



Two New Hot-Vent Peltospirid Snails (Gastropoda: Neomphalina) from Longqi Hydrothermal Field, Southwest Indian Ridge

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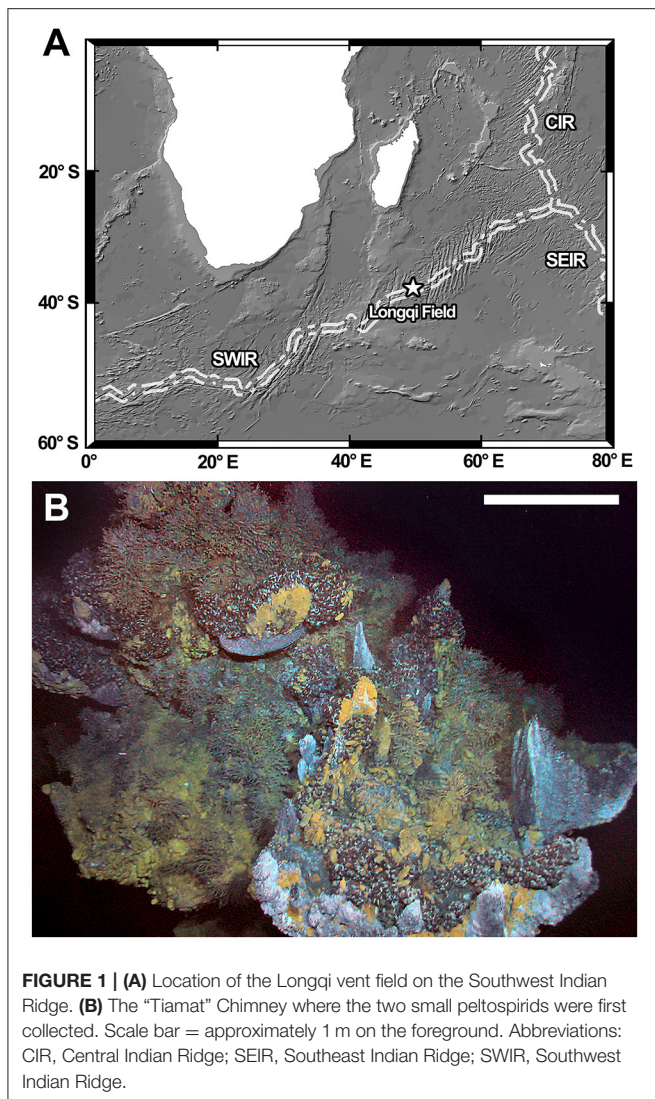
The Longqi hydrothermal vent field is the first deep-sea active vent field to be explored on the ultra-slow spreading Southwest Indian Ridge. Although a number of larger taxa has been described or characterised, many smaller and less conspicuous animals remain undescribed. Here, two small (<7 mm) coiled gastropods belonging to the vent-endemic family Peltospiridae are characterised and formally named from Longqi. *Lirapex politus* n. sp. is characterised by its entirely smooth shell lacking in axial sculpture, which distinguishes it from the three described congeners from East Pacific Rise and Mid-Atlantic Ridge. *Dracogyra subfuscus* n. gen., n. sp. is conchologically most similar to *Depressigyra globulus* from the northeastern Pacific, differing in having an almost closed umbilicus and lacking a basal notch in the outer lip. Radula characteristics clearly distinguish the two, however, with *Dracogyra* n. gen. having a much wider, shorter, sturdier central tooth and stronger laterals. Molecular phylogeny reconstruction using the cytochrome c oxidase I (COI) barcoding fragment indicate that *Dracogyra* n. gen. is in fact most closely related to *Gigantopelta* and *Lirapex* is sister to *Pachydermia*. The pairwise distance in COI between *Dracogyra* n. gen. and other peltospirid genera (14.4%~26.6%, mean 21.3%) are sufficient to justify separate genera. Both new species were found around diffuse flow venting areas in association with giant holobiont peltospirid snails *Chrysomallon* and *Gigantopelta*. The addition of these two new species increases the total macrofauna species known from Longqi field to 23.

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INTRODUCTION

The Southwest Indian Ridge is an ultra-slow spreading ridge running from the Rodrigues Triple Junction in southwest Indian Ocean to the Bouvet Triple Junction in southeast Atlantic Ocean (Dick et al., 2003). The Longqi hydrothermal vent field (**Figure 1A**), the first active vent visually confirmed on the ridge, was initially discovered in 2007 using an autonomous underwater vehicle and a camera-grab system (Tao et al., 2012, 2014). The earliest exploration of the site with a



submersible was carried out on-board RRS *James Cook* expedition JC67 in 2011 using ROV *Kiel6000* (Copley et al., 2016). Subsequently, the Chinese manned submersible HOV *Jiaolong* also visited the Longqi field on-board R/V *Xiangyanghong 9* on several occasions (Zhou et al., 2017).

Up to this point, 21 megafauna species have been reported from the Longqi field (Copley et al., 2016). Among the dominant fauna of the Longqi field are two large snails in Peltospiridae, the scaly-foot gastropod *Chrysomallon squamiferum* Chen et al., 2015 and *Gigantopelta aegis* Chen et al., 2015 which often co-occur and form large aggregations side-by-side on diffuse flow venting areas (Chen et al., 2015a; Copley et al., 2016). Peltospiridae is one of three families in the gastropod clade Neomphalina, the other two being Melanodrymiidae and Neomphalidae (Heß et al., 2008). The entire clade appears to be restricted to chemosynthetic ecosystems and Peltospiridae is so far only known from hot vents (Chen et al., 2015b). Of the 11 currently recognised peltospirid genera, *Chrysomallon* and *Gigantopelta* are the only two that definitively rely on

endosymbiotic bacteria for nutrition as adults (Chen et al., 2017; although *Hirtopelta* has also been reported to have endosymbionts in gill filaments; Beck, 2002), while most others are known to be deposit feeders and/or grazers (Fretter, 1989; Warén and Bouchet, 1989, 2001). Two other gastropods are reported from the Longqi field, including a *Lepetodrilus* species (Vetigastropoda: Lepetodrilidae) which is likely a grazer or filter-feeder and a species of *Phymorhynchus* (Neogastropoda: Raphitomidae) which is a carnivore/scavenger (Copley et al., 2016).

The species richness of small-sized marine invertebrates is still largely unexplored globally (e.g., Bouchet et al., 2002; Albano et al., 2011), and it is therefore not surprising that careful sorting of materials targeting small species may result in new discoveries. After expedition JC67, sorting of washings from *C. squamiferum* and *G. aegis* fixed and preserved in 99% ethanol on shore revealed two further distinct morphotypes of small (<7 mm) coiled peltospirid snails. The same two peltospirids were also recovered from materials collected by HOV *Jiaolong* in 2015 during the expedition DY35 of China. The two small peltospirids were associated with the two large peltospirids (*C. squamiferum* and *G. aegis*), living together and sometimes found on their body surface, but their small sizes indicate that they are unlikely to be holobionts. Many small peltospirids such as species in genera *Rhynchopelta*, *Peltospira*, *Nodopelta*, *Lirapex*, and *Depressigyra* are known to live on the surface of tubeworm bushes or *Bathymodiolus* deep-sea holobiont mussels where they feed (Warén et al., 2006), and the two small peltospirids from the Longqi field may be associated with *Chrysomallon* and *Gigantopelta* in a similar way. The purpose of the present study is to characterise these two snails and to ascertain their taxonomic and systematic affinity, as well as their ecological roles.

MATERIALS AND METHODS

Collection and Preservation

Small peltospirid snails examined herein were chiefly collected using a suction sampler from the Longqi vent field, Southwest Indian Ridge by ROV *Kiel6000* (Dive 142) during RRS *James Cook* expedition JC67. All specimens were recovered from washings fixed and stored in 99% ethanol. Additional specimens were collected in the same field by HOV *Jiaolong* during dives DV94 and DV100 on-board R/V *Xiangyanghong 9* expedition DY35, fixed and preserved in 95% ethanol. Specifically, the peltospirids were found on chimney structures named “Tiamat” (Figure 1B; HOV *Jiaolong* Marker DFF11) and “Jabberwocky” (HOV *Jiaolong* Marker DFF1). Detailed location maps of each chimney within the Longqi vent field can be found in Copley et al. (2016).

Morphology

For anatomical investigations, shells were dissolved by submerging the specimens in 1 mol/L hydrochloric acid solution for several hours. The periostracum was then carefully peeled using fine tweezers. Since all specimens available for morphological investigation were fixed and preserved in 99% ethanol, the extracted soft parts were then subjected to

rehydration in MilliQ water for 48 h before further dissection and observation using a stereo dissecting microscope (Carl Zeiss SteREO Discovery V.12). This also meant that no specimens were available for histological studies. Photographs of both intact specimens and soft parts were taken using a Nikon D5000 DSLR camera mounted to the microscope trinocular. Shell measurements were taken using a digital calliper (rounded up to one decimal point).

