A new genus and species of Neomphalidae from a hydrothermal vent of the Manus Back-Arc Basin, western Pacific (Gastropoda: Neomphalina)

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ABSTRACT

Lamellomphalus manusensis new genus, new species is described from a hydrothermal vent site of the Manus Back-Arc Basin. The familial assignment is based on morphologies of shell and external anatomy. The new taxon is superficially similar to some members of Peltospiridae McLean, 1989 in general shell shape, but differs from all peltospirids in having sex dimorphism and presence of a copulatory organ. *Lamellomphalus manusensis* is characterized by possessing haliotiform shell with some degree of coiling, which could be considered as an intermediate form in the family Neomphalidae McLean, 1981, between species with regularly coiled shells (*Cyathermia* Warén and Bouchet, 1989; *Lacunoides* Warén and Bouchet, 1989; *Planorbidella* Warén and Bouchet, 1993, and *Solutigyra* Warén and Bouchet, 1989) and limpet-like shells (*Neomphalus* McLean, 1981 and *Symmetromphalus* McLean, 1990). This feature thus distinguishes the new taxon from other neomphalids. A phylogenetic reconstruction based on cytochrome *c* oxidase I gene (COI) also supports its placement within Neomphalidae.

Additional keywords: Gastropoda, Neomphaloidea, chemosynthetic environment, new taxon

INTRODUCTION

The Manus Back-Arc Basin is of particular biological interest due to its location between the biologically well studied Mariana Trough and the vent communities of the North Fiji and Lau Back-Arc Basins. That special geographical environment yields many interesting and new gastropods, attracting the interest of many scientists (e.g. Desbruyères and Laubier, 1989; Beck, 1991, 1992a, 1992b, 1993; Bouchet and Warén, 1991; Warén and Bouchet, 1993).

Neomphalina (Warén and Bouchet, 1993) are a group of gastropods that inhabits chemosynthetic environments (Desbruyères et al., 2006; Sasaki et al., 2010) and sunken wood (Hess et al., 2008). Among them, Neomphalidae is a particular family that by far is consisting of six genera and eight species, known from East Pacific Rise (Warén and Bouchet, 1989), Galapagos Rift (McLean, 1981; Warén and Bouchet, 1989), Lau Basin (Warén and Bouchet, 1993), Axial Seamount (Warén and Bouchet, 2001) and Mariana Back-Arc Basin (McLean, 1990).

In June 2015, during a scientific investigation carried out by the Institute of Oceanology, Chinese Academy of Sciences (IOCAS), several limpet-shaped gastropods were collected in the Manus Back-Arc Basin by a dive of the ROV Faxian (based on mother ship R/V Kexue). Observations on their shell, radula features and external anatomy confirmed that they represent a new genus and a new species belonging to the family Neomphalidae McLean, 1981. In present study, we describe and illustrate this new taxon, comparing it to its closest relatives.

MATERIALS AND METHODS

More than 130 specimens were collected during single dive of the ROV Faxian (IOCAS) in June, 2015, at a hydrothermal vent site in the Manus Back-Arc Basin. This vent field is composed of both fissure areas and more active zones with small anhydrite and tall sulfide and silica chimneys ejecting greyish-black fluids (see Fourre et al., 2006 for details). The entire area is partially colonized by vestimentiferan worms (Siboglinidae) associated with the large gastropods *Ifremeria nautilei* Bouchet and Warén, 1991, mussels, shrimps and galatheid crabs.

The specimens described herein were collected by the mechanical arm of the ROV Faxian in the course of sampling the rock where specimens were attached. The materials were fixed in 99.5% ethanol directly after collection. Preserved specimens were brought to Marine

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Table 1. Shell measurements of *Lamellomphalus manusensis* new species.

Measurements (mm)	Shell		
	Length	Width	Height
Lamellomphalus manusensis			
Holotype (MBM283053)	8.8	5.7	2.9
Paratype (MBM283054)	6.6	4.7	2.7
Range	3.5–8.9	2.5–6.5	1.5–3.3
Mean	5.9	4.4	2.6

Biological Museum, Chinese Academy of Sciences (MBMCAS), for further study. Shell measurements were taken with a caliper with accuracy of 0.1 mm (see Table 1).

Scanning Electron (SEM) and Light Microscopies (SEM): Shell and soft part morphologies were examined via both light microscopy and SEM, and the radula by SEM alone. Soft parts of two specimens were critical-point dried for SEM studies. For SEM studies of radulae, radular sacs were removed and placed in 10% NaOH solution for 7–8 hours. The radulae were then dehydrated through an ethanol series and laid on a cover slip to air-dry. Samples were coated with gold and examined under a Hitachi S-3400N scanning electron microscope. Type material was deposited at MBMCAS, Qingdao, China.

