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Levinaespira georgesnyderi gen. et sp. nov., a New Deep-Sea Snail (Gastropoda: Neomphalidae) From Eastern Pacific Methane Seeps

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Deep-sea methane seeps host diverse and abundant animal communities, including an extensive undescribed diversity of small cryptic invertebrates. We describe a new genus and species of neomphalid snail, *Levinaespira georgesnyderi* gen. et sp. nov., from the Mound 12 methane seep at 1000 m depth on the Pacific margin of Costa Rica, and we report a closely related singleton specimen from the Hydrate Ridge seep off Oregon, USA, at ca. 600 m depth. Molecular phylogenies based on the mitochondrial cytochrome c oxidase subunit I (COI) gene and the complete mitochondrial genome support the placement of the new genus within Neomphalidae (Gastropoda: Neomphalida), a group originally described from hydrothermal vents. *Levinaespira georgesnyderi* gen. et sp. nov. is separated from species in other described genera by at least 15.2% COI distance. It is morphologically distinctive in having lateral projections on the anterior foot, a lobe-shaped right cephalic lappet, and bilaterally symmetric cephalic tentacles without obvious reproductive modifications. This species represents the first genetically confirmed record of Neomphalidae at methane seeps and the shallowest known occurrence of this group at any environment. The new genus is named in honor of Professor Emerita Lisa Levin and the new species is named in memory of Collection Manager H. George Snyder (1931–1990) for their contributions to deep-sea invertebrate biology.

Key words: chemosynthetic ecosystem, COI, molecular phylogeny, Mollusca, Neomphalida, Neomphaliones, new species, taxonomy

INTRODUCTION

Gastropods are abundant, diverse, and ecologically wide-ranging in marine environments, though the members of Neomphaloidea McLean, 1981 (Neomphaliones: Neomphalida) are known only from deep-sea chemosynthesis-based ecosystems (Sasaki et al., 2010; Zhang et al., 2024; Chen et al., 2025). Encompassing a variety of body plans from small limpets to the iconic "scaly-foot snail" *Chrysomallon squamiferum* Chen, Linse, Copley and Rogers, 2015, Neomphaloidea includes 61 presently described species, within Melanodrymiidae Salvini-Plawen and Steiner, 1995; Neomphalidae McLean, 1981; Peltospiridae McLean, 1989; and genera of uncertain placement such as *Helicrenion* Warén and Bouchet, 1993 (Sasaki et al., 2010; Bouchet et al., 2017; Kaim, 2022).

The family Neomphalidae comprises 13 extant species in the genera *Cyathermia* Warén and Bouchet, 1989; *Lacunoides* Warén and Bouchet, 1989; *Lamellomphalus* Zhang and Zhang, 2017; *Neomphalus* McLean, 1981; *Planorbidella* Warén and Bouchet, 1993; *Retiskenea* Warén and Bouchet, 2001 (Neomphaloidea *incertae sedis*); *Solutigyra* Warén and Bouchet, 1989; and *Symmetromphalus* McLean, 1990 (Warén and Bouchet, 2001; MolluscaBase eds., 2010). Morphologies include limpet-shaped forms, haliotiforms, and regularly coiled (helicospiral) snails (Zhang and Zhang, 2017; Chen and Sigwart, 2023; Chen et al., 2024). All known neomphalid species have been recorded only from the Pacific Ocean, and most were originally described from hydrothermal vents (Sasaki et al., 2010; Zhang and Zhang, 2017; Chen and Sigwart, 2023; Chen et al., 2024; Zhang et al., 2024). Several vent-dwelling species have been listed as

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critically endangered due to the threat of deep-sea mining (Thomas et al., 2021). The as-yet undescribed diversity of neomphalids includes seep and vent taxa (Zhong et al., 2022; Chen et al., 2023) and the deepest gastropod records to date, from > 9500 m depth in the Kuril-Kamchatka Trench (Fukumori et al., 2019a).

We describe a previously unnamed neomphalid snail from the Mound 12 methane seep at 1000 m depth on the Pacific margin of Costa Rica. Mound 12 (Fig. 1A) is one of more than 100 seep sites located ca. 50 km off Costa Rica and southern Nicaragua, at the subduction of the Cocos Plate beneath the Caribbean Plate (Sahling et al., 2008). The active seepage of methane-rich fluids supports extensive formations of authigenic carbonates and sustains chemosynthesis-associated animal communities (Sahling et al., 2008; Levin et al., 2015). Conspicuous megafaunal assemblages at Mound 12 include beds of mussels (*Bathymodiolus nancyschneiderae* McCowin, Feehery and Rouse, 2020 and *Bathymodiolus earlougheri* McCowin, Feehery and Rouse, 2020), clusters of the Costa Rican dancing yeti crab (*Kiwa puravida* Thurber, Jones and Schnabel, 2011), and aggregations of vestimentiferan tubeworms (*Lamellibrachia donwalshi* McCowin and Rouse, 2018 and *Escarpia spicata* Jones, 1985) (Fig. 1B, C) (Thurber et al., 2011; McCowin and Rouse, 2018; McCowin et al., 2020; Seid et al., 2025). More than 488 animal species have been documented from the Costa Rica seeps, including numerous macrofaunal gastropods at Mound 12 (Betters et al., 2024; Shen et al., 2024; Kroesche and Rouse, 2025; Seid et al., 2025). A similar neomphalid specimen was also collected from the Hydrate Ridge seep off Oregon, USA (Fig. 1A), at ca. 600 m depth. We show through integrative taxonomy that *Levinaespira georgesnyderi* gen. et sp. nov. represents a distinctive new genus and species, increasing the known diversity at eastern Pacific methane seeps.

MATERIALS AND METHODS

Specimen collection and vouchering

Dives at methane seeps were conducted by the crewed submersible (Human Occupied Vehicle, HOV) *Alvin* during R/V *Atlantis* cruises AT15-44 (2009), AT15-59 (2010), AT13-37 (2017), and AT42-03 (2018) off Puntarenas, Costa Rica, and cruise AT15-68 (2010) at Hydrate Ridge, off Oregon, USA (Fig. 1A). Authigenic carbonates and small clusters of tubeworms were collected into a Delrin storage box using the *Alvin* manipulator arms. Large aggregations of tubeworms were collected using the Bushmaster Jr. device, a hydraulically operated net that maximizes retention of associated fauna (Bergquist et al., 2002). Only a single specimen of *Levinaespira* gen. nov. (SIO-BIC M19168) was collected from Hydrate Ridge.

Specimen collection in Costa Rica was performed under permits SINAC-SE-CUS-PI-R-035-2017 and SINAC-CUSBSE-PI-R-032-2018 issued by SINAC (Sistema Nacional de Áreas de Conservación) under MINAE (Ministerio de Ambiente y Energía), Government of Costa Rica. DNA sequencing for this project was authorized by the Contract for the Grant of Prior Informed Consent between MINAE-SINAC-ACMC and Jorge Cortés Nuñez for the Basic Research Project: “FK190106 - Cuantificación de los vínculos biológicos, químicos y físicos entre las comunidades quimiosintéticas con el mar profundo circundante” (“Quantifying the biological, chemical, and physical linkages between chemosynthetic communities and the surrounding deep sea”).

