Chrysomallon squamiferum* Chen, Linse, Copley & Rogers, 2015 and other representatives by Chen *et al.* (2015, 2017) and a recently mitogenome-based phylogeny discussed the dispersal of Peltospiridae to the Indian Ocean (Zhang *et al.* 2024).

Recently, Chen *et al.* (2021) described three new species of the family Neolepetopsidae McLean, 1990; Hoffman *et al.* (2022); and Kniesz *et al.* (2025) described four species of the genus *Anatoma* S.P. Woodward, 1859, solely known from the vent fields in CIR and SEIR and Gu *et al.* (2026) reported on four new species of the family Lepetodrilidae McLean, 1988. Contrasting this pattern of regional endemism, the bivalve *Bathymodiolus septemdierum* Hashimoto & Okutani, 1994, recently reviewed by Tunnicliffe & Breusing (2022), remains the only vent-related mollusc with a wide Indo-Pacific distribution (Breusing *et al.* 2015; Mao *et al.* 2025).

During the INDEX cruises in 2012, 2015, 2018 and 2019, several specimens identified as genus *Melanodrymia* Hickman, 1984 (Gastropoda: Melanodrymiidae Salvini-Plawen & Steiner, 1995) were collected from the CIR and SEIR. Species of *Melanodrymia* are small, less than 2 mm, and often characterised by thin, translucent shells with one or more strong spiral cords and a simple paucispiral protoconch (Hickman 1984; Warén & Bouchet 1989, 1993, 2001; Chen *et al.* 2024). Although Melanodrymiidae currently comprises four extant genera with in total 18 species (MolluscaBase 2026), only five species are known in *Melanodrymia* and they all occur near hydrothermal vents in the eastern Pacific Ocean (Hickman 1984; Warén & Bouchet 1993, 2001; Chen *et al.* 2024; Mullineaux *et al.* 2025). Chen *et al.* (2024) and Mullineaux *et al.* (2025) indicated that *M. galeronae*, *M. telperion* and *M. laurelin* live in inactive areas near hydrothermal vents (Chen *et al.* 2024; Mullineaux *et al.* 2025). In contrast, the type species *M. aurantiaca* and *M. brightae* are associated with active vents (Chen *et al.* 2024). In this study, we provide the first description for a species of this genus from the Indian Ocean along with DNA barcodes, to facilitate identification.

Material and methods

The material used for the present study was collected during the INDEX2012, INDEX2015, INDEX2018, and INDEX2019 cruises on the RV Pelagia and Sonne using the Canadian ROV (Remotely Operated Vehicle) ROPOS (Remotely Operated Platform for Ocean Sciences). All samples were collected using ROV-operated manipulators, with individual specimens hand-picked and preserved in 96% ethanol for DNA sequence analysis at the DZMB in Wilhelmshaven.

Eight lots of specimens assigned to Melanodrymiidae, containing a total of 345 live-collected specimens and 13 shells, were obtained during four cruises from six different vent field areas. Detailed specimen data, including taxonomy and collection sites for specimens identified by a unique voucher specimen

code and museum number, is available in the Barcode of Life Data Systems (BOLD; https://boldsystems.org/) (Ratnasingham *et al.* 2024). This information can be accessed directly within the public dataset "DS-INMAC02", (https://doi.org/10.5883/DS-INMAC02).

DNA methods

Nucleotide sequences of the mitochondrial cytochrome c oxidase subunit 1 (*COI*) gene fragment were generated at the German Centre for Biodiversity Research (DZMB) department at Senckenberg am Meer (SaM). *COI* was selected as the marker for this analysis due to its known suitability for species delimitation in Melanodrymiidae (Chen *et al.* 2024) and the availability of comparative congeneric species sequences in the public data bases BOLD (DS-INMAC02) 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 ml of soft tissue was immersed in 30 ml of Chelex and activated for 30 min at 56°C followed by a chemical deactivation for 10 min at 99°C. Polymerase chain reaction (PCR) was performed to amplify the *COI* barcode fragment using the primers jgLCO (TITCIACIAAYCAYAARGAYATTGG)/ jgHCO (TAIACYTCIGGRTGICCRAARAAYCA) (Geller *et al.* 2013) and M13 tails: M13-FP (TGTAAAACGACGGCCAGT) (Schuelke 2000)/ M13R-pUC (CAGGAAACAGCTATGAC) (Messing 1983). PCR reactions were conducted using an Eppendorf Mastercycler Pro S (Eppendorf, Hamburg, Germany) and each PCR reaction contained: 13.0 ml of AccuStart II PCR ToughMix (2X) (QuantaBio), 9.0 ml of highly purified water, 0.5 ml of each primer (10 pmol/µl) and 2.0 µl of DNA template in a mixture of total 25.0 µl. 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 visualized 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.

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 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 (Camacho *et al.* 2009; Kearse *et al.* 2012) from Geneious Prime 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 Melanodrymiidae sequences published by Chen *et al.* (2024) were downloaded from GenBank (Table 1). The cocculinid limpet *Cocculina messingi* J.H. McLean & Harasewych, 1995 and *Chrysomallon squamiferun* C. Chen, K. Linse, Copley & A.D. Rogers, 2015 were used as outgroups, following the previous study (Chen *et al.* 2024).

All sequences were aligned using MAFFT (Katoh *et al.* 2005) in Geneious Prime 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 specimens 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 1,000 ultrafast bootstrapping replicates (uBS). IQ-TREE analyses were performed using R packages "ape", "seqinr", "treeio" and "ggtree".

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 package "ape" (Paradis & Schliep 2019).

Imaging methods

A few live-collected specimens were selected for morphological imaging of the shell and the radula, using a Scanning Electron Microscope (SEM, VEGA3-Tescan) with incident energy of 10 keV electrons; shells were gold-coated to improve image quality.

Sample retention

The type material was stored in the Senckenberg Museum at Frankfurt am Main (SMF). Other reference material is kept in the voucher collection at SaM.