Molecular Analyses: Five specimens were subjected to molecular analysis. Genomic DNA from each individual was extracted with the Column Genomic DNA Isolation Kit (Beijing TIANGEN, China) according to the manufacturer's instructions. DNA was eluted in elution buffer and stored at −20°C until use. The COI region was amplified by polymerase chain reaction (PCR) using the primers LCO1490 (forward: 5′-GGTCAACAAAT CATAAAGATATTGG-3′) and HCO2198 (reverse: 5′-TTA ACTTCAGGGTGACCAAAAAATCA-3′) (Folmer et al., 1994). PCR reactions were carried out in a total volume of 50 μL, including 2 mL DNA template, 1.5 mM $MgCl_2$, 0.2 mM of each dNTPs, 1 μL of both forward and reverse PCR primers, 10×buffer and 2.5 U Taq DNA polymerase. Thermal cycling was performed under the following conditions: 95°C for 3 min (initial denaturation), followed by 35 cycles of 95°C for 30s (denaturation), 42°C for 30s (annealing), 72°C for 60s (extension) and a final extension at 72°C for 10 min. PCR products were verified on a GelRed-stained 1.5% agarose gel and purified with the Column PCR Product Purification Kit (Shanghai Sangon, China). Purified products were sequenced in both directions using the BigDye Terminator Cycle Sequencing Kit (ver. 3.1, Applied Biosystems) and an AB PRISM 3730 (Applied Biosystems) automatic sequencer. Sequence alignments were generated using Clustal X (Larkin et al., 2007). For phylogenetic analyses, COI sequence from present study and those from GenBank were used (see Table 2). Neighbor-joining (NJ) tree was performed by MEGA 6.06 (Tamura et al., 2013), using Kimura 2-parameter (K2P) model (Kimura, 1980). Bootstrap analyses were performed with 1000 replications.

SYSTEMATICS

Superfamily Neomphaloidea McLean, 1981
Neomphalidae McLean, 1981

Table 2. Works from which the COI sequences derived.

Family	Species	Accession number	Reference
Melanodrymiidae	*Leptogyra inflata*	AB330998.1	Heβ et al., 2008
Melanodrymiidae	*Leptogyropsis inflata*	AB365258.1	Kano, 2008
Melanodrymiidae	*Melanodrymia aurantiaca*	GQ160763.1	Aktipis and Giribet, 2012
Melanodrymiidae	*Melanodrymia aurantiaca*	AB429220.1	Heβ et al., 2008
Neomphalidae	*Cyathermia naticoides*	AY923926.1	Geiger and Thacker, 2005
Neomphalidae	*Cyathermia naticoides*	DQ093518.1	Giribet et al., 2006
Neomphalidae	*Lamellomphalus manusensis*	KY399885	this study
Peltospiridae	*Depressigyra globulus*	AY296825.1	Colgan et al., 2003
Peltospiridae	*Depressigyra globulus*	DQ093519.1	Giribet et al., 2006
Peltospiridae	*Gigantopelta chessoia*	KU312688.1	Roterman et al., 2016
Peltospiridae	*Gigantopelta chessoia*	KU312689.1	Roterman et al., 2016
Peltospiridae	*Nodopelta subnoda*	GU984280.1	Matabos et al., 2011
Peltospiridae	*Nodopelta subnoda*	GU984281.1	Matabos et al., 2011
Peltospiridae	*Pachydermia laevis*	AB429222.1	Heβ et al., 2008
Peltospiridae	*Pachydermia laevis*	GU984266.1	Matabos et al., 2011
Peltospiridae	*Peltospira delicata*	AY923931.1	Geiger and Thacker, 2005
Peltospiridae	*Peltospira operculata*	GU984279.1	Matabos et al., 2011
Peltospiridae	*Peltospira smaragdina*	GQ160764.1	Aktipis and Giribet, 2012
Peltospiridae	*Rhynchopelta concentrica*	GU984283.1	Matabos et al., 2011
Pleurotomariidae	*Bayerotrochus delicatus*	KU759008.1	Zhang et al., 2016

Lamellomphalus new genus

Type Species: *Lamellomphalus manusensis* new species, by original designation.

Diagnosis: Shell haliotiform. Coiled earlier whorl offset to posterior right. Protoconch and first teleoconch whorl with coiling axis parallel to adult aperture. Protoconch surface sculptured with irregular network of low ridges. First 1.2 teleoconch whorl rounded, sculptured with weak axial threads; subsequent teleoconch whorl rapidly expanding, with developed reticulated sculpture. Operculum present, mutispiral with wide free edge. Neck short, dorso-ventrally compressed. Mouth opening triangular; snout apically strongly bilobed and drawn out laterally into points. Cephalic tentacles short, postero-laterally oriented, left tentacle of male greatly enlarged, serving as copulatory organ, deep ventral sperm groove connecting with groove on left side of neck. Epipodial tentacles present posteriorly and laterally. Ctenidium bipectinate, afferent membrane absent; efferent axis merged with floor of mantle cavity by thickened efferent membrane; gill lamellae elongate. Mantle cavity open anteriorly. Radula rhipidoglossate, has a formula of (ca. 10)+4+1+4+(ca. 10), cusps of inner three lateral teeth similar to those of rachidian teeth with smooth cutting edges, fourth lateral teeth strongly serrate on outer edge; marginal teeth with long, broad shafts, cusp edges deeply divided into about 20 serrations.

Etymology: The name of new genus refers to the lamellae-like structures formed on shell periostracum.

