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# *Siamochlamys panhai*, a New Limestone Karst-Restricted Terrestrial Snail from Thailand (Eupulmonata: Helicarionidae)

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**ABSTRACT.–** A new genus and new species of helicarionid snail, *Siamochlamys panhai*, is described from limestone outcrops in Thailand. This new genus differs from all helicarionid genera based on morphological characters of shell, radula, and genitalia. The diagnostic characters of *Siamochlamys panhai* **gen. et sp. nov.** are depressed shell, well-polished surface, umbilicus opened, and aperture less covered by reflection of columellar margin. The genitalia exhibit a straight epiphallic caecum and small flagellum but lack a dart apparatus; radula has tricuspid central and lateral teeth and bicuspid marginal teeth. The discovery of this karst-associated land snail increases the knowledge of endemic malacofauna in Thailand, and also suggests that many taxa remain undiscovered.

**KEYWORDS: endemic, Indochina, land snail, limestones, taxonomy**

## INTRODUCTION

Helicarionoidea Bourguignat, 1877 is a large and diverse group of snails and semislugs widely distributed from Africa to Australia and Asia (Blanford and Godwin-Austen, 1908; Hausdorf, 2000; Schileyko, 2002, 2003; Hyman et al., 2007; Hyman and Ponder, 2010). The superfamily was defined to contain three families: Helicarionidae Bourguignat, 1877, Ariophantidae Godwin-Austen, 1883, and Urocyclidae Simroth, 1889. Their members share the key characters of the presence of an epiphallic caecum and a flagellum; however, these appendages may be absent in some taxa (Hausdorf, 1998). These three families can be divided by the position of the penial sheath: it is open at the distal end in Helicarionidae, whereas it is fused to the epiphallus at the distal end in Ariophantidae and Urocyclidae. Ariophantidae contains taxa in which fibres of the penial nerve do not run through the cerebral ganglion, while Urocyclidae is characterized by the presence of fibres of the penial nerve running through the cerebral ganglion (Hausdorf, 1998). Up to now, 19 genera belonging to two families (Ariophantidae and Helicarionidae) are reported from Thailand (Blanford and Godwin-Austen, 1908; Solem, 1966; Panha, 1996; Hemmen and Hemmen 2001; Pholyotha et al., 2018, 2020a, b, c, 2021a, b, c; Tumpeesuwan and Tumpeesuwan, 2019; Sutcharit et al., 2021; Sutcharit and Panha, 2021; MolluscaBase, 2022).

Thailand is a part of the Indo-Burma biodiversity hotspot located in tropical Asia (Myers et al., 2000). In recent years, intensified malacofaunal surveys across the country, especially within limestone areas known to support highly localized diversity of land snails (Clements et al., 2006; Naggs et al., 2006; Sutcharit et al., 2020), have led to discoveries of rare species and many new taxa of helicarionoid snails (i.e., Tanmuangpak et al., 2017; Pholyotha et al., 2018, 2020a, b, c, 2021a, b, c; Tumpeesuwan and Tumpeesuwan, 2019; Sutcharit et al., 2021; Sutcharit and Panha, 2021). However, the knowledge of helicarionoid snails in Thailand is far from complete because living animals are not abundant and most of the new materials collected are only empty shells. Many of these shells likely represent species that are new to science. Hence, living snails are necessary and are key to improving the morphology-based taxonomy of malacofauna in Thailand.

The field surveys along the southern slope of Phi Pan Nam Range in Lampang and Sukhothai provinces in Thailand have yielded an unknown taxon with a glossy, depressed heliciform shell that was initially presumed to be a member of *Macrochlamys* s.l. The genus *Macrochlamys* Gray, 1847 is one of the most speciose in Helicarionoidea, comprising over a hundred described species distributed from South to Southeast Asia and the southern part of China (Blanford and Godwin-Austen, 1908; Schileyko, 2003; Pholyotha et al., 2018, 2020b). This genus has a few informative shell morphologies, and because of morphological convergence or the similar phenotypic shell traits that result when snails are facing similar ecological pressures (Chiba, 2004; Schilthuizen et al., 2006; Haase and Misof, 2009; Okajima and Chiba, 2009; Khalik et al., 2020), most species are in a controversial taxonomic position (Blanford and Godwin-Austen, 1908; Pholyotha et al., 2018, 2020b). Surprisingly, however, the unknown taxon can be clearly separated from *Macrochlamys* s.s because it lacks a dart apparatus, a structure that is well developed in *Macrochlamys* s.s. (Blanford and Godwin-Austen, 1908; Pholyotha et al., 2018, 2020a, b, c). The reproductive anatomy of this unknown taxon is similar to that of *Aenigmatoconcha* Tumpeesuwan & Tumpeesuwan, 2017 but its radular