Electron Microscopy

Prior to scanning electron microscopy (SEM) radula sacs were dissected out and tissues dissolved for a couple of minutes in diluted commercial bleach. As all specimens had apex covered by mineral deposits and no very young individuals were available, attempts to reveal the protoconch was carried out by softening the deposits using diluted commercial bleach and then carefully peeling with a fine needle. For investigation of shell microstructure small fragments of shells were broken off the aperture and also washed in bleach. Following bleach treatments

specimens were washed in MilliQ water twice and 99% ethanol twice before being mounted on SEM stubs using carbon tapes. For examination of digestive tract contents, materials inside the stomach and the intestine were dissected out from one specimen of each species and directly mounted on SEM stubs using carbon tapes, and pre-examined with a dissection microscope (as above) before SEM examination. These were then air-dried and subjected to uncoated SEM imaging with a Hitachi TM-3000 SEM at 15 kV.

Genetics

Barcoding sequences of the cytochrome *c* oxidase subunit I (COI) gene of the small peltospirids were sequenced using the primer pair LCO1490 and HCO2198 (Folmer et al., 1994) and compared with other neomphaline data available on GenBank (taxa, accession number, and voucher information of sequences used are listed in **Table 1**). A COI sequence of *Lirapex costellatus* Warén & Bouchet, 2001 (392bp; collection data: Tour Eiffel, Lucky Strike, Mid-Atlantic Ridge; 37°17'N, 32°16'W; 1693 m

TABLE 1 | List of taxa used for phylogenetic analysis using COI gene, with GenBank accession number, voucher number (where available), and original references shown.

Family	Taxa	GenBank	Voucher	References
Neomphalidae	<i>Lamellomphalus manusensis</i> Zhang & Zhang, 2017	KY399885	MBMCAS 283054	Zhang and Zhang, 2017
Neomphalidae	<i>Lacunooides</i> sp. <i>sensu</i> Heß et al., 2008	AB330999	YK #245	Heß et al., 2008
Neomphalidae	<i>Cyathernia naticoides</i> Warén & Bouchet, 1989	DQ093518	MCZ DNA100855	Aktipis and Giribet, 2010
Peltospiridae	<i>Chrysomallon squamiferum</i> Chen et al., 2015	AB540646	JAMSTEC 1090003793	Nakamura et al., 2012
Peltospiridae	<i>Nodopelta subnoda</i> McLean, 1989	GU984280	-	Matabos et al., 2011
Peltospiridae	<i>Rhynchopelta concentrica</i> McLean, 1989	GU984282	-	Matabos et al., 2011
Peltospiridae	<i>Peltospira delicata</i> McLean, 1989	FJ977764	MCZ DNA101609	Aktipis and Giribet, 2010
Peltospiridae	<i>Peltospira operculata</i> McLean, 1989	GU984278	-	Matabos et al., 2011
Peltospiridae	<i>Peltospira smaragdina</i> Warén & Bouchet, 2001	GQ160764	MCZ DNA102425	Aktipis and Giribet, 2012
Peltospiridae	<i>Gigantopelta chessoia</i> Chen et al., 2015	KR024336	NHMUK 20150068	Chen et al., 2015a
Peltospiridae	<i>Gigantopelta aegis</i> Chen et al., 2015	KR024376	NHMUK 20150072	Chen et al., 2015a
Peltospiridae	<i>Dracogyra subfuscus</i> n. sp. #1	MF977760	SIOSEA RSIO3556	This study
Peltospiridae	<i>Dracogyra subfuscus</i> n. sp. #2	MF977761	SIOSEA RSIO3557	This study
Peltospiridae	<i>Depressigyra globulus</i> Warén & Bouchet, 1989	DQ093519	MCZ DNA101123	Aktipis and Giribet, 2012
Peltospiridae	<i>Lirapex pollitus</i> n. sp. #1	MF977762	SIOSEA RSIO3558	This study
Peltospiridae	<i>Lirapex pollitus</i> n. sp. #2	MF977763	SIOSEA RSIO3559	This study
Peltospiridae	<i>Lirapex costellatus</i> Warén & Bouchet, 2001	Kano and Warén, unpublished data	YK#838/SMNH-89170	Kano and Warén, unpublished data
Peltospiridae	<i>Pachydermia laevis</i> Warén & Bouchet, 1989	AB429222	FMNH 307194	Heß et al., 2008
Melanodrymiidae	<i>Leptogyropsis inflata</i> Hasegawa, 1997	AB365258	YK #237	Heß et al., 2008
Melanodrymiidae	<i>Melanodrymia aurantiaca</i> Hickman, 1984	GQ160763	MCZ DNA102421	Aktipis and Giribet, 2012
Melanodrymiidae	<i>Leptogyra inflata</i> Warén & Bouchet, 1993	AB330998	YK #236	Heß et al., 2008
Cocculinidae	<i>Cocculina messingi</i> McLean & Harasewych, 1995 (Outgroup)	AY923910	-	Geiger and Thacker, 2005

FMNH, Field Museum of Natural History, Chicago; JAMSTEC, Japan Agency for Marine-Earth Science and Technology; MBMCAS, Marine Biological Museum, Chinese Academy of Sciences; MCZ, Museum of Comparative Zoology, Harvard University; NHMUK, Natural History Museum, London; SIOSEA, Second Institute of Oceanography, Hangzhou, China; SMNH, Swedish Museum of Natural History; YK, Department of Biological Production and Environmental Science, University of Miyazaki, Japan.

deep; Momareto 2005, sta. PL251) was kindly supplied by Dr. Yasunori Kano (the University of Tokyo) and Dr. Anders Warén (Swedish Museum for Natural History). Detailed procedures for DNA extraction, amplification, purification, and sequencing are as detailed in Chen et al. (2015a). Pairwise distance of COI sequences were calculated using MEGA7 (Kumar et al., 2016) with the Tamura-Nei (Tamura and Nei, 1993) model estimated by the composite likelihood method (Tamura et al., 2004). The alignment of COI gene used for phylogenetic reconstruction was 569 bp in length. The most suitable substitution model for each codon was selected using the programme PartitionFinder v.2.1.1 (Lanfear et al., 2017), using scores for the Bayesian information criterion. The models selected were GTR+I+G for all codons. MrBayes v.3.2.6 (Ronquist et al., 2012) was used for phylogenetic reconstruction using Bayesian inference. Metropolis-coupled Monte Carlo Markov Chains were run for one million generations, with topologies sampled every 100 generations. To ensure convergence Tracer v.1.6 (Rambaut et al., 2013) was used to visualise traces and calculate adequate burn-in values (2500 in this case). Newly generated sequences in this study are deposited in GenBank under the accession numbers MF977760- MF977763.

Type Repository

Type specimens are deposited at the Natural History Museum, London (NHMUK), the Swedish Museum of Natural History (SMNH), the University Museum, the University of Tokyo (UMUT), and the Second Institute of Oceanography, State Oceanic Administration, Hangzhou, China (SIOSEA).

RESULTS

Systematics

Clade Neomphalina McLean, 1990

Superfamily Neomphaloidea McLean, 1981

Family Peltospiridae McLean, 1989

Lirapex Warén & Bouchet 1989

Type species: *Lirapex humatus* Warén & Bouchet, 1989 (by original designation).

Diagnosis: Coiled, skeneimorph peltospirids, small to medium sized (<5 mm) for the family. A film-like operculum always present. Shell usually with distinct axial sculpture that is strongest at shoulder and umbilicus. Protoconch initially with distinct spiral ridges which disappear toward the last half. Radula with hook-like marginals. Sexes separate. Snout even in breadth, tentacles smooth and not modified into copulatory organ (Warén and Bouchet, 1989, 2001).

Lirapex politus n. sp.

ZooBank registration: urn:lsid:zoobank.org:act:C5BB998D-34B1-4B4F-B095-F3E5974D5F76

Diagnosis: A *Lirapex* with a totally smooth shell surface lacking in significant axial sculpture and a less disjunct final whorl in adults when compared with other known species.

Type locality: Longqi vent field, Southwest Indian Ridge, 37°47.03' S, 49°38.97'E ("Tiamat" Chimney/DFF11), 2785 m

deep, RRS *James Cook* expedition JC67, ROV *Kiel6000* Dive 142, 2011/xi/29.

Type material: Holotype, **Figures 2A–D**, NHMUK 20170383. Paratype 1, one specimen, **Figures 2E–F**, SMNH Type-8948. Paratype 2, one specimen, **Figures 2G–J**, UMUT RM32664. Paratype 3, one specimen, **Figures 2K–L**, SIOSEA RSIO35614. Paratype 4, one specimen, NHMUK 20170384. Paratype 5, two specimens with shell dissolved (one intact, one dissected), **Figures 4A–D**, UMUT RM32665. Paratype 6, a lot of 20 specimens, NHMUK 20170385. Paratype 7, a lot of 20 specimens, SMNH Type-8949. Paratype 8, a lot of 20 specimens, UMUT RM32666. Paratype 9, a lot of 20 specimens, SIOSEA RSIO35615. All types from a single collecting event at the type locality as indicated above; fixed and stored in 99% ethanol.

Additional Materials Examined:

Approximately 50 specimens, same data as type locality.

Fourty specimens fixed and stored in 95% ethanol, Longqi vent field, Southwest Indian Ridge, 37° 47.03' S/49° 39.01' E ("Tiamat" Chimney/DFF11), 2761 m deep, R/V *Xiangyanghong* 9 expedition DY35, HOV *Jiaolong* Dive 94, 2015/i/11.