Abbreviations

Morphological abbreviations

H	=	height of shell from apex to anterior en
Ha	=	height of aperture
L	=	length of shell, perpendicular to height measurement in ventral view

Institutional abbreviations

DZMB	=	Deutsches Zentrum für Marine Biodiversitätsforschung, Wilhelmshaven, Germany
SaM	=	Senckenberg am Meer, Wilhelmshaven
SMF	=	Senckenberg Museum Frankfurt, Frankfurt am Main, Germany

Geographical abbreviations

CIR	=	Central Indian Ridge
SEIR	=	Southeast Indian Ridge

Analytical abbreviation

bp	=	Base pairs

Results

DNA sequence analyses

A total of 17 sequences were obtained from the 22 specimens examined, with an amplification rate of 77.3%. The obtained sequences ranged in length from 594 to 658 bp; no indels (insertions or deletions) or stop codons were found. Overall mean nucleotide frequencies were G (18.3%), C (15.2%), A (27.5%), T (39.1%). All sequences were barcode compliant and placed in BOLD BIN: AEF6501.

The results of 31 *COI* sequence (567 bp) analyses are given in a ML tree (Fig. 2). The analysis confirms *Melanodrymia* as a well-supported clade, that is placed as sister group to *Leptogyra* Bush, 1897. Together these two genera are positioned as sister group to *Leptogyropsis* Marshall, 1988, consistent with previous work (Chen *et al.* 2024). All 17 specimens of *M. biconica* sp. nov. cluster together in a strongly supported clade and BOLD BIN data, confirming they represent a single species despite being found across different vent habitats and ocean ridges from the Indian Ocean. Within the genus, *M. biconica* sp. nov. is most closely related to the clade containing *M. galeronae* and *M. laurelin*, other species found in inactive vents (Chen *et al.* 2024). Interestingly, the three specimens of *M. aurantiaca* are mapped to two distinct clades and BOLD BINs: BOLD: AAX4484 and BOLD: ACQ5634, indicating hidden genetic diversity and suggesting a species complex.

Table 1. List of COI sequences from GenBank used for the DNA analyses in this study. Species name, GenBank accession number and reference are given.

Species	Accession numbers	Reference
Chrysomallon squamiferum C. Chen, K. Linse, Copley & A.D. Rogers, 2015	PZ721843	Present study
Cocculina messingi J.H. McLean & Harasewych, 1995	AY923910	Geiger & Thacker 2005
Leptogyra inflata Warén & Bouchet, 1993	AB330998	Hess *et al.* 2008
Leptogyropsis inflata Hasegawa, 1997	AB365258	Kano 2008
Melanodrymia aurantiaca Hickman, 1984	AB429220	Hess *et al.* 2008
M. aurantiaca Hickman, 1984	BK064863	Zhang *et al.* 2024
	GQ160763	Aktipis & Giribet 2011
M. brightae Warén & Bouchet, 1993	Sequencing project available under BioProject number: PRJNA962978	Unpublished genome shotgun
M. brightae Warén & Bouchet, 1993	BK064862	Zhang *et al.* 2024
M. biconica sp. nov.	PZ721833, PZ721834, PZ721835, PZ721836, PZ721837, PZ721838, PZ721839, PZ721840, PZ721841, PZ721842, PZ721844, PZ721845, PZ721846, PZ721847, PZ721848, PZ721849, PZ721850	Present study
M. galeronae Warén & Bouchet, 2001	OR828527	Chen *et al.* 2024
	NC085482, OR852748	Zhang *et al.* 2024
M. laurelin C. Chen, Y.-L. Li, J. Sun, Beaulieu & Mullineaux, 2024	OR828529	Chen *et al.* 2024
M. telperion C. Chen, Y.-L. Li, J. Sun, Beaulieu & Mullineaux, 2024	OR828528	Chen *et al.* 2024

All genetic distances reported hereafter refer to p-distances unless otherwise specified. The percentage pairwise genetic distance in the *COI* gene among the six species of *Melanodrymia* (Fig. 3) averaged at 10.4%, with the minimum being 6.9% (between *M. biconica* and *M. galeronae*) and the maximum being 15.5% (between *M. brightae* and *M. galeronae*). Taking in account the pairwise distance of all 17 specimens of *M. biconica* sp. nov. against each other, the mean intraspecific distance was 0.8%, with values ranging from 0% to 2.1%. Comparing *M. biconica* sp. nov with other species, pairwise distance ranged between 6.9% (compared to *M. galeronae*) up to a maximum of 13.8% (compared to *M. brightae*). Values for *M. aurantiaca* supported the allocation of the three samples to two separated BOLD BINs as sequences AB429220 and BK064863 have a distance of only 0.4%, but both are separated from sequence GQ160763 by a distance ranging from 4.6% to 5.0%, which is intermediate between the maximum intraspecific (2.1%) and minimum interspecific (6.9%) distances shown for the other, more clearly delineated species.

Systematic results

Class Gastropoda Cuvier, 1795
Subclass Vetigastropoda Salvini-Plawen, 1980
Superfamily Neomphaloidea McLean, 1981
Family Melanodrymiidae Salvini-Plawen & Steiner, 1995

Genus ***Melanodrymia*** Hickman, 1984

Type species

Melanodrymia aurantiaca Hickman, 1984, by original designation. Recent, East Pacific Rise.

Melanodrymia biconica sp. nov.
urn:lsid:zoobank.org:act:50D63A29-84FC-4AED-924D-4ECB33F74973
Figs 1–6, Tables 1–2

Diagnosis

Small, biconical, melanodrymiform shell; angular whorls, rounded apex and peripheral keel, apical angle 83°; wavy microsculpture, numerous prosocline growth lines at about 40° with spire axis; deeply impressed suture. Height up to 1.5 mm, height to length ratio 86–90%; height of aperture about 60% of total height; ultimate whorl to total shell height ratio 80% (Table 2). Colour of shells in ethanol: shell young specimens weakly translucent, white shell with thin, light yellowish-green periostracum; adult specimens with opaque, white shell with thick, amorph, brown, corneous periostracum.

Etymology

Biconica refers to the biconical shape of the shell.

Type material

Holotype

CENTRAL INDIAN RIDGE – **Vent Field 2** • shell; 23.88° S, 69.61° E; depth 3185 m; 11 Nov. 2019; INDEX 2019-31RO-SF2; on rocks, inactive vent area; Fig. 4; SMF376630.