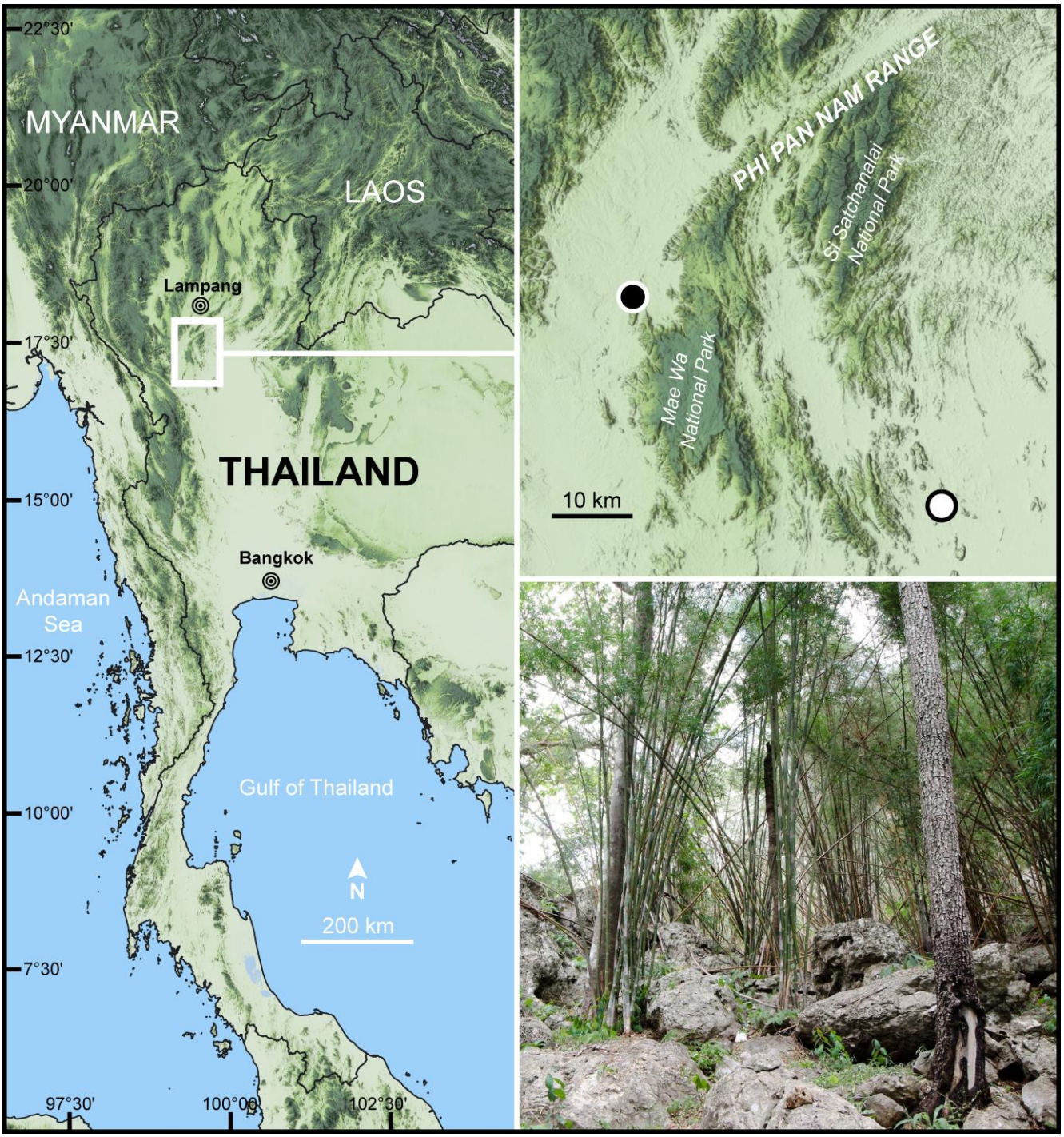


**FIGURE 1.** Distribution and microhabitat structure of the limestone at the type locality of *Siamochlamys panhai* gen. et sp. nov. in Thailand. Black circle indicates type locality: Wat Tham Pha Ngam, Lampang Province. White circle indicates a second locality: Tham Lom-Tham Wang, Sukhothai Province.

morphology and mantle extensions are distinct from this latter genus (Pholyotha et al., 2021c). Therefore, we propose a new genus and new species, *Siamochlamys panhai* gen. et sp. nov., for this unknown taxon and provide appropriate taxonomic descriptions.

## MATERIALS AND METHODS

Land snail specimens were collected from Lampang and Sukhothai provinces, Thailand (Fig. 1). Animal use protocol was approved by the Chulalongkorn University Animal Care and Use Committee (CU-ACUC) under the approval number 1723018. All specimens were hand-collected from several limestone habitats.

Prior to preservation of the collected snail specimens in the field, we took colour photographs of each individual in life using a Nikon camera (DSLR D850) with a Nikon 105 Macro lens (AF-S VR Micro-Nikkor 105mm f/2.8G IF-ED). Living snails were euthanized by a two-step method following the AVMA Guidelines for the Euthanasia of Animals (American Veterinary Medical Association, 2020) and then fixed in 95% (v/v) ethanol for further morphological work as well as molecular studies.

Identification of species was made based on the literature of Blanford and Godwin-Austen (1908), Solem (1966), Páll-Gergely et al. (2016), Tumpeesuwan and Tumpeesuwan (2017, 2019), Bhosale et al. (2019), Pholyotha et al. (2018, 2020a, b, c, 2021a, b, c), and Sutcharit et al. (2020, 2021), and was then compared to the reference collection at the Chulalongkorn University Museum of Zoology (CUMZ), Bangkok, Thailand, and the Natural History Museum, London, UK (NHM; NHMUK when citing specimens deposited in the NHM). For the descriptive work, adult shells were examined and were imaged using the Nikon camera, the whorls were counted, and shell size was measured using a Vernier caliper. Three to 10 preserved specimens were examined under an Olympus SZX2-TR30 stereoscopic light microscope. Whole genitalia were imaged using the Nikon camera and their inner sculpture was imaged by a stereo microscope with the Cell'D Imaging Software. Radulae were extracted, soaked in 10% (w/v) sodium hydroxide, cleaned with distilled water, and imaged by scanning electron microscopy (SEM; JEOL, JSM-6610 LV).

The holotype and most paratypes are housed in the Chulalongkorn University Museum of Zoology (CUMZ), Bangkok, Thailand. Moreover, some paratypes have been donated to the collections of the Natural History Museum, London, UK (NHMUK).

The following abbreviations listed below are used in the figures:

ant-ldl = anterior left dorsal lobe
at = atrium
e1 = portion of epiphallus nearer to penis
e2 = portion of epiphallus nearer to retractor muscle
ec = epiphallic caecum
fl = flagellum
fo = free oviduct
gd = gametolytic duct
gs = gametolytic sac
lsl = left shell lobe
p = penis
post-ldl = posterior left dorsal lobe
pp = penial pilaster
prm = penial retractor muscle
ps = penial sheath
rdl = right dorsal lobe
rsl = right shell lobe
v = vagina
vd = vas deferens

## RESULTS

### Taxonomy

#### Superfamily Helicarionoidea Bourguignat, 1877
#### Family Helicarionidae Bourguignat, 1877
#### Subfamily Durgellinae Godwin-Austen, 1888

#### Genus *Siamochlamys* Pholyotha gen. nov.

http://zoobank.org/urn:lsid:zoobank.org:act:B2A6A094-D89F-4542-AD0A-4F24A2CFEA7F

**Type species.**− *Siamochlamys panhai* Pholyotha sp. nov.; here designated.

**Etymology.**− The name combines '*Siam*', which is a former name of Thailand, chosen because this snail is restricted to the country as far as we know, and the Greek word '*chlamys*', meaning "mantle or cloak". Therefore, the generic name means the land snail with well-developed mantle extensions from Thailand.

**Diagnosis.**− Depressed, glossy shell with open umbilicus, straight epiphallic caecum, short flagellum, no dart apparatus, radula with tricuspid central and lateral teeth and bicuspid marginal teeth, and five mantle extensions well-developed.

**Description.**− See below under the type species.

**Constituent species.**− *Siamochlamys* gen. nov. currently contains only the type species, *Siamochlamys panhai* sp. nov.

**Distribution.**− This new genus is only known to occur in the southern portion of the Phi Pan Nam Range, northern Thailand.