Fifteen specimens fixed and stored in 95% ethanol, Longqi vent field, Southwest Indian Ridge, 37° 47.00' S/49° 39.01' E ("Jabberwocky" Chimney/DFF1), 2736 m deep, R/V *Xiangyanghong* 9 expedition DY35, HOV *Jiaolong* Dive 100, 2015/ii/02.

Description

Shell (**Figure 2**) solid, skeneimorph, usually at least partly encrusted by mineral deposits. Tightly coiled, loosening in the final 0.25 whorls but does not become obviously disjunct. Medium-sized for the group, as tall as wide, the largest specimen had a shell height of 4.4 mm and shell width of 4.5 mm. For more measurements see **Table 2**. Cross-section almost round. Covered by a layer of semi-transparent greyish green periostracum that is usually covered in turn by mineral deposit. Protoconch (**Figure 3A**) just less than half a whorl (diameter 220 μm), initially sculptured with five distinct spiral ridges and finer wrinkles, disappearing before reaching the centre part of the protoconch. Distal part of the protoconch remains smooth without any significant sculpture. Teleoconch consists of 3–3.5 whorls, white, entirely smooth and lacking in sculpture (except fine growth lines; **Figure 3B**), without nacreous layer. Aperture weakly opisthocline, nearly circular, not significantly thickened in adults. Umbilicus narrow. Shell microstructure (**Figure 3C**) comprises of two distinct layers, a thick cross-lamellar layer on the inside and a thin granular layer on the outside. Shell pores opening to the interior of the teleoconch present, gradually tapering toward the granular layer but does not reach it.

Radula (**Figures 3D,E**) rhipidoglossate, formula ~25 + 4 + 1 + 4 + ~25. Central and laterals rigid, well-reinforced. Central teeth triangular, with a smooth, triangular overhanging cusp. The three inner laterals are similar in shape with bifurcating reinforcement but while the innermost lateral has smooth cusp the other two tend to have minor serrations. The outer lateral is much broader and have conspicuous serrations. The laterals all have a minor protuberance near the base. Marginal teeth

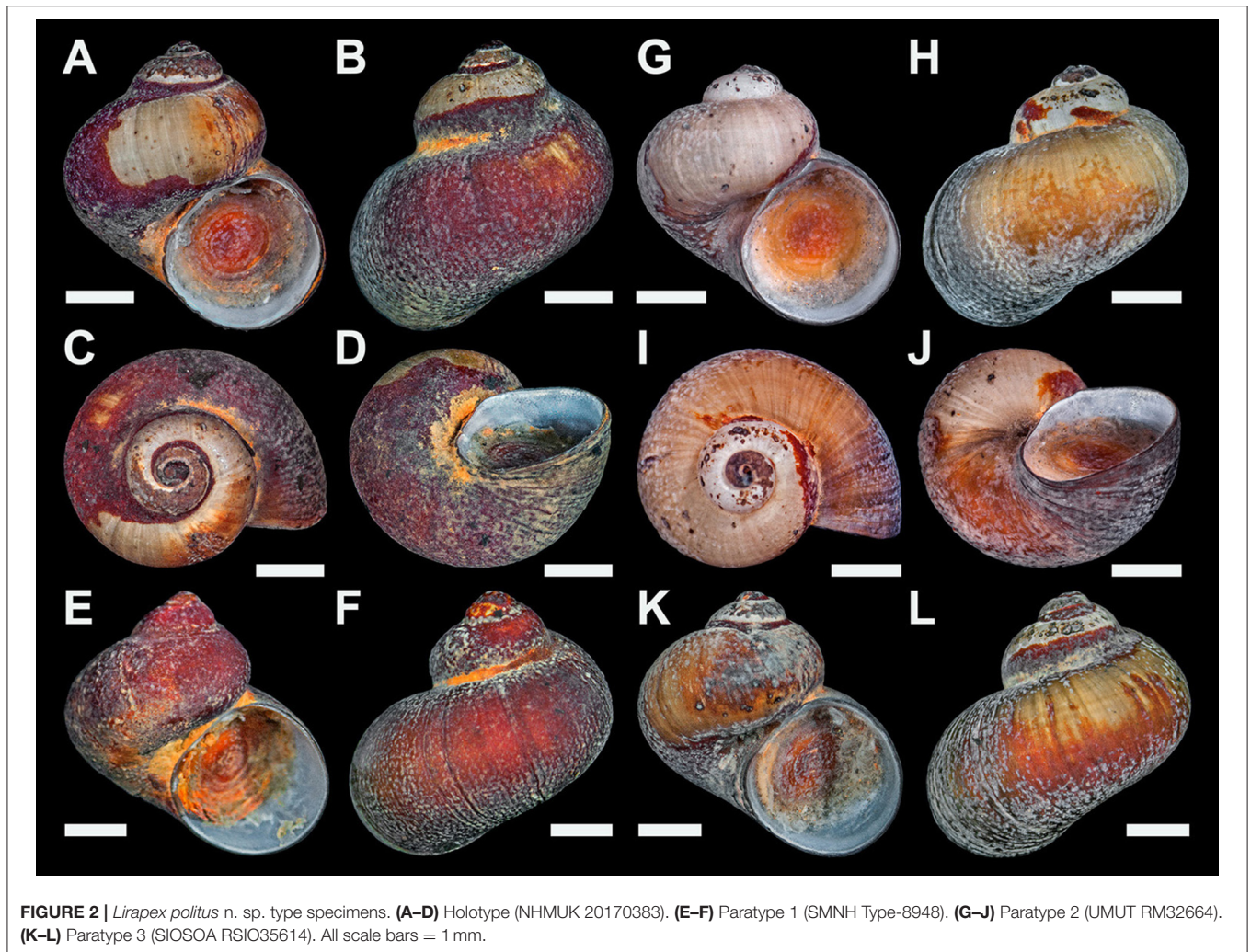


TABLE 2 | Shell parameters of *Lirapex politus* n. sp. and *Dracogyra subfuscus* n. gen., n. sp.

	<i>Lirapex politus</i> n. sp.						<i>Dracogyra subfuscus</i> n. gen., n. sp.					
	SH (mm)	SW (mm)	SH/SW	AH (mm)	AW (mm)	AH/AW	SH (mm)	SW (mm)	SH/SW	AH (mm)	AW (mm)	AH/AW
Holotype	4.0	3.9	1.03	2.2	2.2	1.00	4.1	5.5	0.75	3.4	3.6	0.94
Paratype 1	4.3	4.3	1.00	2.6	2.5	1.04	3.0	3.9	0.77	2.4	2.6	0.92
Paratype 2	4.0	4.0	1.00	2.4	2.2	1.09	3.2	4.6	0.70	2.6	2.7	0.96
Paratype 3	3.9	3.8	1.03	2.2	2.1	1.05	2.3	3.3	0.70	2.1	2.3	0.91
Paratype 4	4.2	4.2	1.00	2.3	2.1	1.10	2.5	3.5	0.71	2.1	2.3	0.91
Largest	4.4	4.5	0.98	2.7	2.6	1.04	4.6	6.3	0.73	4.2	4.6	0.91
Smallest	2.3	2.4	0.96	1.6	1.6	1.00	2.3	3.3	0.70	2.1	2.3	0.91
Average	3.9	3.9	1.00	2.3	2.2	1.04	3.3	4.5	0.73	2.8	3.0	0.93

SH, Shell Height, SW, Shell Width, AH, Aperture Height, AW, Aperture Width.

long and thin, tapering distally. The innermost two have wider, triangular cusps that are serrated into about 10 denticles. The outer marginals have hook-like cusps that are serrated into very fine denticles. Size of outer marginals decreases outwards.

Operculum (Figure 3F) multispiral, with over 20 volutions in adults, film-like and transparent. In later volutions the edge of the

previous volution extends freely to form an obvious fringe over the next.

