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Research Article

Two new melanodrymiid snails from the East Pacific Rise indicate the potential role of inactive vents as evolutionary stepping-stones

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Since their discovery in 1977, animals specialized to life in active deep-sea hydrothermal vents have been the focus of many studies. Inactive spires in the vent periphery, however, have received little attention. Recent shifts of deep-sea mining interests from active vents to inactive sulphide deposits have led to an urgent need to characterize the inactive vent fauna. Here, we report two new species of the vent-endemic genus *Melanodrymia* that are apparently specific to surfaces of inactive sulphides on the East Pacific Rise. *Melanodrymia laurelin* sp. nov. and *M. telperion* sp. nov. are easily distinguished from other congeners by shell shape and sculpture; their standings as distinct species are supported by molecular analyses using the mitochondrial cytochrome *c* oxidase subunit I (COI) gene. They were collected together with numerous specimens of *M. galeronae*, another species originally described some distance away from active vents. Phylogenetic reconstruction indicates *Melanodrymia* species living in active vents likely evolved from ancestors specializing in inactive spires, and in turn from sunken wood. Our findings add to the growing evidence that inactive sulphides host unique species, bolstering the need to better understand these systems before any anthropogenic exploitation takes place.

https://zoobank.org/urn:lsid:zoobank.org:pub:D8E8EB3F-B246-4962-B70C-1CD94AEB134D

Key words: Deep sea, hydrothermal vent, Melanodrymiidae, Neomphalida, Neomphalina, Neomphaliones, polymetallic sulphides

Introduction

Hydrothermal vents were first discovered on the Galápagos Rift in 1977, opening a door to the realm of chemosynthesis that changed our understanding of life on Earth (Corliss et al., 1979). Thriving on microbial primary production, these deep-sea 'oases' host biomass comparable to shallow-water coral reefs. Over 600 animal species are now known from vents worldwide, and as living at vents requires special adaptations most are endemics that can live nowhere else (Chapman et al., 2019). As vents also produce polymetallic sulphide deposits, they have been eyed as targets for deep-sea mining (Amon et al., 2022). As a result, many specialist species of active vents are now considered by the IUCN (International Union for the Conservation of Nature) Red List as endangered from anthropogenic activities (Thomas et al., 2022). Lately, interest in exploitation is shifting from active vent fields to inactive or extinct features. Although lacking in dense aggregations typical of active vents, we currently have little to no baseline data of biodiversity at inactive vents required to understand the impact of potential mining there (Amon et al., 2022; Van Dover, 2019).

Several recent studies have shown that some species are likely specialists of inactive sulphide spires, belonging to genera or families typical of vent habitats but absent from nearby active vent sites (Chen, Zhou, et al., 2021; Zhou et al., 2019). These findings suggest inactive spires may be a unique ecosystem home to

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another suite of specialist fauna, which remain understudied (Amon et al., 2022). Here, we report the discovery of two previously undescribed melanodrymiid snails belonging to genus *Melanodrymia* from inactive spires on the East Pacific Rise (EPR). Neither of these species has previously been found at active sites of the EPR despite considerable sampling efforts (Desbruyères et al., 2006; Warén & Bouchet, 1993, 2001).

Melanodrymiidae is a family of gastropods in the order Neomphalida, which is restricted to chemosynthesis-based ecosystems including hydrothermal vents, hydrocarbon seeps, and organic falls (Zhong et al., 2022). Melanodrymiid snails currently include three genera from sunken wood (*Leptogyra*, *Leptogyropsis*, and *Xyleptogyra*) and one, *Melanodrymia*, from hydrothermal vents (Hess et al., 2008; Hickman, 1984; Marshall, 1988). The genus *Melanodrymia* is clearly distinguished from the rest by having both cephalic tentacles modified into copulatory organs in males (Haszprunar, 1989) and by a unique discordant shell sculpture where fine elements appearing at the suture and disappearing at the periphery generate a texture resembling coarse frosted glass (Hickman, 1984; Warén & Bouchet, 1993, 2001). Three species are known at present, all from the eastern Pacific vents. The type species *Melanodrymia aurantiaca* Hickman, 1984 was first described from 20°50′N on the EPR (Hickman, 1984) and later found in more localities between 21°N to 17°S between 2500 and 2600 m deep (Warén & Bouchet, 2001). *Melanodrymia brightae* Warén & Bouchet, 1993 is only known from Endeavour vents at the Juan de Fuca Ridge (Warén & Bouchet, 1993), and the third species *M. galeronae* Warén & Bouchet, 2001 was recovered from EPR near 13°N (Warén & Bouchet, 2001). We characterize and describe our two new species below, and also examine the phylogenetic relationships among the five *Melanodrymia* species using the mitochondrial cytochrome *c* oxidase subunit I (COI) gene to shed light on their evolution.

Materials and methods

Sample collection and preservation

Sampling took place at two inactive sulphide deposits near 9°50′N on the EPR, including Lucky's Mound and Sentry Spire (McDermott et al., 2022; Wu et al., 2022), during R/V *Atlantis* cruise AT50-06 (cruise https://doi.org/10.7284/909880). Parts of inactive sulphide spires were collected by the manipulators of the human-occupied vehicle (HOV) *Alvin*. After recovery on deck, animals were either rinsed or gently scraped off the surfaces of sulphides. The animal samples were placed into 4 °C chilled seawater and then sorted on Petri dishes. Some gastropods were preserved in 80% ethanol and stored at −20 °C, while others were fixed in 10% buffered formalin. The formalin material was accidentally placed in a −80 °C freezer onboard the research vessel after transferring to 80% ethanol. The specimens were thawed and transported by courier in room temperature. Specimens examined in the present study are deposited in Senckenberg Natural History Museum, Frankfurt (SMF), National Museum of Nature and Science, Tsukuba (NSMT), or Muséum national d'Histoire naturelle, Paris (MNHN).