Live specimens were sorted in chilled seawater, relaxed with isotonic magnesium chloride (7.5% $MgCl_2$ in fresh water), and photographed using a stereomicroscope (Leica S8 Apo or MZ9.5) with an attached camera (Canon PowerShot G9 or EOS Rebel T6s). Specimens for morphological analysis were fixed in 10% seawater formalin for at least 24 h, rinsed with fresh water, and transferred to 50% ethanol for long-term archival. Specimens or tissue subsamples for genetic analysis were preserved in 95% ethanol, with the fluid replaced at least twice during the first 2 days and stored at −20°C for long-term archival. Voucher specimens were deposited

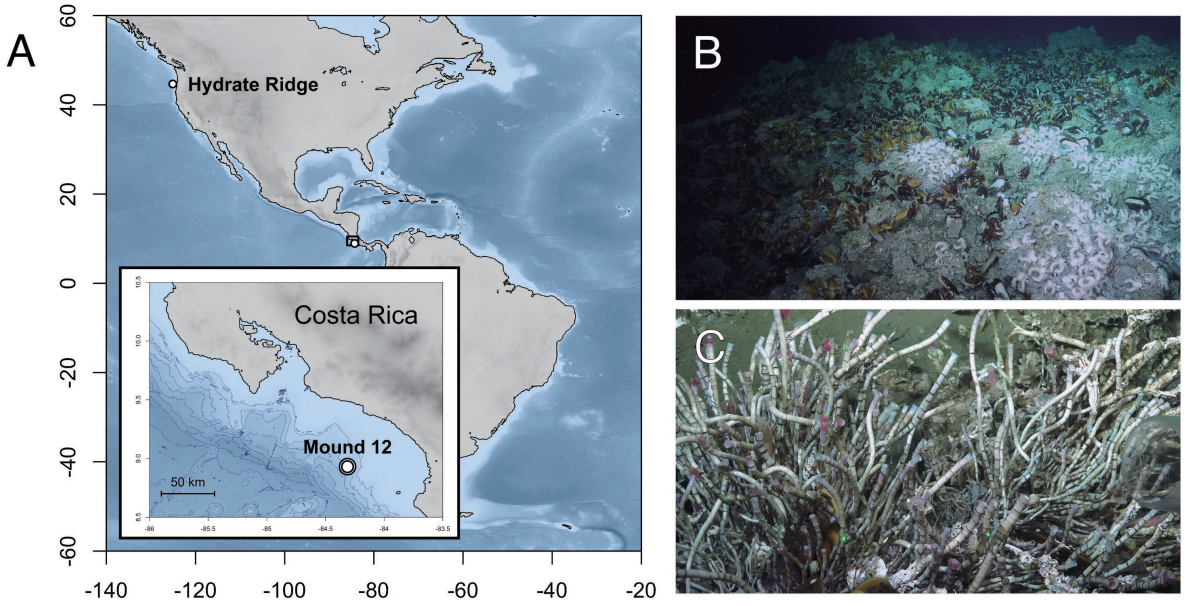


Fig. 1. Collection localities of *Levinaespira georgesnyderi* gen. et sp. nov. **(A)** Map of Mound 12 (type locality), off Costa Rica, and Hydrate Ridge, off Oregon, USA. In situ images of representative habitats at Mound 12: **(B)** authigenic carbonates harboring mussels and yeti crabs, **(C)** aggregations of vestimentiferan tubeworms. The map was generated using the R package marmap (Pante and Simon-Bouhet, 2013) and bathymetric data from NOAA (https://www.ncei.noaa.gov/maps/autogrid/, accessed 25 August 2021). Credit **(B, C)**: ROV *SuBastian*/Schmidt Ocean Institute, Dive S0215.

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in the Scripps Institution of Oceanography Benthic Invertebrate Collection (SIO-BIC), La Jolla, California, USA; Museo de Zoología de la Universidad de Costa Rica (MZUCR), San José, Costa Rica; and Senckenberg Museum Frankfurt (SMF), Frankfurt am Main, Hesse, Germany.

DNA extraction and sequencing

DNA was extracted from six ethanol-fixed specimens using the Qiagen DNeasy kit (for SIO-BIC M19062 and the Hydrate Ridge specimen M19168) or the Zymo Research *Quick*-DNA Microprep Plus Kit (Zymo Research, Irvine CA) (all other specimens). Polymerase chain reaction (PCR) amplification of mitochondrial cytochrome c oxidase subunit I (COI) for SIO-BIC M19062 and M19168 was performed as described by Kano (2008) using the primer pair LCO1490 and COIa-NER (Folmer et al., 1994; Kano and Kase, 2004). For all other specimens, PCR amplification of COI was performed using the primer pair jgLCO1490 and jgHCO2198 (Geller et al., 2013). Each reaction contained 1 μl of each primer (10 μM), 2 μl of genomic DNA, 12.5 μl Apex 2.0× *Taq* Red DNA Polymerase Master Mix (Genesee Scientific, El Cajon, CA), and 8.5 μl ddH_2O. The reaction was performed on an Eppendorf thermal cycler using the following temperature profile: 95°C for 300 s; 35 cycles of (95°C for 30 s, 48°C for 30 s, and 72°C for 45 s); and 72°C for 300 s. The nuclear 18S subunit ribosomal RNA (18S) was also targeted, to provide reference sequences for future multi-gene phylogenetic analyses or detection from environmental DNA (metabarcoding). PCR amplification of 18S was performed using the primer pair 18A1 and 1800r (Steiner and Dreyer, 2003), with an annealing temperature of 55°C, as described by Kano (2008). PCR products were purified with ExoSAP-IT (USB Corporation, Cleveland, OH).

For most specimens, Sanger sequencing was performed by Eurofins Genomics, followed by consensus sequence assembly using Geneious 10.1.0 or Geneious Prime 2021.1.1–2022.0.1 (https://www.geneious.com). Sanger sequencing for SIO-BIC M19062 and M19168 was performed at the Ocean Research Institute, University of Tokyo, using a Big Dye Terminator Cycle Sequencing Kit v. 3.1 (Applied Biosystems, Waltham, MA), a Big Dye XTerminator Purification Kit, and analysis on an ABI PRISM 3130xl sequencer, as described by Kano (2008). For these two specimens, the COI sequencing primers were the same as the COI PCR primers, whereas the 18S sequencing reactions used the 18S PCR primers and additional primers 188f and 189r (Kano, 2008).

A paratype of *Levinaespira georgesnyderi* gen. et sp. nov. (SIO-BIC M14646A) was selected for mitochondrial genome sequencing. To confirm the phylogenetic placement of *Levinaespira* gen. nov., we compared its mitochondrial genome to that of *Chrysomallon squamiferum*, as COI is insufficient to resolve higher-level relationships within Neomphalida and phylogenies based only on COI have recovered *C. squamiferum* within Neomphalidae rather than Peltospiridae (Chen et al., 2015b, 2017; Zhong et al., 2022). We generated a mitochondrial genome for *C. squamiferum* (paratype SIO-BIC M13766A; details in Chen et al. [2015a]), although another mitochondrial genome for this species was published first (Zhong et al., 2022). We have included both *C. squamiferum* mitogenomes in our analysis for completeness.

Library preparation and mitochondrial genome sequencing were performed by Novogene using the Illumina NovaSeq 6000 system for paired-end reads of length 150 base pairs (bp), generating 7,223,767 raw reads for *Levinaespira georgesnyderi* gen. et sp. nov. and 8,369,091 for *Chrysomallon squamiferum*. Raw reads were trimmed using Trimmomatic v. 0.39 (Bolger et al., 2014) to remove adapters (Illumina TruSeq3) and low-quality reads (settings "LEADING:3 TRAILING:3 SLIDINGWINDOW:4:15 MINLEN:36"). The retained reads were assembled into circularized mitogenomes using MitoFinder v. 1.4 (Allio et al., 2020), producing assemblies of 13,924 reads with an average sequencing coverage of 131× for *Levinaespira georgesnyderi* gen. et sp. nov. and 64,570 reads with an average sequencing coverage of 622× for *Chrysomallon squamiferum*. The assemblies were annotated using the integrated MitoFinder pipeline with MEGAHIT v. 1.2.9 (Li et al., 2016) and ARWEN v. 1.2.3 (Laslett and Canbäck, 2008), checked using the MITOS Web server (Bernt et al., 2013), and manually finalized with Geneious Prime 2022.0.1.

Sequences were submitted to the National Center for Biotechnology Information GenBank database (Clark et al., 2016), with COI and 18S accession numbers listed in the Material examined section below and mitogenome accession numbers PV448932 (*Levinaespira georgesnyderi* gen. et sp. nov.) and PV448933 (*Chrysomallon squamiferum*).

Phylogenetic analysis

Newly generated sequences were compared to representatives of all available species of Neomphalida on GenBank (accessed 13 February 2025), with representatives of Cocculinida Hazsprunar, 1987 as outgroups, following the most recent COI phylogeny (Chen et al., 2024) and mitogenome phylogeny (Zhong et al., 2022) of Neomphalida. Preliminary identification was facilitated by the nucleotide BLAST suite (Zhang et al., 2000; Boratyn et al., 2013). FigTree v. 1.4.4 (Rambaut, 2018) was used to visualize trees with bootstrap values.