Soft parts (Figure 4). Head large, eyes lacking, with no apparent cephalic copulation appendages. Snout short, flattened and even in breadth, with a ventral mouth. Cephalic tentacles smooth, elongated, about twice as long as the snout when

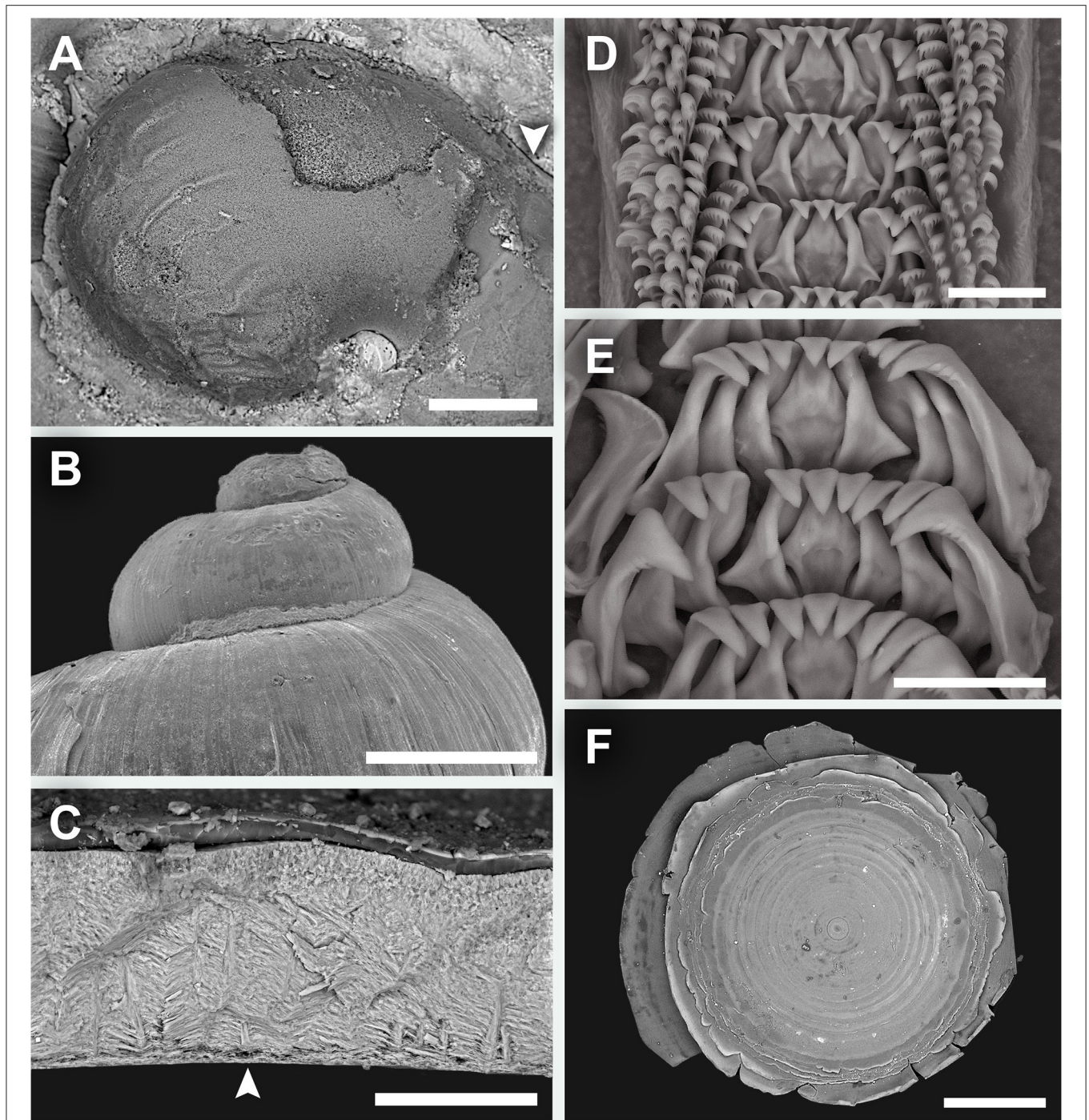


FIGURE 3 | *Lirapex politus* n. sp. scanning electron micrographs. (A) Protoconch, (B) Shell surface of the upper half of the shell, as seen from the abapertural view, (C) Shell microstructure, (D) Radula, (E) Close-up of central and lateral teeth, (F) Operculum. Scale bars: (A) 50 μ m, (B) 1 mm, (C) 50 μ m, (D–E) 25 μ m, (F) 0.5 mm.

contracted, conical and gradually decrease in size distally. Neck-lobe and cephalic lappets lacking. Foot rather well developed with a distinct transverse furrow separating propodium and mesopodium. Epipodial tentacles present between the operculum and foot, arranged in a semi-circular series surrounding posterior two-thirds of the opercular attachment and numbering 9–11 on each side (18–22 in total).

Size of epipodial tentacles decrease slightly anterodorsally. Sexes separate, head-foot of both sexes identical in external anatomy. Pallial edge smooth and lacks appendages. Columellar muscle shallow, reaches about 0.3 whorls behind pallial edge, with a large attachment area on the right side of body connected to a smaller attachment area on the left side by a rather thick band of ventral muscular tissue.

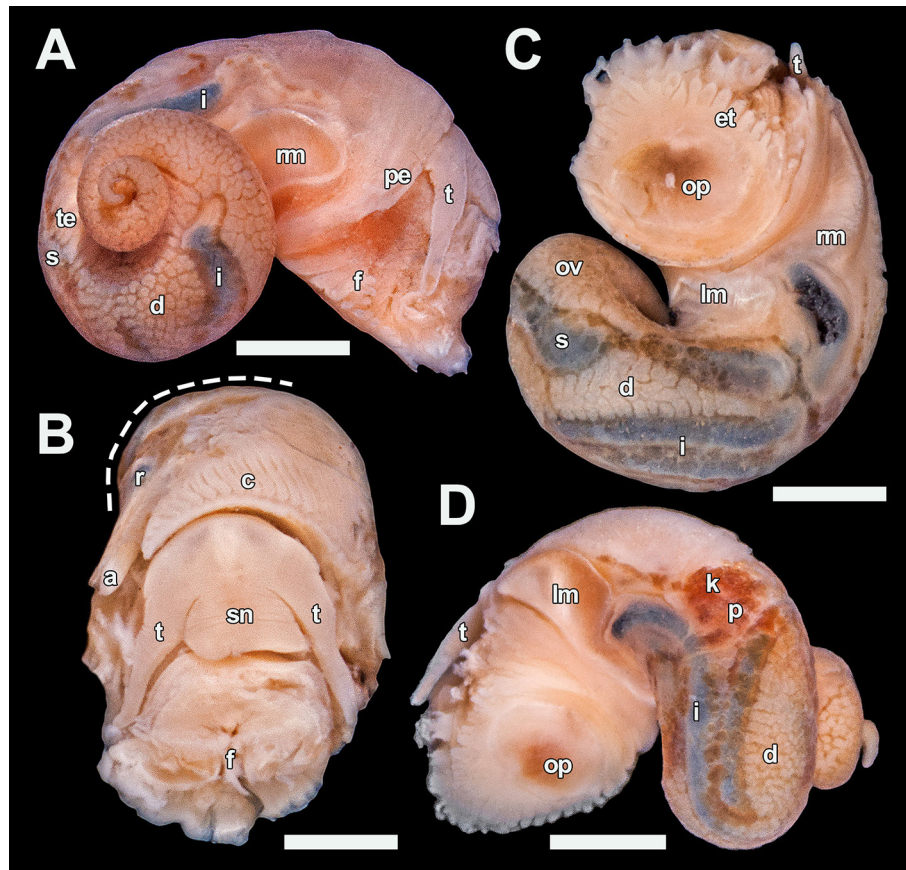


FIGURE 4 | *Lirapex politus* n. sp. soft parts, paratype 5 (UMUT RM32665). **(A)** Right view, **(B)** Anterior view with part of the mantle roof removed to expose the ctenidium (visceral mass cut away at dashed line), **(C)** Ventral view, **(D)** Left view. Scale bars: **(A), (C,D)** 1 mm, **(B)** 0.5 mm. a, anus; c, ctenidium; d, digestive gland; et, epipodial tentacle; f, foot; i, intestine; k, right kidney; lm, left columellar muscle; ov, ovary; op, opercular attachment; p, pericardium; pe, pallial edge; r, rectum; mm, right columellar muscle; s, stomach; sn, snout; t, cephalic tentacle; te, testis.

Mantle cavity moderate in size, extending 0.4 whorls posterior of pallial edge. Ctenidium sizeable, bipectinate with approximately 40 pairs of leaflets. Digestive tract easily visible due to shiny, dark mineral deposits in the tract contents. Stomach quite large and significantly thickened compared to the intestine, situated one whorl posterior of the pallial edge. Rectum curves only slightly after entering the mantle cavity. It is attached to mantle ceiling and only becomes detached just posterior of the anus. Intestine long, looping twice between the left kidney and the stomach, partly concealed by the overlying digestive gland. Pericardium not penetrated by the intestine. Heart monocardian with a posteroventral ventricle and an anterodorsal auricle. Other than the large stomach and intestine the visceral mass is occupied dorsally by digestive gland up to the apex and ventrally by the gonad. Gonopore simple, opens just behind the anus.

Stomach and intestine filled by organic material, mixed with numerous conspicuous shiny mineral particles which are dark in colouration. Outline of mid- and hindgut highly conspicuous from exterior due to these dark mineral particles.

Distribution: Only known from Longqi hydrothermal vent field, Southwest Indian Ridge. Found on active chimneys among assemblages dominated by the two giant peltospirids *C. squamiferum* and *Gigantopelta aegis*. It is frequently found underneath the two species which often form dense aggregations in the same location (see Chen et al., 2015a), and also sometimes seen on body surface of the two giant peltospirids.

Etymology: “*Politus*” (Latin), meaning polished or smoothed. This refers to the smooth shell surface lacking in significant sculpture.

