

Hidden Lineages in the Mountains: The Genus *Glyptaulax* Gude, 1914 and *Maelamaodiscus* gen. nov. (Heterobranchia: Stylommatophora: Charopidae and Ariophantidae) with Description of Two New Species from Western Thailand

CHIRASAK SUTCHARIT* AND ARTHIT PHOLYOTHA

Animal Systematics Research Unit, Department of Biology, Faculty of Science, Chulalongkorn University, Bangkok 10330, THAILAND

*Corresponding author. Chirasak Sutcharit (jirasak4@yahoo.com; chirasak.s@chula.ac.th)

Received: 2 August 2022; Accepted: 27 October 2022

<http://zoobank.org/urn:lsid:zoobank.org:pub:DDE2F560-FA61-4083-8C64-CCCB00ADB96>

ABSTRACT.– The Tenasserim Range runs from north to south and forms not only a natural border between Thailand and Myanmar, but also the backbone of the Indo-Burma biodiversity hotspot, which is rich in endemic species, especially of the malacofauna. Knowledge of land snail diversity in Thailand is continuously expanding and being refined, and various groups have been revised recently. From field surveys throughout the country, unique snails with delicate shell shape and sculpture hidden in mountainous areas have been discovered and described. Firstly, a new species of the Charopidae, *Glyptaulax spectabilis* sp. nov. has round tubercles arranged on spiral ridges. Second, *Maelamaodiscus somsakpanhai* gen. et sp. nov. of the Ariophantidae is described from the Moei River Basin. These new taxa differ from all Southeast Asian ariophantids by having a prominent radial ridge, peculiar aperture with wide sinulus, and an impression on the last whorl. This discovery of endemic taxa reflects the high biodiversity in this region, and suggests that many more land snail treasures are still waiting to be revealed.

KEYWORDS: endemism, limestone, Pulmonata, systematics, Tenasserim Range

INTRODUCTION

The Tenasserim Range is part of the Indo-Malayan Mountain system of Southeast Asia (Laudee and Malicky, 2018; Poyarkov et al., 2018), and runs from north to south, forming the backbone of the Indo-Burma biodiversity hotspot (Myers et al., 2000; Critical Ecosystems Partnership Fund, 2012). It has complex biogeography and has long been considered species-rich in vertebrate groups (e.g., Clements et al., 2006; Grismer et al., 2018, 2021; Chomdej et al., 2021; Poyakov et al., 2022), but has received comparatively little attention for its invertebrate fauna. Thus, ongoing fieldwork along the Tenasserim Range in western Thailand continues to bring to light new land snails, particularly in speciose but less explored groups, i.e., Helicarionoidea Bourguignat, 1877 and Punctoidea Morse, 1864. Even though these taxa are among the dominant groups of land snails in such a species-rich ecosystem, they have often been overlooked. This is likely due to the absence of comprehensive surveys like those done for various vertebrate groups; also, many of the land snails are extremely difficult to distinguish.

Over the last century, the prevailing classification of the land snails (Heterobranchia) in the Indo-Burma region has followed the classic publications of Godwin-Austen (1882–1920), Blanford and Godwin-Austen (1908), and Gude (1914). In this early litera-

ture, only a handful of spirit specimens of the Helicarionoidea and Punctoidea were examined and published, and instead, the collections that were studied were mainly composed of empty shells. However, the most variable and taxonomically informative characters are found in the morphology of the male and female reproductive organs and the spermatophores (i.e., Páll-Gergely et al., 2016; Hyman et al., 2017; Hyman and Köhler, 2018; Pholyotha et al., 2020b, 2021b; Sutcharit et al., 2020, 2021). Still, the shell morphology offers diagnostic characters in some genera, i.e., *Sesara* Albers, 1860, *Glyptaulax* Gude, 1914 and *Teraia* Solem, 1966, with their ridges or coarse shell surfaces, widely opened umbilicus, and unique apertural barriers (Schileyko, 2001, 2002, 2003).

One enigmatic genus of the Charopidae Hutton, 1884 known from Indo-Burma, with medium shell size and elaborate shell sculpture is *Glyptaulax*. The genus was originally nominated to include only the type species; no other information or additional species have been reported since then (Gude, 1914; Thiele, 1929; Zilch, 1959). This has created some anticipation for a second species in the genus to be found from the Tenasserim Range, and it should be recognizable by distinctive shell sculptures (Schileyko, 2001). In addition, the past two decades have seen impressive progress in the systematic review of the snails of Thailand, particularly the helicarionoidids. Several ariophantid groups with helicoid, smooth and polished shells have been systematically studied and revised,

TABLE 1. Key characters of shells and genitalia of some Indochinese ariophantid and charopid genera that have a small to medium shell size and that possess ribbed shells. The familial classification follows Schileyko (2002, 2003) and Bouchet et al. (2017). ? = data not available.

	Ariophantidae			Charopidae		
	<i>Sesara</i> Albers, 1860	<i>Khasiella</i> Godwin-Austen, 1899	<i>Teraia</i> Solem, 1966	<i>Maelamaodiscus</i> gen. nov.	<i>Glyptaulax</i> Gude, 1914	<i>Thysanota</i> Albers, 1860
type species	<i>Helix infrendens</i> Gould, 1844	<i>Helix vidua</i> Hanley and Theobald, 1876	<i>Teraia thailandica</i> Solem, 1966	<i>Maelamaodiscus somsakpanhai</i> gen. et sp. nov.	<i>Helix artificiosa</i> Benson, 1856	<i>Helix guerini</i> Pfeiffer, 1842
peristomal lip	thickened	simple	simple	thickened and little expanded at base	simple	simple
apertural dentition	present / absent ¹	absent	absent	absent	absent	absent
umbilicus	imperforate	perforate	umbilicate	widely umbilicate	perforate	umbilicate
shell shape	depressed to dome shape	depressed to dome shape	depressed conic	flattened to depressed	subdiscoid	trochoid to dome shape
shell sculpture	smooth radial ridges or smooth ²	smooth radial ridges, smooth	smooth radial ridges	serrate radial ridges	serrate spiral ridges	smooth radial ridges
dart apparatus	absent	present	present	present	?	?
epiphallic caecum	straight / coiled ³	coiled	absent	straight	?	?
attachment of retractor muscle	middle or tip of epiphallic caecum ⁴	middle of epiphallic caecum	epiphallus	tip of epiphallic caecum	?	?
flagellum	present	present	present	present	?	?
references	Blanford and Godwin-Austen, 1908; Solem, 1966; Tanmuangpak et al., 2017	Blanford and Godwin-Austen, 1908; Schileyko, 2002	Solem, 1966; Schileyko, 2003	this study	Gude, 1914; Schileyko, 2001	Gude, 1914; Schileyko, 2001

¹*Sesara galea* (Benson, 1859), *Sesara inermis* Theobald, 1876b and *Sesara annamitica* (Möllendorff, 1900) have no apertural dentition (MolluscaBase, 2022).

²*Sesara inermis* Theobald, 1876b and *Sesara triodon* Tanmuangpak & Tumpeesuwan, 2017 have smooth and polished shell surface (MolluscaBase, 2022).

³*Sesara parva* Solem, 1966 have a coiled epiphallic caecum (Solem, 1966).

⁴Attached at tip of epiphallic caecum in *Sesara infrendens* (Gould, 1844) and at middle of epiphallic caecum in *Sesara parva* (Solem, 1966).

with the addition of many new species (i.e., Pholyotha et al., 2018, 2020a, b, c, 2021a, b, 2022; Sutcharit et al., 2020). The coarse and discoidal shell and unique shape of the aperture of an unfamiliar ariophantid taxon first became known to us in material collected from the limestone karsts in the vicinity of the Tenasserim Range, western Thailand. They show several shell morphological characteristics that do not conform to any generic definition of the Ariophantidae, for example, a coarse, discoidal shell, apertural lip expanded, and dorsal side descending. Because no existing generic name applies to these unique shells, a new genus is established herein.

The Animal Systematics Research Unit of Chulalongkorn University (ASRU), is currently engaged in revising the land snails in the Kingdom of Thailand, based on an integrative approach involving morphological and anatomical studies and DNA barcoding. Our efforts have focused on extensive fieldwork for collecting fresh materials, reviewing new morphological and molecular data, and addressing the taxonomic

status of every existing taxon by re-examining the types and/or authenticated specimens available in well-known natural history museums (i.e., Nantararat et al., 2014; Sutcharit et al., 2015, 2019, 2021; Sutcharit and Panha, 2021; Jirapatrasilp et al., 2022). This study formally describes a new species of the charopid genus *Glyptaulax* as well as a new genus and new species of the ariophantids as part of our ongoing effort towards a complete revision of the land snail fauna of the Kingdom of Thailand.