**Remarks.**− *Siamochlamys* gen. nov. is conchologically similar to some South and Southeast Asian helicarionids including *Aenigmatoconcha*, *Chalepotaxis* Ancey, 1887, *Eurychlamys* Godwin-Austen, 1899, and *Sophina* Benson, 1859. Among these four genera, *Siamochlamys* gen. nov. has a straight epiphallic caecum, short flagellum, and no dart apparatus, similar to *Aenigmatoconcha*. However, this new genus can be distinguished by its radular morphology with tricuspid central and lateral teeth, and bicuspid marginal teeth

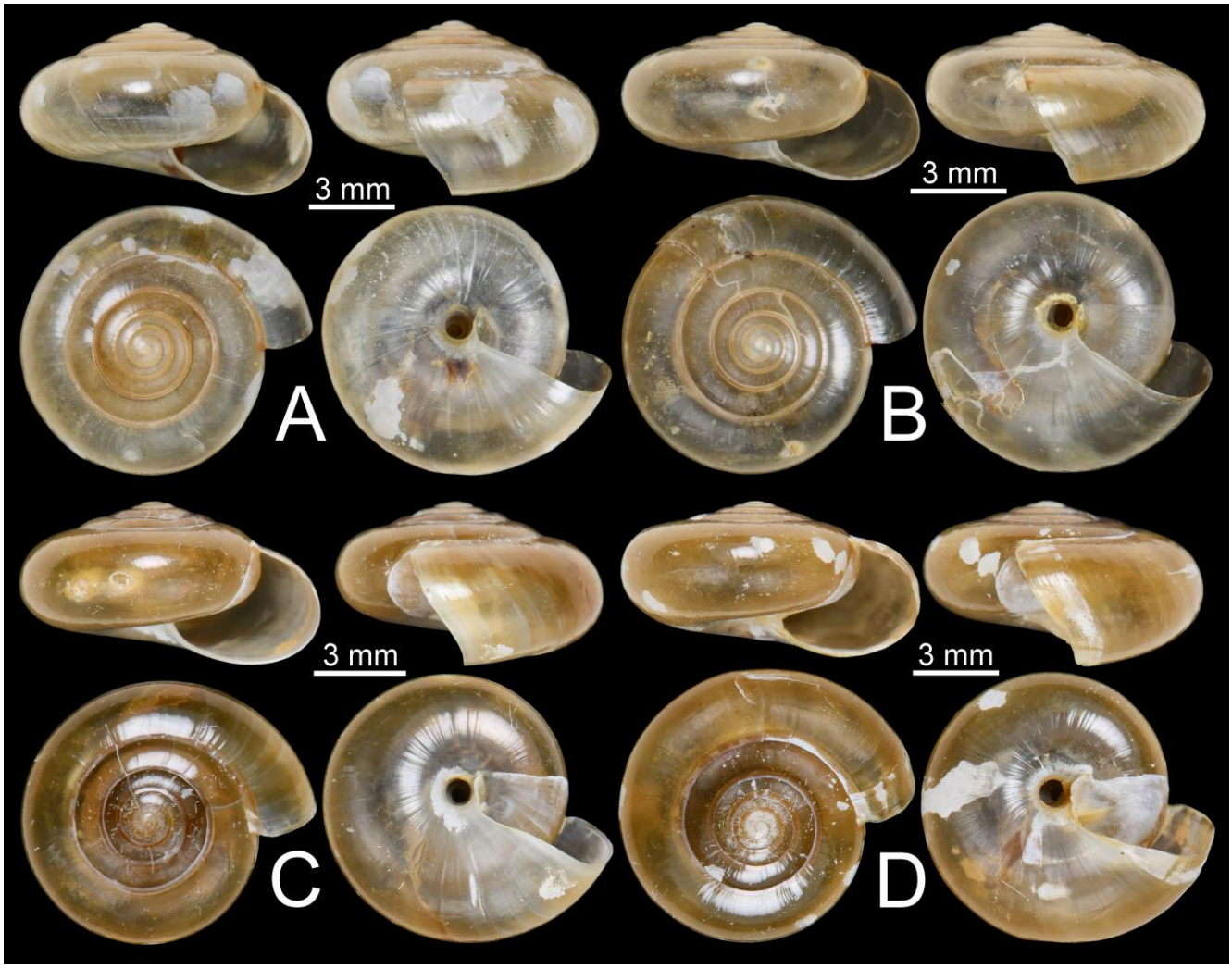


**FIGURE 2.** Shells of *Siamochlamys panhai* gen. et sp. nov. **A.** holotype CUMZ 14209, and (**B**) paratype CUMZ 14210 from Wat Tham Pha Ngam, Lampang Province. **C, D.** paratype CUMZ 14212 from Tham Lom-Tham Wang, Sukhothai Province.

(Fig. 5A). In contrast, *Aenigmatoconcha* has monocuspid and spatulate-shaped teeth (Fig. 5B), which are also found in *Chalepotaxis* and *Sophina* (Páll-Gergely et al., 2016; Sutcharit et al., 2020; Pholyotha et al., 2021c). Similarly, the helicarionid genera *Durgella* Blanford, 1863 and *Burmochlamys* Pholyotha & Panha, 2022 are an example of taxa that have similar genital organs (that have dart apparatus and no flagellum), but are considered as different genera on the basis of radular morphology. Radula of *Durgella* has a unicuspid, bicuspid or asymmetrical tricuspid central tooth and very numerous bicuspid marginal teeth with several small cusps on the outer edge (Fig. 5C), while *Burmochlamys* has a monocuspid central tooth; laterals and marginals undifferentiated and monocuspid (Blanford and Godwin-Austen, 1908; Solem, 1966; Pholyotha et al., 2022). *Siamochlamys* gen. nov. can be distinguished from the Indian endemic genus *Eurychlamys* (type species = *Macrochlamys platychlamys* Blanford, 1881) by having a well-developed epiphallic caecum, whereas it is absent in the latter genus (Bhosale et al., 2019).

With its few informative shell characteristics (glossy, smooth and depressed heliciform), *Siamochlamys* gen. nov. has shell morphology similar some other ariophantid genera, namely *Macrochlamys*, *Sakiella* Godwin-Austen, 1908, *Sarika* Godwin-Austen, 1907, and *Taphrenalla* Pholyotha & Panha, 2021. However, the shell of this new genus has an open umbilicus, while the other genera have a much narrower umbilicus, and their genitalia differ by possessing a dart apparatus (Blanford and Godwin-Austen, 1908; Pholyotha et al., 2018, 2020c, 2021b).