Morphology

Gastropod specimens were gently cleaned using small brushes, and observed under a stereo dissecting microscope (Olympus SZX9). Shell width (SW) and shell height (SH) were measured using an eyepiece graticule and a stage micrometre to the nearest tenth of a millimetre. Specimens were photographed using a digital single-lens reflex camera (Olympus E-M5 Mark III) attached on to the trinocular of the same dissecting microscope. Several photographs were taken at different focal depths, which were subsequently stacked using Adobe Photoshop CC.

To obtain the operculum and radula for scanning electron microscopy (SEM), dissections were done under the microscope using fine forceps and tungsten needles. The dissected radula ribbons were placed in diluted household bleach (10%) until the remaining tissues dissolved, and then washed twice in MilliQ water and twice in 99% ethanol before mounting on aluminium stubs using carbon tape. For SEM observations of the operculum and shell sculpture, specimens were placed into the same diluted bleach for 30 s and then gently cleaned with a fine-tipped brush. They were then washed in a similar manner to the radula ribbon and mounted on aluminium stubs. A Hitachi TM-3000 tabletop SEM was used for observation and micrography, all stubs were observed uncoated at 15 kV.

Genetics

One specimen each of the two new *Melanodrymia* species as well as a specimen of *Melanodrymia galeronae* (Lucky's Mound, 9°47.4132′N, 104°17.2325′W, 2511 m deep, HOV *Alvin* dive 5135) were sequenced. Due to the small size, genomic DNA was extracted from whole snail individuals using the DNeasy Blood & Tissue kit (Qiagen) following the manufacturer's protocols. The barcoding region of the mitochondrial COI gene was amplified using the universal primer pair HCO2198-LCO1490 (Folmer et al., 1994), following a previously published method for thermal cycling and sequencing (Zhou et al., 2018). Sequences from both directions were assembled in Geneious Prime 2023.2 (https://www.geneious.com/) (Kearse et al., 2012) and checked by eye to obtain alignments of 658 bp. New sequences generated are deposited on NCBI (National Center for Biotechnology Information) GenBank under accession numbers OR828527–OR828529.

For phylogenetic reconstruction, GenBank sequences of *Melanodrymia aurantiaca* and *M. brightae* (COI sequence extracted from an unpublished genome shotgun sequencing project available under BioProject number PRJNA962978) as well as other Neomphalida gastropods were downloaded. The cocculinid limpet *Cocculina messingi* (in Cocculinida, the sister order of Neomphalida) and the turbinid vetigastropod *Turbo sazae* were used as outgroups, following previous studies (Chen, Zhou, et al., 2017, 2021). All COI sequences were aligned using Geneious Prime 2023.2, resulting in an alignment length of 572 bp for phylogenetic inferences. Phylogeny was reconstructed in MrBayes v.3.2.6 (Ronquist et al., 2012) using Bayesian inference, using the GTR + I + G model selected by PartitonFinder v.2.1.1 (Lanfear et al., 2016). Metropolis-coupled Monte Carlo Markov chains were run for 2 million generations, with topologies sampled every 100 generations. Convergence was checked using Tracer v.1.7.2 (Rambaut et al., 2021) and 3000 was selected as the appropriate burn-in value. Pairwise distances of COI sequences between pairs of the five *Melanodrymia* species were estimated based on a 658 bp alignment using the software package MEGA7 (Kumar et al., 2016).

Results

Three species of *Melanodrymia* were found from washings of inactive sulphide deposits at both Lucky's Mound and Sentry Spire, including *M. galeronae* and two undescribed species. Previously, *M. galeronae* has only been collected from 13°N on the EPR (Desbruyères et al., 2006; Warén & Bouchet, 2001), and therefore our present record of this species from 9°50′N represents a southward range extension of about 300 km. Specimens of *M. galeronae* from the two localities are deposited in SMF as vouchers: 5 specimens (SMF 374499), 80% ethanol, Lucky's Mound inactive sulphide, East Pacific Rise (9°47.4132′N, 104°17.2325′W), 2511 m deep, HOV *Alvin* dive 5135, 2022/xii/19, R/V *Atlantis* cruise AT50-06; 5 specimens (SMF 374521), 10% buffered formalin transferred to 80% ethanol, Sentry Spire inactive sulphide, East Pacific Rise (9°46.3361′N, 104°17.2229′W), 2543 m deep, HOV *Alvin* dive 5142, 2022/xii/27, R/V *Atlantis* cruise AT50-06. The two new species are described below.

Systematics

Order NEOMPHALIDA McLean, 1981
Superfamily NEOMPHALOIDEA McLean, 1981
Family MELANODRYMIIDAE Salvini-Plawen & Steiner, 1995
Genus *Melanodrymia* Hickman, 1984
Type species: *Melanodrymia aurantiaca* Hickman, 1984, by original designation

Melanodrymia laurelin sp. nov.
(Figs 1–2)

ZooBank registration LSID. urn:lsid:zoobank.org:act:1B5D6F22-5B94-4DEB-8CA7-DDCCDF5F19E2

Diagnosis. A small-sized *Melanodrymia* with a depressed trochoid shell carrying a very strong peripheral keel and a weaker basal keel, peripheral keel carrying numerous short open spines. Protoconch with very fine netted sculpture at similar densities throughout.

Type locality. From surface of inactive sulphide, Lucky's Mound, East Pacific Rise (9°47.4132′N, 104°17.2325′W), 2511 m deep, HOV *Alvin* dive 5135, 2022/xii/19, R/V *Atlantis* cruise AT50-06.

Type material. Holotype (SMF 374491; SW 1.6 mm, SH 1.1 mm; Fig. 1A), 80% ethanol. Paratype 1 (NSMT-Mo 79495; SW 1.6 mm, SH 1.0 mm; Fig. 1B), 80% ethanol. Paratype 2 (SMF 374492; SW 1.4 mm, SH 0.8 mm; Fig. 1C), 80% ethanol. Paratype 3 (MNHN-IM-2012-2401; SW 1.8 mm, SH 1.2 mm; Fig. 1D), 10% buffered formalin transferred to 80% ethanol. Paratype 4 (NSMT-Mo 79496; SW 1.6 mm, SH 1.1 mm), 10% buffered formalin transferred to 80% ethanol. Paratype 5 (MNHN-IM-2012-2402; SW 1.5 mm, SH 0.9 mm), 80% ethanol. Paratype 6 (NSMT-Mo 79497; SW 1.4 mm, SH 0.9 mm), 80% ethanol. Paratype 7 (SMF 374493), growth series of three specimens, 10% buffered formalin transferred to 80% ethanol. Paratype 8 (NSMT-Mo 79498), growth series of three specimens, 10% buffered formalin transferred to 80% ethanol. Paratype 9 (MNHN-IM-2012-2403), growth series of three specimens, 10% buffered formalin transferred to 80% ethanol. All types were collected from the type locality.