MATERIALS AND METHODS

Zoology collection. Additional specimens from Myanmar were collected under an MOU between the Forest Department, Ministry of Natural Resources and Environmental Conservation and Forestry, Myanmar, and Fauna & Flora International, Myanmar, from 2015 to 2017. Snails were collected by direct visual searching and hand collecting from all accessible localities,

mainly among limestone habitats along the Tenasserim Range from Tak Province to Kanchanaburi Province. Snails were then euthanized following the standard two-step protocol (American Veterinary Medical Association, 2020) and preserved in 95% (v/v) ethanol for further morphological and molecular work.

Species identification was made based on literature (i.e., Godwin-Austen, 1882–1920; Blanford and Godwin-Austen, 1908; Gude, 1914) and then compared with the available reference collection at the Natural History Museum in London. For the descriptive work, adult shells and genitalia were photographed. Adult shells were measured for size using a vernier caliper. All preserved specimens (spirit specimens) were dissected and examined under a stereo microscope. Radulae were extracted, soaked in 10% (w/v) sodium hydroxide, cleaned with distilled water, and then imaged by scanning electron microscopy (SEM; JEOL, JSM-6610 LV).

Abbreviations

CUMZ	Chulalongkorn University Museum of Zoology, Bangkok
NHMUK	The Natural History Museum, London
UMZC	University Museum of Zoology, Cambridge University, Cambridge

RESULTS

Taxonomy

Superfamily Punctoidea Morse, 1864

Family Charopidae Hutton, 1884

Subfamily Thysanotinae Godwin-Austen, 1907

Genus *Glyptaulax* Gude, 1914

Type species.— *Helix artificiosa* Benson, 1856, by original designation.

Diagnosis.— Uniquely characterized among all other SE Asiatic Charopidae by shell small, subdiscoidal, and light yellowish or corneous color. Protoconch with radial ridges. Shell surface above periphery consists of tubercles arranged in spiral ridges; below periphery consists of smooth spiral ridges. Aperture lunate and lip simple. Umbilicus widely opened and deep.

Remarks.— A '*Glyptaulax* sp.' (= *Glyptaulax* 'tempurung 1' in Foon et al., 2017: 66, fig. 25d) has been reported from Perak, Peninsular Malaysia. This unidentified and unnamed species seems to represent an intermediated form between *Glyptaulax* s.s. and *Sundacharopa* Vermeulen and Liew, 2022 (Charopidae), and

could possibly be recognized as its own genus. The presence of spiral ridge sculptures is shared among these three taxa, while a tiny shell size (width less than 2 mm) and sealed umbilicus possibly make '*Glyptaulax* sp.' more closely related to *Sundacharopa* (Vermeulen and Liew, 2022). In addition, a large shell size (width about 15 mm), with tubercles arranged on spiral ridges above the periphery and a widely opened umbilicus are the unique characteristics distinguishing *Glyptaulax* s.s. from '*Glyptaulax* sp.' and *Sundacharopa*. Based on these distinct synapomorphic traits, we have excluded '*Glyptaulax* sp.' (sensu Foon et al., 2017) from possible membership in *Glyptaulax* s.s. However, additional specimens and further examination of the genitalia anatomy and molecular phylogeny will clarify their relationship.

Currently, the genus *Glyptaulax* is comprised of the type species and a new species described herein. It is probably endemic to the Tenasserim Range both in Myanmar and Thailand. The genus is generally defined by its unique shell sculpture and without mention of the soft anatomy, which has made the higher classification of the genus provisional (Table 1). Originally, Gude (1914) placed *Glyptaulax* together with the other oriental genera under the Endodontidae (Thysanotinae), probably due to the unique shell sculpture. Later, Thiele (1929) united the Thysanotinae together with the Endodontinae and placed *Glyptaulax* under the Endodontidae (Endodontinae), which was followed by Zilch (1959). More recently, Schileyko (2001) followed the original classification by Gude (1914). However, the recently revised classification of the gastropods by Bouchet et al. (2017) and the Mollusca Base (2022) database both place *Glyptaulax* under the Charopidae (Thysanotinae), and this classification has been adopted in this study.

Glyptaulax artificiosa (Benson, 1856)

(Figs 1, 2A, B)

Helix artificiosa Benson, 1856: 249, 250. Type locality: ad Phie Than vallis Tenasserim. Theobald, 1857: 250. Pfeiffer, 1859: 178. Pfeiffer, 1860: 131, 132, pl. 36, figs 8–10. Hanley and Theobald, 1872: 26, pl. 55, fig. 3. Tryon, 1887: 33, pl. 7, fig. 82. Preece et al., 2022: 143, 144, fig. 63c–e.

Macrochlamys (?) *artificiosa*—Theobald, 1876a: 19.

Nanina artificiosa—Nevill, 1878: 54.

Glyptaulax artificiosa—Gude, 1914: 14.

Material examined.— Syntypes UMZC I.103035.A (4 shells) from Burmah. Specimens NHMUK 1888.12.4. 629–631 (3 shells; Fig. 2B) from Phaiethan Hill. NHMUK 1906.2.2.160 (2 shells; Fig. 2A) ex. W.T.

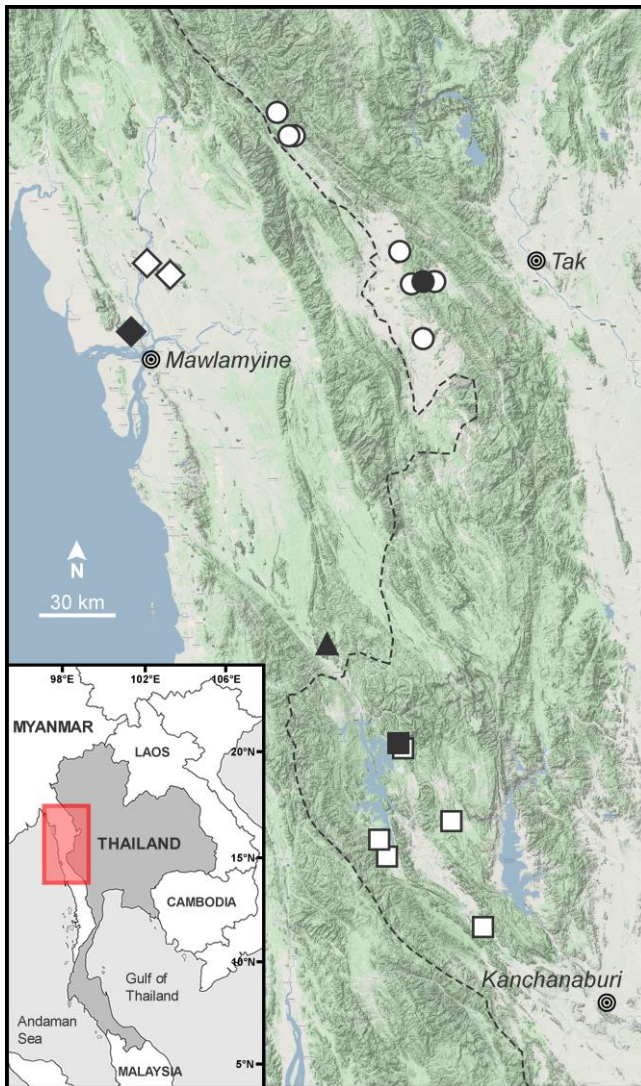


FIGURE 1. Distribution map of *Glyptaulax artificiosa* (triangle), *Glyptaulax spectabilis* sp. nov. (square), *Maelamaodiscus somsakpanhai* gen. et sp. nov. (circle), and *Maelamaodiscus atkinsoni* (diamond). Each filled symbol indicates approximate type locality of its respective taxon.

Blanford collection from Tenasserim Valley. NHMUK (2 shells) ex. H.F. Blanford collection from Tenasserim Valley.