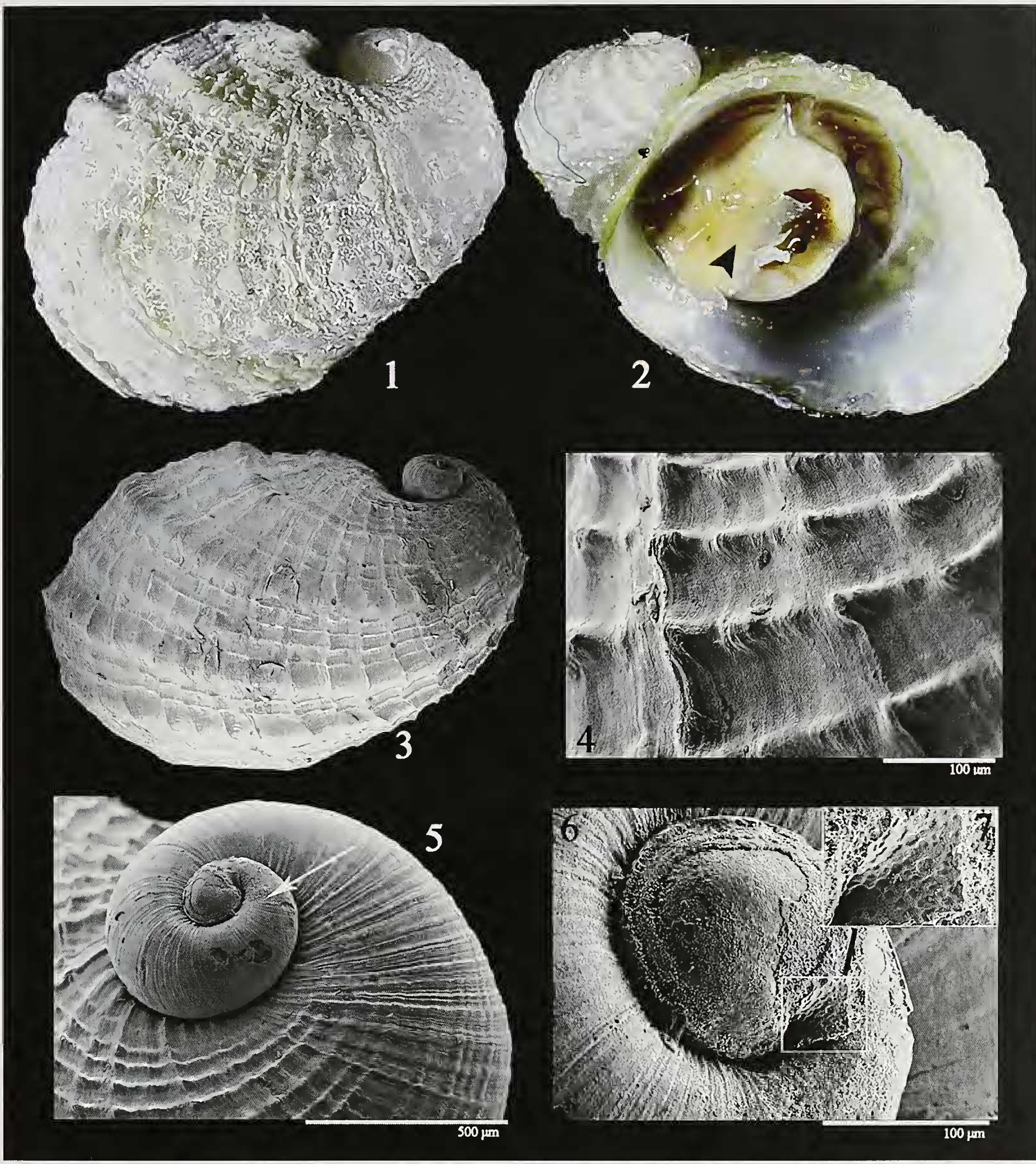
Remarks: *Lamellomphalus* superficially resembles some members Peltospiridae (e.g. *Hirtopelta hirta* McLean, 1989; *Ctenopelta porifera* Warén and Bouchet, 1993, and *Hirtopelta tufari* Beck, 2002) in having haliotiform shell with coiling axis of earlier whorls parallel to final aperture, but differs from them by displaying sexual dimorphism and a copulatory organ, lack of gill afferent membrane and by the non-serrated cusps of the rachidian and lateral teeth. Within Neomphalidae, *Cyathermia*, *Lacunoides*, *Planorbidella*, and *Solutigyra* can be clearly separated from *Lamellomphalus* by their regularly coiled shells. In addition, *Cyathermia* and *Lacunoides* differs from *Lamellomphalus* by having a left tentacle with closed sperm groove and two proximal cirri, and by serration on cusps of rachidian and lateral teeth; *Planorbidella* and *Solutigyra* mainly differ by having cephalic tentacles of equal size in both female and male. *Neomphalus* and *Symmetromphalus* somewhat resemble *Lamellomphalus* in their limpet-shaped shell. However, *Neomphalus* and *Symmetromphalus* can be differentiated from *Lamellomphalus* by having the coiling axis of earlier whorls perpendicular rather than parallel to the adult aperture.

Lamellomphalus manusensis new species
(Figures 1–32)

Description: **Shell** (Figures 1–6) of medium size for family (maximum length 8.9 mm for female and 6.6 mm for male), shell color white. Periostracum olive-green, extending beyond shell margin. Shell haliotiform, profile moderately depressed. Spire small, appressed to the posterior right side of the shell. Protoconch (Figures 5–7) with one rounded whorl, maximum diameter 260 µm, usually heavily eroded, surface sculpture an irregular network of low ridges. Protoconch and first teleoconch whorl with coiling axis parallel to final aperture. Suture deep. First 1.2 teleoconch whorls rounded, sculptured with weak axial threads; subsequent teleoconch whorls rapidly expanding, surface sculpture of radial ribs crossing by thin, curved concentric threads, the two forming sharp nodules on intersections (Figure 4). Radial ribs of varying strengths, primary ones thick, raised, 7–8 in number, each interspace of two adjacent primary ribs with 2–3 secondary ribs. Outline of aperture elongate-oval to nearly rounded, aligned on a single plane or gently arched from side to side. Margin of aperture very thin and fragile, extending into short digitations that correspond to primary radial ribs. Periostracum forming lamellar processes that correspond to intersections of radial ribs and concentric threads.

