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Exploring the Almost Unknown *Trochomorpha* (Eupulmonata: Trochomorphidae) from Laos, with Description of Three New Species

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ABSTRACT.– Terrestrial malacofauna in Laos is expected to comprise a large number of species because the country has a large variety of suitable habitats for snail colonization and diversification. The genus *Trochomorpha*, which exhibits a depressed trochiform shell, is a group of Laotian terrestrial snails for which much is still to be discovered. This study was based on historical records and the recent land snail collections obtained from Laos during 2013–2014. Our results uncovered seven species in Laos based on their distinct shell morphological characters. These comprise four nominal species (*T. benigna*, *T. paviei*, *T. albofilosa*, and *T. thachi*) and three new species (*T. buotia* **sp. nov.**, *T. speirofascia* **sp. nov.**, and *T. somsakpanhai* **sp. nov.**). Additionally, the geographic distribution of *Trochomorpha* species in Laos, except *T. benigna*, and photos of type specimens of the Indochinese *Trochomorpha* species are provided.

KEYWORDS: diversity, Indochina, land snail, morphology, taxonomy, *Trochomorpha*

INTRODUCTION

Terrestrial snails with generally trochiform to lenticular shells with an angulated or carinated periphery have traditionally been placed in family Trochomorphidae Möllendorff, 1890 (Baker, 1941; Schileyko, 2002; Delsaerdt, 2016). Among the genera within this family, *Trochomorpha* Albers, 1850 is the most species rich, containing more than a hundred species described to date, and it has been further divided into several subgenera (MolluscaBase, 2022). The genus has wide distribution in Indochina, the Malay Peninsula, Indonesia, New Guinea, North Australia, and Polynesia as far as the Society Islands (Thiele, 1931; Solem, 1959; Schileyko, 2002). However, because studies are lacking that include reliable anatomical investigation, and most taxonomic works on trochomorphid snails rely on shell information only, their systematic position remains provisional and has differed markedly from author to author. The Southeast Asian taxa, especially, need confirmation of their generic classification because there are more than two trochomorphid genera distributed in the region, e.g., *Trochomorpha*, *Geotrochus* van Hasselt, 1823 and *Videna* Adams & Adams, 1855 (Gude, 1914; Baker, 1941; Schileyko, 2002, 2011; Inkhavilay et al., 2019; Sutcharit et al. 2020; Vermeulen and Liew, 2022).

Laos is located in Southeast Asia, where it is globally recognised as supporting ecoregions that are highly important for biodiversity (Myers et al., 2000). The country has a wide diversity of limestone hills and outcrops, mountainous areas, and different types of forests (King et al., 1975; Gupta, 2005); these are home to many animal taxa, especially terrestrial molluscs (Inkhavilay et al., 2019). The recent research on land snails in the country by Inkhavilay et al. (2019), whose study was based on both historical evidence and new materials, emphasizes that land snail fauna in Laos is more diverse than previously thought; however, many species remain undescribed, especially the taxonomically problematic trochomorphid snails.

Three snails reported in the aforementioned study were unknown *Trochomorpha* species from Laos (Inkhavilay et al. 2019) that we formally describe here as new to science. All other known *Trochomorpha* recorded from Laos are herein re-described, and all recognised species with trochomorphid shell forms recorded from mainland Indochina are reviewed (Table 1). Additionally, an updated species list together with images of the type materials are provided. We hope this article provides useful information for future research on trochomorphid snails in Indochina (Laos, Cambodia, and Vietnam) and inspires young Laotian zoologists to take an interest in the land snails of their country.

MATERIALS AND METHODS

This study was based on voucher specimens deposited in the Chulalongkorn University Museum of Zoology (CUMZ), Bangkok, obtained from all available habitats in Laos during the years 2013–2014 (Fig. 1). Species identifications are based on original and subsequent literature (i.e., Pfeiffer, 1863; Crosse, 1867; Morlet, 1885; Mabille, 1887a, b; Heude, 1890; Möllendorff, 1901; Fischer and Dautzenberg, 1904; Bavay and Dautzenberg, 1909a, b; Schileyko, 2011;

TABLE 1. Species list of *Trochomorpha* s.l. recorded from mainland Indochina. References: 1 = this study; 2 = Pfeiffer (1863); 3 = Crosse (1867); 4 = Morlet (1885); 5 = Mabille (1887a); 6 = Heude (1890); 7 = Möllendorff (1901); 8 = Bavay and Dautzenberg (1909a); 9 = Thach (2018; 2020); 10 = Sutcharit (2020).

Species	Figure in this study	whorls	Maximum shell size (mm)		Type locality	Reference
			Width	Height		
1. *T. benigna* (Pfeiffer, 1863)	2A	6	32.5	11.0	Lao Mountains, Camboja [Laos or Cambodia]	2
2. *T. saigonensis* (Crosse, 1867)	7A	6	11.0	5.0	Saigonensi et Poulo-Condor, Cochinchinae [South Vietnam]	3
3. *T. paviei* (Morlet, 1885)	2C–F	5¾–7	15.3	6.1	Kampot et Phnom-Penh [Cambodia]	1, 4, 10
4. *T. subtricolor* Mabille, 1887	7B	6–7	17.0	6.0	Tonkin [North Vietnam]	5
5. *T. sapeca* (Heude, 1890)	7C	~6	17.0	6.0	Tay-ninh Cochinchinae [South Vietnam]	6
6. *T. montana* Möllendorff, 1901	7D	7	18.5	6.0	Mansongebirge [North Vietnam]	7
7. *T. albofilosa* Bavay & Dautzenberg, 1909a	3A–C	5¾–6¼	16.0	7.0	Muong-Bo, Muong-Hum, Gia-Phu [North Vietnam]	1, 8
8. *T. latior* Bavay & Dautzenberg, 1909a	7E	7	20.0	8.0	Muong-Bo, Muong-Hum, Nat- Son, Phong-Tho [North Vietnam]	8
9. *T. vinhensis* Thach, 2018	2B	6	22.9	9.6	Vinh city, Nghe An Province, North Vietnam	9
10. *T. thachi* Huber in Thach, 2020	3D	6	12.6	7.8	Kasi, Vientiane Province, North Laos	9
11. *T. buotia* sp. nov.	5A, B	6¼	22.1	11.9	Tam Nang Rod, Yommalath District, Khammouan Province, Laos	1
12. *T. speirofascia* sp. nov.	5C, D	6¾–7	15.2	6.8	Par-Houak limestone, Vieng Phoukha District, Luang Namtha Province, Laos	1
13. *T. somsakpanhai* sp. nov.	5E, F	6¾–7	14.9	7.7	Tam Xang, Thakhek District, Khammouan Province, Laos	1

Inkhavilay et al., 2019; Thach 2020; Sutcharit et al. 2020) and comparisons with the type specimens and/or reference collections from the Natural History Museum, London (NHM; NHMUK when citing specimens deposited in the NHM), the Senckenberg Forschungsinstitut und Naturmuseum, Frankfurt am Main (SMF), the Royal Belgian Institute of Natural Sciences, Brussels (RBINS), and the Muséum National d'Histoire Naturelle, Paris (MNHN). For the descriptive work, adult shells were examined and imaged using a Nikon camera with a macro lens. The number of whorls (± 0.25) was counted according to Vermeulen and Liew (2022: 10). Shell size was measured using a vernier calliper. Shell sculpture was imaged by scanning electron microscopy (SEM; JEOL, JSM-6610 LV).

The holotypes and paratypes are housed in the Chulalongkorn University Museum of Zoology (CUMZ), Bangkok, Thailand.

RESULTS

Taxonomy

Superfamily Trochomorphoidea Möllendorff, 1890
Family Trochomorphidae Möllendorff, 1890

Genus *Trochomorpha* Albers, 1850

Helix (Trochomorpha) Albers, 1850: 116.