Paratypes

CENTRAL INDIAN RIDGE – **Vent Field 3** • Paratype 1; 1 shell; 25.47° S, 69.93° E; depth 2646 m; 14 Nov. 2019; INDEX 2019-36RO-SG1; in sediment, inactive vent area; Figs 5A–C; SMF376631 • Paratype 2; 1 shell; same data as for paratype 1; Fig. 5D–E; SMF376632 • Paratype 3; shell, same data as for paratype 1; Fig. 5F–G; SMF376633 • Paratype 4; 1 specimen; same data as for paratype 1; Fig. 5H; SMF376634 • Paratype 5; 1 specimen; same data as for paratype 1; Fig. 5I; SMF376635 • 8 specimens; same data as for paratype 1; SMF376636; in ethanol.

Other material examined

CENTRAL INDIAN RIDGE – **Vent Field 1** • 2 haplotype specimens (I15-Ma7, 10) and 3 specimens; 23.78° S, 69.55° E, depth 3041 m; 28 Nov. 2015; INDEX 2015-49RO-B2-1; active vent area; SaM • 1 specimen; 23.78° S, 69.55° E; depth 3012 m; 2 Dec. 2015; INDEX 2015-49RO-J; inactive vent area; SaM – **Vent Field 2** • 284 specimens + 10 shells; 23.88° S, 69.61° E; depth 3296 m; 8 Dec. 2015; INDEX 2015-62RO-B3; inactive vent area; SaM89288 • 3 haplotype specimens (I19-Ma103-104, 134); 23.88° S, 69.61° E; 3185 m; 11 Nov. 2019; INDEX 2019-31RO-SF-01/02; on rocks, inactive vent area; SaM. – **Gauss Vent Field** • 3 haplotype specimens (I19-Ma131-133); 23.868º S, 69.606º E; 3026 m; 12 Nov. 2019; INDEX 2019-33RO-PF-01; on rocks, inactive vent area; SaM. – **Vent Field 3** • 12 specimens; 25.32° S, 70.04° E; depth 2444 m; 1 Dec. 2012; INDEX 2012-36RO-TVG; on rocks,

active vent area; SaM89284 • 18 specimens; 25.47° S, 69.93° E; depth 2631 m; 14 Nov. 2019; INDEX 2019-36RO-PASA-01; on rocks, active vent area; SaM • 1 specimen; 25.47° S, 69.93° E; depth 3064 m; 15 Nov. 2019; INDEX 2019-40RO-PASA-01; on rocks, non-vent area; SaM • 6 haplotype specimens (I19-Ma101-102, 139-142) and 24 specimens; 25.47° S, 69.93° E; depth 2933 m; 16 Nov. 2019; INDEX 2019-42RO-PF-01; on rocks, inactive vent area; SaM.

SOUTHEAST INDIAN RIDGE – **Vent Field 9** • 3 specimens; 27.64° S, 73.88° E; depth 2480 m; 23 Nov. 2018; INDEX 2018-63RO-J-001; on rocks, active vent area; SaM. – **Vent Field 8** • 4 haplotype specimens (I19-Ma135-138) and 1 specimen; 27.64° S, 73.86° E; depth 2541 m; 5 Dec. 2019; INDEX 2019-102RO-PASA-01; on rocks, inactive vent area; SaM.

Description

Protoconch (Fig. 4C). Raised globular shell, slightly more than ½ whorl; fine network with shallow pits (partly eroded); raised sharp lip at the transition to teleoconch with thickened rim towards periphery, transition to teleoconch clear by change in sculpture; diameter 240 mm.