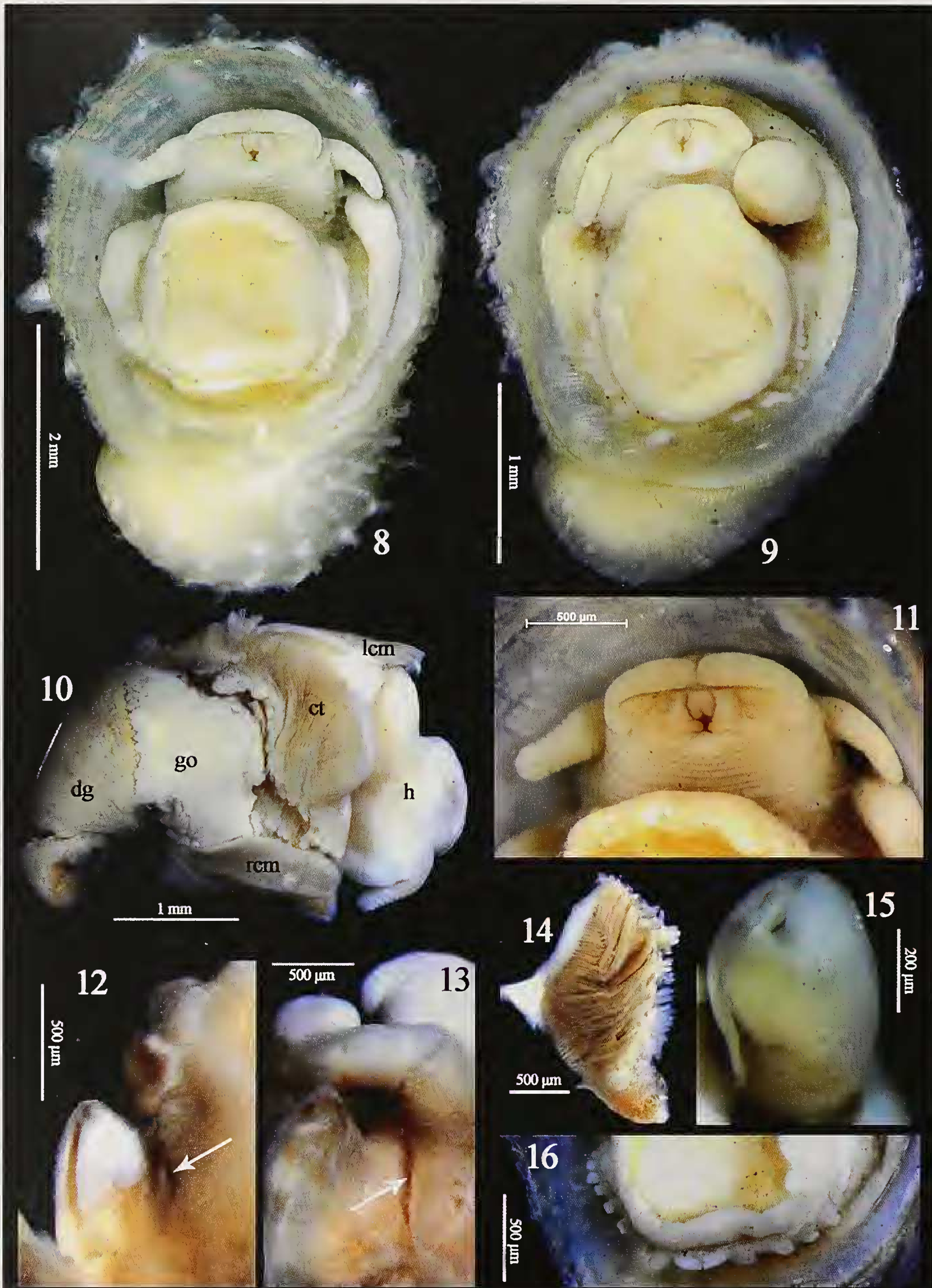
Operculum (Figures 2, 24): Very thin, transparent, attached vertically to posterior region of foot, multispiral, with large, wide final whorl, margin frayed.

External Anatomy (Figures 8–25): Neck short, widened, dorso-ventrally flattened, ventral side with regularly spaced transversal furrows, each side with rounded projection or lobe; males with deep groove on left lateral side, extending to posterior region of mantle cavity; females with short groove (Figures 12, 13). Mouth triangular, perioral area with radial furrows; snout strongly bilobed apically and drawn out laterally into points. Eyes absent. Cephalic tentacles postero-laterally directed, of equal size in female; left tentacle of male very enlarged, relatively thin where attached to head, becoming abruptly thicker distally, about four times as thick as right tentacle, scroll-like in shape, distal end with a seminal opening, ventrally with a deep, open sperm groove that continuous as deep groove on left edge of neck. Mantle skirt very thin. Pallial margin thickened, without papillae, its edge with one dorsal notch, about 3 mm deep. Mantle cavity opened anteriorly, deep and spacious. A pallial vein prominently visible on mantle skirt, originating in right anterior part of mantle skirt and extending posteriorly to end of mantle cavity. Ctenidium enlarged, bipectinate, its large size indicative of filter-feeding, afferent membrane absent; efferent axis arising at posterior of mantle cavity on left, attached to floor of mantle cavity by thickened efferent membrane; gill lamellae elongated and curved, with a blunt pointed