We tentatively assign *Siamochlamys* gen. nov. to the subfamily Durgellinae together with *Aenigmatoconcha* and *Eurychlamys*, as they appear to be closely related taxa based on shared morphological and anatomical characters including open umbilicus, short and bulbous gametolytic organ, small flagellum, and no dart apparatus (Bhosale et al., 2019; Pholyotha et al., 2021c).

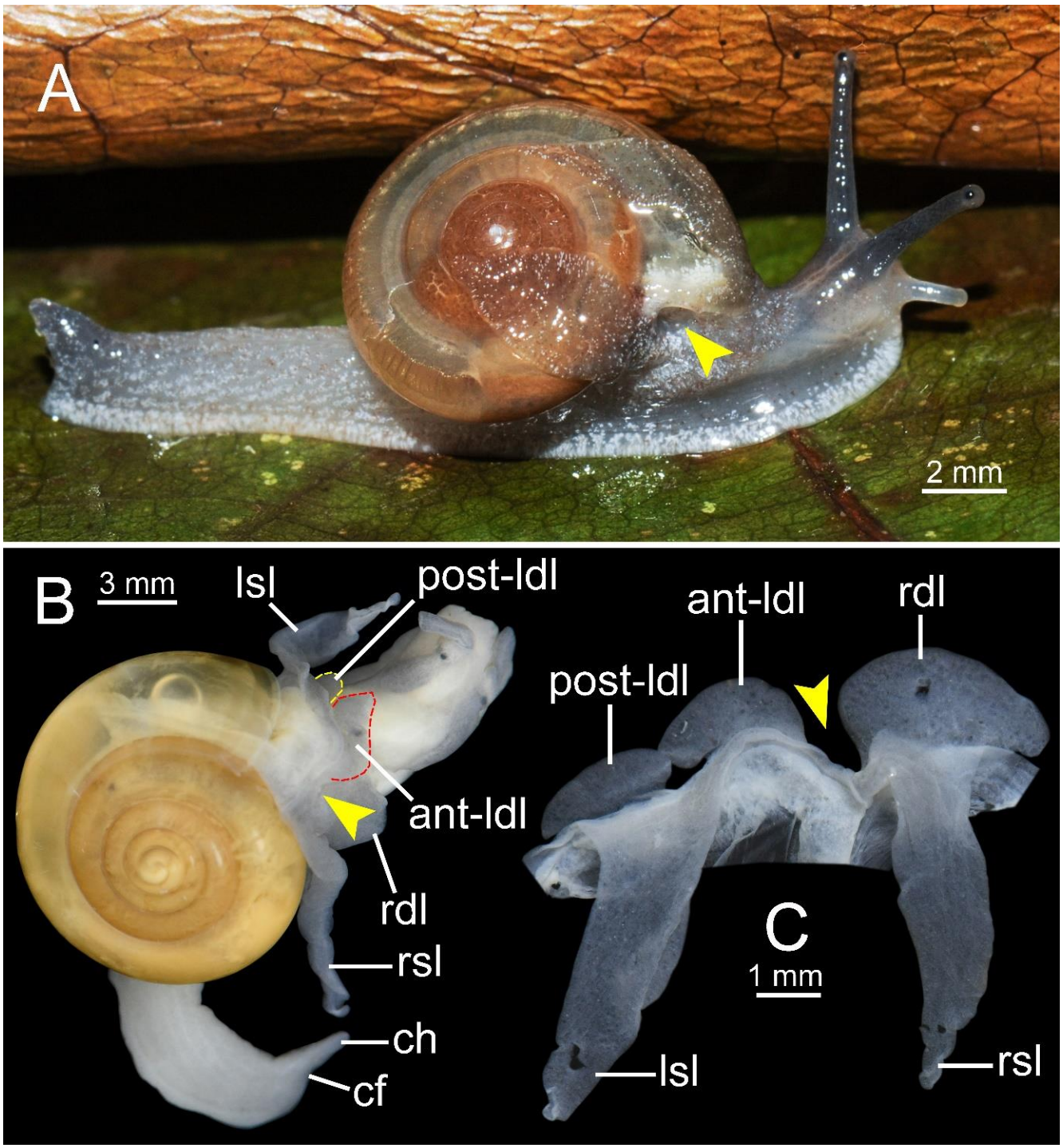


**FIGURE 3.** Living snails and mantle extensions of *Siamochlamys panhai* gen. et sp. nov. paratype CUMZ 14211. **A.** living snail during relaxed position showing the expansion of mantles **B.** alcohol-preserved snail showing shell lobes and dorsal lobes and posterior body **C** dorsal view of mantle extensions (shell lobes and dorsal lobes).

***Siamochlamys panhai* Pholyotha, sp. nov.**

http://zoobank.org/urn:lsid:zoobank.org:act:C278D991-F7E2-45F2-98A2-F5764CE0DED2

(Figs 1–4, 5A)

**Type locality.**− Limestone outcrops at Wat Tham Pha Ngam, Mae Phrik District, Lampang Province, Thailand (17°28'48.8"N, 99°10'07.2"E).

**Material examined.**− Holotype: CUMZ 14209 (Fig. 2A, width 10.1 mm, height 6.0 mm). Paratypes: same locality as holotype: CUMZ 14210 (seven shells and 38 alcohol-preserved specimens; Fig. 2B, width 9.4 mm, height 5.0 mm), CUMZ 14211 (five shells and 10 alcohol-preserved specimens), and NHMUK (two shells). Limestone outcrops at Tham Lom-Tham Wang, Si Samrong District, Sukhothai Province, Thailand

(17°13'24.6"N, 99°31'51.5"E): CUMZ 14212 (10 shells and 21 alcohol-preserved specimens; Fig. 2C, width 9.6 mm, height 5.3 mm; Fig. 2D, width 10.3 mm, height 5.4 mm).

**Diagnosis.**− Shell depressed, small to nearly medium sized and pale to dark, brownish with well-rounded body whorl. Umbilicus narrowly opened such that columellar margin does not reflect over umbilicus and a few preceding whorls can be seen. Genitalia with a long penis; inner sculpture of penis with several small conical penial pilasters and one prominent longitudinal fold inside; epiphallic caecum straight and long.

**Etymology.**− The specific epithet '*panhai*' is named in honor of Professor Dr. Somsak Panha from the Center of Excellence on Biodiversity, Faculty of Science, Chulalongkorn University, who has outstandingly contributed to the study of the biodiversity and the systematics of the fauna in Thailand.