Description.— Shell small (shell width up to 15.0 mm, shell height up to 7.0 mm), discoidal to subdiscoidal and rather solid. Shell color light yellowish or corneous; periostracum thin corneous. Spire little elevated; suture wide and impressed. Whorls 6–7, increasing regularly and not descending. Protoconch about 2 whorls, with very weak tubercles arranged on radial ridges. Last whorl with large and rounded periphery. Shell surface with delicate sculpture: above periphery (penultimate whorl) bears elongate tubercles arranged in about five rows of spiral ridges; below periphery (from upper to lower junction of peristome)

consists of about ten spiral ridges, first to sixth ridges very strong and distinct, then gradually weaker and disappearing around umbilical area. Aperture lunate; parietal callus thin. Peristome continuous; lip simple to slightly thickened; below periphery lip very little expanded. Columella margin short, straight and little thickened. Umbilicus widely opened and deep.

Distribution.— This species is probably restricted to the limestone karsts in Kayin State, Myanmar; no further specimens with precise locality have been reported after the original description (Fig. 1).

Remarks.— In the original description, Benson (1856) clearly stated that the specimen examined was provided by W. Theobald, but the number of the type series was not stated other than one set of shell measurements. The catalog of Benson's type specimens in Cambridge University lists four syntypes and one of them is illustrated (Preece et al., 2022).

***Glyptaulax spectabilis* sp. nov.**

<http://zoobank.org/urn:lsid:zoobank.org:act:36986DD5-1E77-46A8-A496-23CA33D8190C>
(Figs 1, 2C, D)

Type material.— Holotype CUMZ 5485/1 (Fig. 2D) from the type locality. Paratypes CUMZ 5185/2 (6 shells; Fig. 2C), CUMZ 5184 (11 shells), CUMZ 5186 (9 juvenile shells) and NHMUK (2 shells), and all from the type locality.

Other material examined.— **THAILAND:** Limestone karsts at Khao Khat (Hellfire Pass, Thai-Burma Railway), Sai Yok District, Kanchanaburi Province (14°21'18.9"N, 98°57'08.8"E): CUMZ 5280 (1 juvenile shell). Wat Pak Lam Pilok, Thong Pha Phum District, Kanchanaburi Province (14°37'46.1"N, 98°34'27.1"E): CUMZ 5281 (1 shell). Limestone karsts at Sahakon Nikhom Village, Thong Pha Phum District, Kanchanaburi Province (14°45'05.2"N, 98°48'42.5"E): CUMZ 5279 (1 shell). Limestone outcrop at Wat Tham Khao Noi, Thong Pha Phum District, Kanchanaburi Province (14°41'52.8"N, 98°31'31.8"E): CUMZ 5182 (2 shells). Ka Teng Cheng Waterfall, Sangkhla Buri District, Kanchanaburi Province (15°01'20.9"N, 98°35'49.5"E): CUMZ 5183 (4 shells + 5 broken shells).

Type locality.— A small limestone outcrop at Wat Pa Tham Sukho, Sangkhla Buri District, Kanchanaburi Province, Thailand (15°02'14.4"N, 98°34'57.7"E). The locality is within a limestone forest near a small village.

Etymology.— The specific name is from the Latin word '*spectabilis*' meaning 'notable or remarkable', and

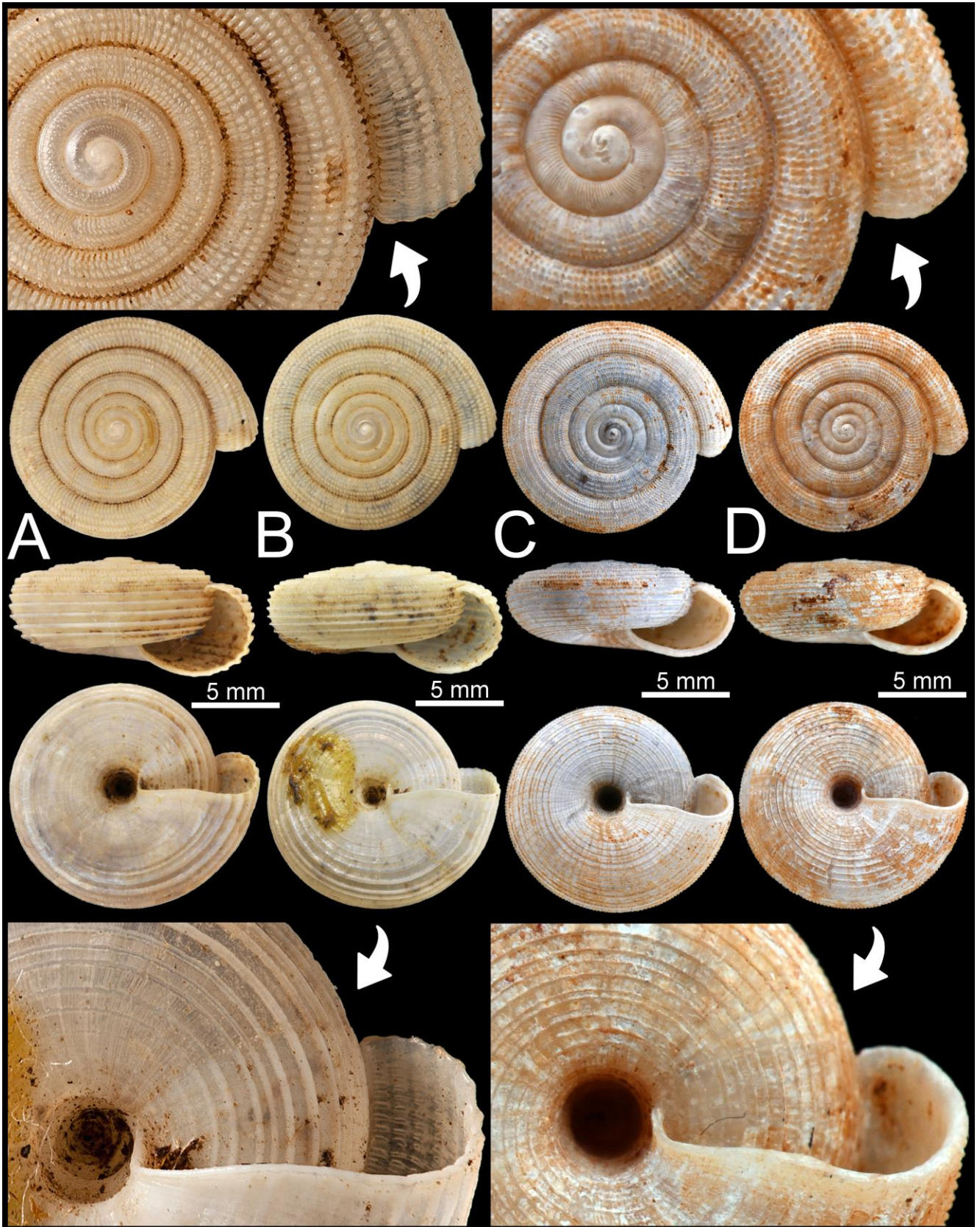


FIGURE 2. Shell morphology. **A, B.** *Glyptaulax artificiosa* (Benson, 1856), **A.** specimen NHMUK 1906.2.2.160 from Tenasserim Valley and **B.** specimen NHMUK 1888.12.4.629–631 from Phaiethan Hill with magnification of apex and umbilicus. **C, D.** *Glyptaulax spectabilis* sp. nov., **C.** paratype CUMZ 5185/2 from Tham Sukho, Kanchanaburi, and **D.** holotype CUMZ 5185/1 from the type locality with magnification of apex and umbilicus.

TABLE 1. Shell measurements of *Glyptaulax spectabilis* sp. nov. and *Maelamaodiscus somsakpanhai* gen. et sp. nov. from several localities.