Other material examined. One specimen from the type locality, 80% ethanol, whole specimen used for DNA sequencing. 10 specimens (SMF 374494), 80% ethanol, inactive sulphide at Sentry Spire, East Pacific Rise

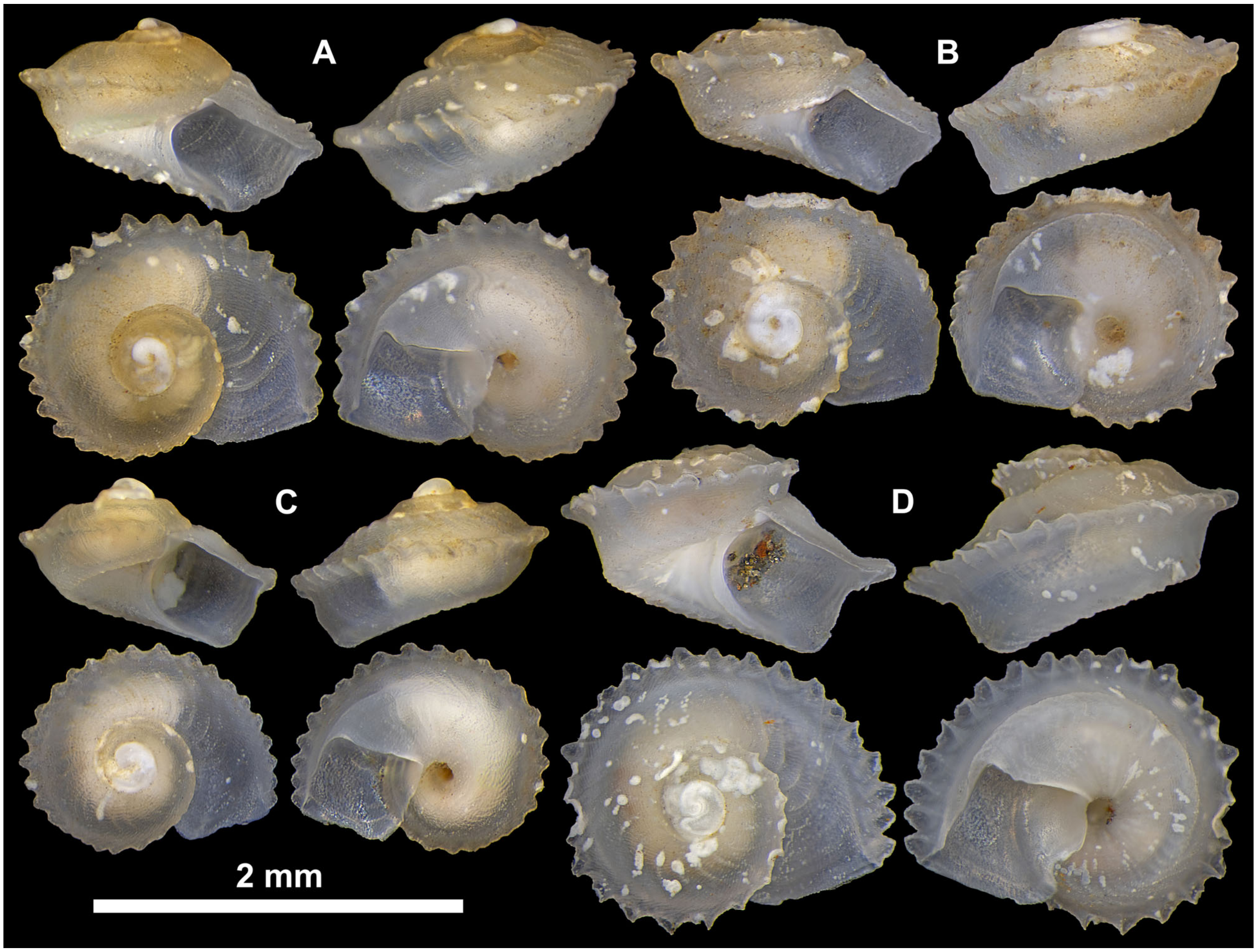

Fig. 1. *Melanodrymia laurelin* sp. nov., representative type specimens shown from apertural, abapertural, apical, and basal views. **A**, holotype (SMF 374491); **B**, paratype 1 (NSMT-Mo 79495); **C**, paratype 2 (SMF 374492); **D**, paratype 3 (MNHN-IM-2012-2401).

(9°46.3361′N, 104°17.2229′W), 2543 m deep, HOV *Alvin* dive 5142, 2022/xii/27, R/V *Atlantis* cruise AT50-06. 20 specimens (SMF 374495), 10% buffered formalin transferred to 80% ethanol, same data as the previous lot.

Description

Shell (Figs 1, 2A, B). Depressed trochoid, small for genus. Robust, whitish, and translucent. Periostracum very thin, virtually transparent. Early teleoconch whorls often with light mineral deposit appearing as golden-brown staining. Peripheral keel starting 0.5 whorls after protoconch, very strong, carrying 24–28 short, open spines on periphery. Each peripheral spine corresponds to a weak, oblique axial rib that is strongest in middle of shell but fades at periphery. Basal keel weaker but still prominent, connects to basal corner of peristome. Axial ribs cause low bumps on basal keel but not drawn out to form spines like in peripheral keel. Shell surface densely covered by fine, discordant sculpture which start immediately after protoconch, overlaid on very fine axial growth striae (Fig. 2A, B). Spiral sculpture other than peripheral and basal keels lacking. Suture deep but narrow. Umbilicus wide, deep. Columella strong, obliquely connected to basal keel. Outer lip not thickened. Early whorls and shell surface show some signs of corrosion in large specimens (Fig. 1D). Protoconch (Fig. 2A) about 250 µm in length, approximately 0.75 whorls, entirely and densely covered in very fine net sculpture that does not change in density or strength throughout. Peristome of protoconch distinctly expands into a clearly defined, strongly sinuous lip. Coiling loosens considerably in adults, with suture shifting from just below peripheral keel (Fig. 1C) to just above basal keel (Fig. 1D).