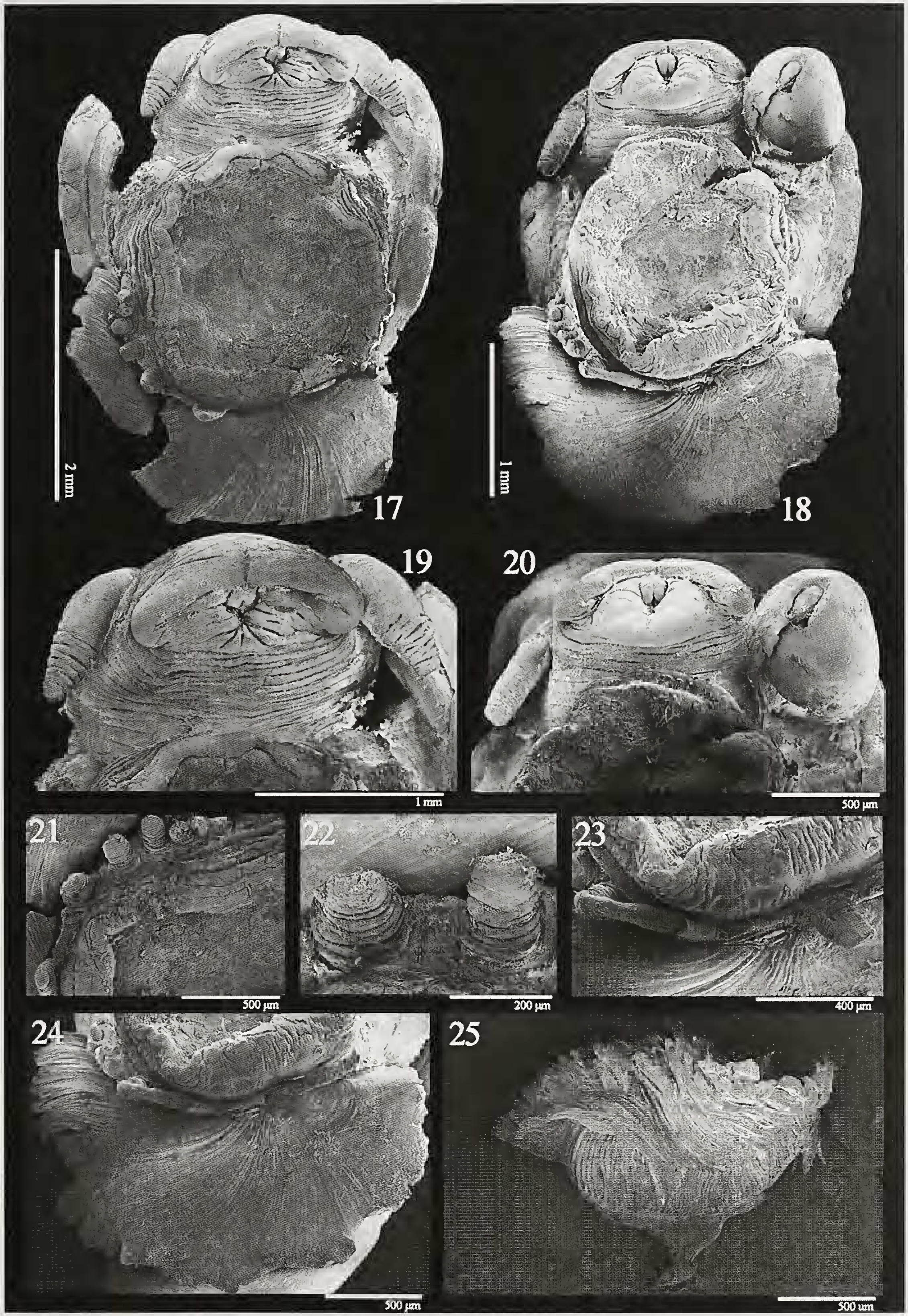


Figures 1–7. Shell of *Lamellomphalus manusensis* new species. **1, 2.** Holotype, length 8.8 mm, black triangle refers to operculum. **3.** Paratype (with periostracum removed), length 6.6 mm. **4.** Sculpture. **5.** Earlier whorls, white arrow indicate protoconch/teleoconch transition. **6.** Protoconch. **7.** Net-like sculpture on protoconch.