Locality and CUMZ nos.	No. of specimens	Range, mean \pm S.D. (mm)		
		Shell width	Shell height	H/W ratio
<i>Glyptaulax spectabilis</i> sp. nov.				
Wat Pa Tham Sukho, Sangkhla Buri, Kanchanaburi: 5184, 5185/1, 5185/2	19	11.0–13.1	4.7–5.9	0.43–0.50
		11.80 \pm 0.67	5.40 \pm 0.34	0.46 \pm 0.02
Ka Teng Cheng Waterfall, Sangkhla Buri, Kanchanaburi: 5183	4	11.3–12.5	4.9–5.5	0.43–0.44
		11.34 \pm 0.55	5.19 \pm 0.29	0.44 \pm 0.01
<i>Maelamaodiscus somsakpanhai</i> gen. et sp. nov.				
Phra Wor Shine, Mae Sod, Tak: 5284, 5286, 5287, 5288, 5300/2	11	11.5–13.7	4.6–7.2	0.39–0.60
		12.40 \pm 0.54	5.94 \pm 0.67	0.48 \pm 0.05
Wat Phothikun, Mae Sod, Tak: 5290	10	10.3–12.0	5.3–6.1	0.47–0.53
		11.22 \pm 0.49	5.71 \pm 0.26	0.51 \pm 0.02
Wat Phratat Rattana Chedi, Tha Song Yang, Tak: 5291	5	12.5–14.7	6.2–7.1	0.46–0.52
		13.57 \pm 0.88	6.73 \pm 0.40	0.50 \pm 0.02
Km 89 (Road 105), Tha Song Yang, Tak: 5296	6	11.5–13.1	5.2–7.1	0.45–0.57
		12.29 \pm 0.52	6.08 \pm 0.65	0.49 \pm 0.04
Tam Mae U-Su, Tha Song Yang, Tak: 5292, 5293, 5298	7	13.4–14.8	4.8–6.2	0.36–0.44
		13.90 \pm 0.63	5.81 \pm 0.44	0.42 \pm 0.03
Km 87 (Road 105), Tha Song Yang, Tak: 5297	6	12.1–13.7	6.0–7.6	4.49–0.59
		12.71 \pm 0.57	6.65 \pm 0.63	0.52 \pm 0.04
Tam Mae Kasa, Mae Sod, Tak: 5289, 5294	20	12.3–15.1	4.8–6.5	0.38–0.48
		13.77 \pm 0.84	5.73 \pm 0.45	0.42 \pm 0.03
Thararak Waterfall, Mae Sod, Tak: 5285, 5299	92	9.0–11.5	3.8–4.9	0.36–0.48
		10.31 \pm 0.53	4.33 \pm 0.27	0.42 \pm 0.02

refers to the notable spiral ridges around the entire shell of the new species.

Diagnosis.– Shell small, flattened to depressed, and corneous in color. Protoconch with prominent radial ridges. Shell surface with delicate sculpture: above periphery with tubercles arranged in about 10 rows of spiral ridges; below periphery with about 17 rows of smooth spiral ridges. Umbilicus widely opened and deep.

Differential diagnosis.– Based on shell morphology alone, this new species differs from *G. artificiosa* by having ten rows of spiral ridges above the periphery and seventeen rows of spiral ridges below the periphery. In contrast, *G. artificiosa* bears about five rows of spiral ridges above the periphery and about ten to twelve weak to strong rows of spiral ridges below the periphery.

Description.– Shell small (shell width up to 14.0 mm, shell height up to 6.0 mm), flattened to depressed and rather solid. Shell color light yellowish or corneous; periostracum thin corneous. Spire generally flattened to little elevated; apex little elevated; suture wide and impressed. Whorls 5–7, increasing regularly and not descending. Protoconch about 2 whorls, with very

weak tubercles arranged on prominent radial ridges. Last whorl large and slightly shouldered periphery. Shell surface with delicate sculpture of tubercles and spiral ridges. Above periphery (penultimate whorl) consists of rounded and distinct tubercles arranged in about ten rows of spiral lines. Below periphery (from upper to lower junction of peristome) with indistinct tubercles that gradually transform to nearly even-sized spiral ridges, in about seventeen rows. Aperture lunate; parietal callus thin. Peristome continuous; lip simple to little thickened; below periphery lip little expanded. Columella margin short, straight and little thickened. Umbilicus widely opened and deep.

Distribution.– Currently, this new species is recorded from several localities on the limestone ridges in Khwae Noi River Basin, Kanchanaburi Province, Thailand (Fig. 1).

Remarks.– This new species currently is described based only on the empty shells. No living materials of this species have been found in any of the localities surveyed thus far. Therefore, more sampling effort, along with comprehensive anatomical examination and molecular phylogenetic analyses are required to clarify the relationship of this species with the other confamilials.

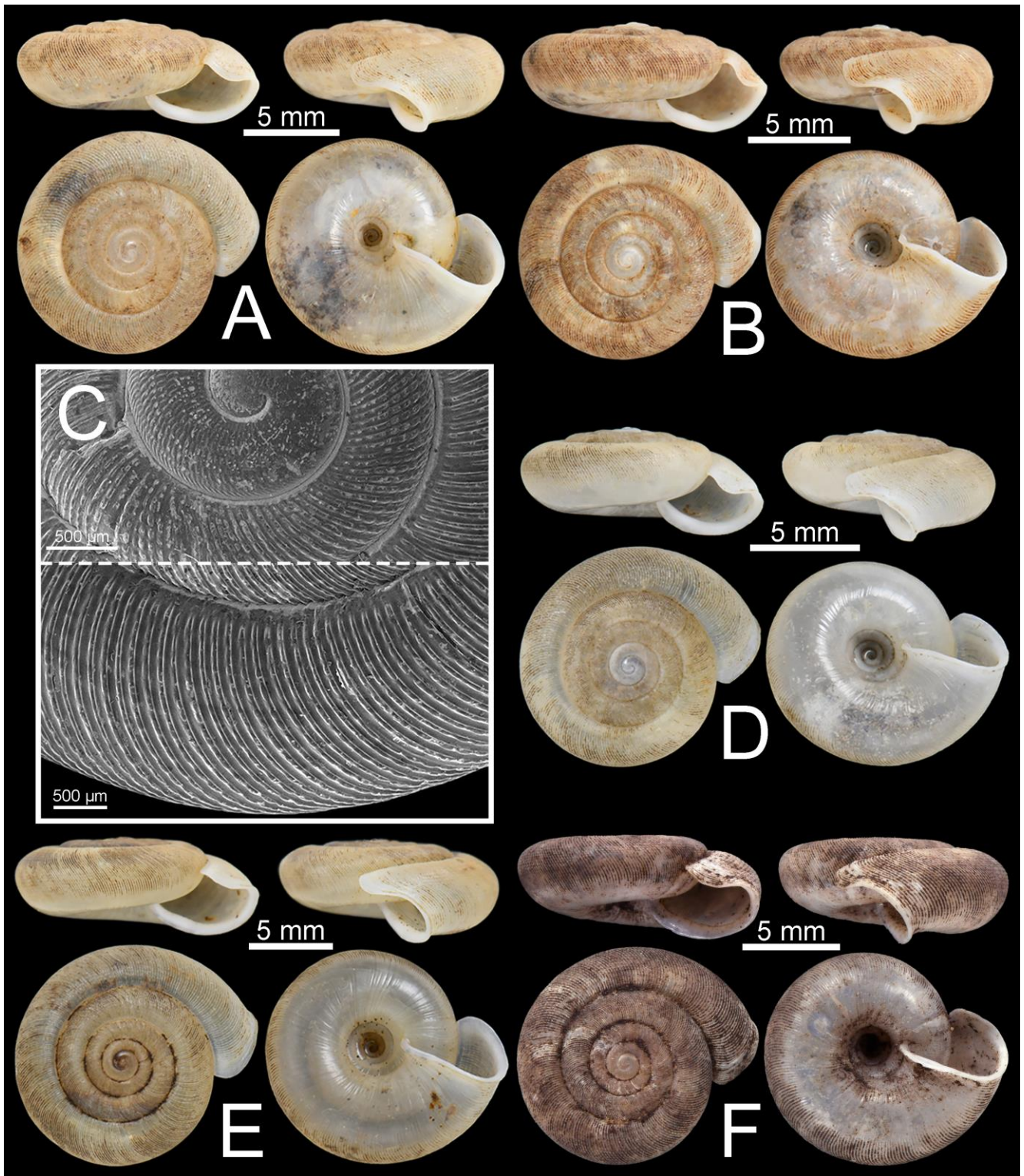


FIGURE 3. Shell morphology of *Maelamaodiscus somsakpanhai* gen. et sp. nov. **A.** holotype CUMZ 5300/1 from the type locality, **B.** paratype CUMZ 5300/2 from the type locality, **C.** SEM images of the paratype CUMZ 5287 showing sculpture of protoconch (upper image) and teleoconch (lower image), **D.** specimen CUMZ 5299 from Thararak Waterfall, Mae Sod, Tak, **E.** specimen CUMZ 5289 from Tam Mae Kasa, Mae Sot, Tak, and **F.** specimen NHMUK ex. Godwin-Austen collection from near Moulmein.