Operculum (Fig. 2C). Multispiral, round. Light brownish, very thin, nearly transparent.

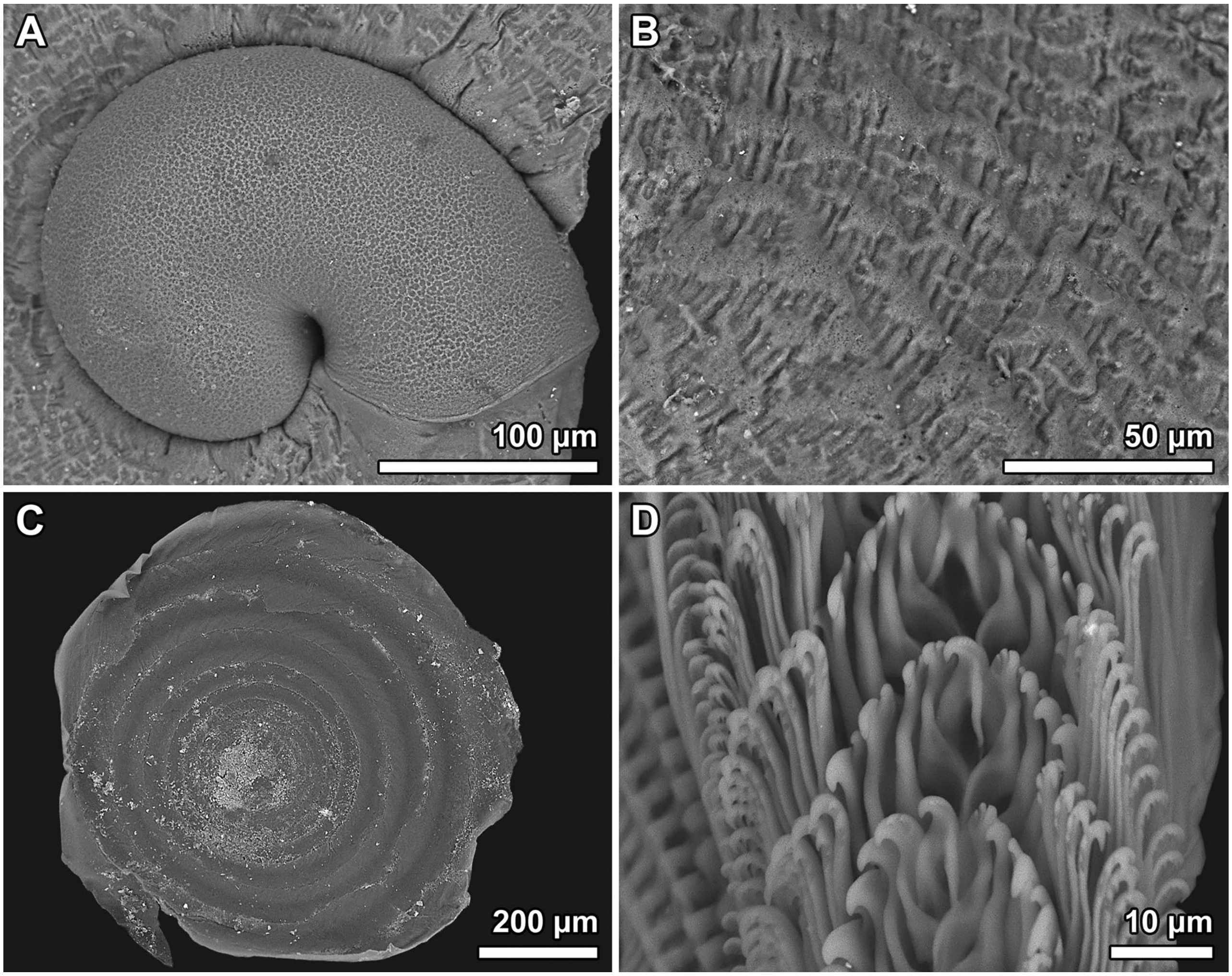

Fig. 2. *Melanodrymia laurelin* sp. nov., scanning electron micrographs. **A**, protoconch; **B**, discordant shell surface sculpture on an early teleoconch whorl; **C**, operculum; **D**, radula.

Radula (Fig. 2D). Rhipidoglossate, formula *c.* 20 + 4 + 1 + 4 + *c.* 20. Teeth very slender, elongated overall. Central tooth with laterally expanded strong supporting ridges, cusp overhanging, with finely serrated cutting edges. Lateral teeth with strongly interlocking supporting ridges, shaft becoming gradually more bent and sinuous towards central tooth. Cusps of lateral teeth split into 3–4 sharp, claw-like denticles, of which outermost is the strongest. Inner marginal teeth flat, claw-like, with cusps splitting into 6–8 hook-like denticles. Outer marginal teeth gradually becoming smaller in size outwards, with finely serrated cusps. Position of each tooth shifts down (posterior) considerably from central tooth outwards, leading to teeth in each row having a strongly angled arrangement.

Soft parts. Tissue quality of the formalin-fixed specimens was not ideal, likely due to the samples being accidentally frozen at −80 °C during onboard sample treatment and then thawed. Nevertheless, we confirm that the gross external anatomy is not significantly different from that of *M. aurantiaca*, with several epipodial tentacles underneath the operculum (Haszprunar, 1989; Warén & Bouchet, 1989).