ZooBank registration: urn:lsid:zoobank.org:act:C5BB998D-34B1-4B4F-B095-F3E5974D5F76

Remarks: Three species are currently placed in *Lirapex* other than the present new species: *L. humatus* and *L. granularis* Warén & Bouchet, 1989 from East Pacific Rise (21°N) and *L. costellatus* Warén & Bouchet, 2001 from Mid-Atlantic Ridge (Lucky Strike and Eiffel Tower) (Warén and Bouchet, 1993, 2001). The protoconch and radula morphology as well as the shell shape of *L. politus* n. sp. does not deviate significantly from other members of *Lirapex* and unambiguously places this new species in that genus. *Lirapex politus* n. sp. is easily distinguished

from the three congeners by a lack of any significant axial teleoconch or periostracal sculpture in all specimens examined ($n > 100$). Although other *Lirapex* species are usually quite variable in surface sculpture within a species, they always have axial sculpture present at least on the shoulder and around the umbilicus (Warén and Bouchet, 2001). In *L. humatus* and *L. costellatus* the sculpture is on the teleoconch itself. In the case of *Lirapex granularis* apparently the sculpture is only on the periostracum and not the shell itself (Warén and Bouchet, 2001), but that species is much smaller (shell height to 1 mm in adult) that no confusion with the present new species is possible. The smooth cusps of the central tooth, as well as the narrower umbilicus, helps separating the new species from *L. humatus*. Furthermore, the extent of whorl detachment in the final stage of growth in *L. politus* n. sp. is less than that of other *Lirapex* species.

***Dracogyra* n. gen.**

ZooBank registration: urn:lsid:zoobank.org:act:F3A5936A-34EC-46EA-A074-CFC2CEFEDD26

Type species: *Dracogyra subfuscus* n. sp. (by original designation).

Diagnosis: Coiled, depressed globular peltospirids of medium size for the family (<7 mm shell diameter). Protoconch indistinctly coiled, approximately 0.5 whorls (sculpture unknown). Teleoconch smooth, without any distinct sculpture. Aperture opisthocline, without basal notch. Periostracum thick, leathery. A rather thick, opaque operculum always present. Gonochoristic. Snout equal in breadth, cephalic tentacles simple and exhibiting no sexual dimorphism. Central radular tooth very compressed, wide and rigid, nearly equilateral triangular in shape. The shafts of lateral teeth significantly longer than that of the central teeth, also rigid and well-supported.

Description: See that of *D. subfuscus* n. sp. below.

Etymology: “*Draco*” (Latin), dragon; “*gyrus*” (Latin), to circle or coil. Named for the Longqi vent field; “Longqi” means “dragon flag” in Chinese and “Dragon vent field” has been used as an alternative name (Roterman et al., 2013; Copley et al., 2016).

ZooBank registration: urn:lsid:zoobank.org:act:F3A5936A-34EC-46EA-A074-CFC2CEFEDD26

***Dracogyra subfuscus* n. sp.**

ZooBank registration: urn:lsid:zoobank.org:act:DE688815-288B-45EF-802A-0EC470D567AC

Diagnosis: See that of *Dracogyra* n. gen. above.

Type locality: Longqi vent field, Southwest Indian Ridge, 37°47.03' S, 49°38.97' E (“Tiamat” Chimney), 2785 m deep, RRS *James Cook* expedition JC67, ROV *Kiel6000* Dive 142, 2011/xi/29.

Type material: Holotype, **Figures 5A–D**, NHMUK 20170386. Paratype 1, one specimen, **Figures 5E,F**, SMNH Type-8950. Paratype 2, one specimen, **Figures 5G,H**, UMUT RM32667. Paratype 3, one specimen, **Figures 5I,J**, SIOSOA RSIO35616. Paratype 4, one specimen, NHMUK 20170387. Paratype 5, two specimens with shell dissolved (one intact, one dissected), **Figures 7A–D**, UMUT RM32668. Paratype 6, two empty shells,

NHMUK 20170388. Paratype 7, one empty shell, SMNH Type-8951. Paratype 8, one empty shell, UMUT RM32669. Paratype 9, one empty shell, SIOSOA RSIO35617. All types from a single collecting event at the type locality as indicated above; fixed and stored in 99% ethanol.

Additional materials examined:

Five dead shells with calcareous layer dissolved and only periostracum remaining, same data as in type locality above.

About 100 specimens fixed and stored in 95% ethanol, Longqi vent field, Southwest Indian Ridge, 37° 47.03' S/49° 39.01' E (“Tiamat” Chimney/DFF11), 2761 m deep, R/V *Xiangyanghong* 9 expedition DY35, HOV *Jiaolong* Dive 94, 2015/i/11.

Twelve specimens fixed and stored in 95% ethanol, Longqi vent field, Southwest Indian Ridge, 37° 47.00' S/49° 39.01' E (“Jabberwocky” Chimney/DFF1), 2736 m deep, R/V *Xiangyanghong* 9 expedition DY35, HOV *Jiaolong* Dive 100, 2015/ii/02.

Description

Shell (**Figure 5**) tightly coiled, strongly depressed with a low spire, shape between skeneiform and neritiform. Medium-sized for the family, the largest specimen available (a dead shell) measured 4.6 mm in shell height and 6.3 mm in shell width. More measurements shown in **Table 2**. Protoconch (**Figure 6A**) indistinctly coiled, 200 μm in diameter. Specimen with protoconch sculpture preserved was not found in materials available. Teleoconch white and lacks nacreous layer, moderately thick, consist of about 2.7 whorls, depressed oval in cross section. Perfectly smooth except fine growth striations (**Figure 6B**). Aperture opisthocline to the coiling axis, oval in shape, lacking any significant notch. Outer lip simple, not thickened in adults. Inner lip with a small section of columellar callus extending toward the umbilical area. Umbilicus extremely narrow, sometimes obscured by callus. Microstructure (**Figure 6C**) of a thin, granular outer layer and a thick, cross-lamellar inner layer. The inner layer bears shell pores which open to the interior of the teleoconch, pores do not reach the outer layer. Periostracum thick, leathery. Initially light reddish brown, gradually darkening to near-black in last 0.5 whorls of adults. Lacks significant sculpture or pattern except fine growth lines. Outer edge extends over the outer lip, enveloping it. Never seen covered by thick mineral deposits in specimens available, although scattered deposits and evidence of corrosion is commonplace.

Radula (**Figure 6D,E**) rhipidoglossate, formula $\sim 35 + 4 + 1 + 4 + \sim 35$. Central tooth solid with a smooth triangular cusp and very robust antero-lateral supports. The shaft is unusually horizontally compressed in impression as it is rather short and rapidly broadening basally to become almost equilateral triangle in shape. Lateral teeth have sturdy shafts that are interlocking, and becomes taller laterally. The innermost lateral has a significantly stronger, more oblique lateral supporting ridge compared to the second and third laterals which are essentially the same. All three inner laterals have elongate, triangular cusps, cutting edge smooth without serration. The outermost lateral is much broader than the rest and carry a few coarse serrations on the outer edge of its cusp. Marginal teeth truncated at the