For species delimitation based on COI, sequences were aligned using the MAFFT online service v. 7.511, option L-INS-I (Katoh et al., 2019). Maximum Likelihood (ML) analysis was conducted using W-IQ-TREE v. 1.6.11 (Trifinopoulos et al., 2016) with 1000 ultrafast bootstrap pseudoreplicates (Hoang et al., 2018) and the ModelFinder option (Kalyaanamoorthy et al., 2017), by which GTR + F + I + G4 was chosen as the best-fit model according to the Bayesian Information Criterion. Uncorrected pairwise distances (*p*-distances) and Kimura 2-parameter distances (*K2P*) (Kimura, 1980), for comparison with previous work, were calculated using PAUP* v. 4.0a169 (Swofford, 2003). A haplotype network of *Levinaespira georgesnyderi* gen. nov. COI sequences was created with PopART v. 1.7 (Leigh and Bryant, 2015) using the TCS algorithm (Clement et al., 2002).

For the mitogenome phylogeny, the 13 protein-coding genes (PCGs) were translated into amino acid sequences in Mesquite v. 3.81 (build 955) (Maddison and Maddison, 2025). Using the Align package v. 1.8 within Mesquite (Maddison et al., 2016), each PCG amino acid sequence was aligned via the MUSCLE5 Align tool (Edgar, 2022), and the nucleotide sequences of the 12S rRNA (*rrnS*) and 16S rRNA (*rrnL*) genes were each aligned via the MAFFT Align tool (Katoh and Standley, 2013). Alignments were concatenated in raxmlGUI 2.0 v. 2.0.16 (Edler et al., 2021). A partitioned ML analysis with thorough bootstrapping was performed in RAxML-NG v. 1.2.2 (Kozlov et al., 2019) with settings "--all --seed 228542 --bs-metric fbp --tree rand{100} --bs-trees 100". The following substitution models were used for each partition: MtZoa (Rota-Stabelli et al., 2009) for the PCGs and TIM3 + I + G for *rrnS* and *rrnL*.

Scanning electron microscopy (SEM)

Overall, SEM material was prepared following Geiger et al. (2007) and imaged at the Swedish Museum of Natural History or Scripps Institution of Oceanography. For external anatomy of soft parts, three individuals of SIO-BIC M19055 were critical-point dried via 99.5% ethanol and carbon dioxide. For radula preparation, the head of the ethanol-preserved paratype SIO-BIC M18569 was dissected from the body and digested with pancreatin to remove the soft tissue, based on a previous protocol (Álvarez-Padilla and Hormiga, 2007). Briefly, the tissue was treated for > 24 h at room temperature with a filtered solution of 7 mg/ml pancreatin 4× USP (United States Pharmacopoeia specifications) enzyme complex buffered with 21% v/v sodium borate. The radula was rinsed with deionized water, air-dried, and mounted on an aluminum stub. The radula and selected shells were sputter-coated with gold-palladium

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and imaged with a Zeiss EVO 10 SEM at 20 kV (Scripps Institution of Oceanography) or a Hitachi S-4300 SEM at 5–10 kV (Swedish Museum of Natural History, Stockholm).

RESULTS

Mitochondrial genome

The mitochondrial genome of *Levinaespira georgesnyderi* gen. et sp. nov. contained 13 protein-coding genes, two rRNA genes, and 22 tRNA genes (Fig. 2), consistent with the other known examples of Neomphalidae and most of the known examples of other Neomphalida (Zhong et al., 2022). The gene order arrangement was identical to that of the two other available neomphalids (*Lamellomphalus manusensis* Zhang and Zhang, 2017 and Neomphalidae gen. et sp. Hatoma *sensu* Zhong et al., 2022) (Zhong et al., 2022). The mitochondrial genome of *Levinaespira georgesnyderi* gen. et sp. nov. was 15,573 bp in length, with a GC content of 29.5% (Fig. 2). The newly generated mitochondrial genome of *Chrysomallon squamiferum* was 15,935 bp in length with a GC content of 33.8%, closely matching the previously published mitochondrial genome (GenBank AP013032.1; 15,388 bp in length, GC content 33.8%) (Nakagawa et al., 2014; Zhong et al., 2022).

Phylogenetics

The ML COI tree recovered the six specimens of *Levinaespira* gen. nov. as a strongly supported clade within Neomphalidae (Fig. 3A). The ML mitogenome tree confirmed the placement of *Levinaespira* gen. nov. within Neomphalidae (Fig. 3B), as COI is known to be insufficient in resolving higher-level relationships within Neomphalida, e.g., among families (Aktipis and Giribet, 2012; Chen et al., 2015b, 2017, 2024; Zhong et al., 2022). Both phylogenies placed *Levinaespira* gen. nov. with strong support as the sister taxon to the undescribed taxon "Neomphalidae gen. et sp. Hatoma *sensu* Zhong et al., 2022," which was collected from the Hatoma Knoll hydrothermal vent site on the Okinawa Trough at 1482 m depth (Zhong et al., 2022).

Genus and species delimitation

Within Neomphalidae, *Levinaespira* gen. nov. was separated from other described genera by a minimum uncorrected COI distance of 15.18% (17.06% K2P; Table 1), consistent with intergeneric distances of > 15.1% (K2P) in Neomphalidae (Zhang and Zhang, 2017), > 12.8% (ML model-corrected) in Peltospiridae (Chen et al., 2017), and > 20.3% in Melanodrymiidae (Zhang and Zhang, 2017).

Levinaespira georgesnyderi gen. et sp. nov. and Neomphalidae gen. et sp. Hatoma *sensu* Zhong et al., 2022 were separated by 7.34–7.50% uncorrected COI divergence (7.79–7.97% K2P; Table 2), which falls short of the aforementioned intergeneric divergences and is commensurate with interspecific distances in Neomphalidae (3.84–7.54%, K2P) (Chen et al., 2024). We suggest that Neomphalidae sp. Hatoma *sensu* Zhong et al., 2022 would be suitably placed within *Levinaespira* gen. nov., as a new species distinct from *Levinaespira georgesnyderi* gen. et sp. nov., when it is described.

The COI sequences of *Levinaespira georgesnyderi* gen. et sp. nov. specimens from Costa Rica showed minimal variation (<0.5%, Table 2; at most three base pairs, Fig. 4), consistent with intraspecific variation (<3.8% K2P) in other neomphalids (Chen et al., 2024). The single specimen from Hydrate Ridge, ca. 4000 km north of the type locality (Fig. 1A), differed from the type series by 3.67–4.15% uncorrected COI distance (3.79–4.30% K2P; Table 2), corresponding to 23–26 base pairs (Fig. 4). Although this level of divergence could be interpreted as species-level separation in neomphalids based on the distance of 3.84% (K2P) between *Symmetromphalus mcleani* Beck, 2023 and *S. mithril* Chen, Poitrimol and Matabos, 2024, we conservatively designate the Hydrate Ridge specimen as *Levinaespira* cf. *georgesnyderi* gen. et sp. nov. We did not observe any clear morphological distinctions between the Hydrate Ridge specimen and the type series of *Levinaespira georgesnyderi* gen. et sp. nov. (Fig. 5A–N), as the former was preserved in a contracted state and not photographed alive. Genetic data from intermediate localities between Costa Rica and Hydrate Ridge would be helpful to address whether the Hydrate Ridge specimen represents a

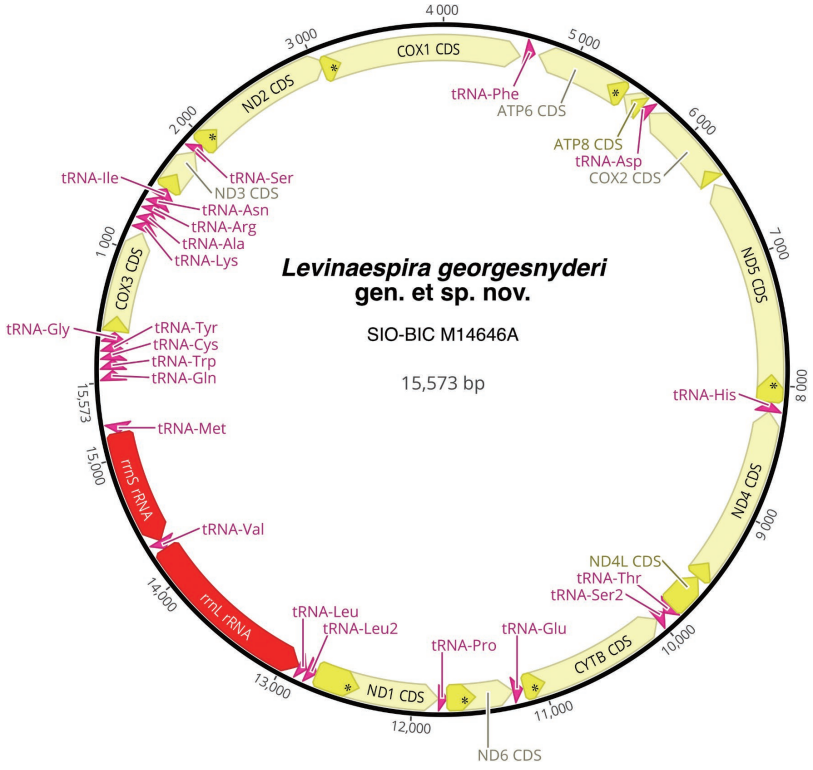


Fig. 2. Mitochondrial genome of *Levinaespira georgesnyderi* gen. et sp. nov., paratype SIO-BIC M14646A. Numbers along the outer circle indicate base pairs along the circularized sequence. Arrows represent the length and direction of genes: protein-coding genes (yellow) including coding sequences (CDS) and predicted stop codons (*), rRNA genes (red), and tRNA genes (pink). Visualization created in Geneious Prime 2025.1.3 (https://www.geneious.com, accessed 26 May 2025).