Etymology

Laurelin (Quenya, ‘Song of Gold’), the Golden Tree; one of the Two Trees of Valinor in J.R.R. Tolkien’s legendarium (Tolkien, 1987). Her last fruit would become the Sun of Middle-earth (Tolkien, 1991) – the apical view of the present new species resembles a sunburst shape, hence the allusion. Used as noun in apposition.

Distribution

Only known from two inactive sulphide mounds near 9°50′N, East Pacific Rise (Lucky’s Mound and Sentry Spire).

Remarks

Melanodrymia laurelin sp. nov. is clearly distinct from all other known congeners by its open spines on the peripheral keel. Its shell and radula morphology most closely resembles *M. aurantiaca* (Hickman, 1984). However, although the peripheral keel of *M. aurantiaca* may become wavy when intersecting with axial ribs, the ribs are never drawn out to form spines. The radula of *M. aurantiaca* is similar to that of *M. laurelin* sp. nov. in having very slender teeth, but the lateral support of the central tooth is much weaker and the cusps of inner laterals are simple triangular in *M. aurantiaca*. The protoconch is also similar to *M. aurantiaca* in being completely covered by fine net sculpture (Warén & Bouchet, 1989), but the netting is much finer in *M. laurelin* sp. nov. The strong ridge above the lip in the protoconch of *M. aurantiaca* is lacking in *M. laurelin* sp. nov. The protoconch illustrated as '*Melanodrymia*? *galeronae*' in Mills et al. (2009) matches *M. laurelin* sp. nov. well and may be this species (Susan Mills, pers. comm.).

Melanodrymia telperion sp. nov.

(Figs 3–4)

ZooBank registration LSID. urn:lsid:zoobank.org:act:B1638373-398A-4C72-90E1-5555946B62A9

Diagnosis

A small-sized *Melanodrymia* with a depressed-trochoid shell carrying peripheral and basal keels of similar strength, lacking in significant axial sculpture. Protoconch small, about 220 µm in length, with moderately fine netting throughout.

Type locality. Surface of inactive sulphide at Lucky's Mound, East Pacific Rise, R/V *Atlantis* cruise AT50-06.

Type material. Holotype (SMF 374496; SW 1.2 mm, SH 0.9 mm; Fig. 3A), 10% buffered formalin transferred to 80% ethanol (9°47.4031'N, 104°17.2122'W, 2513 m deep, HOV *Alvin* dive 5134, 2022/xii/18). Paratype 1 (NSMT-Mo 79499; SW 1.2 mm, SH 0.9 mm; Fig. 3B), 10% buffered formalin transferred to 80% ethanol, same collecting data as the holotype. Paratype 2 (MNHN-IM-2012-2404; SW 0.8 mm, SH 0.6 mm; Fig. 3D), 80% ethanol (9°47.4132'N, 104°17.2325'W, 2511 m deep, HOV *Alvin* dive 5135, 2022/xii/19). Paratype 3 (SMF 374497;

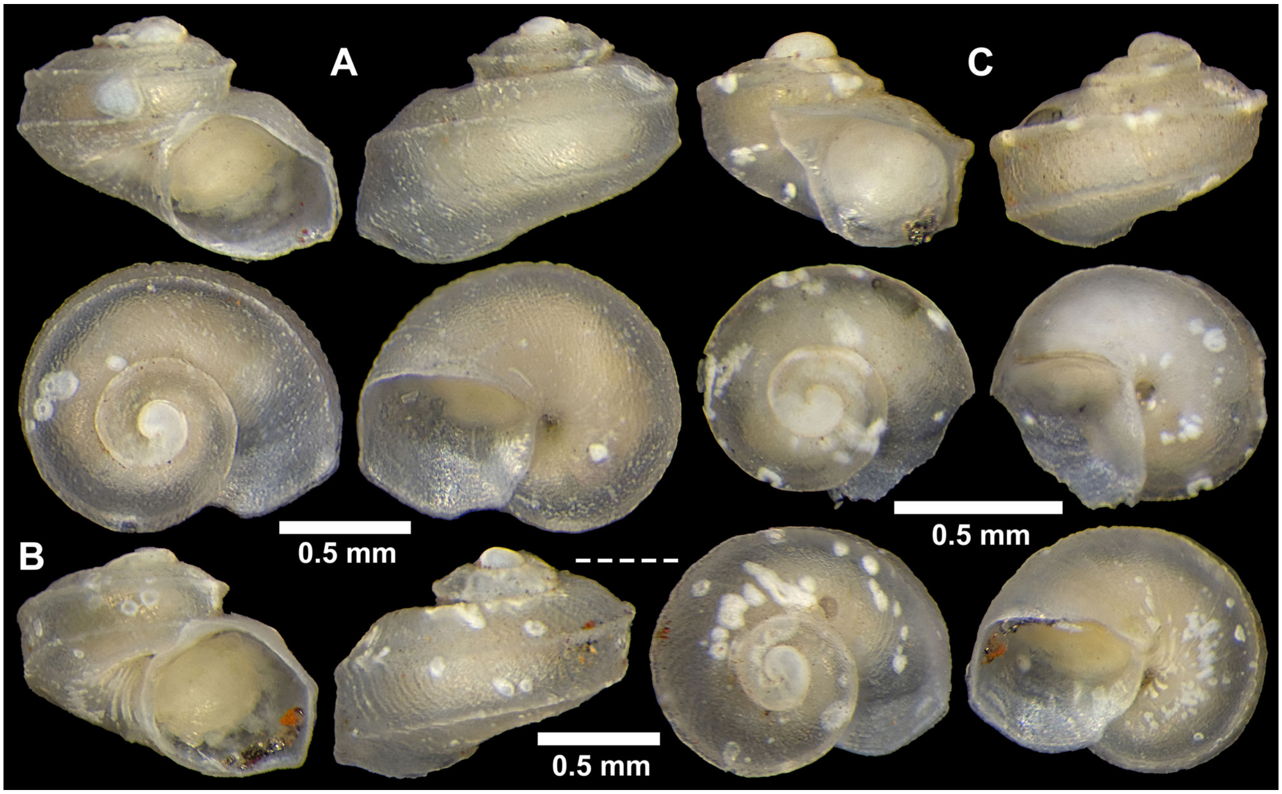

Fig. 3. *Melanodrymia telperion* sp. nov., representative type specimens shown from apertural, abapertural, apical, and basal views. **A**, holotype (SMF 374496); **B**, paratype 1 (NSMT-Mo 79499); **C**, paratype 2 (MNHN-IM-2012-2404).