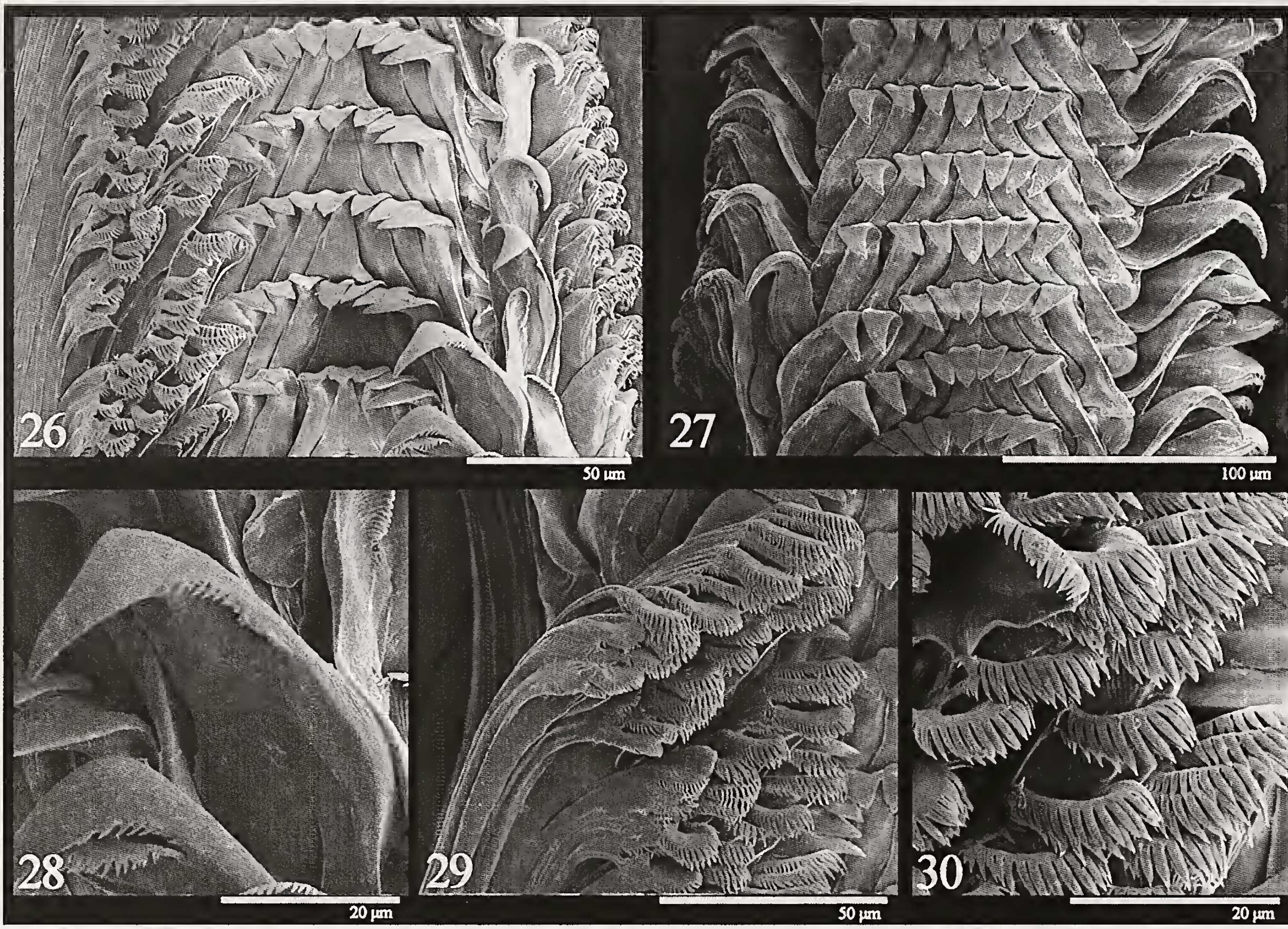
distal end. Columellar muscle horseshoe-shaped, left one long and slender, right one short and broad, both extending anteriorly to middle area of neck. Alimentary groove, or channel, present between right columellar muscle and right neck projection. Gonad located on posterior right, behind right columellar muscle. Pericardium visible as dark structure posterior to gill; ventricle small but solid, rich in brownish pigment, attached on



Figures 8–16. Soft parts of *Lamellomphalus manusensis* new species under light microscope. **8, 9.** Ventral view of animal of female and male, respectively. **10.** Dorsal view of animal (with mantle skirt removed). **11.** Ventral view of head of female; **12, 13.** Left neck portion, white arrows indicate groove on lateral side of female and male, respectively. **14.** Ctenidium. **15.** Left tentacle of male. **16.** Posterior part of foot showing epipodial tentacles. Abbreviations: **ct,** ctenidium; **dg,** digestive gland; **go,** gonad; **h,** head; **lcm,** left columellar muscle; **rcm,** right columellar muscle.



Figures 17–25. Soft parts and operculum of *Lamellomphalus manusensis* new species under SEM. **17–18.** Ventral view of animal of female and male, respectively. **19, 20.** Ventral view of the head of female and male, respectively; **21.** Right lateral epipodial tentacles. **22.** Enlargement of the epipodial tentacles under higher magnification. **23.** Posterior epipodial tentacles. **24.** Operculum. **25.** Ctenidium.



Figures 26–30. Radula of *Lamellomphalus manusensis* new species. **26.** Dorsal view of the radula. **27.** Rachidian and lateral teeth. **28.** Fourth lateral tooth. **29, 30.** Marginal teeth.

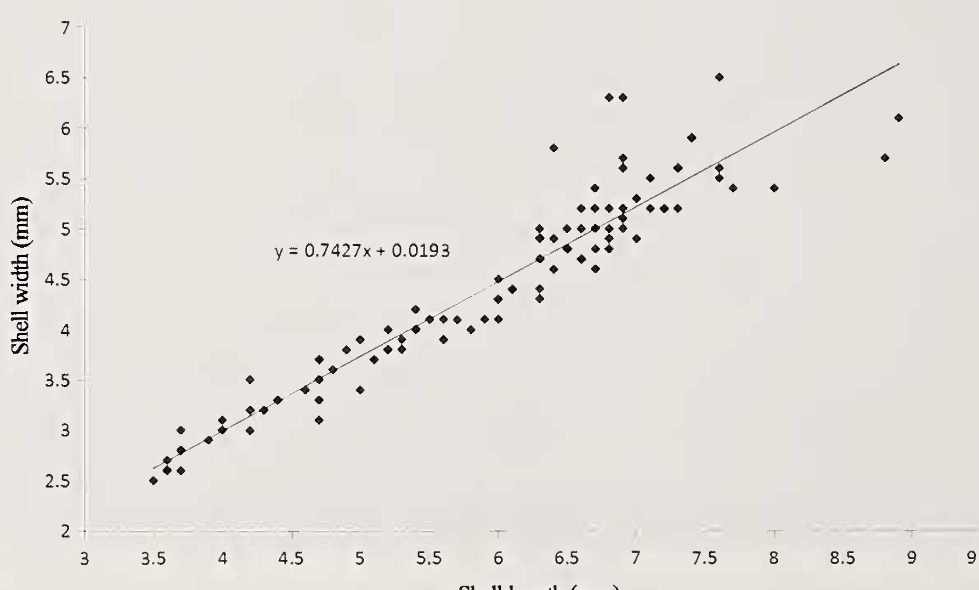


Figure 31. Scatter plot of shell length vs. shell width across the size range of 100 specimens of *Lamellomphalus manusensis* new species.