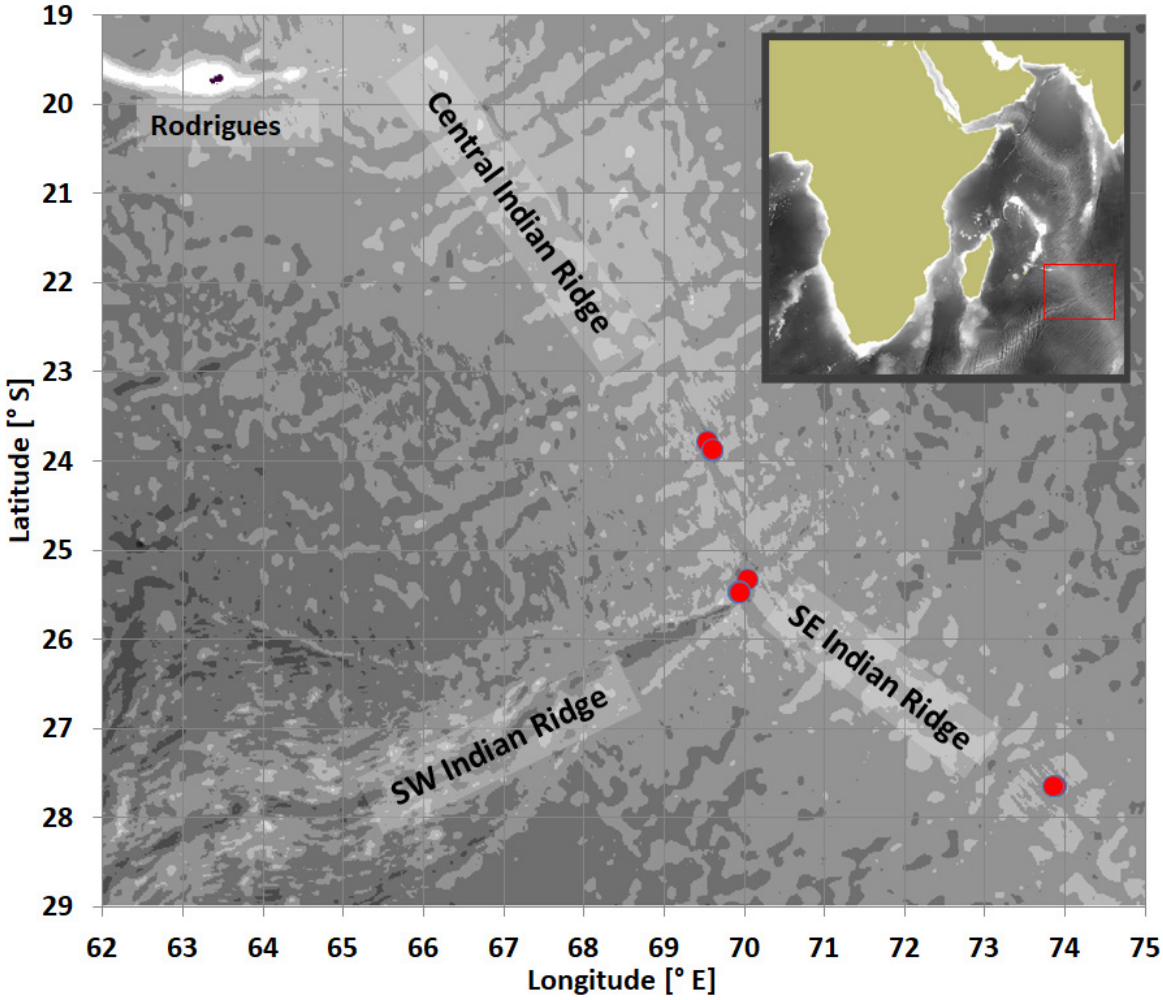


Fig. 1. Location map where *Melanodrymia biconica* sp. nov. has been collected in the Central Indian Ocean; the locations are shown by red dots. The inset map shows the location of the study area with a red rectangle in the western Indian Ocean, East of Madagascar. Bathymetric data GEBCO, isobaths 500 m.

Teleoconch (Fig. 4A–B). 2¼ regular whorls with convex shoulder area, flattened sloping face towards periphery at 40° with spire axis (Fig. 4A); apical angle about 80°. First whorl, simple smooth peripheral keel with part of base whorl below. Ultimate whorl, smoothly rounded protruding peripheral keel (Fig. 4A, D), base convex with broadly rounded umbilical keel. Umbilicus closed by columella and columellar lip (Fig. 4E). Sculpture anatomising rounded spiral grooves descending towards periphery (Fig. 4D), fading towards umbilical area (Fig. 4E). Aperture subcircular (Fig. 4A): lip prosocline with union at 90° to penultimate whorl, weakly pointed anteriorly (rounded in holotype), at peripheral keel and at union with penultimate whorl; columellar/parietal lip concave, distinct, partly covering umbilical area; callus reclining on parietal area (Fig. 4E) or distinct in older specimens (Fig. 5); outer lip sharp; inside aperture smooth, callus thin.

Operculum. Circular, yellowish transparent, thin, corneous, multispiral with central circular nucleus, six whorls.

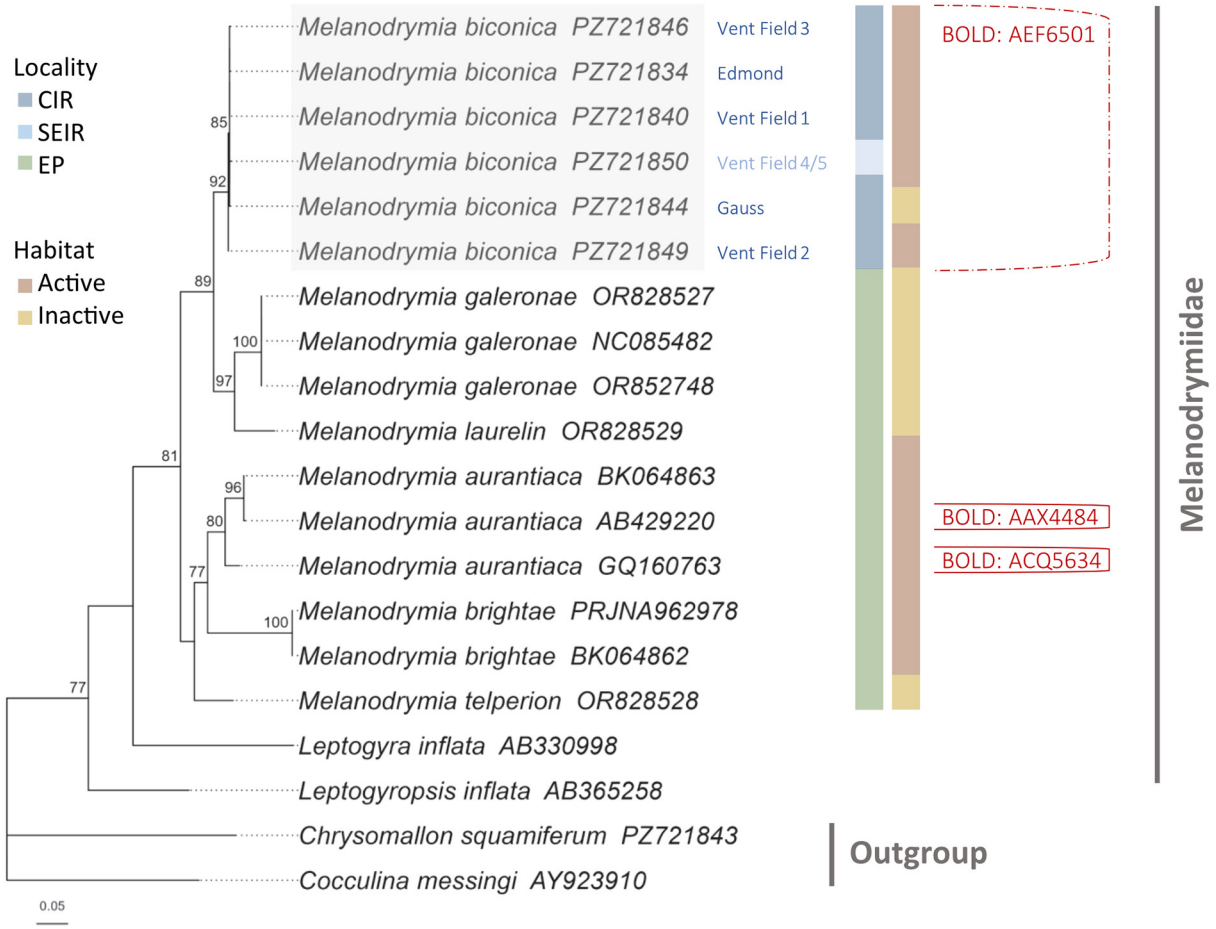


Fig. 2. Maximum-likelihood tree of Melanodrymiidae Salvini-Plawen & G. Steiner, 1995 based on COI sequences with *Cocculina messingi* and *Chrysomallon squamiferun* as outgroups. The GenBank accession numbers are added following species names. The new species is highlighted in light grey. Numbers at nodes indicate ultrafast bootstrap support ≥ 70%. Scale shows substitutions per site. Coloured vent names added following new species name. Coloured squares indicating locality: CIR = Central Indian Ridge; SEIR = Southeast Indian Ridge, and EP = East Pacific. Coloured squares indicating habitat: active vents and inactive vents. BOLD BIN, when available, provided for each species cluster.