**Description.**− ***Shell*** (Fig. 2). Depressed, thin, semi-translucent, pale to dark brownish, and small to nearly medium sized (shell width 9.1–10.3 mm, shell height 4.7–6.0 mm). Shell surface smooth and glossy with very faint growth lines. Whorls 5 to 6, convex, regularly increasing in size, separated by shallow suture. Spire rather elevated. Last whorl well rounded. Aperture oval-lunate, open obliquely; lip simple. Columellar margin oblique, hardly reflected or not reflected over umbilicus. Umbilicus opened, deep, and showing a few preceding whorls.

***External appearance*** (Fig. 3). Living animal pale grey to slightly dark grey with several minute white and brown dots scattered on body and mantle; eye stalks dark grey. Five mantle extensions well-developed. Left dorsal lobe divided into anterior and posterior lobes; both lobes crescent shaped, large but smaller than remaining lobes. Right dorsal lobe enlarged and crescent to ovate. Left and right shell lobes translucent, pale grey, enlarged, triangular shaped or tongue-like, partially covering shell and retracted when disturbed; right shell lobe slightly smaller than left shell lobe. Pallial anatomy typically sigmurethrous (sigmoid-shaped ureter). Foot sole tripartite. Caudal fossa present. Caudal horn raised and rather large, dark grey.

***Genitalia*** (Fig. 4). Atrium enlarged and short. Penis long, cylindrical, and with one longitudinal groove through its length (observed clearly when penial sheath is removed) (yellow arrow in Fig. 4A). Penial sheath thick and covering atrium and nearly two-thirds of penis. Inner sculpture of penis with small conical penial pilasters, and one large and prominent longitudinal fold (corresponding to external groove) running from atrium to epiphallus (Fig. 4B). Epiphallus (e1+e2) approximately three-fourths of penis length: e1 an elongate and slender tube and e2 bulbous and slightly shorter than e1. Inner sculpture of e1 nearly smooth with small, thin, and longitudinal folds; and inner sculpture of e2 with loose small papillate. Epiphallic caecum straight, elongate and slightly shorter than e2. Penial retractor muscle thin and connecting at head of epiphallic caecum. Flagellum small, bulbous, and approximately half the length of e2. Vas deferens a long, thin tube. Vagina short, enlarged, thickened and cylindrical in shape. Dart apparatus absent. Gametolytic duct slightly shorter than half of penis length, rather thick and enlarged near vagina, then its diameter becoming smaller and more slender near gametolytic sac. Gametolytic sac large and elongate bulbous. Free oviduct short, cylindrical.

***Radula*** (Fig. 5A). Teeth arranged in wide-angle U-shape with half row formula: 1–(11–12)–62 teeth. Central tooth symmetrical tricuspid with pointed cusps; mesocone large lanceolate; ectocones smaller. Lateral teeth asymmetrical tricuspid; mesocone large with pointed cusp; ectocone larger than endocone, located in middle of tooth; endocone very small, located near tip. Marginal teeth obliquely bicuspid, starting around tooth number 11 or 12. Inner marginal teeth elongate bicuspid with lanceolate endocone and small ectocone. Outermost marginal teeth gradually reduced in size.

**Distribution.**− *Siamochlamys panhai* gen. et sp. nov. can be found from two localities. The type locality is situated on the western side of an isolated limestone hill that is covered by bamboo forest (Fig. 1). It also occurs on limestone outcrops at Si Samrong District, Sukhothai Province, about 50 km southeast of the type locality. The occurrence of this new species between the two limestone areas is expected (Fig. 1).

**Remarks.**− The generic assignment of several Indochinese *Macrochlamys* species with medium shell size and unknown genitalia is unclear. These species include *M. excepta* (Mabille, 1887), *M. zero* (Mabille, 1887), *M. callojuncta* Ancey, 1898, and *M. brunnea* Möllendorff, 1902. *Siamochlamys panhai* gen. et sp. nov. can be distinguished from these equivocal species by having a wider and larger umbilicus that shows the preceding whorl, while these Indochinese *Macrochlamys* species have a narrow and small umbilicus, and columellar margin generally reflected over the umbilicus (see Pholyotha et al., 2018, 2020a, b, c; Inkhavilay et al., 2019).