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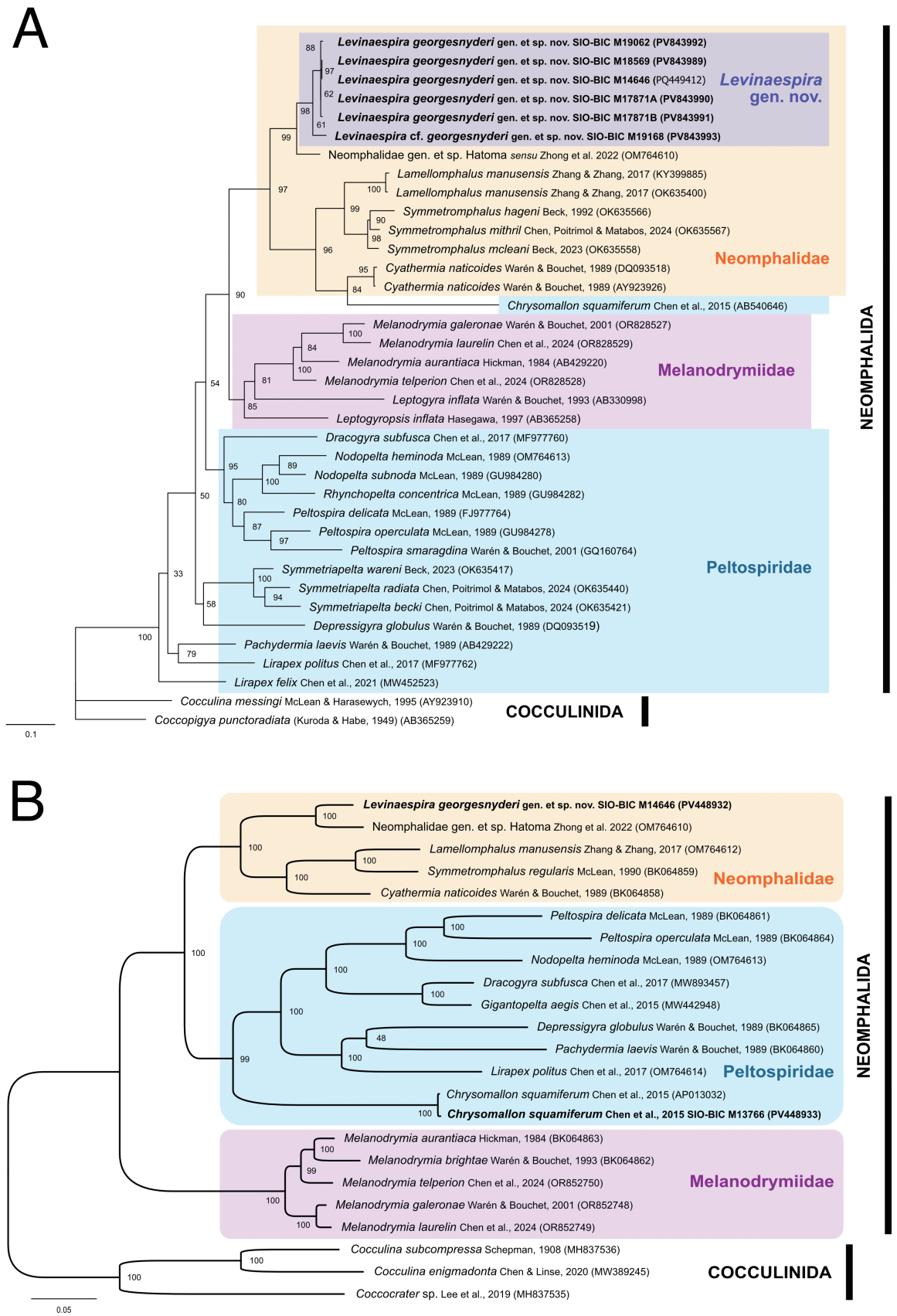


Fig. 3. Maximum likelihood trees generated from **(A)** mitochondrial COI (alignment of 554 bp) and **(B)** 13 protein-coding mitochondrial genes (as amino acid sequences) and two mitochondrial rRNA genes (as nucleotide sequences). Newly generated sequences are shown in bold and GenBank accession numbers are shown in parentheses. Node labels indicate bootstrap values.

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northern range extension of *Levinaespira georgesnyderi* gen. et sp. nov. or a narrowly diverged, separate undescribed species.

SYSTEMATICS

Family **Neomphalidae** McLean, 1981
Levinaespira gen. nov.

Levinaegyra: Levin et al., 2015: supplemental table 1 (line 160), supplemental table 2 (line 144) (*nomen nudum*; incorrectly formulated).

Type species. *Levinaespira georgesnyderi* gen. et sp. nov. by original designation.

Diagnosis. Shell regularly coiled, dextral. Operculum present, multispiral. Cephalic tentacles simple. Eyes absent. Snout simple, with apicoventral mouth. Ctenidium bipectinate. Anterior margin of foot with lateral projections. Epipodial tentacles present posterolaterally. Radula rhipidoglossate with formula n-4-1-4-n. Rachidian tooth and inner three lateral teeth similar in shape and size, without strong serration; outermost lateral tooth strongly serrated on outer margin. Marginal teeth with long, slender shafts and serrated cusps.

Etymology. Dedicated to Distinguished Professor Emerita Lisa Levin (Scripps Institution of Oceanography, University of California San Diego), for her contributions to deep-sea ecology and deep-sea stewardship, including serving as Chief Scientist during the first three cruises on which this species was collected. The genitive form *Levinae* is combined with the Latin *spira* (a spiral or coil, referencing the shell shape), a feminine singular noun in the nominative case.

Remarks. *Levinaespira* gen. nov. is unique among neomphalids in having lateral projections on the anterior foot, a lobe-shaped right cephalic lappet more prominent than the left, and bilaterally symmetric cephalic tentacles without obvious reproductive modifications. We refrain from emending the diagnosis of Neomphalidae until potential apomorphies can be assessed further, as shell shape and other characters in this group can vary greatly (Sasaki et al., 2010; Zhang and Zhang, 2017) and genetic data are not presently available for *Lacunoides*, *Neomphalus*, *Planorbidella*, or *Solutigyra*.

Several fossil taxa from northeastern Pacific seep-carbonate formations warrant comparison to *Levinaespira* gen. nov.: *Retiskenea statura* (Goedert and Benham, 1999) (late Oligocene to middle Eocene, Washington), *Retiskenea*? *kieli* Campbell, Peterson and Alfaro, 2008 (Late Jurassic to Early Cretaceous, northern California), and *Retiskenea*? *tuberculata* Campbell, Peterson and Alfaro, 2008 (Early Cretaceous, northern California) (Goedert and Benham, 1999; Campbell et al., 2008; Kaim et al., 2014). Additional *Retiskenea*-like gastropods have been reported from west-

Table 1. Minimum pairwise COI distances (uncorrected [*p*] and *K2P*) among genera of Neomphalidae, calculated from the maximum likelihood dataset.