Trochomorpha—Albers, 1860: 60, 61. Stoliczka, 1873: 20. Garrett, 1884: 23. Gude, 1914: 1. Thiele, 1931: 988. Baker, 1941: 285. Solem, 1959: 107. Zilch, 1959: 274. Vaught, 1989: 98. Schileyko, 2002: 1143. Delsaerdt, 2016.

Type species.– *Helix trochiformis* Pfeiffer, 1842 (non Montagu, 1803; = *Trochomorpha typus* Baker, 1941); subsequent designation by Martens in Albers (1860).

Diagnosis for the Indochinese species.– Shell rather small to large, dextral, and more or less trochiform. Shell surface with microsculpture; last whorl with keeled periphery. Umbilicus widely opened and conical.

Remarks.– A nominal name '*Trochomorpha*' was originally proposed as a subgenus of *Helix* Linnaeus, 1758 and included 16 nominal species as members but without designation of the type species (Albers 1850: 116). Later, when reclassified '*Trochomorpha*' as a subgenus of *Nanina* Gray, 1834, Martens in Albers (1860: 60) also clearly designated '*Helix trochiformis* Fér.' as the type species. Then, '*Trochomorpha*' was redefined and raised as a distinct genus level by Martens (1867: 245), and this classification was widely accepted and followed since then (Stoliczka, 1873;

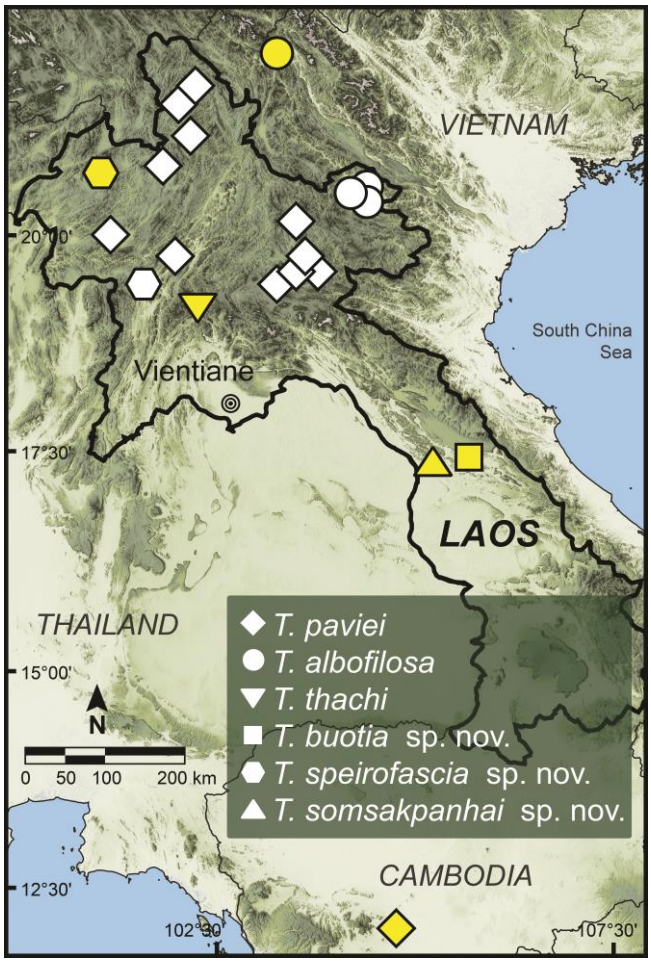

FIGURE 1. Distribution of the genus *Trochomorpha* in Laos. Yellow symbol indicates the type locality of each species. White symbol indicates the other localities of each species. *Trochomorpha benigna* (Pfeiffer, 1863) is not shown on this map because the exact collection location is still uncertain.

Garrett, 1884; Godwin-Austen, 1895; Gude, 1914; Thiele, 1931; Zilch, 1959).

The type species, '*Helix trochiformis* Fér.' Férussac (1821: 45 or 49) has been proposed without description, definition or indication and was thereby unavailable (ICZN 1999: Art. 12). This numen nudum was firstly redefined and used as valid in Pfeiffer (1842a [October]: 304) which therefore made available (ICZN 1999: Art. 12), and consecutively re-described in Pfeiffer (1842b [December]: 40). Concerning this name '*Helix trochiformis* Pfeiffer, 1842' was found to be a junior homonym of Montagu (1803: 427). However, '*Helix trochiformis* Pfeiffer, 1842' was reclassified to either subgenus (see Albers, 1860: 60) or genus *Trochomorpha* (see Martens, 1867: 245), and this latter classification was followed until now (i.e., Stoliczka, 1873; Garrett, 1884; Godwin-Austen, 1895; Gude, 1914; Thiele, 1931; Zilch, 1959). While '*Helix trochiformis* Montagu, 1803' was recognised as a synonym of '*Hyalina fulvus* Drap.' (see Albers, 1860: 73, 348) and never been used as valid again (see Horsáková et al., 2020: 152). These two taxa have not been considered congeneric since Albers (1860), thus the prevailing usage is to be maintained (ICZN, 1999: Arts 23.9.5, 59.2).

A hundred years later, H.B. Baker (1941) recognised this homonym and then propose '*Trochomorpha typus* Baker, 1941' as a substitute name, and listed Férussac's (1821) unavailable name and Pfeiffer's (1842) name in the synonym usage of this species. However, Baker's (1941) proposal of new name did not conform with the criteria set out for replacement names (ICZN 1999: Arts 67.8, 72.7). For an instant, Baker's (1941) did not expressly state it was a replacement name and designated a unique name-bearing type 'type and paratype'. Therefore, '*Trochomorpha typus* Baker, 1941' has separately available and valid, and becoming a junior synonym of *Trochomorpha trochiformis* (Pfeiffer, 1842).

In this study, we apply *Trochomorpha* to Southeast Asian trochiform specimens with wide umbilicus, but we caution that this decision should be verified with anatomical and molecular phylogenetic data. The inclusion of the *Trochomorpha* species listed below in Table 1 is based solely on shell similarity. Because the tiny or dot-like umbilicus of '*Trochomorpha huberi* Thach, 2018' (Fig. 7F) from Vietnam is clearly distinct from *Trochomorpha* s.s., which has an opened and wide umbilicus, we suggest transferring this nominal species to the endemic Vietnamese genus *Trochositala* Schileyko, 2002, although this placement requires further confirmation through anatomical examination.

Trochomorpha benigna (Pfeiffer, 1863)

(Figs 1, 2A)

Helix benigna Pfeiffer, 1863[1862]: 269, pl. 36, figs 11, 12. Type locality: Lao Mountains, Camboja [Cambodia or Laos].

Trochomorpha benigna—Fischer and Dautzenberg, 1904: 398. Inkhavilay et al., 2019: 72, fig. 32f. Páll-Gergely et al., 2020: 47.

Material examined.− Syntypes NHMUK ex. Cuming collection (three shells; Fig. 2A) from 'Lao Mountains, Camboja'.