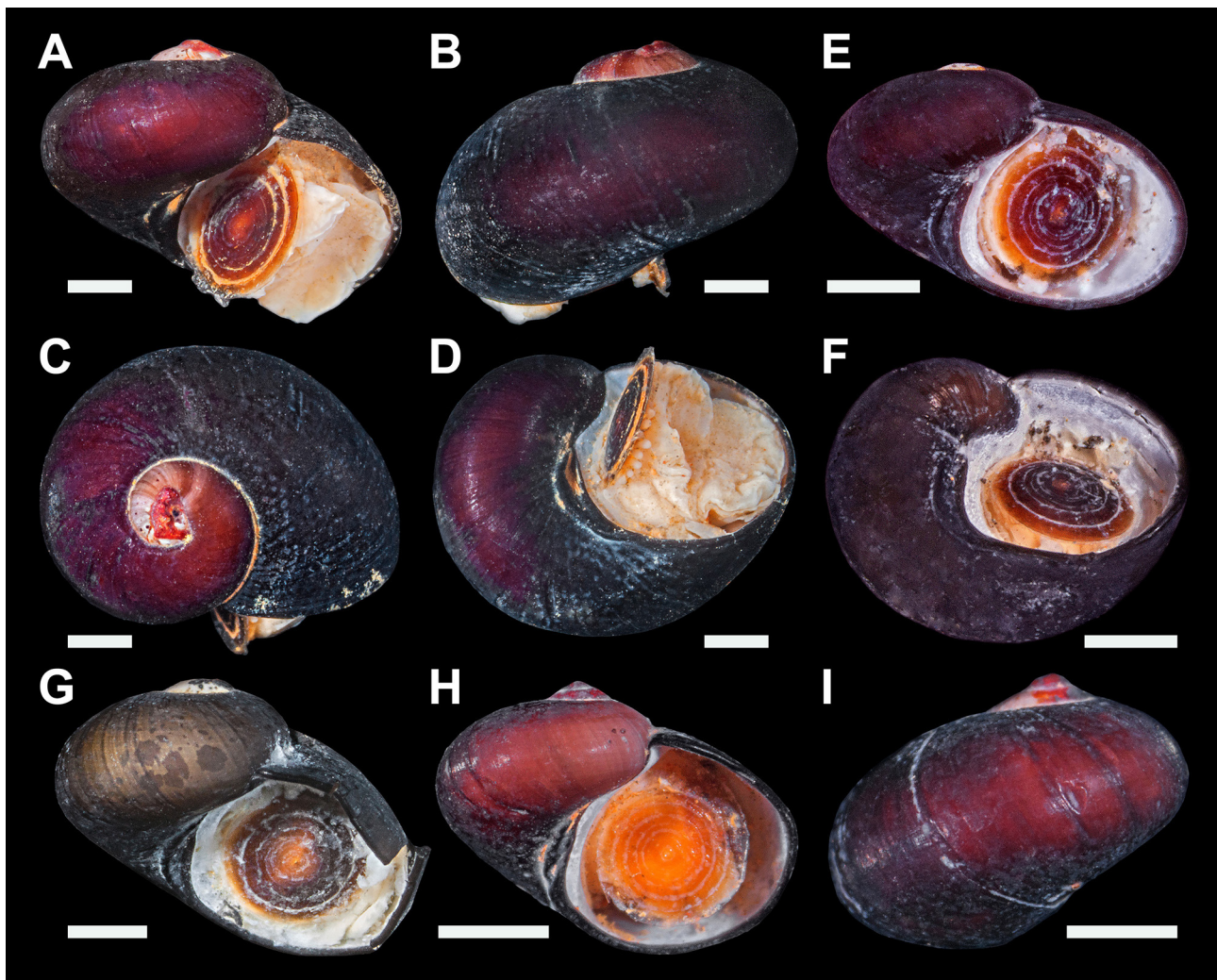


FIGURE 5 | *Dracogyra subfuscus* n. gen. n. sp., type specimens. (A–D) Holotype (NHMUK 20170386). (E–F) Paratype 1 (SMNH Type-8950). (G) Paratype 2 (UMUT RM32667). (H–I) Paratype 3 (SIOSEA RSIO35616). All scale bars = 1 mm.

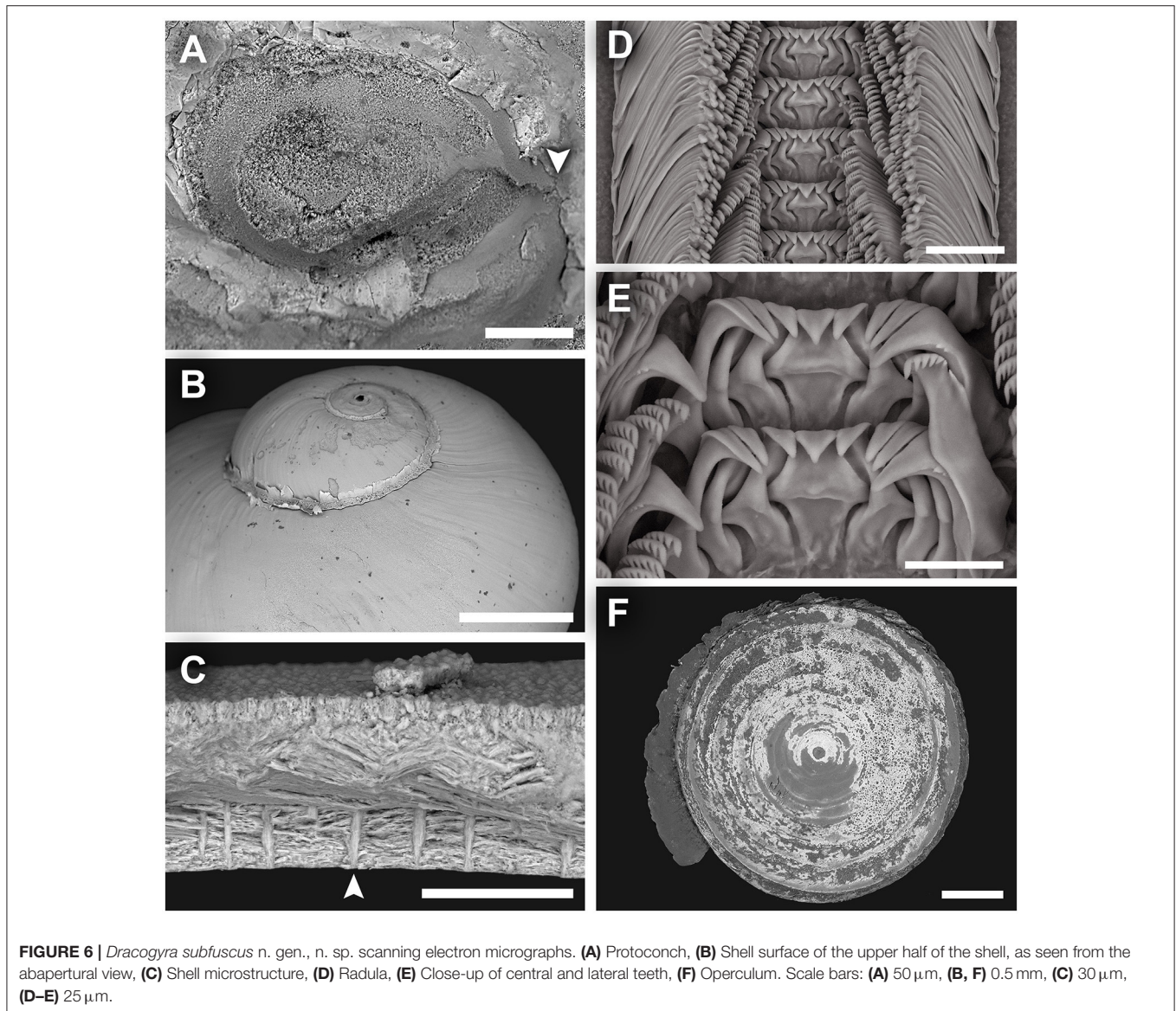
distal end with a rather flattened cusp which is serrated into 8–15 denticles. Outer marginals smaller than inner marginals, with somewhat finer serration.

Operculum (**Figure 6F**) multispiral, about 8 volutions, slightly convex. Brown, thick and opaque near centre (in adults) and becoming semi-transparent toward the edge, often covered by rusty mineral deposit. The outermost volutions often has a thin fringe projecting freely outwards and over the next.

Soft parts (**Figure 7**) occupy 2.5 whorls from the apex to the pallial margin. Head large with a short snout of equal breadth and a subventral mouth, eyes lacking. Cephalic tentacles very broad and stout, slightly tapering and approximately 1.5 times as long as the snout when contracted. The animal is gonochoristic but lacks sexual dimorphism on the head-foot, cephalic tentacles are not modified into copulation appendages. Propodium and mesopodium separated by a furrow. Epipodial tentacles numbering about 20 (10 on each side), arranged like a fringe around the posterior 2/3 of the opercular attachment.

The sizes of the tentacles gradually decrease anterodorsally. Pallial margin simple without tentacles or other appendages. Columellar muscle horse-shoe shaped, with two attachment areas on each side of the body connected by a thin band of ventral musculature, the right attachment area is much larger than the left.

Mantle cavity extends to approximately 0.3 whorls behind the pallial margin, largely occupied by a rather large bipectinate ctenidium with about 50 rows of leaflets. Only a small section of the intestine is visible between the left kidney and the stomach, as much of it is hidden under the mass of digestive gland. Stomach positioned half a whorl posterior of the pallial margin, clearly visible from outside as a dark patch. Pericardium not penetrated by the intestine, heart monocardian with the ventricle positioned posteroventral to the single auricle. The visceral mass, other than the stomach and the intestine loop, is occupied by an extensive digestive gland on the dorsal half (filling the apex) and a large mass of gonad on the ventral half.



The rectum turns half a loop clockwise after entering mantle cavity (right side), it remains attached to the mantle wall except a very short stretch just before the anus.

Stomach and intestine contents consist of mostly fine organic material, mixed with a small amount of very fine mineral particles.

Distribution: Only known from Longqi hydrothermal vent field, Southwest Indian Ridge. Found on diffuse flow chimneys in association with *C. squamiferum* and *Gigantopelta aegis*.

Etymology: From Latin “*subfuscus*” (“*sub-*” + “*fuscus*,” black), meaning brownish and darkish. Refers to the colouration of the periostracum which is initially brownish but gradually darkens to black.

ZooBank registration: urn:lsid:zoobank.org:act:DE688815-288B-45EF-802A-0EC470D567AC

Remarks: *Dracogyra subfuscus* n. sp. is most similar conchologically to *Depressigyra globulus* Warén & Bouchet,

1989, the only species currently assigned to *Depressigyra* (Warén and Bouchet, 2001). The shells of the two are of a similar size and shape, although the shell of *D. subfuscus* n. sp. tends to be more depressed with a narrower umbilicus and the aperture lacks a basal notch present in *Depressigyra*. Radular characters, however, unambiguously separates the two genera. The central and lateral teeth of *D. globulus* is unusually narrow, which is starkly different from that of *D. subfuscus* n. sp. which has very rigid central and laterals. The central tooth of *D. subfuscus* n. sp. especially, is very wide and compressed compared to the laterals. The distinctive shape of the central teeth is also useful in distinguishing the new species from juvenile *G. aegis* (also with central and laterals being similar in length) which may be confused due to the co-occurrence of the two species. *Dracogyra subfuscus* n. sp. is also discernable from *G. aegis* of a similar size conchologically by its much lower spire and more depressed shell form. As the protoconch sculpture could not be examined