Superfamily Helicarionoidea Bourguignat, 1877
Family Ariophantidae Godwin-Austen, 1888

Genus *Maelamaodiscus* gen. nov.

<http://zoobank.org/urn:lsid:zoobank.org:act:9ED7BE0F-F127-470B-AAE6-73BF4B9F0853>

Type species.— *Maelamaodiscus somsakpanhai* gen. et sp. nov., by original designation.

Etymology.— The name '*Maelamaodiscus*' is a combination of the Thai locality name 'Mae Lamao' and the Latin word '*discus*', meaning 'flat or circular plate', which refers to the flattened shape of the shells. The Mae Lamao pass is a historical name of the Mae Sot District, the type locality of the type species. It has served as the main terrestrial route across the Dawna-Tenasserim Range between Thailand and Myanmar since ancient times (ca. sixteenth century).

Diagnosis.— Among the Southeast Asian Ariophantidae, it is uniquely characterized by the flattened to depressed shell, prominent radial ridges, and wide umbilicus.

Description.— Shell flattened to depressed; last whorl angular to little shouldered. Shell surface with prominent radial ridges. Aperture ovate with sinulus; lip thickened, and little expanded below periphery; columella straight and thickened. Umbilicus widely opened.

Animal with well-developed mantle edge with three lobes (one shell lobe and two dorsal lobes); lateral foot margin, caudal foss and caudal horn present. Pedal groove aulacopod type and foot sole tripartite. Pallial anatomy typically sigmurethrous. Genitalia with long penis, penial sheath thin and penial verge present; penial retractor muscle attached at tip of straight epiphallic caecum; flagellum present; gametolytic organ long; dart apparatus large and well developed. Radular teeth with symmetrical tricuspid central tooth, asymmetrical tricuspid lateral teeth, and lanceolate monocuspid marginal teeth.

Remarks.— Currently, this new genus has two constituents, *M. atkinsoni* (Theobald, 1859) and *M. somsakpanhai* gen. et sp. nov. The former is probably endemic to the limestone karsts in Salween River Basin in Myanmar, while the latter is restricted to the Moei River Basin, western Thailand.

***Maelamaodiscus somsakpanhai* gen. et sp. nov.**

<http://zoobank.org/urn:lsid:zoobank.org:act:69BA11A8-FAAA-453C-9084-EE4C42648D0F>

(Figs 1, 3–5)

Type material. Holotype CUMZ 5300/1 (height 5.6, width 12.7; Fig. 3A). Paratype CUMZ 5284 (2 shells), CUMZ 5286 (4 adults + 2 juveniles), CUMZ 5287 (5 shells; Fig. 3C), CUMZ 5288 (1 adult + 1 juvenile), CUMZ 5300/2 (2 shells; Fig. 3B), CUMZ 14295 (4 specimens in ethanol; Fig. 4A), NHUMK (2 shells) all from the type locality.

Type locality.— Limestone hills at Phra Wor Shine, Mae Sot District, Tak Province, Thailand (16°46'17.5" N, 98°41'12.7"E).

Other material.— **MYANMAR:** near Moulmein NHMUK ex. Godwin-Austen collection (7 shells; Fig. 3F). **THAILAND:** Wat Phothikun, Mae Sot District, Tak Province (16°45'44.5"N, 98°38'52.9"E): CUMZ 5290 (12 shells), CUMZ 14296 (1 specimen in ethanol; Fig. 4B). Tam Mae Kasa (U-sa), Mae Sot District, Tak Province (16°51'40.3"N, 98°37'48.3"E): 5289 (20 shells; Fig. 3E), CUMZ 5294 (2 shells). Thararak Waterfall, Mae Sot District, Tak Province (16°34'10.1" N, 98°41'40.1"E): CUMZ 5285 (71 shells), CUMZ 5295 (13 juveniles), CUMZ 5299 (27 shells; Fig. 3D). Wat Phratat Rattana Chedi, Tha Song Yang District, Tak Province (17°18'18.1"N, 98°10'8.4"E): CUMZ 5291 (5 shells). Km 89 (Road105), Mae Tan Village, Tha Song Yang District, Tak Province (17°16'1.7"N, 98°12'9.0"E): CUMZ 5296 (9 shells). Tam Mae U-Su, Tha Song Yang District, Tak Province (17°18'16.2"N, 98°9'22.0"E): CUMZ 5292 (2 shells), CUMZ 5293 (1 shell), CUMZ 5298 (5 shells). Km 87 (Road 105), Mae Tan Village, Tha Song Yang District, Tak Province (17°14'59.6"N, 98°12'48.5"E): CUMZ 5297 (9 shells). Khao Pha-Marn, Tha Song Yang District, Tak Province: CUMZ 5282 (1 juvenile). Mae Tho Village (Taksin), Mueang District, Tak Province: CUMZ 5283 (1 shell), CUMZ 5181 (2 shells).

Etymology.— The specific name '*somsakpanhai*', a joining of the first and family names of Professor Dr. Somsak Panha (Chulalongkorn University), is dedicated to his remarkable contributions to biodiversity in Thailand and in commemoration of his sixty-fifth birthday anniversary.

Diagnosis.— Shell flattened to depressed; last whorl rounded to little shouldered and widely umbilicate. Shell surface with series of tubercles arranged on radial ridges and then gradually diminishing below periphery. Aperture little descending; peristome with impression area close to apertural lip; lip little thickened and little expanded below periphery. Genitalia with thin penial sheath and small penial verge; epiphallic caecum straight; flagellum long and with two small papillae.