Fig. 3. Heat map interspecific genetic distances between species of *Melanodrymia* in COI (K2P: lower-left; p-distance: upper-right).

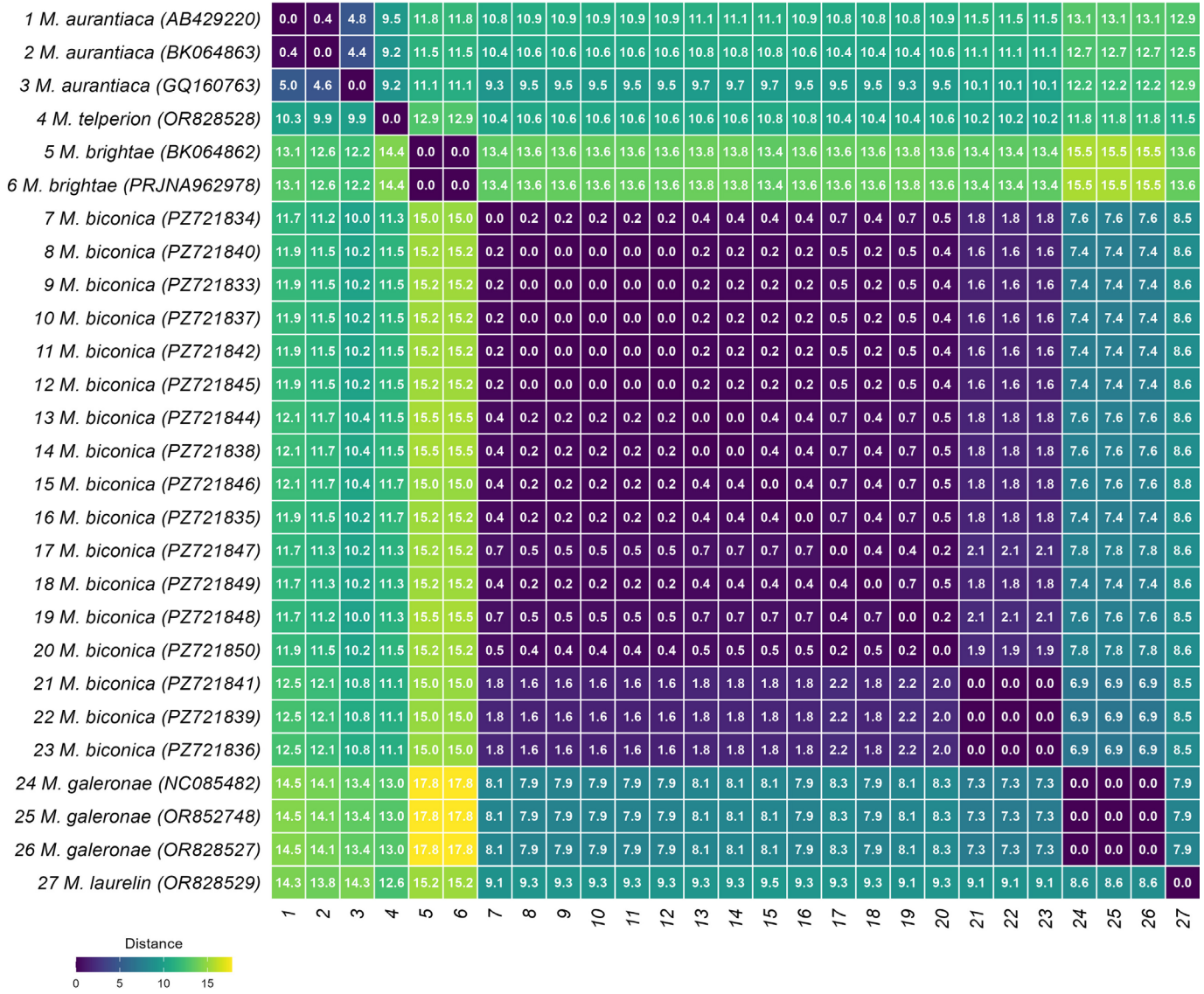


Table 2. *Melanodrymia biconica* sp. nov., dimensions of the figured type specimens.

	Height H [mm]	Length L [mm]	Height aperture Ha [mm]
Holotype	0.94	1.00	0.55
Paratype 1	1.25	1.20	0.74
Paratype 2	1.46	1.31	0.89
Paratype 3	1.33	1.40	0.71
Paratype 4	–	1.29	–
Paratype 5	–	1.19	–