		1	2	3	4
1 *Levinaespira* gen. nov.					
2 *Cyathermia*	p	16.59%			
	K2P	18.86%			
3 *Lamellomphalus*	p	16.43%	13.34%		
	K2P	18.63%	14.88%		
4 *Symmetromphalus*	p	15.18%	14.05%	9.99%	
	K2P	17.06%	15.77%	10.90%	

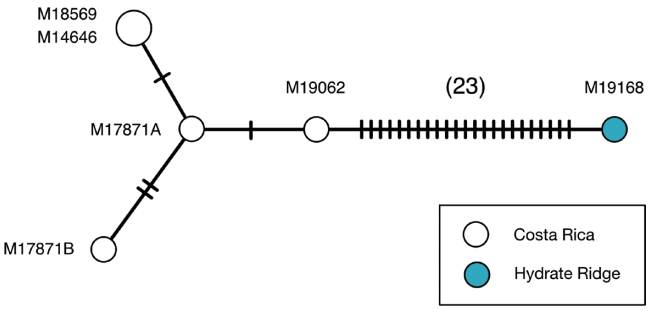


Fig. 4. Haplotype network for *Levinaespira georgesnyderi* gen. et sp. nov. Each circle represents a unique COI sequence of 627 bp, and each tick mark represents one nucleotide difference between the connected sequences. Geographic localities are color-coded and the size of each circle is proportional to the number of specimens sharing the sequence. Labels indicate SIO-BIC catalog numbers for voucher specimens.

Table 2. Pairwise distances of *Levinaespira georgesnyderi* gen. et sp. nov. and closest relatives, calculated from an alignment of 627 bp of COI. Uncorrected (*p*) and *K2P* distances are listed on separate rows if they differ. SIO-BIC catalog numbers or GenBank numbers are indicated in parentheses.

		1	2	3	4	5	6	7
1 *Levinaespira georgesnyderi* gen. et sp. nov. (M18569)								
2 *Levinaespira georgesnyderi* gen. et sp. nov. (M14646)		0.00%						
3 *Levinaespira georgesnyderi* gen. et sp. nov. (M17871A)		0.16%	0.16%					
4 *Levinaespira georgesnyderi* gen. et sp. nov. (M17871B)		0.48%	0.48%	0.32%				
5 *Levinaespira georgesnyderi* gen. et sp. nov. (M19062)		0.32%	0.32%	0.16%	0.48%			
6 *Levinaespira* cf. *georgesnyderi* gen. et sp. nov. (M19168)	p	3.99%	3.99%	3.83%	4.15%	3.67%		
	K2P	4.13%	4.13%	3.96%	4.30%	3.79%		
7 Neomphalidae gen. et sp. Hatoma *sensu* Zhong et al., 2022 (OM764610)	p	7.50%	7.50%	7.34%	7.34%	7.50%	7.82%	
	K2P	7.97%	7.97%	7.79%	7.79%	7.97%	8.33%	

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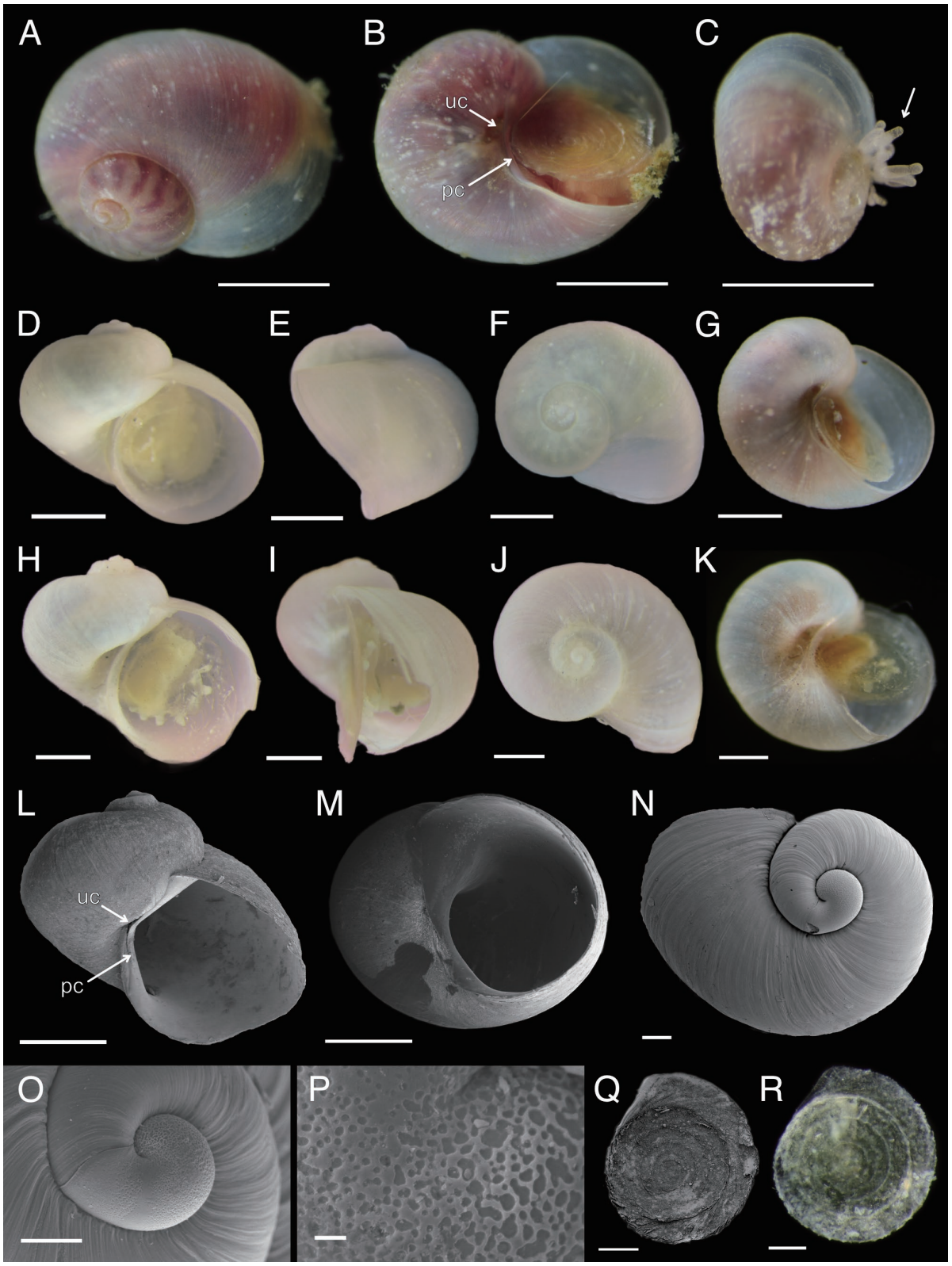


Fig. 5. *Levinaespira georgesnyderi* gen. et sp. nov., shell and operculum. **(A, B)** Live paratype SIO-BIC M11971. **(C)** Live specimen SIO-BIC M16952 with attached bacterial pustules (arrows). **(D–G)** Formalin-fixed holotype SIO-BIC M14645: **(D)** apertural view, **(E)** lateral view, **(F)** apical view, and **(G)** basal view. **(H–L)** Ethanol-fixed specimen SIO-BIC M19168, *Levinaespira* cf. *georgesnyderi* gen. et sp. nov. from Hydrate Ridge: **(H)** apertural view, **(I)** lateral view, **(J)** apical view, and **(K)** basal view. **(L–Q)** SEM images: paratype SIO-BIC M12101A, **(L)** apertural view and **(M)** basal view; **(N)** paratype SIO-BIC M12101B, apical view; paratype SIO-BIC M12101C, **(O)** protoconch and **(P)** detail of protoconch sculpture; **(Q)** operculum, specimen not retained. **(R)** Operculum of ethanol-fixed paratype SIO-BIC M19055. Scale bars: 1 mm **(A–M)**, 100 µm **(N, O)**, 10 µm **(P)**, 0.5 mm **(Q, R)**. Abbreviations: pc, parietal callus; uc, umbilical chink.

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ern Pacific and southeastern Pacific fossil seeps (Kaim, 2022). Although paleontological investigation is beyond the scope of this work, the similarities of these fossils to *Levinaespira* gen. nov. suggest the continuous presence of this genus at cold seeps for at least 145 million years (Kaim et al., 2014).

Levinaespira georgesnyderi gen. et sp. nov. (Figs. 5–7)

Levinaegyra sp.: Levin et al., 2015: supplemental table 1 (line 160), supplemental table 2 (line 144) (*nomen nudum*; incorrectly formulated).

Neomphalidae sp. SIO_BIC_M14645: (Seid et al., 2025): 104–105, fig. 39E–F.

Diagnosis. Same as genus.