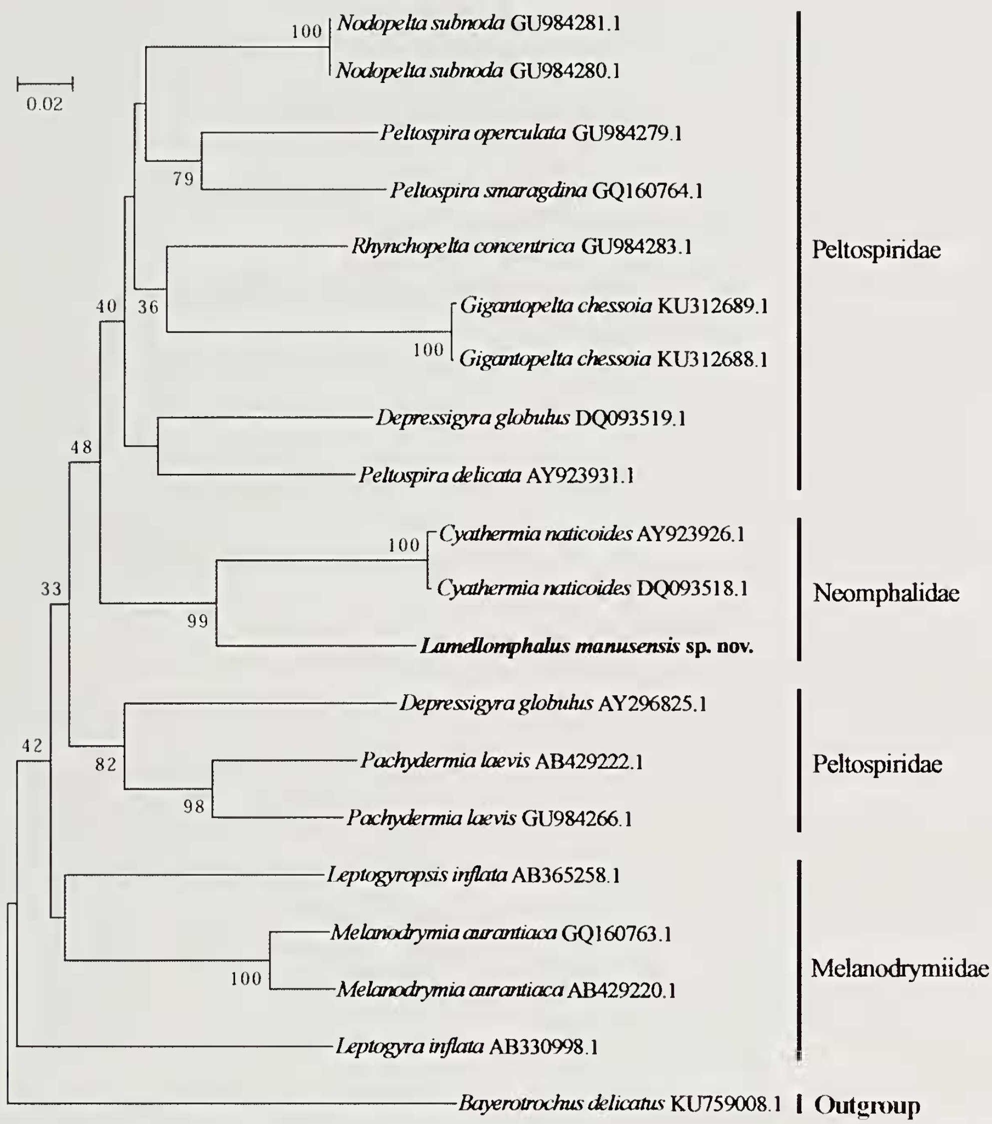


Figure 32. Neighbour-joining tree for Neomphalina based on suitable COI sequences from GenBank and this study. Numbers above branches indicate the bootstrap values.

posterior part of efferent membrane of gill. Foot well developed, rounded, muscular; anterior edge of foot with transverse furrow marking opening of pedal gland. Posterior part of foot encircled by epipodial ridge; epipodial ridge laterally with 4–6 pairs of short, cylindrical epipodial tentacles, posteriorly with one pair of relatively developed ones. Epipodial tentacles becoming smaller anteriorly (Figures 16, 21–23).

Radula (Figures 26–30): Rhipidoglossate, with formula (ca. 10)+4+1+4+(ca. 10). Rachidian teeth and four pairs of lateral teeth of similar morphology. Base of rachidian tooth broad, overhanging moderately long cusp with smooth cutting edges. First to third lateral teeth slightly less prominent than rachidian tooth, innermost bases behind that of adjacent lateral tooth. Fourth lateral tooth with relatively thinner but longer cusp, outer cutting edge serrated. Marginal teeth with long shaft, bearing about 20 long denticles at distal end.