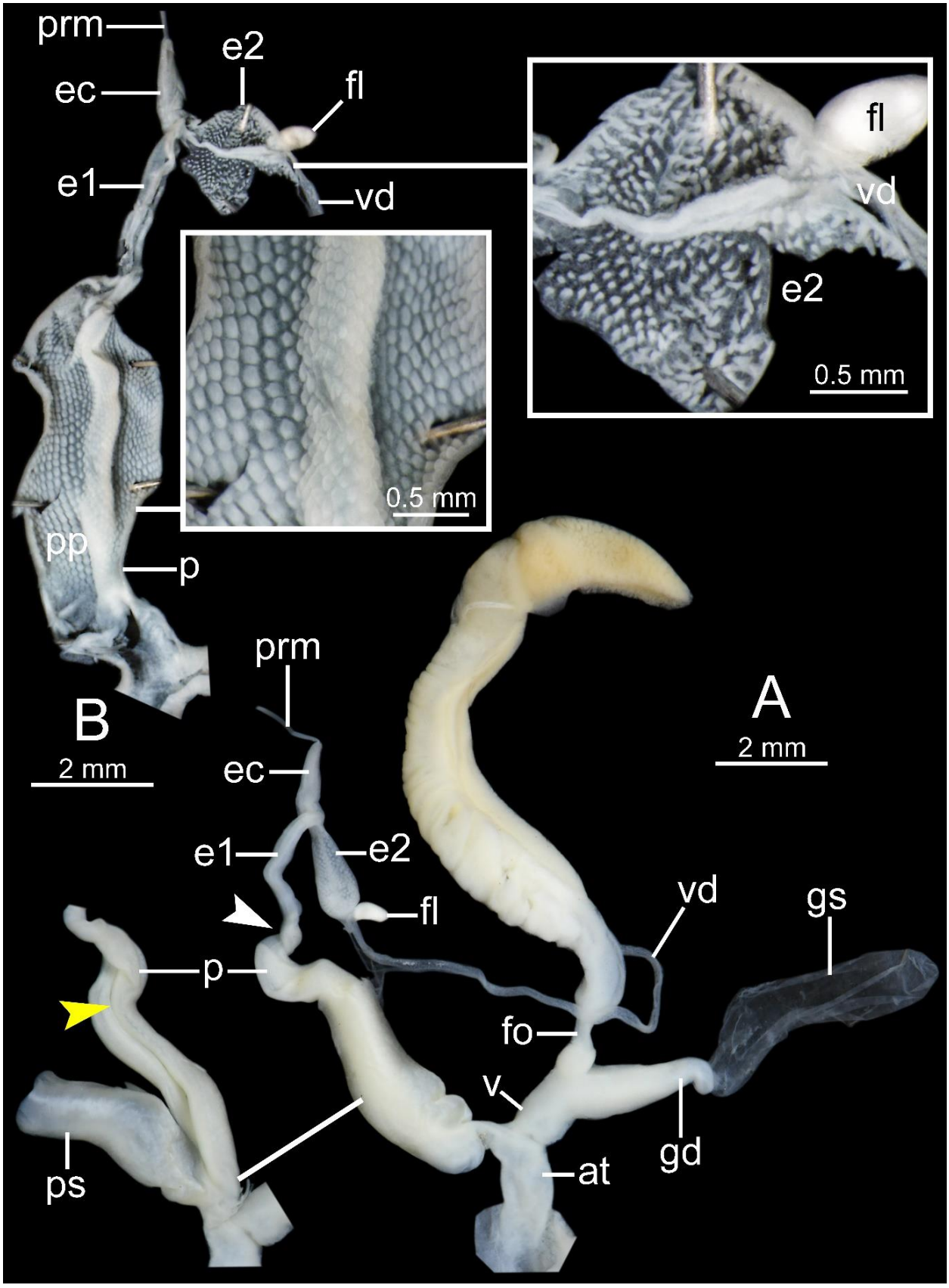


**FIGURE 4.** Genitalia of *Siamochlamys panhai* gen. et sp. nov. paratype CUMZ 14211. **A.** general view of genital system. **B.** internal structure of penis and epiphallus. White arrow indicates the end of the penis. Yellow arrow indicates longitudinal groove on penis after penial sheath is removed.

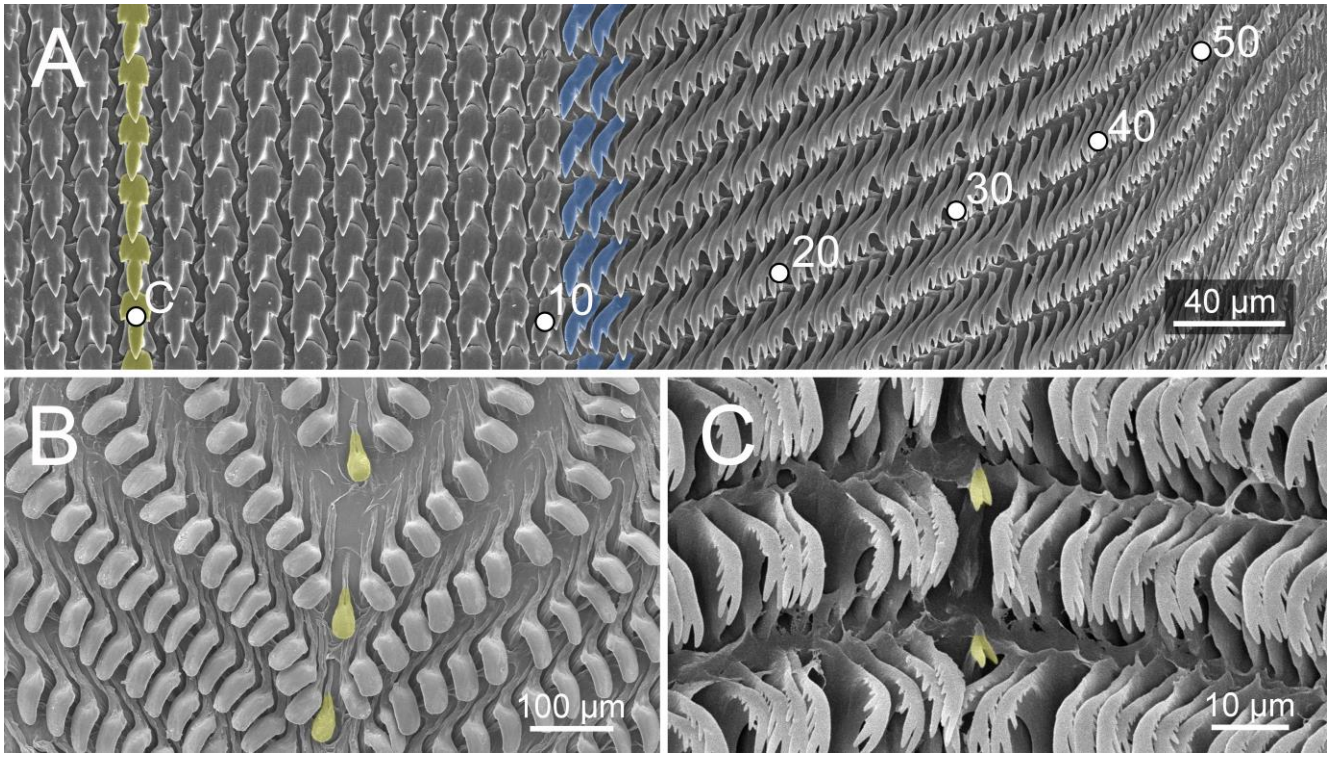


**FIGURE 5.** SEM images of radula. **A.** radula of *Siamochlamys panhai* gen. et sp. nov. paratype CUMZ 14211. **B.** radula of *Aenigmatoconcha clivicola* Tumpeesuwan & Tumpeesuwan, 2017 specimen CUMZ 7928. **C.** radula of *Durgella levicula* (Benson, 1859) specimen CUMZ 14245. Central tooth indicated by 'C'; yellow colour indicates central tooth row; blue colour indicates the transition from lateral to marginal teeth.

## CONCLUSION

There are 10 genera of Ariophantidae and 9 genera of Helicarionidae in Thailand plus a new genus proposed herein. Assigning genera to these families remains difficult because the molecular phylogeny of the Thai Ariophantidae and Helicarionidae has not yet been resolved. Therefore, a comprehensive revision using comparative morpho-anatomy and molecular phylogenetics will be necessary to clarify their systematic classification.

Based on the known distribution ranges and habitats, all of the *Aenigmatoconcha* species, most of the *Taphrenalla* species, and some species of the genera *Macrochlamys*, *Sarika*, and *Sesara* Albers, 1860 are restricted to karst ecosystems (Tanmuangpak et al., 2017; Pholyotha et al., 2018, 2020a, b, c, 2021a, b, c). This study has also revealed the endemic land snail taxon *Siamochlamys panhai* gen. et sp. nov. living in Thai limestone karsts, confirming the importance of limestone karsts for speciation and endemism of malaco-fauna and as refugia for the snails in disturbed areas.