Material examined. Holotype: SIO-BIC M14645, fixed in 10% seawater formalin and preserved in 50% ethanol, collected from the Mound 12 methane seep off the Pacific margin of Costa Rica (8.9303°, −84.3124°), carbonate rock at 997 m depth, 25 May 2017, HOV *Alvin* dive 4910, collectors Greg Rouse, Todd Litke, and pilot Jefferson Grau.

Paratypes: SIO-BIC M11971, one individual fixed in glyoxal (Prefer fixative, Anatech Ltd., Battle Creek, MI) and preserved in 95% ethanol, collected from Mound 12 (8.93°, −84.31°), ca. 997 m depth, HOV *Alvin* dive 4501, 22 February 2009, collectors Lisa Levin, Anne Dekas, and pilot Mark Spear; SIO-BIC M12094, six individuals fixed in 10% seawater formalin and preserved in 50% ethanol, collected from Mound 12 (8.93°, −84.31°), ca. 997 m depth, HOV *Alvin* dive 4502, 23 February 2009, collectors Victoria Orphan, Brian Wrightsman, and pilot Bob Waters; SIO-BIC M12101, eight individuals fixed and preserved in 95% ethanol (of which three shells were prepared for SEM), same collection data as M12094; SIO-BIC M14646, two individuals fixed and preserved in 95% ethanol (of which one was subsampled for DNA extraction; GenBank COI PQ449412, mitogenome PV448932), collected from Mound 12 (8.9296°, −84.3121°), tubeworm cluster at 995 m depth, HOV *Alvin* dive 4917, 1 June 2017, collectors Greg Rouse, Ben Moran, and pilot Jefferson Grau; SIO-BIC M18569, one individual fixed and

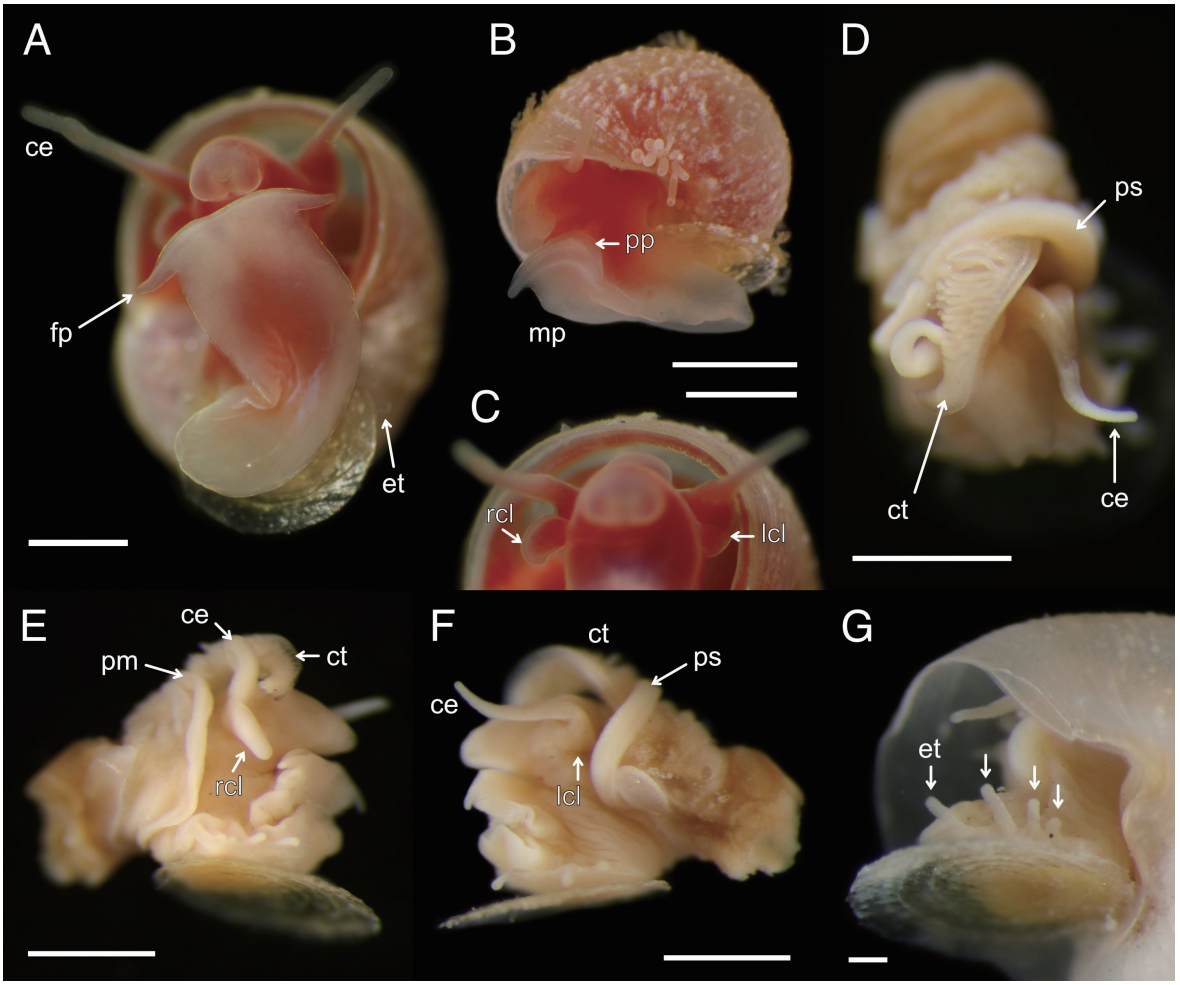


Fig. 6. *Levinaespira georgesnyderi* gen. et sp. nov., soft parts. **(A–C)** Live specimens from lot comprising holotype SIO-BIC M14645 and paratype SIO-BIC M18569, prior to holotype selection. **(D–G)** Ethanol-fixed paratypes, lot SIO-BIC M19055: **(D)** dorsal view, **(E)** right lateral view, and **(F)** left lateral view of the same individual, removed from shell; **(G)** left lateral view of a different individual. Scale bars: 1 mm **(A–F)**, 0.1 mm **(G)**. Abbreviations: ce, cephalic tentacle; ct, ctenidium; et, epipodial tentacle; fp, foot projections; lcl, left cephalic lappet; mp, mesopodium; pm, pallial margin; pp, propodium; ps, pallial skirt; rcl, right cephalic lappet.

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preserved in 95% ethanol (radula prepared for SEM and most soft tissue destroyed for DNA extraction; GenBank COI PV843989), same collection data as holotype; SIO-BIC M18833, nine individuals fixed and preserved in 95% ethanol, collected from Mound 12 (8.9306°, −84.3128°), carbonate rock at 997 m depth, HOV *Alvin* dive 4589, 10 January 2010, collectors Guillermo Mendoza, William Ussler, and pilot Mark Spear; MZUCR 10786, five individuals fixed and preserved in 95% ethanol, same collection data as SIO-BIC M18833; SIO-BIC M18868, 14 individuals fixed and preserved in 95% ethanol, collected from Mound 12 (8.9305°, −84.3124°), carbonate rock at 995 m depth, HOV *Alvin* dive 4511, 5 March 2009, collectors Tony Rathburn, Paola Lopez, and pilot Bruce Strickrott; MZUCR 10787, five individuals fixed and preserved in 95% ethanol, same collection data as SIO-BIC M18868; SIO-BIC M19055, 16 individuals fixed and preserved in 95% ethanol with soft parts exposed (three additional individuals destroyed for critical-point drying), collected from Mound 12 (8.9304°, −84.3125°), carbonate rock at 997 m depth, HOV *Alvin* dive 4588, 9 January 2010, collectors Greg Rouse, Benjamin Grupe, and pilot Dave Walter; SIO-BIC M19062, 32 individuals fixed and preserved in 95% ethanol (of which one was subsampled for DNA extraction; GenBank COI PV843992, 18S PV843603), same collection data as SIO-BIC M19055; SMF 383096, three individuals fixed and preserved in 95% ethanol with soft parts exposed, same collection data as SIO-BIC M19055; SMF 383097, seven individuals fixed and preserved in 95% ethanol, same collection data as SIO-BIC M19062.