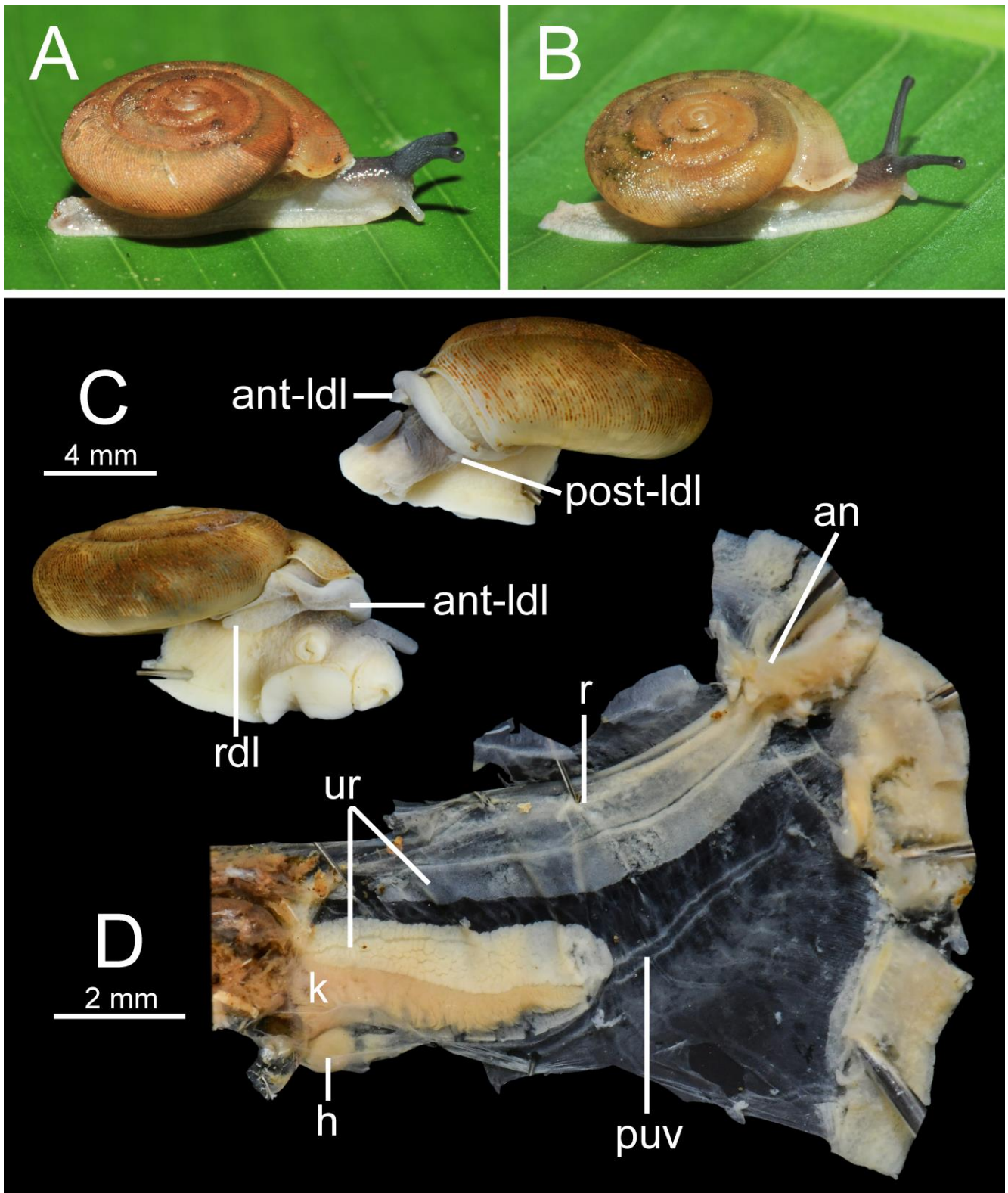


FIGURE 4. *Maelamaodiscus somsakpanhai* gen. et sp. nov. Living snails showing color in life, **A**, paratype CUMZ 14295 and **B**, specimen CUMZ 14296 from Wat Phothikun, Tak Province. **C**, **D**, paratype CUMZ 14295, **C**, ethanol-preserved (without posterior body) showing the arrangement of mantles and **D**, pulmonary cavity and mantle collar. Abbreviations: an: anus, ant-ldl: anterior left dorsal lobe, k: kidney, post-ldl: posterior left dorsal lobe, puv: pulmonary vein, r: rectum, rdl: right dorsal lobe, ur: ureter.

Radular teeth with symmetrical tricuspid central tooth, asymmetrical tricuspid lateral teeth, and lanceolate marginal teeth.

Description.— Shell small (shell width up to 15.0 mm, shell height up to 7.6 mm; Table 2), flattened to depressed and rather solid. Shell color light yellowish or corneous; periostracum thin corneous. Spire generally flattened to little elevated; apex little elevated; suture wide and depressed. Whorls 6–7, increasing regularly and slightly descending near apertural lip. Protoconch about 2 whorls, similar sculpture with teleoconch but weaker radial ridges. Last whorl large and rounded to little shouldered periphery. Shell surface sculptured with strong radial ridges, series of tubercles arranged on ridges and then gradually diminishing below periphery around umbilicus (below periphery smooth). Aperture ovate and little descending; parietal callus little thickened, and with wide sinus. Peristome continuous; above periphery lip simple to little thickened and with impression area close to apertural lip; below periphery lip little thickened and little expanded. Columella margin short, straight, thickened and expanded. Umbilicus widely umbilicate and showing all preceding whorls.

External features.— Mantle edge with large dorsal lobes. Right dorsal lobe (rdl) large and thick. Left dorsal lobe composed of thin crescentic anterior left dorsal lobe (ant-ldl) and thin elongated posterior left dorsal lobe (post-ldl). Shell lobes absent (Fig. 4A–C).

Pulmonary cavity typically sigmurethran, heart (h; auricle and ventricle) located left of kidney (on the right in figure). Pulmonary cavity approximately two times longer than wide. Pulmonary vein (puv) and venation on lung cavity well developed and distinct. Kidney (k) elongate, slender, and approximately half the length of pulmonary cavity. Ureter (ur) a sigmoid, closed tube arising from tip of kidney, extending along right side of kidney, and curved adjacent to rectum (r). Anus (an) adjacent to mantle edge (Fig. 4D).

Living snails possess long blackish tentacles (Fig. 4A, B). Skin reticulated brownish with greyish reticulations around head. Foot sole relatively elongate, broad and tripartite. Sole of foot plain brownish; side of body pale brownish; upper part of tail paler color. Tail long, curved mid-dorsally and dome-shaped in cross section. Caudal horn not overhanging; caudal foss a long vertical slit arranged on tail above sole margin. Pedal groove typically aulacopod and well defined.

Genitalia.— Atrium (at) enlarged and very short (Fig. 5A). Penis (p) elongate, cylindrical, with very thin

penial sheath (ps). Inner sculpture of penis covered with smooth surface of longitudinal penial pilasters (pp) running the length of entire penis chamber; proximal area near atrium with very weak pilasters then transforming to large pilasters at distal area near penial verge (Fig. 5B). Penial verge (pv) very small and indistinct. Epiphallus (e) cylindrical, slightly long, almost same length as penis. Epiphallic caecum (ec) slightly long, straight, diameter nearly equal to proximal epiphallus and located close to penis. Penial retractor muscle (prm) very long and thin, and attached at tip of epiphallic caecum. Flagellum (fl) a very long slender tube, approximately same length as epiphallus. Two small papillae located on flagellum close to vas deferens junction (inset in Fig. 5A). Vas deferens (vd) a thin tube and connected between epiphallus and free oviduct.

Vagina (v) cylindrical, slightly short and about half of penis length (Fig. 5A). Dart apparatus (da) enlarged cylindrical and joined to atrium at vagina and penis junction. Gametolytic sac (gs) bulbous; gametolytic duct (gd) a long cylindrical tube. Free oviduct (fo) long cylindrical, approximately same length as vagina, and proximal part encircled with thick tissue. Oviduct with large lobules; prostate gland running alongside oviduct.

Radula.— Teeth arranged in nearly straight row with formula: 1–(9–10)–37 (Fig. 5C). Central tooth symmetrical tricuspid with large mesocone and small ectocones. Lateral teeth asymmetrical tricuspid with large mesocone, and small endocone and ectocone. Marginal teeth starting around tooth number 9 or 10; inner teeth elongate unicuspid and elongate sword-shaped with pointed tip; outermost teeth unicuspid and gradually reduced in size.

Distribution.— This new species is currently known from the type locality and nearby localities in the Moei River Basin in Mae Sot and Tha Song Yang District of Tak Province in western Thailand, less than 5 km from the Thai–Myanmar border (Fig. 1). The type locality has dense vegetation and human-modified habitats such as a shrine and recreation areas; more natural habitat tended to have lower abundance of snails. This snail likely inhabits the montane dry evergreen forest and limestone forest of the northern part of the Tenasserim Range, at elevations from ca. 50–500 m asl. The snails were hidden beneath decaying leaf litter or in crevices of limestone outcrops.

Remarks.— This new species differ from *M. atkinsoni* by having a shouldered last whorl, below periphery with a smooth shell surface, apertural lip little expanded, and with prominent impression area and sinus