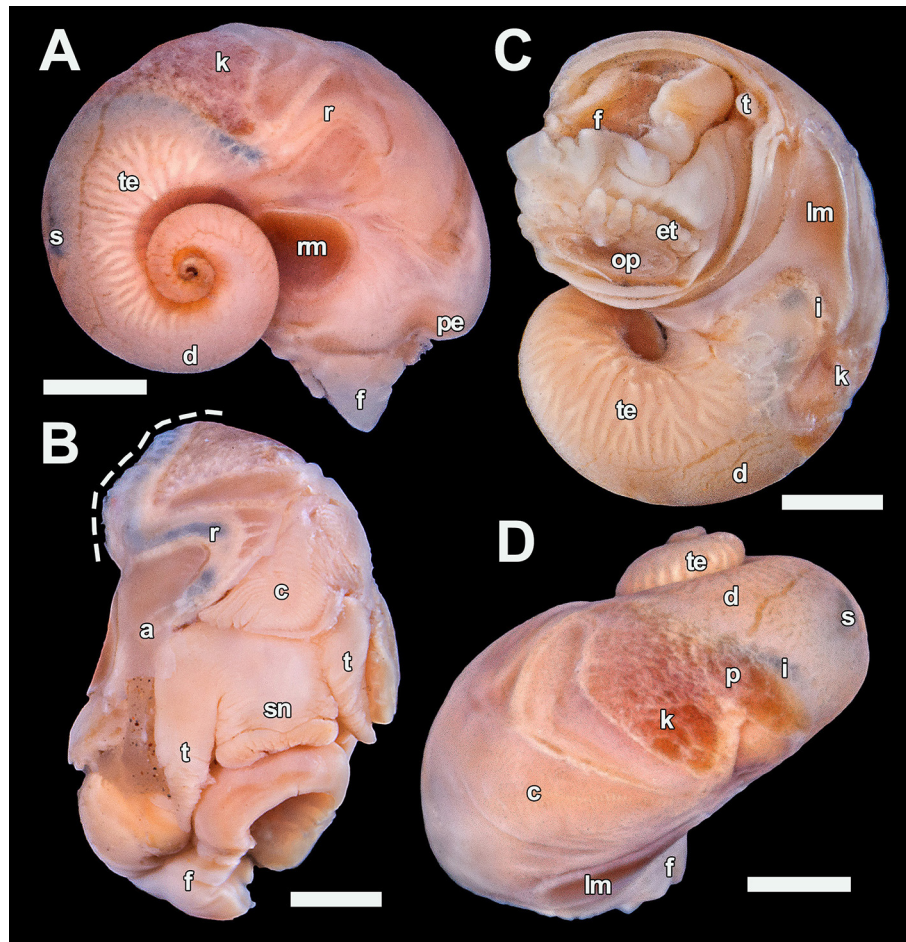


FIGURE 7 | *Dracogyra subfuscus* n. gen., n. sp. soft parts, paratype 5 (UMUT RM32668). **(A)** Right view, **(B)** Anterior view with part of the mantle roof removed to expose the ctenidium (visceral mass cut away at dashed line), **(C)** Ventral view, **(D)** Dorsal view. Scale bars: **(A), (C–D)** = 1 mm. **(B)** 0.5 mm. a, anus; c, ctenidium; d, digestive gland; et, epipodial tentacle; f, foot; i, intestine; k, right kidney; lm, left columellar muscle; op, opercular attachment; p, pericardium; pe, pallial edge; r, rectum; rm, right columellar muscle; s, stomach; sn, snout; t, cephalic tentacle; te, testis.

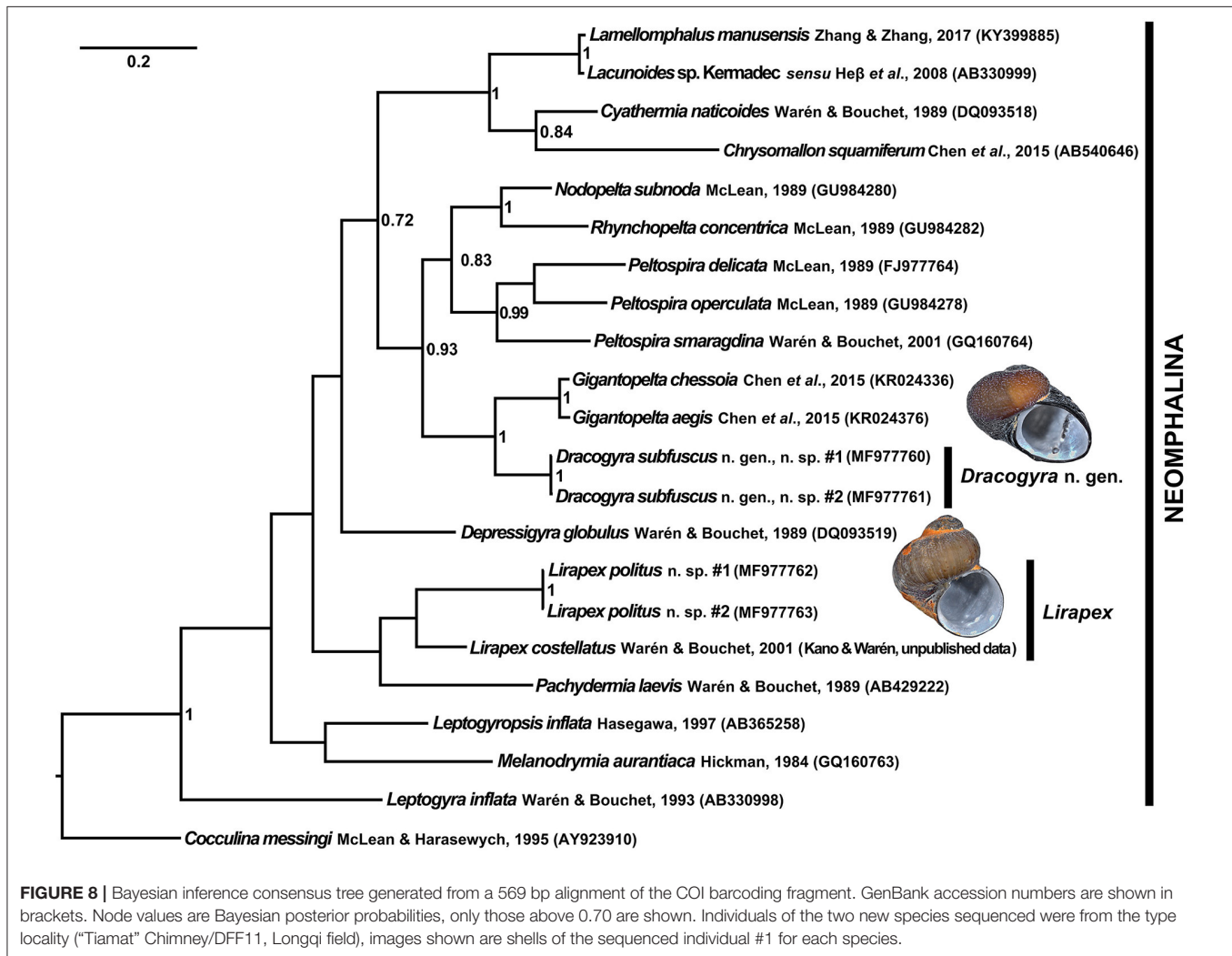
for *Dracogyra* n. gen. based on the existing material, differences in protoconch characters cannot be discussed at this point.

Genetic Support

The Bayesian consensus tree generated based on the COI barcoding fragment is shown in **Figure 8**. Neomphalina was recovered as a fully supported clade (Posterior Probability, PP = 1.00). The placement of both new species within Neomphalina is confirmed, with *L. politus* n. sp. falling sister to *L. costellatus* and the genus *Lirapex* in turn falling sister to *Pachydermia* (although the support was low with PP < 0.70 in both relationships) and *Dracogyra* n. gen. sister to *Gigantopelta* with full support (PP = 1.00). These relationships support the placement of the two new species in family Peltospiridae, and does not contradict with placing *L. politus* n. sp. in genus *Lirapex*. Since it has been well discussed that the barcoding fragment of COI alone is not sufficient to resolve familial relationships among Neomphalina due to saturation (Heß et al., 2008; Chen et al., 2017) and many

branches in the present tree is not well supported, it is difficult to discuss familial assignment of other genera from this tree. This is likely the reason why Peltospiridae appears to be paraphyletic in the present tree, which is not the case in a recent five gene phylogenetic reconstruction (see Chen et al., 2017).