Description.– Shell large (width 29.0–32.5 mm, height 11.0 mm), very depressed trochiform, thickened and rather opaque. Shell colour monochrome yellowish brown or dark brown. Shell surface sculptured with radial and spiral striations. Whorls 6, convex, regularly increasing, separated by shallow suture. Spire with slightly raised apex to low-conical with straight or slightly convex sides. Last whorl distinctly angular,

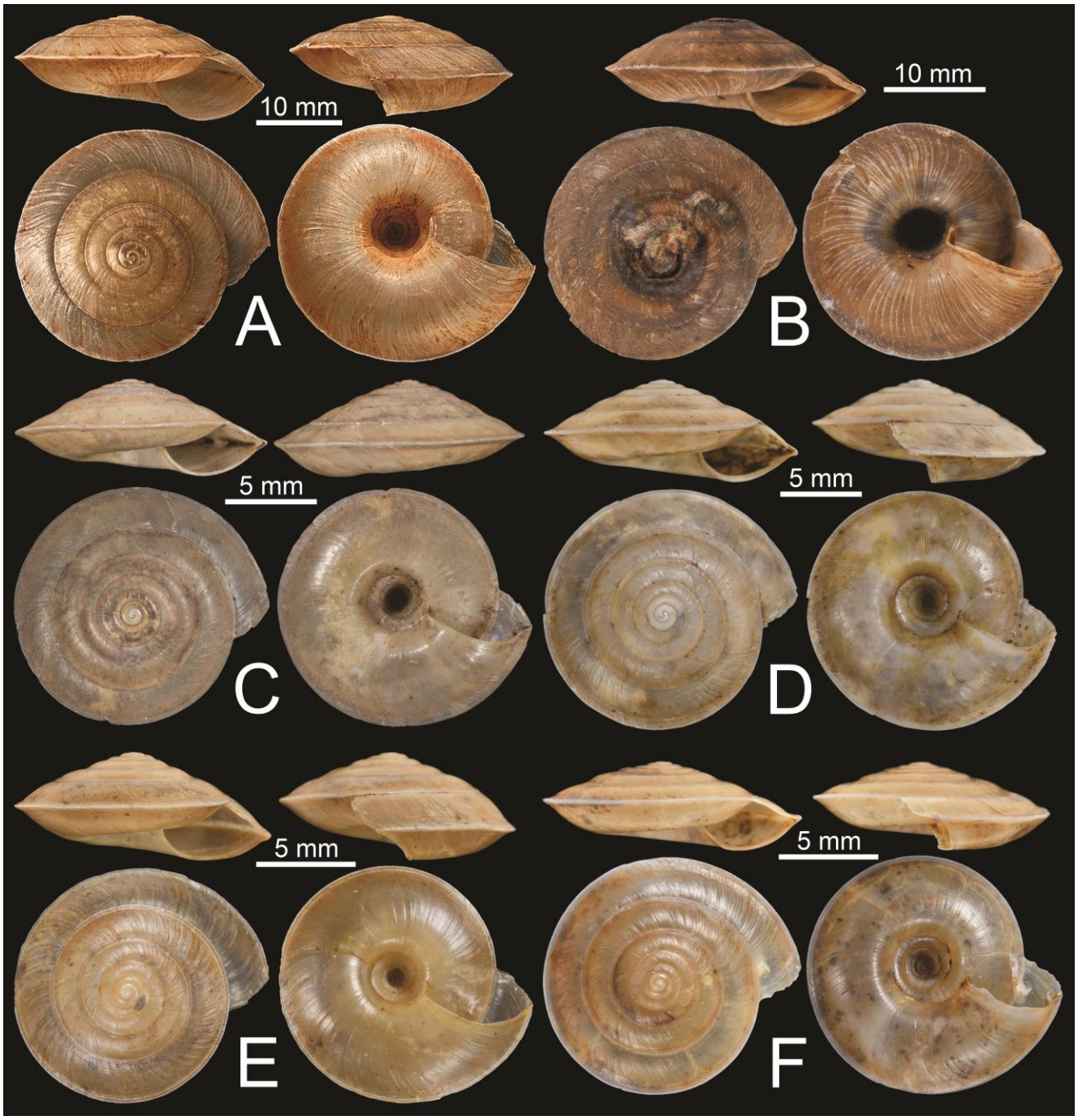

FIGURE 2. Shells of *Trochomorpha* species. **A.** *T. benigna* syntypes NHMUK ex. Cuming collection. **B.** *T. vinhensis* holotype NHMUK 20180285. **C–F.** *T. paviei*, **C.** syntype MNHN-IM-2000-27885, **D.** specimen CUMZ 14290 from Phou Thaleang Bio-Diversity Conservation Area, Phongsaly Province, **E.** specimen CUMZ 14275 from Ban Oudom village, Oudomxay Province, and **F.** specimen CUMZ 14274 from Thamxang Cave, Xieng Khouang Province.

slightly compressed at periphery, and moderately convex below periphery. Aperture oblique and quadrate; peristome slightly thickened; columellar margin suboblique. Umbilicus opened, relatively wide, funnel shaped, showing all preceding whorls (Fig. 2A).

Distribution.− Laos (Fischer and Dautzenberg, 1904) and Vietnam (Thach, 2018).

Remarks.− In this study, no additional material identified as *T. benigna* was found from Laos; thus, only the type specimens were examined. The type locality of this species was stated as 'Lao Mountains, Camboja' probably referring to Laos or Cambodia, which makes the precise collection locality still uncertain (Páll-Gergely, 2020; Pholyotha et al., 2020).

Among the large-sized trochomorphid species, *T. benigna* (Fig. 2A) is similar to *T. vinhensis* Thach,

2018 (Fig. 2B) described from Nghe An Province, central Vietnam, in terms of shell shape, colour, and sculpture (Páll-Gergely et al., 2020; Thach, 2020). The main differences between these two species are the columellar margin and sculpture below the periphery to the umbilicus. The columellar margin of *T. benigna* is simple, whereas in *T. vinhensis* it is thicker and extends slightly inside the umbilicus. An interval of radial sculpture below the periphery of *T. vinhensis* is wider than in *T. benigna*.

Trochomorpha paviei (Morlet, 1885)

(Figs 1, 2C–F, 4A–D)

Helix paviei Morlet, 1885[1884]: 386, 387, pl. 11, fig. 1, 1a. Type locality: dans les forêts, entre Kampot et Phnom-Penh [between Kampot and Phnom Penh].

Trochomorpha tonkinorum Mabille, 1887a: 7. Type locality: Tonkin [North Vietnam]. Mabille, 1887b: 97, 98, pl. 3, figs 1–3. Fischer, 1891: 189. Schileyko, 2011: 35 (source of synonymy).

Plectotropis paviei—Morlet, 1889: 125.

Helix (Plectotropis) paviei—Fischer, 1891: 26.

Sivella paviei—Schileyko, 2011: 35.

Trochomorpha paviei—Fischer and Dautzenberg, 1904: 398. Dautzenberg and Fischer, 1905: 352. Dautzenberg and Fischer, 1908: 173. Fischer, 1973: 91. Inkhavilay et al., 2019: 72, figs 33a, b, 56a. Sutcharit et al., 2020: 23, 24, figs 4c, 10a.

Trochomorpha saigonensis—Inkhavilay et al., 2019: 73, fig. 33d (not Crosse, 1867).

Material examined.− Syntype MNHN-IM-2000-27885 (one shell; Fig. 2C) from Kampoi et Phnom-Penh. **LAOS:** Phou Thaleang Bio-Diversity Conservation Area, Boun Neua District, Phongsaly Province (21°37'30.5"N, 101°55'56.9"E): CUMZ 14290. Ban Nam Lee village, Khoua District, Phongsaly Province (21°11'55.5"N, 102°06'40.2"E): CUMZ 14291. Phou Fa Mountain, Phongsaly District, Phongsaly Province (21°44'07.1"N, 102°06'33.1"E): CUMZ 14283. Tat Kuang Si Waterfalls, Luang Prabang Province (19°44' 58.4"N, 101°59'29.5"E): CUMZ 14267. Tham xang Cave, Ban Hot Ta, Kham District, Xieng Khouang Province (19°35'27.5"N, 103°24'45.3"E): CUMZ 14274. Ban Nam Hom Hot Spring Resort, Kham District, Xiangkhouang Province (19°33'28.7"N, 103°41'13.4" E): CUMZ 14292. Tham Piew Cave, Muang Kham District, Xiangkhouang Province (19°40'24.8"N, 103° 34'05.7"E): CUMZ 14286. Thong Hai Hin (Plain of Jars), Phonsavanh Town, Pek District, Xiangkhouang Province (19°25'49.2"N, 103°09'19.4"E): CUMZ 14276. Ban Oudom village, Pakbeg Ditrict, Oudomxay Province (19°59'55.8"N, 101°16'42.7"E): CUMZ 14275. Nam Ork Roo, Ban Nathong village, Namo District, Oudomxay Province (20°52'22.5"N, 101°46' 58.7"E): CUMZ 14289. Muang Hiam, Houaphanh Province (20°05'42.3"N, 103°22'21.1"E): CUMZ 14288.