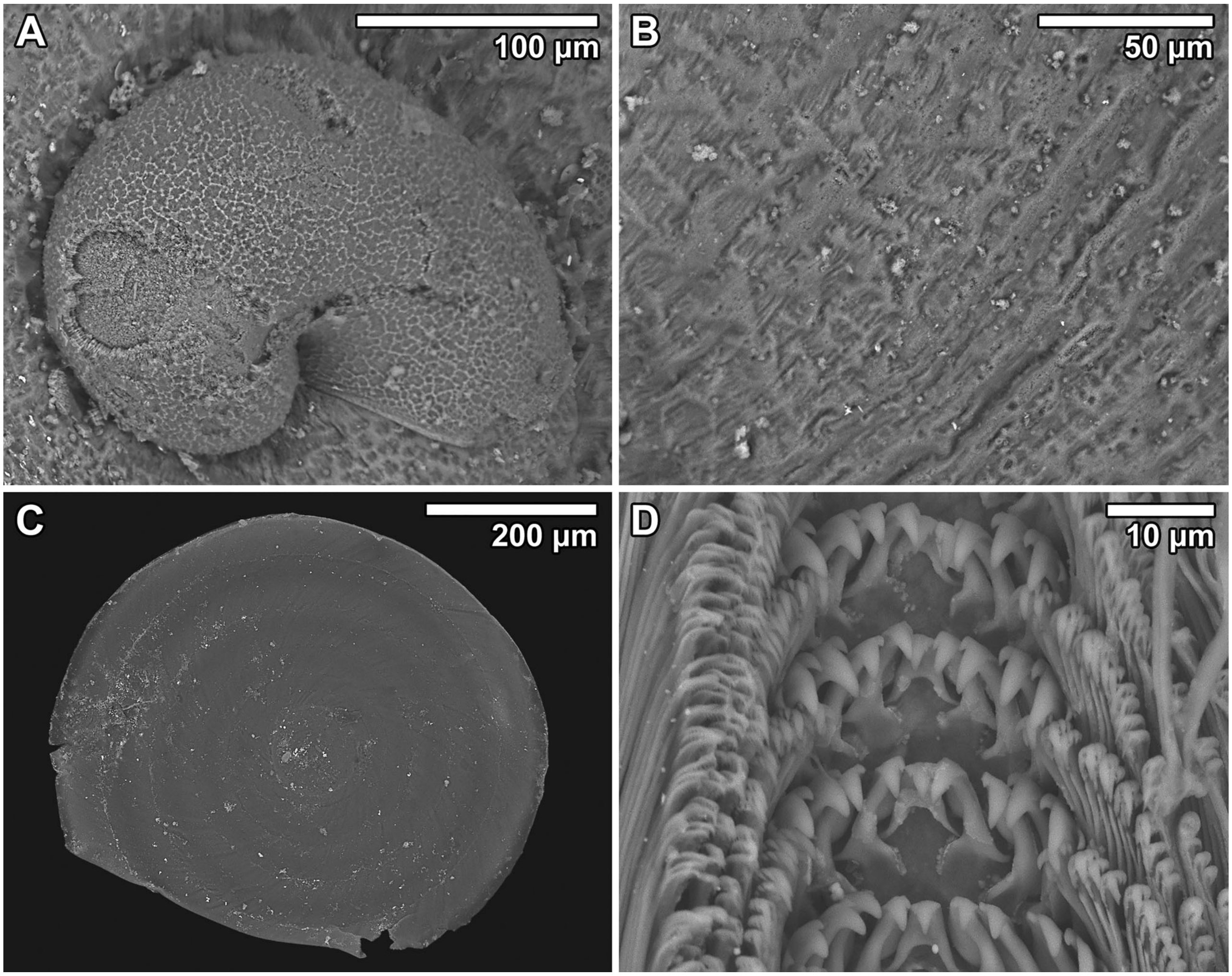

Fig. 4. *Melanodrymia telperion* sp. nov., scanning electron micrographs. **A**, protoconch; **B**, discordant shell surface sculpture on an early teleoconch whorl; **C**, operculum; **D**, radula.

SW 1.0 mm, SH 0.8 mm; Fig. 4), 10% buffered formalin transferred to 80% ethanol, same collecting data as the holotype. All types were collected from the type locality.

Other material examined. One specimen, 80% ethanol, inactive sulfide, Sentry Spire, East Pacific Rise (9°46.3390’N, 104°17.2238’W), 2542 m deep, HOV *Alvin* dive 5142, 2022/xii/27), whole specimen used for DNA sequencing. Two specimens (SMF 374498), 80% ethanol, inactive sulphide, Sentry Spire, East Pacific Rise (9°46.3361′N, 104°17.2229′W), 2543 m deep, HOV *Alvin* dive 5142, 2022/xii/27, R/V *Atlantis* cruise AT50-06.

Description

Shell (Figs 3, 4A, B). Depressed trochoid, small for genus. Thin, fragile, whitish, and translucent. Periostracum very thin, nearly transparent. Peripheral keel prominent, starting immediately after protoconch. Shell surface densely overlaid by fine, discordant sculpture which also start immediately after protoconch (Fig. 4B). This discordant sculpture appears to be on top of very fine growth striation. Axial ribs lacking entirely. Basal keel nearly of same strength as peripheral keel, connecting to basal corner of peristome but often weakens towards it in adults. Spiral sculpture lacking except for the two keels. In all specimens examined shell surface showed signs of minor corrosion. Suture narrow, deep. Umbilicus rather narrow, deep. Columellar strong, well-defined. Outer lip not thickened in adults. In apical view, edge of aperture appears sinuous. Protoconch about 220 µm in length, entirely covered with moderately fine net-like sculpture of similar density throughout. Peristome expanding to form clearly defined, sinuous lip. Coiling loosens slightly with growth, with suture shifting from halfway between peripheral and basal keels (Fig. 3C) to just above basal keel (Fig. 3A, B).