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## LITERATURE CITED

American Veterinary Medical Association. 2020. AVMA Guidelines for the Euthanasia of Animals: 2020 Edition. https://www.avma.org/sites/default/files/2020-01/2020-Euthanasia-Final-1-17-20.pdf [accessed 12 Feb 2020]

Ancey, C.F. 1887. Description of new genera or subgenera of Helicidæ. The Conchologists' Exchange 1(9–10): 53–54, 1(12): 75–76; 2(3): 38–39.

Ancey, C.F. 1898. Notes malacologiques. A – Observations sur les mollusques terrestres et fluviatiles recueillies dans l'Indo-Chine et particulièrement au Laos. B – Descriptions d'espèces nouvelles du centre de l'Afrique. C – Notes sur quelques coupes génériques ou sous-génériques de Mollusques. D – Description d'un mollusque méditerranéen nouveau. Bulletin du Musée d'Histoire Naturelle de Marseille, Série II 1(1): 125–150.

Benson, W.H. 1859. New Helicidae collected by W. Theobald, Esq., jun., in Burmah and the Khasia Hills, and described by W.H. Benson. Annals and Magazine of Natural History series 3, 3: 387–393.

Bhosale, A.R., Muley, D.V., Yadav, O.V. and Raheem, D.C. 2019. Re-description of the land snail *Eurychlamys platychlamys* (Blanford, 1880) (Pulmonata: Helicarionidae) from the Western Ghats of India. Archiv für Molluskenkunde, 148: 117–128. https://doi.org/10.1127/arch.moll/148/117-128

Blanford, W.T. and Godwin-Austen, H.H. 1908. Mollusca: Testacellidae and Zonitidae. In: Bingham C.T. (ed.) The Fauna of British India including Ceylon and Burma. Taylor and Francis, London.

Blanford, W.T. 1881. Contributions to Indian malacology, No. XII. Descriptions of new land and freshwater shells from Southern and Western India, Burmah, the Andaman Islands, &c. Journal of the Asiatic Society of Bengal, 49 [1880] (4): 181–222. https://www.biodiversitylibrary.org/page/43119260

Bouchet, P., Rocroi, J.-P., Hausdorf, B., Kaim, A., Kano, Y., Nützel, A., Parkhaev, P., Schrödl, M. and Strong, E.E. 2017. Revised classification, nomenclator and typification of gastropod and monoplacophoran families. Malacologia, 61(1–2): 1–526. https://doi.org/10.4002/040.061.0201

Bourguignat, J.R. 1877. Description de deux nouveaux genres algériens, suivie d'une classification des familles et des genres de Mollusques terrestres et fluviatiles du système européen. Bulletin de la Société des Sciences physiques et naturelles de Toulouse, 3(1): 49–101.

Chiba, S. 2004. Ecological and morphological patterns in communities of land snails of the genus *Mandarina* from the Bonin Islands. Journal of Evolutionary Biology, 17: 131–143. https://doi.org/10.1046/j.1420-9101.2004.00639.x

Godwin-Austen, H.H. 1883, 1888, 1899, 1907, 1908 [1882-1920]. Land and freshwater Mollusca of India, including South Arabia, Baluchistan, Afghanistan, Kashmir, Nepal, Burmah, Pegu, Tenasserim, Malay Peninsula, Ceylon, and other islands of the Indian Ocean. Supplementary to Messrs. Theobald and Hanley's Conchologia Indica. London, Taylor & Francis.

Gray, J.E. 1847. A list of the genera of recent Mollusca, their synonyma and types. Proceedings of the Zoological Society, 15: 129–182.

Haase, M. and Misof, B. 2009. Dynamic gastropods: Stable shell polymorphism despite gene flow in the land snail *Arianta arbustorum*. Journal of Zoological Systematics and Evolutionary Research, 47: 105–114. https ://doi.org/10.1111/j.1439-0469.2008.00488.x

Hausdorf, B. 1998. Phylogeny of the Limacoidea sensu lato (Gastropoda: Stylommatophora). Journal of Molluscan Studies, 64: 35–66.

Hausdorf, B. 2000. Biogeography of the Limacoidea sensu lato (Gastropoda: Stylommatophora): vicariance events and long-distance dispersal. Journal of Biogeography, 27: 379–390.

Hemmen, J. and Hemmen, C. 2001. Aktualisierte Liste der terrestrischen Gastropoden Thailands. Schriften zur Malakozoologie, 18: 35–70.

Hyman, I.T., Ho, Y.W.S. and Jermiin, L.S. 2007. Molecular phylogeny of Australian Helicarionidae, Euconulidae and related groups (Gastropoda: Pulmonata: Stylommatophora) based on mitochondrial DNA. Molecular Phylogenetics and Evolution, 45: 792–812. https://doi.org/10.1016/j.ympev.2007.08.018

Hyman, I.T. and Ponder, W.F. 2010. A morphological phylogenetic analysis and generic revision of Australian Helicarionidae (Gastropoda: Pulmonata: Stylommatophora), and an assessment of the relationships of the family. Zootaxa, 2462: 1–148.

Inkhavilay, K., Sutcharit, C., Bantaowong, U., Chanabun, R., Siriwut, W., Srisonchai, R., Pholyotha, A., Jirapatrasilp, P. and Panha, S. 2019. Annotated checklist of the terrestrial molluscs from Laos (Mollusca, Gastropoda). ZooKeys, 834: 1–166. https://doi.org/10.3897/zookeys.834.28800

Khalik, M.Z., Bozkurt, E. and Schilthuizen, M. 2020. Morphological parallelism of sympatric cave-dwelling microsnails of the genus *Georissa* at Mount Silabur, Borneo (Gastropoda, Neritimorpha, Hydrocenidae). Journal of Zoological Systematics and Evolutionary Research, 58: 648– 661. https://doi.org/10.1111/jzs.12352

Mabille, J. 1887. Molluscorum Tonkinorum diagnoses. Meulan.

Möllendorff, von O. 1902. Binnenmollusken aus Hinterindien. 2. Neue Arten und Unterarten von Fruhstorfer in Siam gesammelt. Nachrichtsblatt der Deutschen Malakozoologischen Gesells chaft, 34: 153–160.

MolluscaBase. 2022. MolluscaBase. Helicarionoidea Bourguignat, 1877. Available from https://www.molluscabase.org/aphia.php?p=taxdetails&id=867820 [accessed 5 Mar. 2022].