Description.− Shell medium sized (width 12.8–15.3 mm, height 4.4–6.1 mm), nearly flattened to very depressed trochiform, thin to thick, and semi-transparent to opaque. Shell colour light yellowish to yellowish brown. Protoconch and teleoconch near protoconch sculptured with irregular coarse growth lines and spiral striations varying from faint to obvious (Fig. 4A, C); body whorl sculptured with irregular coarse radial wrinkles, and spiral striation wanting (Fig. 4B, D). Whorls 5¾–7, convex, regularly increasing and separated by shallow suture. Spire with slightly raised apex to low-conical with straight sides. Last whorl distinctly angular and compressed at periphery, and moderately convex at base. Aperture oblique and quadrate; peristome thin or slightly thickened; columellar margin suboblique. Umbilicus opened, very wide, funnel-shaped, relatively shallow or slightly deep and showing all preceding whorls (Fig. 2C–F).

Distribution.− Previous reports of this species were from Laos, Cambodia and Vietnam (Schileyko, 2011; Inkhavilay et al., 2019; Sutcharit et al., 2020). In this study, *T. paviei* is known from several sites in Phongsaly, Luang Prabang, Xiangkhouang, Oudomxay, and Houaphanh provinces in northern Laos (Fig. 1).

Remarks.– Specimens from Laos are tentatively identified to *T. paviei* because shell morphology and shell sculpture of these specimens (Fig. 2D–F) is similar to the syntype of this species (Fig. 2A). However, the colour of live animals, especially the mantle pigmentation visible through the transparent shell, seemed different. The approximate topotype population from Cambodia tended to have scattered irregular black and bright markings (see Sutcharit et al. 2020: 23, 24, fig. 4c), while these pigments were absent in the population from northern Laos (see Inkhavilay et al. 2019: 72, fig. 56a). Unfortunately, we could not compare their reproductive morphology, therefore additional information is necessary to determine whether the differences represent colour variation or cryptic species.

Trochomorpha albofilosa Bavay & Dautzenberg, 1909

(Figs 1, 3A−C, 4E–H)

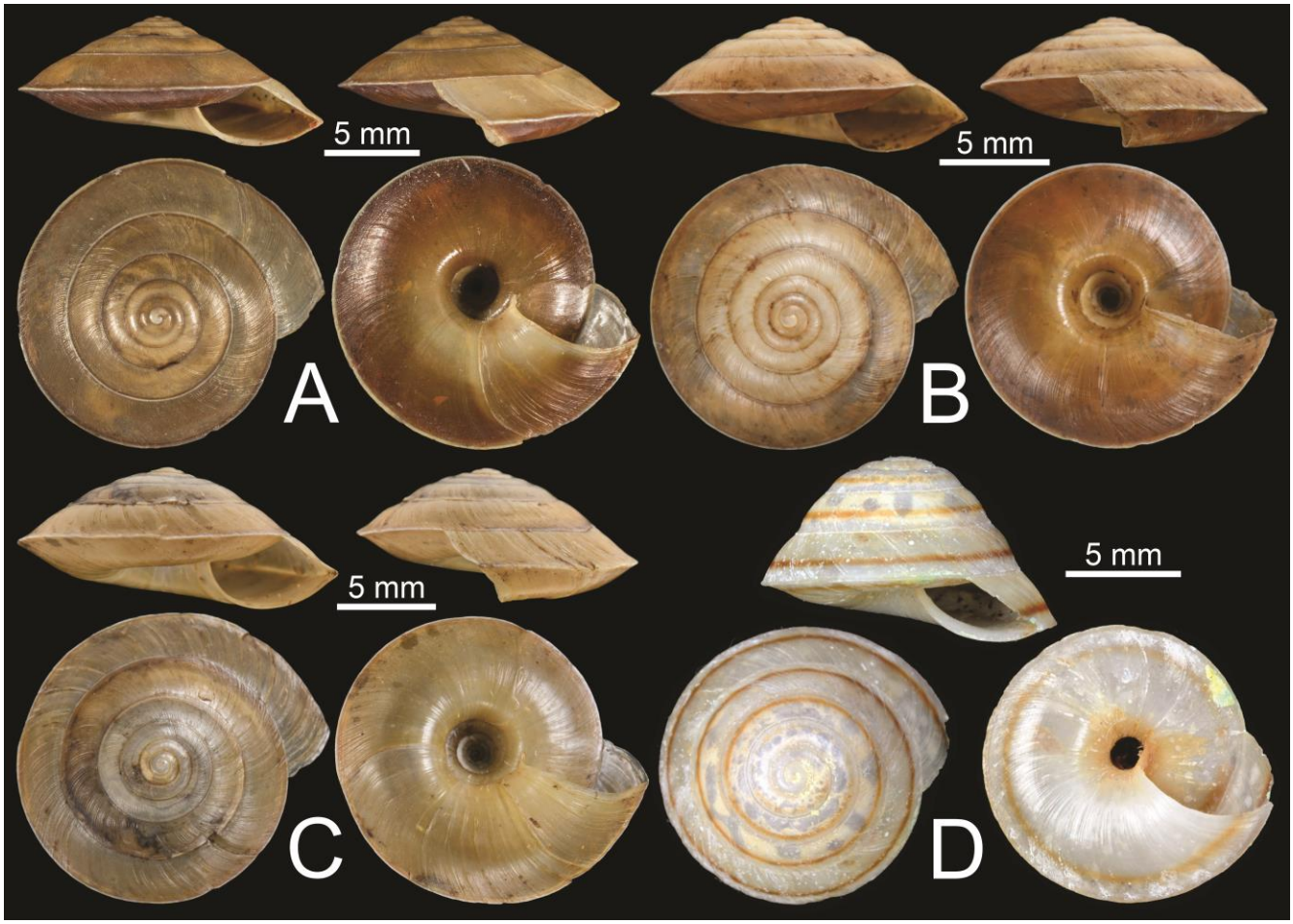

FIGURE 3. Shells of *Trochomorpha* species. **A–C.** *T. albofilosa*, **A.** syntypes MNHN-IM-2000-33109, **B.** specimen CUMZ 14287 from Ban Nathan village, Houaphanh Province, and **C.** specimen CUMZ 14285 from Ban Nawit, Houaphanh Province. **D.** *T. thachi* holotype MNHN-IM-2000-35541.

Trochomorpha albofilosa Bavay & Dautzenberg, 1909a: 233, 234. Type locality: Muong-Bo, Muong-Hum, Gia-Phu [North Vietnam]. Bavay and Dautzenberg, 1909b: 170, 171, pl. 4, figs 23−25. Fischer-Piette, 1950: 174.

Sivella albofilosa—Schileyko 2011: 35.

Material examined.− Syntypes MNHN-IM-2000-33109 (one shell; Fig. 3A) from Muong-Bo. **LAOS:** Nam Noua, Viengxay District, Houaphanh Province (20°27'11.9"N, 104°10'38.6"E): CUMZ 14284. Ban Nawit, Viengxay District, Houaphanh Province (20°22' 37.3"N, 104°16'43.2"E): CUMZ 14285. Ban Nathan village, Viengxay District, Houaphanh Province (20° 27'28.1"N, 104°08'43.4"E): CUMZ 14287.