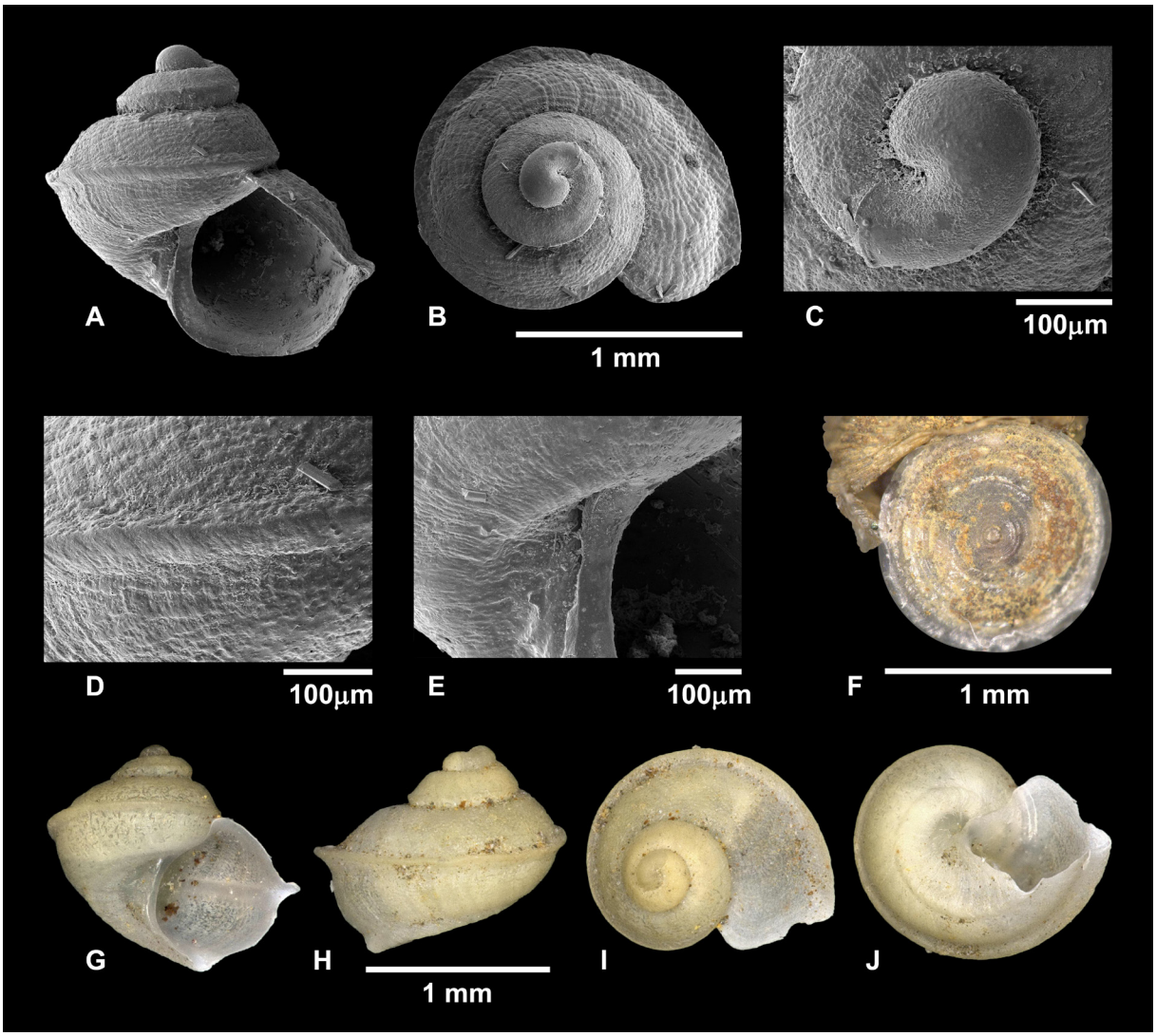


Fig. 4. *Melanodrymia biconica* sp. nov., Central Indian Ridge. **A–E**. holotype, INDEX 2019-31RO-SF2, SEM images, SMF376630. **A**. Apertural view, H = 0.94 mm, L = 1.00 mm, Ha = 0.55 mm. **B**. Apical view. **C**. Protoconch, L = 240 mm. **D**. Microsculpture and peripheral keel body whorl. **E**. Umbilical area and columella. **F**. INDEX 2012-36RO- TVG, SaM89283, operculum, diameter = 1.0 mm. **G–J**. INDEX 2015-62RO-B3xx+, SaM89218, colour images. **G**. Apertural view, H = 1.20 mm, L = 1.40 mm, Ha = 0.89 mm. **H**. Abapertural view. **I**. Apical view. **J**. Abapical view. Scale bars: A–B, F–J = 1 mm; C–E = 100 mm.