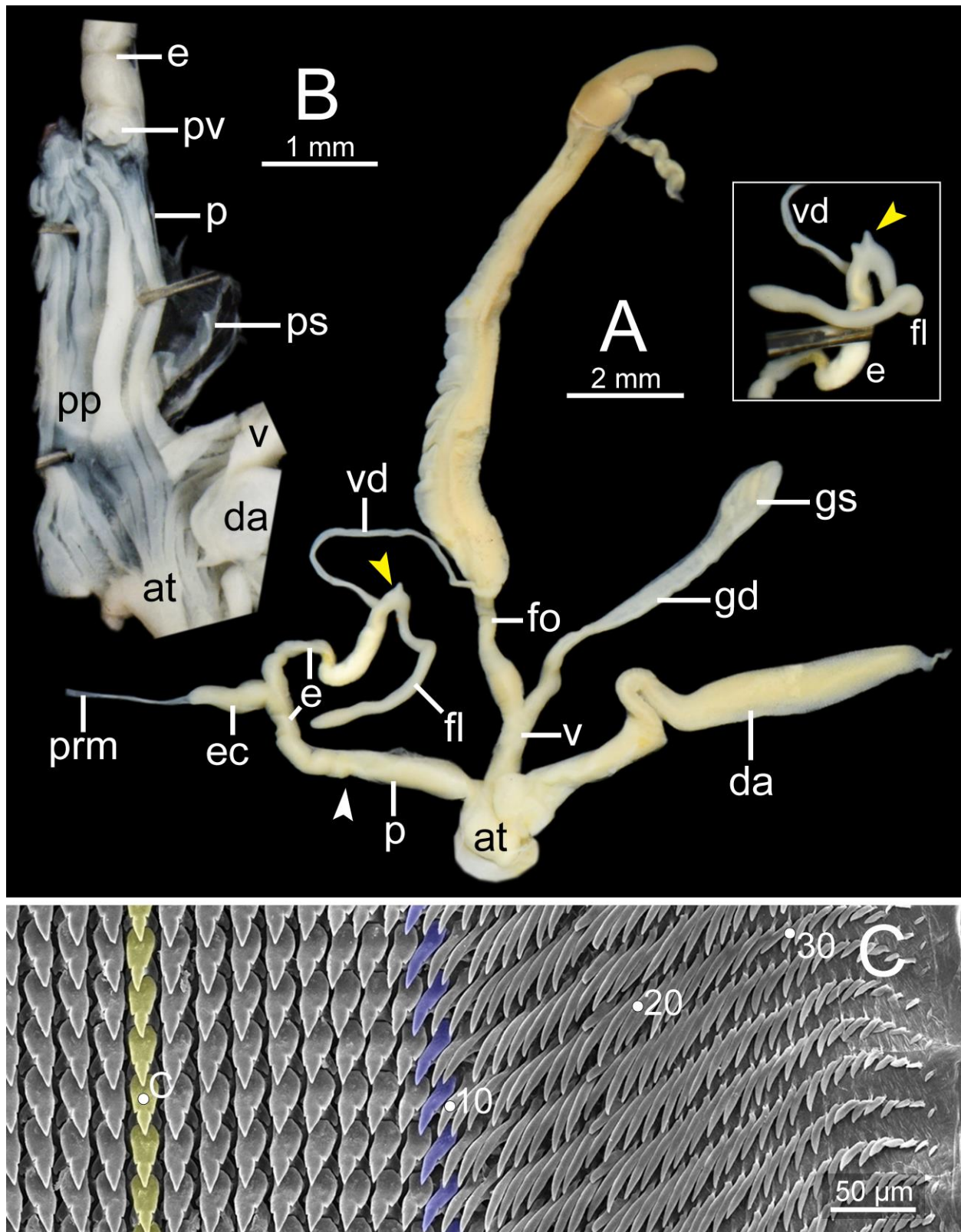


FIGURE 5. Genitalia and radula *Maelamaodiscus somsakpanhai* gen. et sp. nov. paratype CUMZ 14295. **A.** external morphology of genitalia with small inset showing the two protruding knobs on proximal part of the flagellum, **B.** internal wall sculpture of penis, and **C.** radula morphology with yellow highlight indicating central teeth (C) and blue highlight the transition of lateral to marginal teeth. Abbreviations: at: atrium, da: dart apparatus, e: epiphallus, ec: epiphallic caecum, fl: flagellum, fo: free oviduct, gd: gametolytic duct, gs: gametolytic sac, p: penis, pp: penial pilaster, prm: penial retractor muscle, ps: penial sheath, pv, penial verge, v: vagina, vd: vas deferens.



FIGURE 6. Shell morphology of *Maelamaodiscus atkinsoni* (Theobald, 1859). **A.** holotype NHMUK 1888.12.4.622 from the type locality and **B.** specimen CUMZ 4759 from Kaw Ka Taung Cave, Kayin State, Myanmar.

(Fig. 3). For comparison, *M. atkinsoni* possesses an angular last whorl, prominent radial ridges over the entire shell, apertural lip not expanded, with inconspicuous impression area, and without (or indistinct) sinulus (Fig. 6). However, only a limited number of *M. atkinsoni* specimens were available to observe the shell variation. Additional field surveys for living specimens and taxonomic analyses that integrate molecular data and reproductive anatomy are necessary to clarify their placement.

***Maelamaodiscus atkinsoni* (Theobald, 1859)
comb. nov.
(Figs 1, 6)**

Helix atkinsoni Theobald, 1859: 305. Type locality: prope Maulmein [Mawlamyine District, Mon State, Myanmar]. Hanley and Theobald, 1870: 8, pl. 15, fig. 9. Hanley and Theobald, 1874: 36, pl. 84, figs 2, 3.

Helix (Trachia) atkinsoni—Tryon, 1888: 56, pl. 12, figs 83–85.

Planispira (Trachia) atkinsoni—Pilsbry, 1894: 116.

Planispira atkinsoni—Gude, 1914: 156.

Trachia atkinsoni—Richardson, 1985: 297

Material examined.— Holotype NHMUK 1888.12.4.622 (height 5.7, width 14.0; Fig. 6A) from Moulmein. Specimen CUMZ 7459 (1 shell, broken; Fig. 6B) from Kaw Ka Taung Cave (Golden valley), Hpa-an Township, Hpa-an District, Kayin State, Myanmar (16°50'32.4"N, 97°37'10.9"E). CUMZ 7458 (1 shell, broken) from Taung Wine Cave, near Thiri Hpa-an Hotel, Hpa-

an Township, Hpa-an District, Kayin State, Myanmar (16°50'31.1"N, 97°37'18.4"E).

Description.— Shell small (shell width up to 15.0 mm, shell height up to 7.6 mm; Table 2), flattened to depressed and rather solid. Shell color light yellowish or corneous; periostracum thin corneous. Spire generally flattened to little concave; suture wide and depressed. Whorls 6–7, increasing regularly and slightly descending near apertural lip. Protoconch about 2 whorls, similar sculpture with teleoconch but with weaker radial ridges. Last whorl large and angular periphery. Shell surface sculptured with strong radial ridges over entire shell, and series of weak tubercles arranged on ridges. Aperture ovate and very little descending; parietal callus little thickened. Peristome continuous; lip little thickened. Columella margin short, straight and thickened. Umbilicus widely umbilicate and showing all preceding whorls.

Distribution.— This species is known from the type locality and new localities recorded herein from Hpa-an, Kayin State (Fig. 1). These new localities are very close together and situated on an isolated limestone hill on the east bank of Salween River. The two empty (broken) shells were collected from topsoil among decaying leaf litter.

Remarks.— As Theobald (1859) clearly stated ‘a single dead shell was found...’, we know that this species was described based on a single specimen received from E. Atkinson. The single shell in Theobald’s collection purchased by the NHM closely matches the original description, and therefore this is the holotype fixed by monotypy.

DISCUSSION

The Indochinese land snail genus that is most similar to *Maelamaodiscus* gen. nov. in terms of shell morphology with medium shell size, and coarse shell sculpture with either radial or spiral ridges is *Glyptaulax* (Table 1). The genus *Glyptaulax* is currently placed in the subfamily Thysanotinae of the family Charopidae (see Bouchet et al., 2017; MolluscaBase, 2022). The charopids comprise six subfamilies, mainly distributed in the southern hemisphere (Schileyko, 2001), whereas the thysanotinids are distributed from South and Southeast Asia to New Guinea (Schileyko, 2001). Unfortunately, anatomical information of *Glyptaulax* species has never been presented. Regardless of the soft part anatomy (Table 1), *Maelamaodiscus* gen. nov. differs from *Glyptaulax* in having prominent tubercles arranged on radial ridges, widely opened umbilicus showing all preceding whorls, aperture with wide sinulus, and lip little thickened and expanded. In comparison, *Glyptaulax* possesses a prominent series of tubercles arranged on spiral ridges, opened umbilicus, aperture without sinulus, and simple lip. In addition, this new genus shows vast anatomical distinctions from all of the thysanotinid genera distributed in South Asia in having large caudal foss with short caudal horn, and a well-developed dart apparatus. In contrast, the thysanotinids have a simple apertural lip, without dart apparatus, caudal foss or horn (see Schileyko, 2001 for further comparison).

The presence of the caudal foss and horn and the well-developed dart apparatus suggest the placement of *Maelamaodiscus* gen. nov. in the limacoid clade (Hausdorf, 1998; Wade et al., 2001). The shell morphology of *Maelamaodiscus* gen. nov. shows high similarity with the Southeast Asian limacoid genera of medium shell size, coarse shell surface, i.e., *Khasiella* Godwin-Austen, 1899, *Sesara* Albers, 1860 and *Teraia* Solem, 1966 (Table 1). These three genera are traditionally classified in either Helicarionidae or Ariophantidae (Bouchet et al., 2017; MolluscaBase, 2022). On the other hand, Schileyko (2002, 2003) classifies these three genera with the Ariophantidae. Resolving the higher classification of the genera mentioned above is impossible without conclusive phylogenetic study. Here, we provisionally classify *Maelamaodiscus* gen. nov. in Ariophantidae sensu Schileyko (2002, 2003). In addition, this new genus and other ariophantid genera have many characteristics in common, such as a well-developed dart apparatus, long epiphallic caecum, long flagellum and a thin penial sheath connected to the penis at the proximal end, close to the genital orifice

(Fig. 5A, B; Table 1). Some ariophantid genera such as *Sesara*, however, possibly lost their dart apparatus secondarily, which has occurred multiple times in the limacoid lineages (Wade et al., 2006; Jordaens et al. 2009).