Description.− Shell medium sized (width 13.7–16.0 mm, height 6.0–7.0 mm), depressed trochiform, thin to thick, and semi-transparent to opaque. Shell colour monochrome yellowish brown or with yellowish brown on upper periphery and reddish brown below periphery. Protoconch and teleoconch sculptured with obliquely striated growth lines and no spiral striation (Fig. 4E–H). Whorls 5¾–6¼, convex, regularly increaseing in size and separated by shallow suture. Spire with slightly raised apex to low-conical with straight or slightly convex sides. Last whorl sharply angled on periphery, nearly flat or slightly convex at base. Aperture oblique and quadrate; peristome thin or slightly thickened; columellar margin suboblique. Umbilicus opened, relatively wide, funnel-shaped, deep, and showing all preceding whorls (Fig. 3A–C).

Distribution.− Original locality data are from Muong-Bo, Muong-Hum, Gia-Phu in North Vietnam (Bavay and Dautzenberg 1909a; Schileyko 2011). In this study, this species is known from three localities at Viengxay District, Houaphanh Province in northern Laos (Fig. 1).

Remarks.– *Trochomorpha albofilosa* was first described from multiple localities as ‘Muong-Bo’, ‘Muong-Hum’ and ‘Gia-Phu’, which are sites in northern Vietnam and are close to the localities where

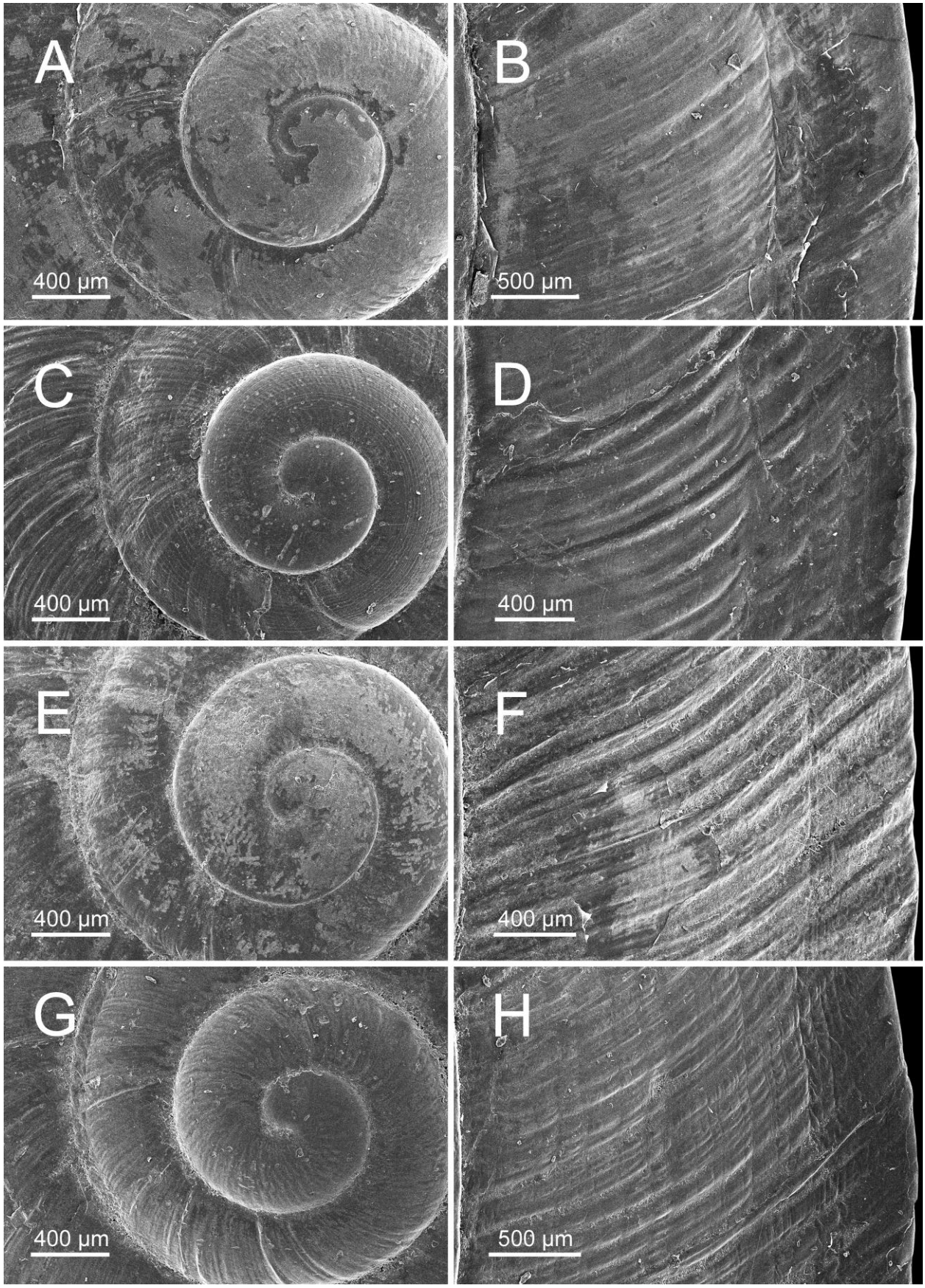

FIGURE 4. Representative SEM images of shells of *Trochomorpha* species. **A–D.** *T. paviei*, **A, B.** specimen CUMZ 14290, **C, D.** specimen CUMZ 14274. **E–H.** *T. albofilosa*, **E, F.** specimen CUMZ 14287, **G, H.** specimen CUMZ 14285. **A, C, E, G.** protoconch. **B, D, F, H.** body whorl.

we obtained specimens. The specimens (Fig. 3B) from Viengxay, Houaphanh, Laos were identical to the syntype (Fig. 3A) in terms of shell shape (depressed trochiform), colour (yellowish brown above the periphery and reddish brown below), and sculpture (spiral striation wanting). We further noticed that *T. albofilosa* has two morphotypes: the typical one with reddish-brown coloration below the periphery (Fig. 3A, B) and a monochrome morphotype with yellowish shell (Fig. 3C). However, these two morphs are identical in having no spiral striation on the shell sculpture (Fig. 4E–H), therefore we considered these as morphological variations. There are several cases of colour dimorphism that occur in the helicarionoid snails such as *Sarika siamensis* (Pfeiffer, 1856) and *Hemiplecta funerea* (Smith, 1896), and these variations have been confirmed by both anatomical and molecular evidence (Sutcharit and Panha 2021, Pholyotha et al. 2022).

Trochomorpha thachi Huber, 2020
(Figs 1, 3D)

Trochomorpha thachi Huber, 2020 in Thach, 2020: 41, pl. 39 figs 484−486, pl. 40 fig. 487. Type locality: Kasi District, Vientiane Province, North Laos.

Material examined.− Holotype MNHN-IM-2000-35541 (Fig. 3D) from Kasi District, Vientiane Province, North Laos.

Description.− Shell medium sized (width 11.5–12.6 mm, height 6.2–7.8 mm), rather thickened, dome shaped, nearly flat on underside and opaque. Shell colour yellowish with two reddish brown spiral bands: a darker one on upper periphery and a paler one below periphery. Shell surface sculptured with closely-spaced radial riblets. Whorls 6, convex, regularly increasing and separated by very shallow suture. Spire dome shaped. Last whorl distinctly keeled. Aperture oblique and quadrate; peristome moderately thickened; columellar margin suboblique. Umbilicus opened, funnel-shaped, deep and moderately wide (Fig. 3D).

Distribution.− This species is probably restricted to the type locality at Vientiane Province in northern Laos (Fig. 1).

Remarks.− No new specimens of this species were found, and only the type specimen was examined. *Trochomorpha thachi* can be distinguished from all other species from Indochina in having a medium-sized and dome-shaped shell with two spiral bands above and below periphery.

Trochomorpha buotia sp. nov.
http://zoobank.org/urn:lsid:zoobank.org:act:/E3C0B182-0D49-4BDD-9A62-EE34B606B764
(Figs 1, 5A, B, 6A, B)

Trochomorpha (?) sp. 1—Inkhavilay et al., 2019: 73, fig. 33e.

Type locality.− Tam Nang Rod (cave), Na-dan village, Yommalath District, Khammouan Province, Laos (17°30'16.3"N, 105°23'08.8"E).