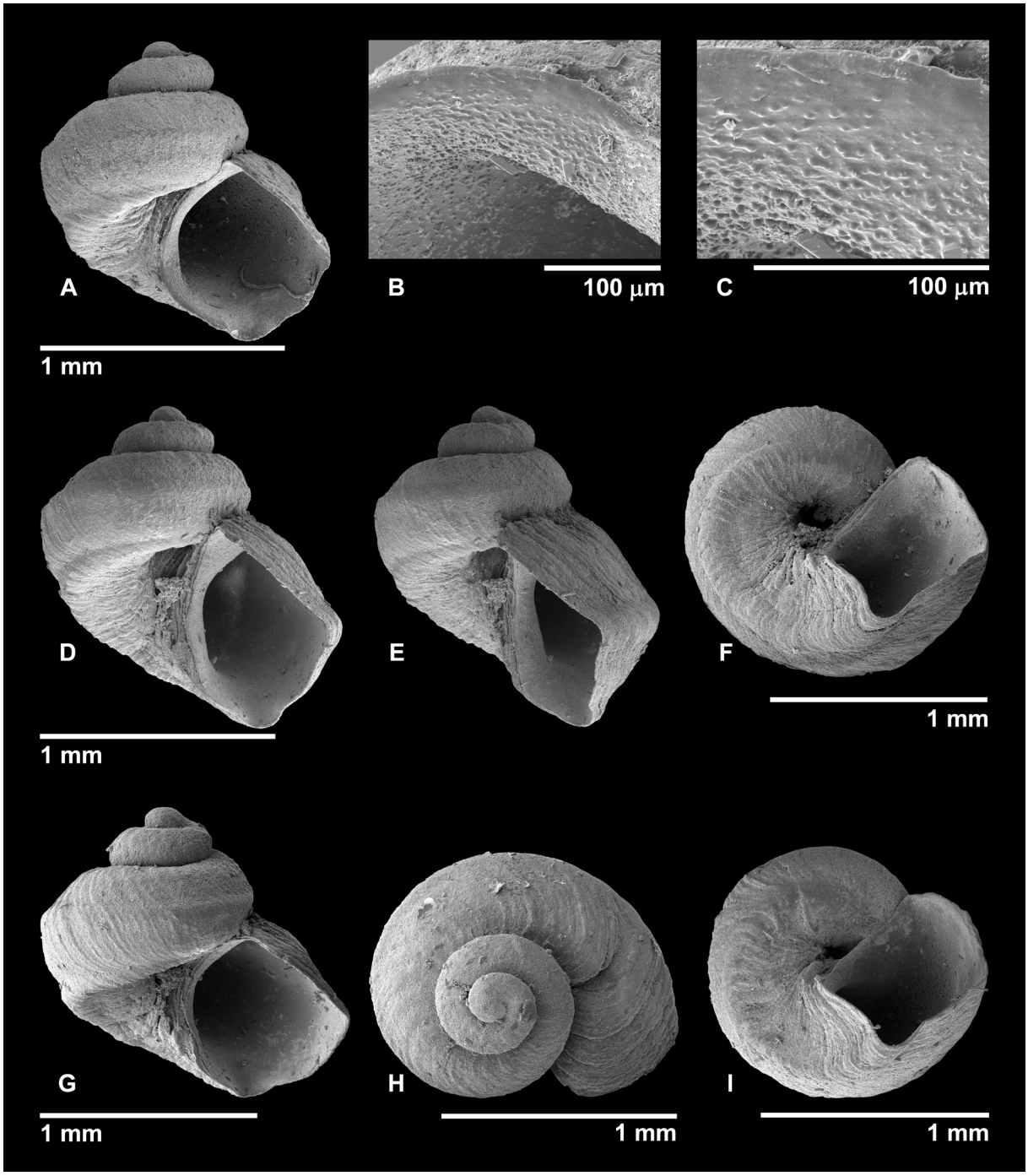


Fig. 5. *Melanodrymia biconica* sp. nov., paratypes, Central Indian Ridge. **A–C**. Paratype 1, INDEX 2019-36RO-SG1, H = 1.25 mm, L = 1.20 mm, Ha = 0.74 mm, SMF376631. **A**. Apertural view. **B–C**. Rough sculpture near base columellar lip. **D–E**. Paratype 2, H = 1.46 mm, L = 1.31 mm, Ha = 0.89 mm, SMF376632. **D**. Apertural view. **E**. Abapical view. **F–G**. Paratype 3, specimen, H = 1.33 mm, L = 1.40 mm, Ha = 0.71 mm, SMF376633. **F**. Abapical view. **G**. Apertural view. **H**. Paratype 4, specimen, L = 1.29 mm, apical view, SMF376634. **I**. Paratype 5, L = 1.19 mm, abapical view, SMF376635. Scale bars: A, D–I = 1 mm; B–C = 100 mm.

Radula. Central (rachidian) tooth, lateral teeth and marginal teeth in symmetric arrangement: 30-4-1-4-30; width of a row about 120 mm (Fig. 6A–C). Central (rachidian) tooth with two broad slightly overlapping curved cusps (Fig. 6B). Four lateral teeth on either side with major curved central cusp and two minor side cusps (Fig. 6B). Thirty marginal teeth on either side on thin stems; proximal teeth with coarsely serrated cusps; distal marginal teeth ovate cusps, curved anteriorly, with about 20 fine spines at the margin (Fig. 6A, C). Inner marginal teeth have an intermediate morphology.

Soft parts. Little is known about the soft parts as the anterior body has been damaged in multiple preparation attempts. The soft parts are 1¾ whorls when contracted.

Variation. The strengths of the umbilical and peripheral keels are variable. The umbilicus may be closed to slightly open, narrow and tortuous.

Distribution

Indian Ocean, Central Indian Ridge and SE Indian Ridge, 23.7°–27.7° S, 69.5°–73.9° E, bathymetric range 2480–3296 m.

Habitat

All live specimens were encountered in abyssal hydrothermal vent fields on rocks and in sediment, near active vents and in inactive vent areas. Microbial mats frequently covered the rocks.

Remarks

Placement in *Melanodrymia* is based on the morphology and the *COI* analyses. Typical morphological features are the peripheral and abapical keels and the micro-sculpture of the teleoconch. The *COI* sequence of *M. biconica* sp. nov. differs by 9–13% from that of the type species *M. aurantiaca* Hickman, 1984.

The new species is the first one known to occur in the Indian Ocean. Five hitherto known species in *Melanodrymia* live in abyssal hydrothermal vent fields on the East Pacific Rise off western North America. The type species *M. aurantiaca* has two peripheral keels, an open umbilicus and broad axial ribs (Hickman 1984: 20; Warén & Bouchet 1989: 75, figs 32–33). *M. brightae* Warén & Bouchet, 1993 from the Juan de Fuca Ridge is very similar but has an open umbilicus and broad axial ribs (Warén & Bouchet 1993: 44–45, fig. 34a–c). *M. galeronae* Warén & Bouchet, 2001 has a raised outline with stepped

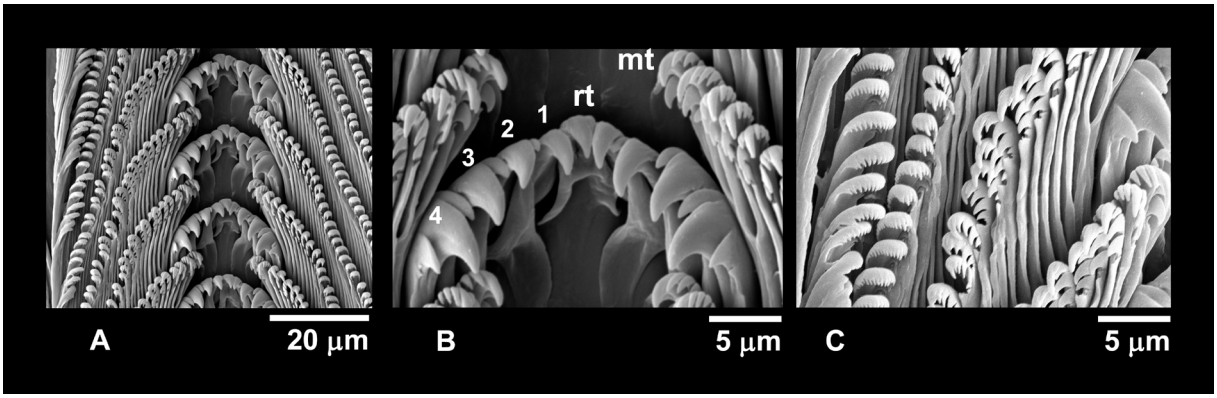


Fig. 6. Radula of *Melanodrymia biconica* sp. nov., Central Indian Ridge, INDEX 2019-42RO-PF01 (haplotype specimen Ma_I19_101, SEM images). **A**. Rows of radular teeth. **B**. Central tooth (rt = rachidian tooth), lateral teeth 1–4, mt = inner marginal teeth. **C**. Left outer marginal teeth, right inner marginal teeth.