Operculum (Fig. 4C). Round, multispiral. Light brownish. Very thin, film-like, nearly transparent.

Radula (Fig. 4D). Rhipidoglossate, formula *c.* 30 + 4 + 1 + 4 + *c.* 30. Teeth short, stubby. Central tooth strong, with laterally expanded supporting ridges. Cusp overhanging, with finely serrated cutting edges. Lateral teeth with interlocking supporting ridges, only slightly curved, not sinuous. Lateral teeth gradually enlarging outwards. Inner three lateral teeth with overhanging cusps split into two claw-like denticles, with the outer one being much stronger; outer edge finely serrated. Fourth lateral tooth similar but with three denticles, the middle one strongest. Marginal teeth gradually becoming smaller in size outwards, also with increasingly serrated cusps. Cusps of inner marginal teeth split into about 5–7 denticles, becoming over 20 in outermost marginals.

Soft parts. As in *M. laurelin* sp. nov. above.

Etymology

Telperion (Quenya/Telerin, 'Silver + *-rion*'), the Silver Tree; one of the Two Trees of Valinor in J.R.R. Tolkien's legendarium (Tolkien, 1987). His last flower would become the Moon of Middle-earth (Tolkien, 1991) – the apical view of the present new species is rounded and resembles a full moon, hence the allusion. Used as noun in apposition.

Distribution

Only known from two inactive sulphide deposits near 9°50′N, East Pacific Rise (Lucky's Mound and Sentry Spire).

Remarks

Melanodrymia telperion sp. nov. is unique among the five known *Melanodrymia* species in lacking significant axial sculpture aside from very fine growth striations (Hickman, 1984; Warén & Bouchet, 1993, 2001). Furthermore, protoconchs of the other described species (not known for *M. brightae*) are all 250–260 μm in size; making the 220 μm protoconch of *M. telperion* sp. nov. significantly smaller. Aside from size, the protoconch of *M. telperion* sp. nov. is very similar to that of *M. laurelin* sp. nov. in having fine net-like sculpture all over, but the netting is considerably coarser in *M. telperion* sp. nov. The radula of *M. telperion* sp. nov. is most similar to that of *M. galeronae* (Warén & Bouchet, 2001), but with stronger lateral support on the central tooth and more numerous marginal teeth (*c.* 30 vs *c.* 20).

Molecular phylogeny

Our molecular phylogeny reconstructed based on the barcoding region of the mitochondrial COI gene (Fig. 5) recovered a strongly supported (Bayesian posterior probability, BPP = 0.99) *Melanodrymia* containing all five nominal species, including *M. laurelin* sp. nov. and *M. telperion* sp. nov. Within *Melanodrymia*, *M. telperion* sp. nov. was sister to the other species with strong support (BPP = 0.99). *Melanodrymia laurelin* sp. nov. was sister to *M. galeronae* (BPP = 1), the two being in turn sister to a clade containing *M. brightae* and *M. aurantiaca* (BPP = 0.89). Moderate support (BPP = 0.81) was found for the sister relationship of the latter two species. *Melanodrymia* was recovered as sister to *Leptogyra* with full support (BPP = 1). The family Melanodrymiidae, represented by *Leptogyra*, *Leptogyropsis*, and *Melanodrymia*, was found to be monophyletic though only with low support (BPP = 0.59). Neomphalidae was fully supported as monophyletic (BPP = 1), but Peltospiridae was paraphyletic. Monophyly of the order Neomphalida as a whole was strongly supported (0.95).

The percentage pairwise genetic distance in the COI gene among the five *Melanodrymia* species (Table 1) averaged at 11.34%, with the minimum being 7.60% (between *M. laurelin* sp. nov. and *M. galeronae*) and the maximum being 14.74% (between *M. galeronae* and *M. brightae*). The pairwise distance of *M. laurelin* sp. nov. from the other species ranged between 7.60% and 13.07%, while the same for *M. telperion* sp. nov. was between 8.97% and 12.61%.

Discussion

The molecular phylogeny presented herein (Fig. 5) is the first to include all *Melanodrymia* species, as genetic data for *M. galeronae* were previously missing (Chen, Zhou, et al., 2021). Recovery of a monophyletic *Melanodrymia* including our two new species supports their placement within this genus. This is further substantiated by the substantial COI pairwise distance (Table 1) between all species pairs in this genus. Although in our tree Peltospiridae was not recovered as monophyletic within Neomphalida, it is well-known that the COI gene does not offer sufficient resolution for resolving familial relationships in this group (Chen, Linse, Copley, et al., 2015; Chen, Linse, Roterman, et al., 2015). We note that Peltospiridae has been recovered as monophyletic based on multi-gene and mitogenome approaches (Chen, Uematsu, et al., 2017; Zhong et al., 2022). The relationships within genus