Other material: SIO-BIC M14644, two individuals fixed in

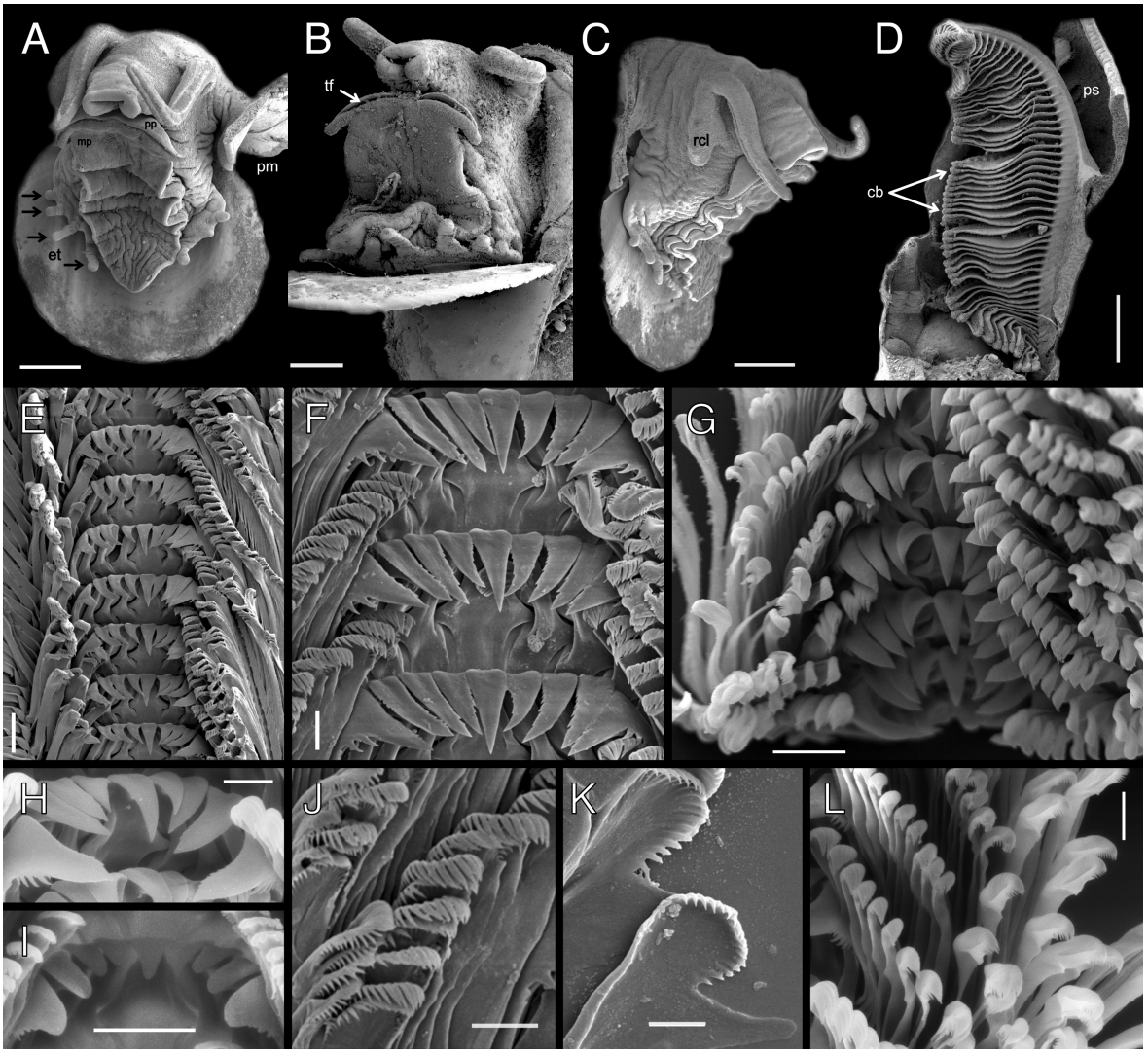


Fig. 7. *Levinaespira georgesnyderi* gen. et sp. nov., soft parts and radula, SEM images. **(A–D)** Soft parts of specimens (not retained) from lot SIO-BIC M19055: **(A–C)** head-foot with operculum and **(D)** ctenidium. Section of radula ribbon (specimen not retained): **(E)** wide view, **(F)** detail of rachidian and lateral teeth. Section of radula ribbon from paratype SIO-BIC M18569: **(G)** wide view, **(H)** detail of selected rachidian and lateral teeth with sharp serration, **(I)** detail of selected rachidian and lateral teeth with blunt serration. **(J)** Detail of marginal teeth from **(F)**. **(K)** Detail of apical end of outer marginal teeth (specimen not retained). **(L)** Detail of stacked marginal teeth showing variation in apical ends, from the same preparation of paratype SIO-BIC M18569 as in **(G–I)**. Scale bars: 0.5 mm **(A–C)**, 20 µm **(D, E, G)**, 5 µm **(F, J)**, 10 µm **(H, I, L)**, 2 µm **(K)**. Abbreviations: cb, ctenidial bursicle; et, epipodial tentacle; mp, mesopodium; pm, pallial margin; pp, propodium; ps, pallial skirt; rcl, right cephalic lappet; tf, transverse furrow.

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10% seawater formalin and preserved in 50% ethanol, two individuals fixed and preserved in 95% ethanol (partially destroyed for DNA extraction of gill bacteria), four individuals fixed and preserved in RNA*later* Stabilization Solution (Ambion, Austin, TX; currently held by Invitrogen, part of ThermoFisher Scientific), collected from Mound 12 (8.9304°, – 84.3128°), 990–999 m depth, HOV *Alvin* dive 4907, 22 May 2017, collectors Lisa Levin, Charlotte Seid, and pilot Pat Hickey; SIO-BIC M16903, one individual minced and preserved in RNAlater, collected from Mound 12 (8.9298°, – 84.3123), tubeworm cluster at 995 m depth, HOV *Alvin* dive 4987, 2 November 2018, collectors Erik Cordes, Emily Cowell, and pilot Jefferson Grau; SIO-BIC M17871, three individuals fixed and preserved in 95% ethanol (destroyed for DNA extraction; GenBank COI PV843990, PV843991), same collection data as SIO-BIC M19055; SIO-BIC M18798, one individual fixed and preserved in 95% ethanol, collected from Mound 12 (8.9296°, – 84.31075°), carbonate rock at 989 m depth, HOV *Alvin* dive 4586, 7 January 2010, collectors Lisa Levin, Graham Nash, and pilot Bruce Strickrott; SIO-BIC M19168, one individual fixed and preserved in 95% ethanol (subsampled for DNA extraction; GenBank COI PV843993, 18S PV843604), collected from a methane seep at Hydrate Ridge, Cascadia Margin, off Oregon, USA, Pacific Ocean (44.670°, – 125.098°), carbonate rock at ca. 618 m depth, HOV *Alvin* dive 4631, 3 August 2010, collectors Victoria Orphan, Jose Patterson, and pilot Bruce Strickrott.

Etymology. Named in memory of H. George Snyder (1931–1990), manager of the Scripps Invertebrate Collection (1959–1966) and the Pelagic Invertebrate Collection (1966–1990), for his dedication to the study and preservation of marine biodiversity. The authors are grateful to Nancy Snyder for her support of the Benthic and Pelagic Invertebrate Collections in honor of her brother's legacy. A Latin singular noun in the genitive case.

Description. Shell (Figs. 5A–G, L–P; 6A–C, G). Regularly coiled, skeneiform, with depressed spire, translucent grayish white, up to 4.9 mm in diameter (largest recorded specimen SIO-BIC M16903). Aperture large, strongly prosocline, approximately circular. Protoconch distinctly demarcated from teleoconch (Fig. 5N, O), consisting of ca. 0.5 whorls, maximum diameter ca. 275 µm, with irregular net (vermiculate) sculpture (Fig. 5P). Teleoconch with up to ca. 2.75 inflated whorls, suture deep, surface relatively smooth, with faint and densely set growth lines of variable strength. Periostracum thin, inconspicuous. Parietal callus thin in adult specimens (Fig. 5B, D, G), less distinct in young ones (Fig. 5L, M). Umbilical chink shallow in adult specimens (Fig. 5B, D, G), less distinct in young ones (Fig. 5L, M).

Operculum (Figs. 5B, G, Q, R; 6A, B, E–G; 7A–C). Circular, multispiral with central nucleus, each volution extending a slight fringe over subsequent volutions. Thin, flexible, translucent, faintly yellow, up to 2.3 mm in diameter, completely filling the aperture.