Material examined.− Holotype: CUMZ 14271 (Fig. 5A, width 22.1 mm, height 11.9 mm). Paratype: CUMZ 14272 (one shell; Fig. 5B, width 21.4 mm, height 11.4 mm) from same locality as holotype.

Diagnosis.− Shell large, moderately umbilicated, dome-shaped, nearly flat or slightly convex at base, sculptured with spiral ridges on body whorl, and sharply angled, compressed and slightly deflexed at periphery.

Etymology.− The specific name '*buotia*' is derived from the Latin prefix '*bu-*' meaning 'large, huge' and the Greek word '*otia*' meaning 'mollusk'. It refers to large shell size, which characterises this species.

Description.− Shell large (width 21.1–22.1 mm, height 11.4–11.9 mm), dome shaped dorsally and nearly flattened ventrally, thick and opaque. Shell yellowish with paler colour on middle between suture and peripheral keel, and nearly creamy near umbilicus (based on old specimen; may be faded and not representative of colour of fresh shell). Protoconch sculptured with unclear growth lines (Fig. 6A); body whorl sculptured with closely spaced spiral ridges (Fig. 6B). Whorls 6¼, convex, regularly increasing in size and separated by shallow suture. Spire with slightly raised apex to low conical with straight or slightly convex sides. Last whorl distinctly angular, slightly compressed and little deflexed at periphery. Aperture oblique, quadrate; peristome thickened; columellar margin suboblique and thickened. Umbilicus opened, slightly to moderately wide, funnel-shaped, deep, and showing most preceding whorls (Fig. 5A, B).

Distribution.– Currently, this new species is known only from the type locality in central Laos (Fig. 1).

Remarks.– This new species differs from all of the recognised Indochinese *Trochomorpha* species by its very solid, dome-shaped, and large-sized shell with a peripheral keel slightly curving downward and body whorl sculptured with spiral ridges. The species most

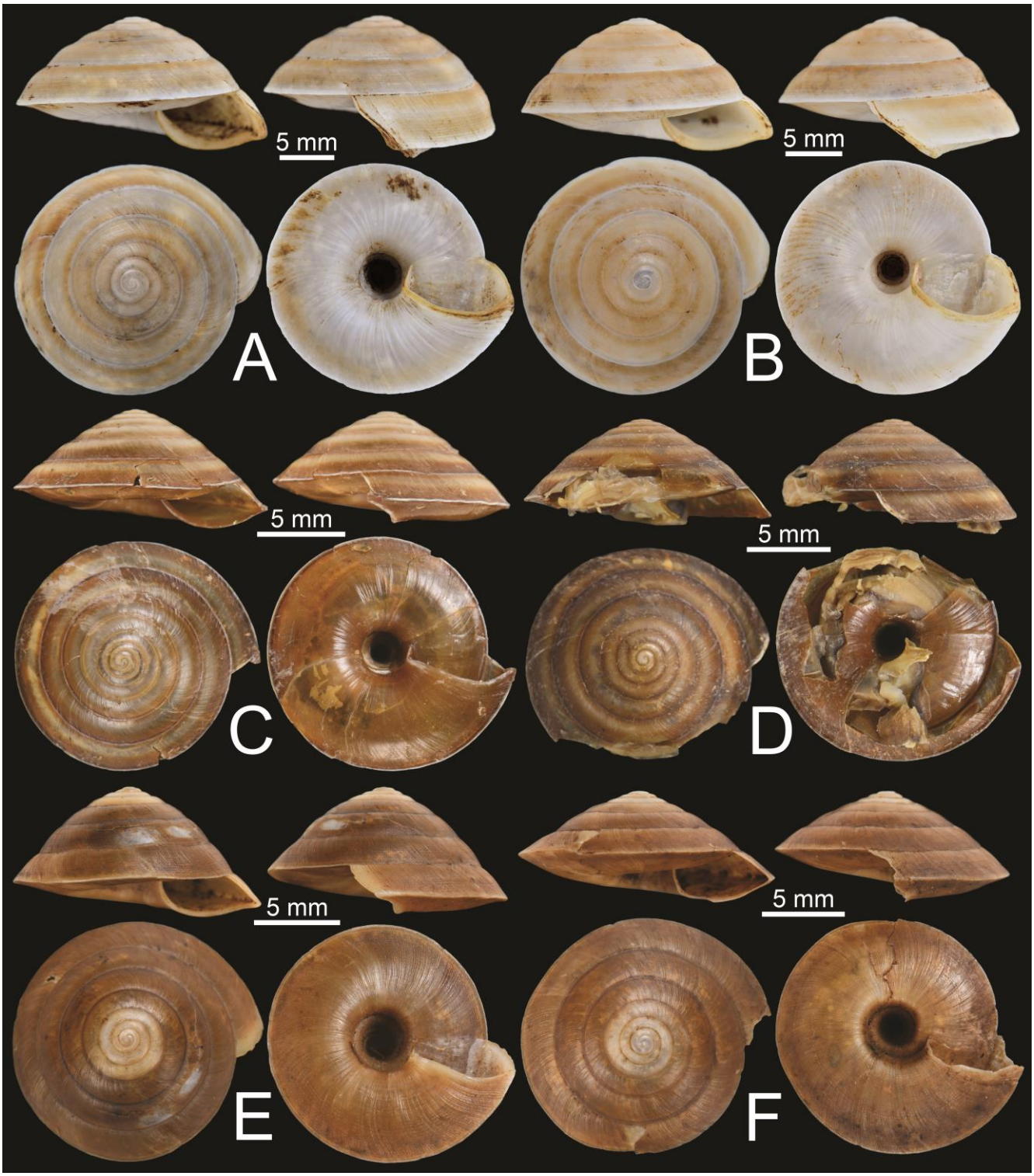

FIGURE 5. Shells of *Trochomorpha* species. **A, B.** *T. buotia* sp. nov., **A.** holotype CUMZ 14271, and **B.** paratype CUMZ 14272 from the type locality. **C, D.** *T. speirofascia* sp. nov., **C.** holotype CUMZ 14268 from the type locality, and **D.** paratype CUMZ 14269 from Xayaboury District, Xayaboury Province. **E, F.** *T. somsakpanhai* sp. nov., **E.** holotype CUMZ 14279, and **F.** paratype CUMZ 14280 from the type locality.

similar to the new species are *T. benigna* and *T. vinhensis* in terms of shell size. In comparison, *T. buotia* sp. nov. has a dome-shaped shell with a peripheral keel slightly curving downward and occurring on the lower surface of the body whorl (Fig. 5A, B), while *T. benigna* and *T. vinhensis* have a more depressed shell with a peripheral keel occurring at the middle of the body whorl (Fig. 2A, B).

***Trochomorpha speirofascia* sp. nov.**
http://zoobank.org/urn:lsid:zoobank.org:act:/CD0DA7B2-A601-46C3-A41A-4EB89830EE97
(Figs 1, 5C, D, 6C, D)

Trochomorpha (?) sp. 3—Inkhavilay et al., 2019: 74, fig. 34a.

Type locality.− Par-Houak limestone, Vieng Swang village, Vieng Phoukha District, Luang Namtha Province, Laos (20°41'14.5"N, 101°04'08.0"E).

Material examined.− Holotype: CUMZ 14268 (Fig. 5C, width 14.6 mm, height 6.8 mm). Paratypes: CUMZ 14269 (one alcohol-preserved specimen; Fig. 5D, width 15.2 mm, height 6.5 mm) from Xayaboury District, Xayaboury Province (19°28'N 101°36'E).

Diagnosis.− Shell medium-sized, rather thin, moderately umbilicated, depressed trochiform, nearly flat or convex at base, sculptured with faintly spiral and radial striation, periphery angulate, slightly compressed at the periphery, reddish brown, and with yellowish subsutural band.