shoulders and broad axial ribs (Warén & Bouchet 2001: 161, fig. 24a–b, d). *Melanodrymia laurelin* Chen, Y.-L. Li, J. Sun, Beaulieu & Mullineaux, 2024 has an open umbilicus, a serrated peripheral keel and a strong peri-umbilical cord (Chen *et al.* 2024: 3–6, figs 1–2) and *M. telperion* Chen, Li, Sun, Beaulieu & Mullineaux, 2024 has a narrow open umbilicus and two peripheral keels with a flattened area in between (Chen *et al.* 2024: 6–8, figs 3–4). *Melanodrymia biconica* sp. nov. differs from the five known species by the bi-conical outline, and the nearly closed umbilicus.

Descriptions of radulae and external soft parts of species in *Melanodrymia* are given in Haszprunar (1989), Warén & Bouchet (1989, 1993, 2001) and Chen *et al.* (2024). The radulae of the type species are figured in Warén & Bouchet (1989: 76, figs 26–27) and they are very similar to those of the present species.

Discussion

Melanodrymia biconica sp. nov. shows a very high *COI* sequence similarity between the vent fields that spread over about 600 km along the CIR and SEIR. Similar observations were recently made in a study on the vent-related gastropods in *Anatoma* (Hoffman *et al.* 2022).

Zhang *et al.* (2024) studied the phylogenetic relationships of taxa in neomphalids including those in Melanodrymiidae. They concluded that the origin of the neomphalids is likely from the Eastern Pacific Rise. The evolution of the taxa in Neomphalida may have involved shifts from vent habitats and sunken wood. Nevertheless, all species of *Melanodrymia* are known from vent fields and five species live in the eastern Pacific Ocean. Currently, *M. biconica* sp. nov. is the only congener and the first representative of Melanodrymiidae in the Indian Ocean. These locations are some 20 000 km away from the Eastern Pacific Rise. Currently, our understanding of the distributions of melanodrymiids is probably hindered by undersampling along the tectonic plate margins of the Indo-Pacific, Atlantic and Southern Ocean.

The simple protoconch of species in *Melanodrymia* suggests a non-planktonic larval stage; a development that is shared with most vetigastropods (Haszprunar 1989). It is unclear how the genus has been able to evolve across the Indo-Pacific oceans considering that its known habitats are scarce and spaced over thousands of kilometres. It is possible that a common ancestor had planktonic larvae and that its Recent descendants developed a non-planktonic larval stage.

The type species *M. aurantiaca* has similar radulae (Warén & Bouchet 1989: figs 26–27) as *M. biconica* sp. nov. (Fig. 6) and a similar food source is likely. The stomach contents of the former type species included predominantly mineral remains mixed with organic material (Warén & Bouchet 1989: 75); this suggests a benthic grazer and/or scavenger. An abundant food source may be Bacteria or Archaea present in mats that were observed on the sea rocky floor near the vents (Mullineaux *et al.* 2025; this study).

Melanodrymia biconica sp. nov. has been found in areas near active and inactive vents albeit that the latter seem more common. Chen *et al.* (2024) and Mullineaux *et al.* (2025) investigated gastropod fauna in vent areas and indicated that *M. telperion*, *M. laurelin* and *M. galeronae* are known from inactive vent areas and *M. aurantiaca* and *M. brightae* occur near active vents. Mullineaux *et al.* (2025) provided more gastropods related to inactive vent areas: *Anatoma* sp., *Neolepetopsis densata* McLean, 1990, and *Sutilizona theca* McLean, 1989. In contrast, they also identified a set of species associated with active vents: *Eulepetopsis vitrea* McLean, 1990, *Lepetodrilus elevatus* McLean, 1988, *Pachydermia laevis* Warén & Bouchet, 1989 and *Solutigyra reticulata* Warén & Bouchet, 1989.

At the CIR and SEIR, we collected congeners of *Melanodrymia* (this study), *Anatoma* (Hoffman *et al.*2022; Kniesz *et al.* 2025), *Neolepetopsis*, *Sutulizona*, *Eulepetopsis*, and *Lepetodrilus*. The teeth of the radulae from these species are similar in arrangement and size and it is likely that all are grazers (Warén & Bouchet 2001). Some species and genera may be more tolerant to extreme environmental conditions

near active vents whereas others live near inactive vents or within the wider periphery of vents that are also influenced by sulphide precipitation. Sulphides are an energy source for sulphide-oxidising microbes, which in turn may provide food for grazing gastropods (Mullineaux *et al.* 2025). A systematic analysis of habitats of gastropods from the CIR and SEIR will be completed as part of our ongoing studies.

Most of the species occuring on the CIR and SEIR are solely known from habitats related to hydrothermal vents from this region. Exploitation of poly-metallic sulphide deposits will jeopardise the habitats of these vulnerable species. Consequently, extreme care should be taken when deciding to develop these subsea regions. We hope that similar inventories of fauna from hydrothermal vent areas will contribute to informed decisions by authorities striking a balance between the value of an unharmed natural environment and commercial interests.

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Data availability

Detailed specimen data, including taxonomy and collection sites for specimens identified by a unique voucher specimen code and museum number, is available in the Barcode of Life Data Systems (BOLD; www.boldsystems.org). This information can be accessed directly within the public dataset "DS-INMAC02" (https://doi.org/10.5883/DS-INMAC02).

Author contribution

Conceptualization, Data curation, Formal analysis, Investigation & Validation, Investigation & Validation, Methodology, Project administration, Writing - review and editing: LH, KK, TK. Supervision: LH, TK. Visualization: LH, TK. Writing - original draft: LH, TK.

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