Soft parts (Figs. 6, 7A–D). Live animals (Fig. 6A–C) translucent, perfused with bright pinkish crimson color in intensity proportional to the thickness of tissue. Cephalic tentacles bilaterally symmetrical, slender and gently tapering to a blunt point, each approximately as long as aperture diameter when extended in life, no obvious reproductive modifications. Left cephalic lappet semicircular (Fig. 6A, C, F), right cephalic lappet extended into an anterolaterally projecting fleshy lobe (Figs. 6A, C, E; 7C). Eyes absent. Snout tubular, flexible, with mouth apicoventrally situated. Perioral surface unornamented, with small transverse furrow. Foot flexible, approximately twice as long as wide, posteriorly tapering and rounded, low and thin in profile. Anterior margin of foot drawn out into symmetrical lateral horn-like projections, each extending approximately one-third the width of the main sole. Propodium separated from mesopodium by a transverse furrow (Figs. 6B, 7A–C). Typical extended size of mesopodium in live animals projecting slightly beyond shell contours anteriorly and posteriorly, but not laterally. Epipodial tentacles present posterolaterally on a low epipodial ridge, four on each side, barely projecting beyond operculum, approximately uniform in diameter with the two posteriormost tentacles diminishing in length (Figs. 6E–G, 7A–C). Head-foot completely retractable into shell. Ctenidium (Figs. 6D, 7D) bipectinate, attached along approximately half its length, equipped with ca. 60 leaflets, each with a slightly broadened bursicle close to the tip. Internal anatomy not assessed.

Radula (Fig. 7E–L). Rhipidoglossate, formula: n-4-1-4-n, where n is ca. 20. Approximately eight times as long as broad. Rachidian tooth (Fig. 7E–I) smooth, triangular, tapering distally to a sharp point, with steeply folded overhanging cusp approximately twice as long as wide. Lateral teeth (Fig. 7E–I) similar in overall shape and size to rachidian tooth, slightly falcate and arcing towards the center, cusps indistinctly serrated, outer margin of the outermost lateral tooth strongly serrated. Marginal teeth densely packed, shafts long and slender, with rake-like cusps bearing ca. 17 denticles at distal end (Fig. 7J, K). Rachidian and lateral teeth with interlocking bases, marginal teeth stacked.

Remarks. No individuals of *Levinaespira georgesnyderi* gen. et sp. nov. were observed with an enlarged left cephalic tentacle modified to serve as copulatory organ, as is diagnostic of males in *Cyathermia*, *Lacunoides*, *Lamellomphalus*, *Neomphalus*, and *Symmetromphalus*. In *Retiskenea*, the appearance of the left cephalic tentacle in mature males is uncertain because the few available specimens appeared to be reproductively immature (Warén and Bouchet, 2001). Considering the relatively large sizes of the specimens examined for *Levinaespira georgesnyderi* gen. et sp. nov., we provisionally interpret the largest specimens as reproductively mature, and we infer that the cephalic tentacles are bilaterally of equal size in both sexes, as in *Planorbidella* and *Solutigyra* (Warén and Bouchet, 1989, 1993).

Ecology. In all cases where the exact habitat type was recorded, specimens were associated with authigenic carbonate rocks or clusters of vestimentiferan tubeworms, *Lamellibrachia donwalshi* and *Escarpia spicata*. Both habitats are considered indicators of active methane-rich fluid seepage (Levin et al., 2015). Representative environmental conditions at Mound 12 are: temperature 5.11°C, oxygen 0.99–1.60 ml/l, pH 7.6–7.7 (Levin et al., 2015). The gut contents of *Levinaespira georgesnyderi* gen. et sp. nov. appeared to contain unsorted sediment with small pieces of rigid debris, suggesting that this species feeds nonselectively by sweeping the surface of rocks and vestimentiferan tubes.

The shells of *Levinaespira georgesnyderi* gen. et sp.

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nov. were often covered by elongated pustules (Figs. 5C, 6B) resembling the sulfur-oxidizing bacteria that have been reported on other gastropods from the Costa Rica and Hydrate Ridge methane seeps (Bailey et al., 2011) and from northeastern Pacific hydrothermal vents (Warén and Bouchet 1989; Johnson et al., 2006; Warén, 2006; Warén et al., 2006). Bacterial DNA from the gills of *Levinaespira georgesnyderi* gen. et sp. nov. did not suggest the presence of chemosynthetic symbionts (Shana Goffredi, personal communication, 8 February 2025). The protoconch of *Levinaespira georgesnyderi* gen. et sp. nov. resembles those of other neomphalids that have been collected as plankton at vents (Mills et al., 2009), suggesting that the new species may also disperse planktonic larvae along bottom currents.

The bright reddish internal color of live animals (Figs. 5A–C, 6A–C) disappeared upon fixation (Fig. 6D–G), suggesting that the blood of *Levinaespira georgesnyderi* gen. et sp. nov. may contain hemoglobin or myoglobin. The soft tissues of the vent peltospirids *Depressigyra globulus* Warén and Bouchet, 1989 and *Chrysomallon squamiferum* are also red in life (Warén and Bouchet, 1989; Chen et al., 2015a), and the transcriptome of the latter suggests that the coloration is due to myoglobin (Sun et al., 2020). Hemoglobin occurs widely among gastropods, especially in the radular muscle of species with energy-intensive feeding modes (Wittenberg and Stein, 1995; Alyakrinskaya, 2004; Fukumori et al., 2019b; Zhang et al., 2023).

Distribution. Confirmed only from the type locality, the Mound 12 methane seep off Costa Rica, Pacific Ocean, ca. 1000 m deep. Possibly extends to the Hydrate Ridge methane seeps on the Cascadia Margin, off Oregon, USA, ca. 600 m depth.

DISCUSSION

Morphology and phylogenetics support the designation of *Levinaespira georgesnyderi* gen. et sp. nov. as a new genus and species within Neomphalidae. At the Costa Rica margin, *Levinaespira georgesnyderi* gen. et sp. nov. has been recorded only from the Mound 12 seep at ca. 1000 m depth, despite extensive sampling of similar habitats at other seep sites at ca. 400–1800 m depth (Levin et al., 2012, 2015; Betters and Cordes, 2024; Betters et al., 2024; Seid et al., 2025). These apparent absences may reflect differences in abundance, unintended sampling bias, or depth restriction as has been reported for other invertebrates at the Costa Rica seeps (McCowin and Rouse, 2018; McCowin et al., 2020; Rouse and Kupriyanova, 2021).

Neomphalidae have been considered “hot vent specialists”, with the possible exception of *Retiskenea*, which occurs at seeps (Sasaki et al., 2010; Zhang et al., 2024). The placement of *Retiskenea* within Neomphalidae is tentative (Warén and Bouchet, 2001), as this genus also shows morphological affinities to *Melanodrymia* Hickman, 1984 (presently within Melanodrymiidae), Seguenziidae Verrill, 1884, and Skeneidae Clark, 1851 (Warén and Bouchet, 2001; Okutani and Fujikura, 2002). *Levinaespira georgesnyderi* gen. et sp. nov., with clear phylogenetic placement and no known vent occurrences, represents the first genetically confirmed record of Neomphalidae at methane seeps. This habitat preference also distinguishes *Levinaespira georgesnyderi* gen. et sp. nov. from its sister taxon Neomphalidae gen. et sp. Hatoma *sensu* Zhong et al., 2022, which is presently known only from the Hatoma Knoll submarine volcano, where the temperatures of hydrothermal vent fluids can exceed 300°C (Watanabe, 2001; Kedzior et al., 2016).

All presently known Neomphalidae have been recorded only from the Pacific Ocean at depths > 1500 m (Warén and Bouchet, 1993; Sasaki et al., 2010; Zhang and Zhang, 2017; Chen and Sigwart, 2023; Chen et al., 2024; Zhang et al., 2024). The occurrence of *Levinaespira georgesnyderi* gen. et sp. nov. at < 1000 m represents the shallowest known records of Neomphalidae. Mitogenome data for *Retiskenea* and additional neomphalid taxa, particularly non-vent examples and the type species *Neomphalus fretterae* McLean, 1981, would enable further taxonomic revision and evaluation of habitat shifts and geographic origins.

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COMPETING INTERESTS

The authors have no competing interests to declare.

AUTHOR CONTRIBUTIONS

GWR conceived the project. GWR, AW, and CAS collected specimens. GWR photographed live specimens, GWR and AW performed radula preparations and SEM imaging, and CAS photographed preserved specimens. SH assembled and annotated the mitochondrial genome. YK generated several COI and 18S sequences. CAS, SH, YK, and GWR analyzed the DNA sequences. AW, YK, and CAS drafted the initial versions of the manuscript. All authors reviewed and approved the final version for publication.

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