Etymology.− The specific name '*speirofascia*' is derived from the Greek word '*speira*' meaning 'coil, spiral, twist' and the Latin word '*fascia*' meaning 'band or stripe'. It refers to the spiral band that characterises the shell of this species.

Description.− Shell medium sized (width 14.6–15.2 mm, height 6.5–6.8 mm), depressed trochiform, rather thin and semi-transparent. Shell colour reddish brown or dark brown, with broad, light-yellowish subsutural band. Protoconch sculptured with faint radial striated growth lines; subsequent whorl sculptured with faint radial striated growth lines and spiral striations varying from faint to obvious (Fig. 6C); body whorl sculptured with irregular coarse radial wrinkles and lacking spiral striation (Fig. 6D). Whorls 6¾–7, convex, regularly increasing, and separated by shallow suture. Spire with slightly raised apex to low-conical with straight or slightly convex sides. Last whorl compressed at margin and acutely keeled; nearly flattened to little convex on underside. Aperture oblique and quadrate; peristome rather thin to slightly thick; columellar margin subobblique. Umbilicus opened, slightly to moderately wide, funnel-shaped, deep, and showing most preceding whorls (Fig. 5C, D).

Distribution.– This new species is mainly distributed in Luang Namtha and Xayaboury provinces in northwestern Laos (Fig. 1).

Remarks.– The moderately funnel-shaped umbilicus, reddish-brown colour, and single subsutural band distinguish *T. speirofascia* sp. nov. from the other known Indochinese congeners. In contrast with other species recorded in Indochina having a spiral band (*T. bicolor* Martens, 1864, *T. thachi* and *T. subtricolor*), this new species differs from *T. bicolor*, which was described from Sumatra and Borneo and was introduced to North Vietnam (Schileyko, 2011), by having an elevated conical shell with flattening below the periphery, and a narrower and deeper umbilicus (Marzuki et al., 2021). *Trochomorpha speirofascia* sp. nov. can be differentiated from *T. thachi* by its depressed trochiform shell that does not have a spiral band below the periphery, whereas *T. thachi* has a more dome-shaped shell, is yellowish in colour, and the spiral band is narrower than in this new species and is located at mid-body whorl and below the periphery (Fig. 3D). In addition, *T. speirofascia* sp. nov. is distinguished from the Vietnamese *T. subtricolor* by having a deeply opened umbilicus and reddish-brown colour, whereas *T. subtricolor* has a wider and shallower umbilicus, a more depressed shell, and yellowish colour below the periphery to the umbilicus (Fig. 7B).

***Trochomorpha somsakpanhai* sp. nov.**
http://zoobank.org/urn:lsid:zoobank.org:act:/794D91AF-0D2B-42C4-A6B5-322E88C8352C
(Figs 1, 5E, F, 6E, F)

Trochomorpha (?) sp. 2—Inkhavilay et al., 2019: 73, fig. 33f.

Type locality.− Tham Xang (cave), Thakhek District, Khammouan Province, Laos (17°25'48.1"N, 104°51' 54.7"E).

Material examined.− Holotype: CUMZ 14279 (Fig. 5E, width 14.9 mm, height 7.7 mm). Paratypes: CUMZ 14280 (two shells; Fig. 5F, width 14.8 mm, height 6.5 mm) from same locality as holotype.

Diagnosis.− Shell medium-sized, thick, reddish brown or dark brown, moderately to widely umbilicated, depressed trochiform to dome shaped, nearly flat to moderately convex below the periphery, sculptured with very weak tubercles arranged on radial striation, periphery angulate, slightly compressed at the periphery.

Etymology.− This species is dedicated to Professor Dr. Somsak Panha from the Center of Excellence on Biodiversity, Faculty of Science, Chulalongkorn University, who has outstandingly contributed to the

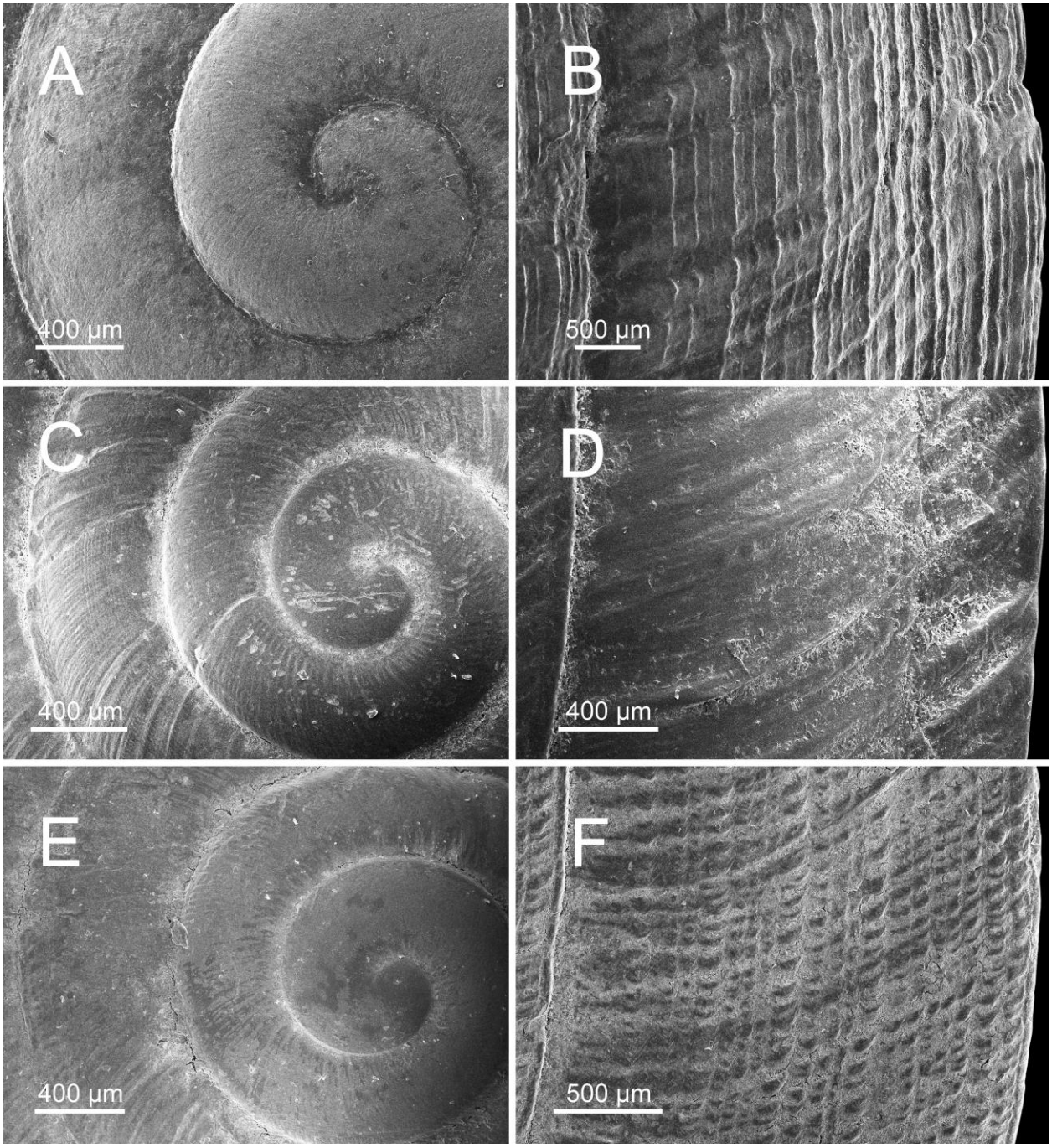

FIGURE 6. Representative SEM images of shells of *Trochomorpha* species. **A, B.** *T. buotia* sp. nov. holotype CUMZ 14271, **A.** protoconch, **B.** body whorl. **C, D.** *T. speirofascia* sp. nov. holotype CUMZ 14268, **C.** protoconch, **D.** body whorl. **E, F.** *T. somsakpanhai* sp. nov. paratype CUMZ 14280, **E.** protoconch, **F.** body whorl.

systematics of invertebrate taxa in Thailand and Southeast Asia.