Okajima, R. and Chiba, S. 2009. Cause of bimodal distribution in the shape of a terrestrial gastropod. Evolution, 63(11): 2877–2887. https ://doi.org/10.1111/j.1558-5646.2009.00780.x

Páll-Gergely, B., Fehér, Z., Otani, J.U. and Asami, T. 2016. An integrative taxonomic approach to infer the systematic position of *Chalepotaxis* Ancey, 1887 (Gastropoda: Stylommatophora: Helicarionidae). Molluscan Research, 37: 113–119. https://doi.org/ 10.1080/13235818.2016.1234996

Panha, S. 1996. A checklist and classification of the land terrestrial pulmonate snail in Thailand. Walkerana, 8: 31–40.

Pholyotha, A., Sutcharit, C. and Panha, S. 2018. The land snail genus *Macrochlamys* Gray, 1847 from Thailand, with descriptions of five new species (Pulmonata: Ariophantidae). Raffles Bulletin of Zoology, 66: 763–781.

Pholyotha, A., Sutcharit, C., Thach, P., Chhuoy, S., Ngor, P.B. and Panha, S. 2020a. Land snail genus *Sarika* Godwin-Austen, 1907 (Eupulmonata: Ariophantidae) from Cambodia, with description of three new species. European Journal of Taxonomy, 674: 1–21. https://doi.org/10.5852/ejt.2020.674

Pholyotha, A., Sutcharit, C., Tongkerd, P., Lin, A. and Panha, S. 2020b. Taxonomic revision of the land snail genera *Macrochlamys* Gray, 1847 and *Sarika* Godwin-Austen, 1907 (Eupulmonata: Ariophantidae) from Southeastern Myanmar, with descriptions of three new species. Molluscan Research, 40: 183–204. https://doi.org/10.1080/13235818.2020.1723041

Pholyotha, A., Sutcharit, C., Tongkerd, P. and Panha, S. 2020c. Integrative taxonomic revision of the land snail genus *Sarika* Godwin-Austen, 1907 in Thailand, with descriptions of nine new species (Eupulmonata, Ariophantidae). ZooKeys, 976: 1–100. https://doi.org/10.3897/zookeys.976.53859

Pholyotha, A., Sutcharit, C. and Panha, S. 2021a. Rediscovering the dancing semislug genus *Cryptosemelus* Collinge, 1902 (Eupulmonata, Ariophantidae) from Thailand with description of two new species. ZooKeys, 1076: 43–65. https://doi.org/10. 3897/zookeys.1076.75576

Pholyotha, A., Sutcharit, C., Tongkerd, P., Jeratthitikul, E. and Panha, S. 2021b. Integrative systematics reveals the new land-snail genus *Taphrenalla* (Eupulmonata: Ariophantidae) with a description of nine new species from Thailand. Contributions to Zoology, 90: 21–69. https://doi.org/10.1163/18759866-bja 10013

Pholyotha, A., Sutcharit, C., Tongkerd, P. and Panha, S. 2021c. Systematic revision of the limestone karst-restricted land snail genus *Aenigmatoconcha* (Eupulmonata: Helicarionidae), with description of a new species. European Journal of Taxonomy, 767: 55–82. https://doi.org/10.5852/ejt.2021.767.1487

Pholyotha, A., Sutcharit, C., Lin, A. and Panha, S. 2022. Uncovering local endemism from southeastern Myanmar: description of the new karst-associated terrestrial snail genus *Burmoch-*

*lamys* (Eupulmonata, Helicarionidae). ZooKeys, 1110: 1–37. https://doi.org/10.3897/zookeys.1110.82461

Schileyko, A.A. 2002. Treatise on recent terrestrial pulmonate molluscs. Part 9. Helicarionidae, Gymnarionidae, Rhysotinidae, Ariophantidae. Ruthenica, supplement 2: 1167–1307.

Schileyko, A.A. 2003. Treatise on recent terrestrial pulmonate molluscs. Part 10. Ariophantidae, Ostracolethidae, Ryssotidae, Milacidae, Dyakiidae, Staffordiidae, Gastrodontidae, Zonitidae, Daudebardiidae, Parmacellidae. Ruthenica, supplement 2: 1309–1466.

Schilthuizen, M., Til, A.V., Salverda, M., Liew, T.S., James, S.S., Elahan, B.B. and Vermeulen, J.J. 2006. Microgeographic evolution of snail shell shape and predator behavior. Evolution, 60: 1851–1858. https://doi.org/10.1111/j.0014-3820.2006.tb00528.x

Solem, A. 1966. Some non-marine mollusks from Thailand. Spolia Zoologia Musei Hauniensis, 24: 1–110.

Sutcharit, C., Jeratthitikul, E., Pholyotha, A., Lin, A. and Panha, S. 2020. Molecular phylogeny reveals high diversity and ende--mism in the limestone karst-restricted land snail genus *Sophina* Benson, 1859 from Myanmar (Eupulmonata: Helicar-ionidae), with description of four new species. Journal of Zoological Systematics and Evolutionary Research, 58: 957–981. https://doi.org/10.1111/jzs.12420

Sutcharit, C. and Panha, S. 2021. Systematic review of the dextral *Hemiplecta* Albers, 1850 (Eupulmonata, Ariophantidae) from Thailand with description of a new species and list of all the Indochinese species. ZooKeys, 1047: 101–154. https://doi.org/10.3897/zookeys.1047.65735

Sutcharit, C., Jeratthitikul, E., Tongkerd, P. and Panha, S. 2021. Reassessment and systematic position of the sinistral snails of genus *Hemiplecta* from Thailand (Eupulmonata: Ariophantidae), with description of two new species. Contributions to Zoology, 90: 183–215. https://doi.org/10.1163/18759866-BJA10016

Theobald, W. 1859. Descriptions of some new Burmese and Indian Helicidae with remarks on some previously described species. Journal of the Asiatic Society of Bengal, 28: 305–309.

Tanmuangpak, K., Tumpeesuwan, C. and Tumpeesuwan, S. 2017. A new species of *Sesara* Albers, 1860 from northeastern Thailand (Stylommatophora: Helicarionidae). Molluscan Research, 37:1–7. https://doi.org/10.1080/13235818.2016.1155431

Tumpeesuwan, C. and Tumpeesuwan, S. 2017. Discovery of an overlooked helicarionid land snail (Helicarionidae: Durgellinae) from northeastern Thailand, with description of a new genus and new species, and a note on radula morphology and genital system. Raffles Bulletin of Zoology, 65: 174–181.

Tumpeesuwan, C. and Tumpeesuwan, S. 2019. *Muangnua arborea*, a new semislug (Gastropoda, Stylommatophora, Helicarionidae, Durgellininae) from Loei Province, northeastern Thailand. ZooKeys, 894: 19–32. https://doi.org/10.3897/zookeys.894.38327