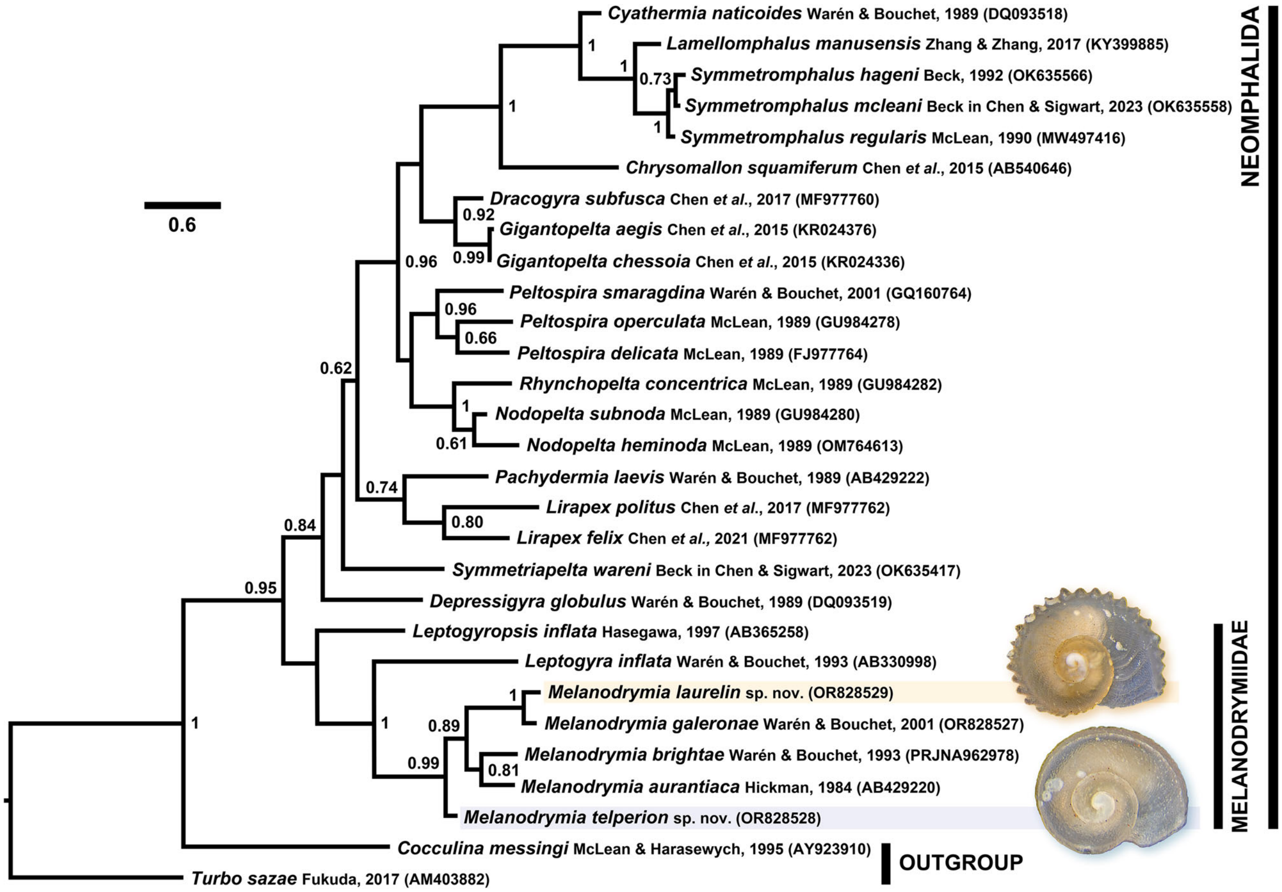

Fig. 5. Phylogenetic tree of the gastropod order Neomphalida reconstructed using Bayesian inference from partial sequences of the mitochondrial COI gene (572 bp). Node values represent Bayesian posterior probabilities, only values over 0.60 are shown. GenBank accession number of each sequence is shown inside parentheses.

Table 1. Percentage pairwise genetic distance between *Melanodrymia* species, calculated using the barcoding fragment of the mitochondrial COI gene (657 bp).

		1	2	3	4	5
1	*Melanodrymia aurantiaca*					
2	*Melanodrymia brightae*	10.94%				
3	*Melanodrymia galeronae*	11.85%	14.74%			
4	*Melanodrymia laurelin* sp. nov.	11.85%	13.07%	7.60%		
5	*Melanodrymia telperion* sp. nov.	8.97%	12.61%	10.79%	10.94%	

Melanodrymia, however, were resolved with high support values in our tree.

The vent fauna of EPR is perhaps the most well-documented of all regions, as this is where deep-sea high temperature venting was first discovered (Chapman et al., 2019; Desbruyères et al., 2006). The fact that *M. laurelin* sp. nov. and *M. telperion* sp. nov. were not found in those samples (Warén & Bouchet, 2001) is evidence that they are specialists of the previously poorly surveyed inactive sulphides. *Melanodrymia aurantiaca* and *M. brightae* have been collected from washings of siboglinid tubeworms (Desbruyères et al., 2006; Warén & Bouchet, 1993). *Melanodrymia aurantiaca* was even collected from washings of *Alvinella* worms, one of the heat-tolerant groups of animals living on the hottest parts of active chimneys (Desbruyères et al., 1998; Warén & Bouchet, 1993). This leaves little doubt that the preferred habitats of these two species are active vents, which is also supported by the corroded apex and thick, golden, sulphide deposits on the shells of *M. aurantiaca* (Hickman, 1984; Warén & Bouchet, 1993). *Melanodrymia galeronae*, however, was collected from 10 km south of the main active venting locality (Warén & Bouchet, 2001). Our finding of *M. galeronae* cooccurring with *M. laurelin* sp. nov. and *M. telperion* sp. nov. at both Lucky's Mound and Sentry Spire inactive sulphide deposits (Wu et al., 2022) suggests that this species is likely also endemic to, or at least primarily inhabiting, surfaces of inactive spires.

As such, genus *Melanodrymia* contains both active vent specialists and inactive spire specialists. In our tree (Fig. 5), *M. telperion* sp. nov. is sister to all other congeners, and the two active vent specialists *M. aurantiaca* and *M. brightae* are sisters. This points to a scenario where the active vent *Melanodrymia* species evolved from an ancestor endemic to inactive spires. As *Melanodrymia* is in a derived position within Melanodrymiidae whose other genera all inhabit sunken wood (Hess et al., 2008), habitat shifts from wood to inactive spires to active vents may have taken place within the family. Though gradual habitat transition from wood to vent has been shown for some taxa such as bathymodioline mussels and cocculinid limpets (Chen & Linse, 2020; Thubaut et al., 2013), the melanodrymiid case adds inactive spires as potentially important evolutionary 'stepping stones' (Smith et al., 2015). Our findings not only add to the growing evidence that inactive vents host a unique ecosystem of specialists (Chen, Zhou, et al., 2021; Van Dover, 2019), but also shed light on their potential importance in the evolution of hot vent fauna – underscoring the need to better understand these systems before deep-sea mining takes place.

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