Existing museum materials of the other two described species of *Lirapex* (i.e., *L. humatus* and *L. granularis*) have been fixed in formalin (Philippe Bouchet, pers. comm.) and they are only known from East Pacific Rise vents where the authors have no plans to visit in the near future, they could not be included in the present phylogeny to compare with *L. politus* n. sp. The genus *Lirapex* is defined by a combination of synapomorphic characters shared by all three described species (after Warén and Bouchet, 1989, 2001), detailed as follows: (1) Coiled, often sculptured, skeneimorph teleoconch with the adults' coiling loosening in the last 0.25 to 0.5 whorls; (2) Radula with formula $n + 4 + 1 + 4 + n$ and outer lateral broader than the inner ones, importantly the outer marginals



possess hook-like, denticulated cusps; and (3) Anterior part of the intestine clearly visible as a double-coil between stomach and the left nephridium. As described above *L. politus* n. sp. possesses: (1) Skeneimorph shell with the coiling loosening toward the final 0.25 whorls (similar to *L. granularis*, does not become obviously disjunct from the previous whorl like in *L. humatus* or *L. costellatus*; **Figure 2**); (2) Formula of the radula is $\sim 25 + 4 + 1 + 4 + \sim 25$ with the outer lateral much broader than the inner three, and outer marginals possess denticulated hook-like cusps (**Figures 3D,E**); and (3) Two coils of the intestine are clearly visible (**Figure 4D**). Two further important characteristics, although not unique to *Lirapex* within Peltospiridae, are shared by *L. humatus*, *L. granularis*, and *L. costellatus* and are important for classification in this genus when combined with the abovementioned synapomorphic characters, namely a protoconch with distinct spiral ridges on first half that disappears toward the protoconch-teleoconch boundary and epipodial tentacles being only present surrounding the opercular attachment. *L. politus* n. sp. possesses a protoconch with five distinct spiral ridges that disappear posteriorly (**Figure 3A**) and

the only epipodial tentacles present are the 18-22 tentacles surrounding opercular attachment (**Figure 4C**). The placement of *L. politus* n. sp. in genus *Lirapex* is therefore also robustly supported by all available morphological characteristics, in addition to its sister relationship with *L. costellatus* in the present phylogeny.

A maximum-likelihood distance matrix of all nine peltospirid genera with available COI sequences was generated using a 579 bp alignment and shown in **Table 3**. The average genetic distance (in pairwise difference) between *Dracogyra* n. gen. and other eight genera averaged 21.3% (range 14.4~26.6%), which is similar to distances among those peltospirid genera other than *Dracogyra* n. gen. which averaged at 22.4% (range 12.8~28.6%). This is in support of the generic status of *Dracogyra* n. gen. within Peltospiridae. The genetic distance between the two individuals used in phylogenetic reconstruction over the same COI alignment was 0.2% for *L. politus* n. sp. and 0.4% for *Dracogyra subfusca* n. sp. It should be noted that the genetic distances in COI among the three *Peltospira* species included ranged between 13.0 and 16.5%, which fit within the range among

TABLE 3 | Maximum-likelihood distance matrix of nine genera in Peltospiridae, including *Lirapex politus* n. sp. representing *Lirapex* and *Dracogyra subfuscus* n. sp. representing *Dracogyra* n. gen.

	1	2	3	4	5	6	7	8	9
1 <i>Peltospira operculata</i>	–								
2 <i>Depressigyra globulus</i>	23.2%	–							
3 <i>Nodopelta subnoda</i>	15.9%	18.7%	–						
4 <i>Pachydermia laevis</i>	22.2%	23.7%	19.9%	–					
5 <i>Rhynchopelta concentrica</i>	18.8%	23.0%	12.8%	23.7%	–				
6 <i>Chrysomallon squamiferum</i>	25.3%	28.6%	25.8%	27.8%	27.5%	–			
7 <i>Gigantopelta chessoia</i>	21.7%	21.7%	19.1%	26.9%	19.1%	27.7%	–		
8 <i>Lirapex politus</i> n. sp.	19.9%	22.2%	20.1%	18.3%	21.6%	27.1%	25.3%	–	
9 <i>Dracogyra subfuscus</i> n. gen., n. sp.	18.4%	23.7%	19.6%	26.6%	19.8%	24.4%	14.4%	23.9%	–

peltospirid genera specified above. The relationship among the three *Peltospira* spp. may require reexamination in future studies.

DISCUSSION

Systematics

Lirapex politus n. sp. is the first species of its genus to be discovered from Indian Ocean, meaning the distribution of *Lirapex* now spans Pacific, Indian, and Atlantic oceans; a first for the clade Neomphalina as a whole. Although *Peltospira* also spans Pacific (three species in East Pacific Rise) and Atlantic (one species in Mid-Atlantic Ridge) oceans, it is not known from Indian Ocean (Warén and Bouchet, 2001). Unfortunately, due to lack of available material, the phylogenetic and biogeographic relationship within genus *Lirapex* (i.e., among *L. politus* n. sp. and its three congeners) could not be examined and remains a topic for future research.

The fact that *Dracogyra* n. gen. appears to be the most closely related peltospirid genus to *Gigantopelta* (although only with COI data at this point) serves to strengthen the lines of reasoning that *Gigantopelta* and *Chrysomallon* independently and convergently evolved the peculiar lifestyle of housing endosymbionts in a “trophosome”-like oesophageal gland (Chen et al., 2017).

During genetic analyses it came to light that *Lamellomphalus manusensis* Zhang & Zhang, 2017, a neomphalid species recently described from Manus Back-Arc Basin, was genetically very close to *Lacunoides* sp. *sensu* Heß et al., 2008 from a vent 1336 m deep in Brothers Caldera, Kermadec Arc, New Zealand (Heß et al., 2008). The pairwise distance between the two was merely 1.4%. The authors of *L. manusensis* only included described species in their phylogenetic tree and thus *Lacunoides* sp. *sensu* Heß et al., 2008 was excluded (Zhang and Zhang, 2017). Since the interspecific pairwise differences in COI of marine gastropods is usually above 3–4% (Meyer and Paulay, 2005) this suggests that *Lacunoides* sp. Kermadec is likely in fact *L. manusensis* and the distribution of *L. manusensis* (or at least the genus *Lamellomphalus*) probably extend to Kermadec Arc. This issue warrants more careful investigation using more genetic markers in the future.

Organismal Biology

Stomach contents suggest both *L. politus* n. sp. and *Dracogyra subfuscus* n. sp. are grazers or deposit feeders like most peltospirids, and some radula wear was seen in both species which is also in support of this. The digestive tract of *L. politus* n. sp. is filled by organic material mixed with a large proportion of conspicuous shiny particles of mineral deposit, making the outline of intestines and stomach easily visible from outside. This is similar to the case in other *Lirapex* species (Warén and Bouchet, 1989, 2001). In *Dracogyra subfuscus* n. sp. the digestive tract contents contain a higher proportion of organic material mixed with only very fine mineral particles, perhaps indicative of difference in food preference compared to *L. politus* n. sp. The lack of hypertrophied oesophageal gland as in *Chrysomallon* and *Gigantopelta* (Chen et al., 2017) or very enlarged ctenidium as in *Hirtopelta* adult individuals (Fretter, 1989; Beck, 2002) further imply that neither new species rely on endosymbiont bacteria for nutrition. A number of small peltospirid genera such as *Peltospira*, *Rhynchopelta*, *Nodopelta* are associated with siboglinid tubeworms such as *Riftia* and *Alvinella*, these peltospirids live on the surface of tubeworms and feed there (Warén and Bouchet, 1993, 2001; Warén et al., 2006). Other species of *Lirapex* are also known to be associated in a similar way with *Bathymodiulus* mussels (Warén et al., 2006). The fact that the two new small peltospirid species live underneath *Chrysomallon* and *Gigantopelta* or even on their body surface implies a similar association. The two giant peltospirids might aid in providing nutrition to them in some way, for example the two small new species may feed on epibionts of *Chrysomallon* or *Gigantopelta* (for epibionts of *Chrysomallon* see Goffredi et al., 2004).

The two new species described herein live amongst dense aggregations of *C. squamiferum* and *G. aegis* meaning the four genera of peltospirids live side-by-side. The situation is similar to Western Pacific vents of North Fiji, Manus, and Lau where two holobiont provannid genera *Alviniconcha* and *Ifremeria* co-occur with two deposit feeding provannid genera *Provanna* and *Desbruyeresia* (Warén and Bouchet, 1993; Johnson et al., 2010). This is interesting as Provannidae is the only gastropod family other than Peltospiridae known to house chemosynthetic symbionts intracellularly (Sasaki et al., 2010), and indicate that both families likely succeeded in chemosynthetic ecosystems

by diversifying into both symbiotic and non-symbiotic feeding niches. Although neomphalines are highly diverse and more than 10 genera across all three families Neomphalidae, Peltospiridae, and Melanodrymiidae co-occur in East Pacific Rise and nearby areas (McLean, 1989; Warén and Bouchet, 2001; Heß et al., 2008), the present work presents the first record of giant holobiont peltospirids (*Chrysomallon* and *Gigantopelta*) co-occurring with other, non-chemosymbiotic peltospirids. Prior to the present study, the two holobiont genera were the only neomphalines reported from East Scotia Ridge and Indian Ocean vents where they occur (Rogers et al., 2012; Chen et al., 2015a,c; Copley et al., 2016). The discovery of *L. politus* n. sp. and *Dracogyra subfuscus* n. sp. increases the number of macro- and megafauna species known from the Longqi field and Southwest Indian Ridge as a whole to 23 species, of which seven are molluscs (Copley et al., 2016).

ETHICS STATEMENT

Study species were gastropod molluscs collected in International Waters and permission for sampling was not necessary. Animals were preserved in ethanol.

AUTHOR CONTRIBUTIONS

CC and YZ conceived the study and participated in the design of the study. CC collected and analysed the morphology data and performed all microscopy; YZ and CC collected and analysed the genetics data. All authors took part in the collection of samples and field data used in this study. CC drafted the manuscript which was critically revised and improved by YZ, CW, and JC. All authors gave final approval for submission and publication.

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Conflict of Interest Statement: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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