Description.− Shell medium sized (width 14.8–14.9 mm, height 6.5–7.7 mm), thickened, depressed-trochiform to dome-shaped and opaque. Shell colour reddish brown or dark brown. Protoconch with irregular coarse growth lines (Fig. 6E); body whorl sculptured with very weak tubercles arranged on radial ridges, caused by spiral lines cutting through the radial (Fig. 6F). Whorls 6¾–7, convex, regularly increasing and separated by very shallow suture. Spire with slightly raised apex to low-conical with straight or slightly convex sides; apex blunt and light yellowish. Last whorl distinctly angular and slightly compressed at periphery and nearly flat to moderately convex below periphery. Aperture oblique and quadrate; peristome moderately thickened; columellar margin suboblique. Umbilicus opened, relatively wide, funnel-shaped, deep and showing all preceding whorls (Fig. 5E, F).

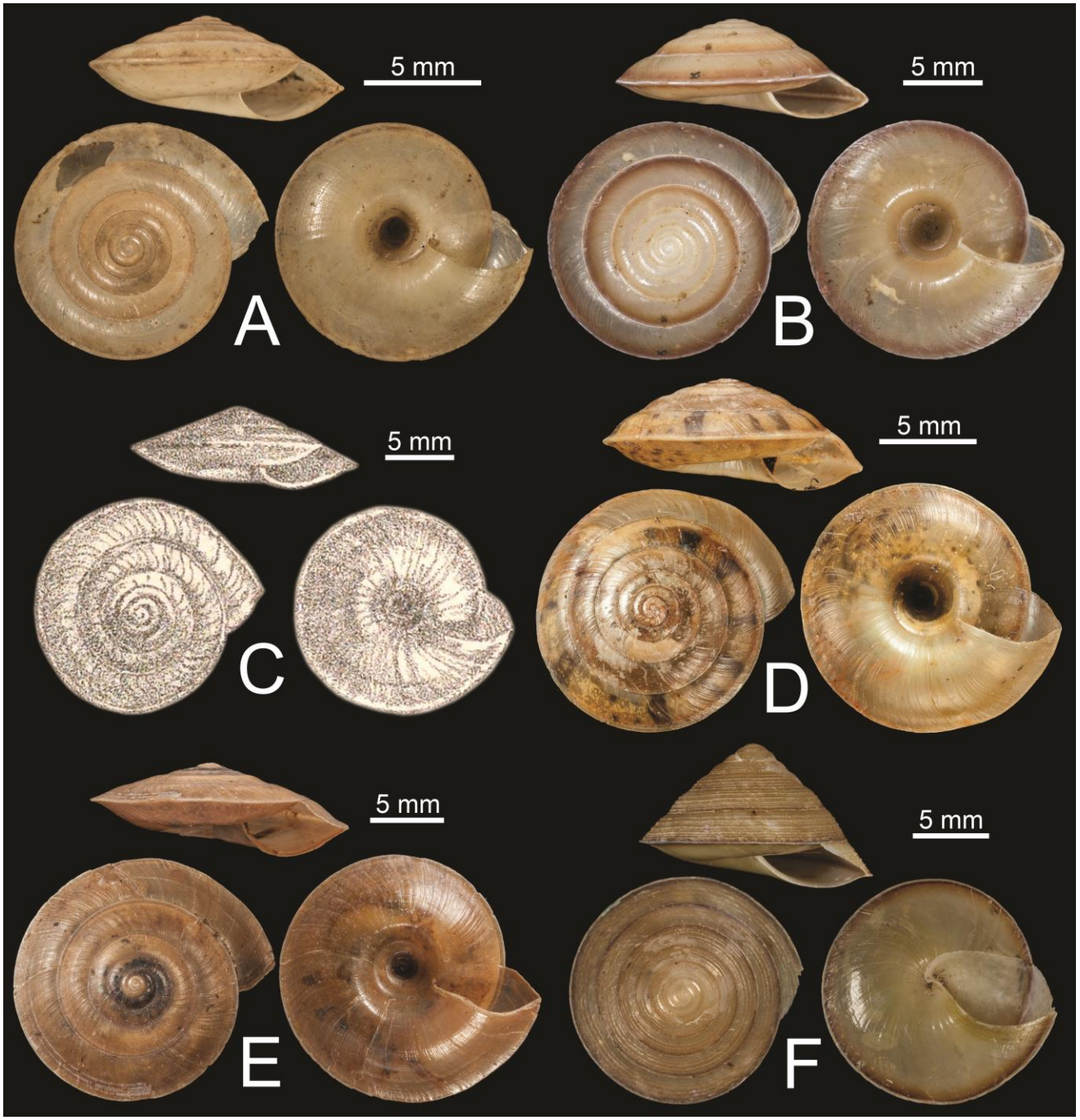

FIGURE 7. Shells of *Trochomorpha* species. **A.** *T. saigonensis*, syntypes MNHN-IM-2000-27875. **B.** *T. subtricolor*, syntypes MNHN-IM-2000-27877. **C.** *T. sapeca*, modified from Heude (1890: pl. 38, fig. 13). **D.** *T. montana*, syntype SMF 70409. **E.** *T. latior*, syntype RBINS-MT2457. **F.** *Trochositala huberi*, holotype MNHN-IM-2000-34069.

Distribution.− As currently known, *T. somsakpanhai* sp. nov. is restricted to Tham Xang Cave, Khammouan Province in the central part of Laos (Fig. 1).

Remarks.– This new species differs from *T. paviei* and *T. albofilosa* from Laos, and *T. saigonensis*, *T. sapeca*, *T. montana* and *T. latior* from Vietnam (Fig. 5) by having the upper periphery dome shaped and the lower periphery flattened, reddish brown, and shell sculpture with very weak tubercles arranged on radial ridges. In contrast, the shell surface of all six of these congeners has only irregular growth lines and is without tubercles. In addition, *T. paviei*, *T. saigonensis*, *T. sapeca*, and *T. latior* have a more depressed-trochiform shell with shallower umbilicus than the new species. *Trochomorpha montana* also has a trochiform shell with the upper periphery depressed, dome shaped, and the lower periphery convex, monochrome yellowish

colour, while the new species is flattened below the periphery and is monochrome dark-brown in colour.

Trochomorpha somsakpanhai sp. nov. differs from *T. buotia* sp. nov. by having a much smaller-sized shell that is sculptured with very weak tubercles arranged on radial striations, while *T. buotia* sp. nov. possesses spiral ridges on the shell surface. Although this new is similar in shell size and shape to *T. speirofascia* sp. nov., *T. somsakpanhai* sp. nov. differs by having monochrome reddish-brown to dark-brown colour and is without a spiral band, while *T. speirofascia* sp. nov. is reddish-brown to yellowish with a broad spiral band on the periphery.

CONCLUSION

Our results enhance the understanding of species diversity of the trochomorphid snails in Indochina, especially Laos. Currently, there are seven *Trochomorpha* species recorded from the country. However, the generic assignment of all seven species in *Trochomorpha* is still provisional. Therefore, future comprehensive revision using comparative anatomy and molecular phylogenetics is necessary to confirm the systematic position of these species.

The seven *Trochomorpha* species from Laos can be divided into two groups based on the presence or absence of a spiral band on the shell. The first group (spiral band present) contains *T. thachi* and *T. speirofascia* sp. nov. The second group (spiral band absent) contains *T. benigna*, *T. paviei*, *T. albofilosa*, *T. buotia* sp. nov., and *T. somsakpanhai* sp. nov. This subdivision has not yet been resolved and requires support from additional observations of living animals, especially regarding mantle pigmentation and genitalia, as well as molecular evidence. This information will help form the first evolutionary hypotheses for the genus in the region.

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