For parameters of shell and scatter plot of shell width against shell length, please see respectively Table 1 and Figure 31.

Type Locality: A hydrothermal vent area at 3°43′ S, 151°40′ E, at depth of 1740 m, Manus Back-Arc Basin.

Type Material: Holotype (registration number: MBM 283053, collection number: M045-1) and about 130 paratypes (registration number: MBM 283054, collection number: M045-2) in MBMCAS. All from type locality, ROV Faxian dive 33, 12 June, 2015.

Distribution and Habitat: Only known from type locality, where they were found on black, hard mineral rock.

Table 3. Pairwise distances among genera of Neomphalina based on Kimura 2-parameter model.

		1	2	3	4	5	6	7	8	9	10
1	*Lamellomphalus*										
2	*Cyathermia*	0.151									
3	*Leptogyropsis*	0.238	0.268								
4	*Melanodrymia*	0.219	0.236	0.203							
5	*Depressigyra*	0.234	0.239	0.216	0.221						
6	*Gigantopelta*	0.248	0.225	0.263	0.252	0.233					
7	*Nodopelta*	0.225	0.197	0.216	0.217	0.185	0.207				
8	*Pachydermia*	0.230	0.221	0.227	0.214	0.191	0.244	0.190			
9	*Peltospiral*	0.214	0.207	0.244	0.224	0.204	0.204	0.154	0.206		
10	*Rhynchopelta*	0.190	0.234	0.208	0.196	0.198	0.170	0.129	0.219	0.170	

Etymology: The name of new species refers to its type locality.

Remarks: Shell surface is covered with a thick olive-green periostracum that extends beyond the shell edge and forms lamellar processes on intersections of radial ribs and concentric threads. This type of periostracum may provide a tighter seal along the shell margin and thus could prevent animal from eventual adverse environmental effects and/or keep potential predators from dislodging the shell from its substrate.

There are some variations in the shape of the aperture, from elongate-oval to nearly rounded, the peristoma aligned on a single plane or gently arched from side to side. As indicated in Figure 31, the ratios shell width: shell length are relatively constant in young snails, but become more variable in adults. We assume that these variations reflect the shape of substratum to which animal need to adapt.

Molecular Analyses: One sequence was obtained for the COI region in *Lamellomphalus manusensis*. The sequence has been deposited in GenBank (Accession number: KY399885). The length of the COI sequence is 629 bp. The Neighbor-joining (NJ) tree (Figure 32) was reconstructed using suitable COI sequences from GenBank and this study. The alignment of COI had a total 437 bp. The NJ tree shows that *Lamellomphalus manusensis* falls into Neomphalidae in which, together with *Cyathermia naticoides* Warén and Bouchet, 1989, it forms a well-supported clade. With available molecular data, the analysis of a 437-bp fragment of the COI gene resulted in 15% pairwise distance between *Lamellomphalus* and *Cyathermia*, whereas the range among *Lamellomphalus* and six genera of Peltospiridae is 19–25% (see Table 3). As COI sequences alone cannot provide sufficient evidence to reflect the familial relationships within this clade, we refrain from discussing any phylogenetic relationships herein. The purpose of the analysis was only to show that *Lamellomphalus* fell into Neomphalidae clade. The phylogenetic relationship of *Lamellomphalus* and other neomphalines needs to be resolved in a multigene phylogenetic study in the future.

DISCUSSION

Based on available morphological information of shell and external anatomy, we placed the new taxon in family Neomphalidae, which confirmed by molecular evidence. Neomphalidae has sexual dimorphism in which the left tentacle in males is modified and serves as a penis, whereas Peltospiridae do not have distinct copulatory organs or modifications of the cephalic tentacles (Fretter, 1989; Israelsson, 1998). In family Neomphalidae, shell shape varies greatly from regularly coiled (*Cyathermia*, *Lacunoides*, *Planorbidella* and *Solutigyra*), to haliotiform (*Lamellomphalus*), to limpet-shaped (*Neomphalus* and *Symmetromphalus*). Thus, *Lamellomphalus manusensis* could be considered as a intermediate form in Neomphalidae. Metapodium with an operculum indicates an incomplete transformation to a limpet-like body plan. These taxa evidently are of common origin, but perhaps underwent a series of divergent evolutionary steps resulting from adaptive radiation. The similarities among *Lamellomphalus* and some peltospirids regarding shell shape, however, should be considered as resulting from convergent evolution.

In addition to the divergent shell morphologies, there is also a wide range of variation in the anatomy among the genera within Neomphalidae, especially in the morphology of the left tentacle in male individuals. *Lamellomphalus manusensis* possesses a postero-laterally oriented, scroll-like left tentacle, with a ventral, open sperm groove and a large proximal seminal opening. However, left tentacles of *Cyathermia* and *Lacunoides* are anterior-laterally directed, have a sausage-shaped distal end, a closed sperm groove, and two prominent proximal cirri; that of *Neomphalus* is posteriorly directed, thick, attached to the neck, tapering to a pointed distal end, and with open sperm groove; that of *Symmetromphalus* is posteriorly directed, sausage-shaped, with dorsal open sperm groove. The left tentacles of species *Solutigyra* and *Planorbidella* are of equal size in both sexes. The divergent morphologies in left tentacles may have resulted from different reproductive strategies in the adaptive radiations of these different clades to chemosynthetic environments. High levels of plasticity in shell and soft parts morphologies could be one of the reasons for the successful colonization of hydrothermal vents by this group of marine gastropods.

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