With respect to its genitalia, *Maelamaodiscus* gen. nov. differs from *Khasiella* in having the penial retractor muscle attached at the tip of the penial caecum, while species of *Khasiella* have a penial retractor muscle attached at the middle of penial caecum, which forms a small coil (Table 1). In addition, this new genus differs from *Sesara* by having a dart apparatus and straight epiphallic caecum, while *Sesara* has no dart apparatus, and straight or coiled epiphallic caecum (Table 1). Comparing these three nominal genera with this new genus, *Teraia* tends to have very similar genitalia characters, differing only in the penial retractor muscle being attached directly to the penis-epiphallus junction, and the penial caecum seemingly absent. These appear to be the only distinct characters of the genus *Teraia* (Table 1).

In genital anatomy, *Maelamaodiscus* gen. nov. resembles *Sarika* Godwin-Austen, 1907 and *Taphrenalla* Pholyotha and Panha, 2021 (see Pholyotha et al., 2021b), which inhabit Indochina. These two genera differ from *Maelamaodiscus* gen. nov. by the presence of shell lobes (left and right shell lobes) and a long and elevated caudal horn. Otherwise, these three genera are very similar in terms of the straight epiphallic caecum, long flagellum, and shape of central teeth.

Morphologically, *Maelamaodiscus* gen. nov. belongs to Ariophantidae based on the absence of a perivaginal gland and presence of a caudal foss and horn, and dart apparatus. This new genus is promptly distinguished from the Oxychilidae Hesse, 1927, which are mainly distributed in the western Palearctic, southwestern Arabian Peninsula and southern China (Neubert, 1998; Schileyko, 2003; Wu and Lui, 2019). In comparison, the oxychilids from southern China of genus *Sinoxychilus* Wu and Lui, 2019 have tripartite sole, oxygnathous jaw, penis sheath and perivaginal gland, and the absence of dart apparatus and a caudal horn. In addition, *Maelamaodiscus* gen. nov. differs from *Sinoxychilus* in having an opaque shell with a delicately sculptured protoconch. The new genus also shows an unusual shell shape that differs from the shells of *Sinoxychilus*. *Maelamaodiscus* gen. nov. and *Sinoxychilus* also share a characteristically radially sculptured shell, and small to medium shell size; however, the latter genus has no caudal horn or thin apertural lip, which suggests that *Maelamaodiscus* gen. nov. does not belong to Oxychilidae.

ACKNOWLEDGMENTS

The authors are indebted to J.D. Ablett (NHM) for kindly allowing us to study the material under his care. The work in Thailand was funded by the TRF-DBG 6080011 and TRF-DPG628001. The field trips in Myanmar were partially funded through grants received from FFI and TRF-RTA 5880002. We wish to thank the Ministry of Natural Resources and the Environmental Conservation Forest Department for the collection and export permits. In addition, we wish to express our gratitude to members of the ASRU members for their help in field collecting.

LITERATURE CITED

- Albers, J.C. 1860. Die Heliceen, nach Natürlicher Verwandtschaft Systematisch Geordnet. Verlag von Wilhem Engelmann, Berlin, 359 pp. <https://doi.org/10.5962/bhl.title.11218>
- American Veterinary Medical Association (AVMA). 2020. 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 2022]
- Benson, W.H. 1856. Descriptions of one Indian and nine new Burmese Helices; and note on two Burmese Cyclostomacea. *Annals and Magazine of Natural History, Series 2*, 17: 249–254.
- Benson, W.H. 1859. New Helicidae collected by W. Theobald, Esq., jun., in Burmah and the Khasia Hills, and described by W.H. Benson, Esq. *Annals and Magazine of Natural History, Series 3*, 3: 387–393.
- Blanford, W.T. and Godwin-Austen, H.H. 1908. The Fauna of British India, including Ceylon and Burma. Mollusca. Testacellidae and Zonitidae. Taylor and Francis, London, 311 pp.
- 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: 1–526. 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: 49–101.
- Chomdej, S., Pradit W., Suwannapoom C., Pawangkhanant P., Nganvongpanit K., Poyarkov N.A., Che, J., Gao, Y. and Gong, S. 2021. Phylogenetic analyses of distantly related clades of bent-toed geckos (genus *Cyrtodactylus*) reveal an unprecedented amount of cryptic diversity in northern and western Thailand. *Scientific Reports*, 11: 2328. doi.org/10.1038/s41598-020-70640-8
- Clements, R., Sodhi, N.S., Schilthuizen, M. and Ng, P.K.L. 2006. Limestone karsts of Southeast Asia: Imperiled arks of biodiversity. *BioScience*, 56: 733–742.
- Critical Ecosystems Partnership Fund (CEPF). 2012. Ecosystem Profile. Indo-Burma Biodiversity Hotspot. 2011 Update. https://www.cepf.net/Documents/final.indoburma_indochina.ep.pdf Accessed February 2022.
- Foon, J.K., Clements, G.R. and Liew, T.-S. 2017. Diversity and biogeography of land snails (Mollusca, Gastropoda) in the limestone hills of Perak, Peninsular Malaysia. *ZooKeys*, 682: 1–94. doi.org/10.3897/zookeys.682.12999
- Godwin-Austen, H.H. 1888, 1899, 1907, [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*, Taylor & Francis, London. Volumes 1 [pp. 1–257, pls 1–62; part 6: pp. 207–257 (1888)], Volume 2 [pp. 1–442, pls 63–158; part 9: pp. 87–146, pl. 83–100 (1899); part 10: pp. 147–238, pls 101–117 (1907)] and Volume 3 [pp. 1–65, pls 159–165].
- Gould, A.A. 1844. Description of land mollusks from the province of Tavoy, in British Burmah. *Boston Journal of Natural History*, 4: 452–459.
- Grismer, L., Wood Jr, P.L., Poyarkov, N.A., Le, M.D., Karunaratna, S., Chomdej, S., Suwannapoom, C., Qi, S., Liu, S., Che, J., Quah, E.S.H., Kraus, F., Oliver, P.M., Riyanto, A., Pauwels, O.S.G. and Grismer, J.L. 2021. Karstic landscapes are foci of species diversity in the World's Third-Largest vertebrate genus *Cyrtodactylus* Gray, 1827 (Reptilia: Squamata: Gekkonidae). *Diversity*, 13: 183. doi.org/10.3390/d13050183
- Grismer, L.L., Wood Jr, P.L., Thura, M.K., Zin, T., Quah, E.S.H., Murdoch, M.L., Grismer, M.S., Lin, A., Kyaw, H. and Lwin, N. 2018. Twelve new species of *Cyrtodactylus* Gray (Squamata: Gekkonidae) from isolated limestone habitats in east-central and southern Myanmar demonstrate high localized diversity and unprecedented microendemism. *Zoological Journal of the Linnean Society*, 182: 862–959. doi.org/10.1093/zoolinnean/zlx057
- Gude, G.K. 1914. The Fauna of British India including Ceylon and Burma. Mollusca II. (Trochomorphidae-Janellidae). Taylor and Francis, London. 520 pp.
- Hanley, S.C.T. and Theobald, W. 1870, 1872, 1874, 1876 [1870–1876]. *Conchologia Indica: Illustrations of the Land and Freshwater Shells of British India*. L. Reeve & Co, Covent Garden, London. i–xviii + 1–65 pp., 160 pls. [pp. 1–18, pls 1–40 (1870); pp. 19–28, pls 41–60 (1872); pp. 29–34, pls 61–80 (1873); pp. 35–48, pls 81–120 (1874); pp. 49–56, pls 121–140 (1875); pp. 57–65, pls 141–160 (1876)] [Published in parts, dates after Prashad (1927)]
- Hausdorf, B. 1998. Phylogeny of the Limacoidea sensu lato (Gastropoda: Stylommatophora). *Journal of Molluscan Studies*, 64: 35–66. doi.org/10.1093/mollus/64.1.35
- Hutton, F.W. 1884. Revision of the land Mollusca of New Zealand. *Transactions of the New Zealand Institute*, 16: 186–212.
- Hyman, I.T. and Köhler, F. 2018. A revision of eastern Australian land snails placed in *Nitor* Gude (Helicarionidae, Stylommatophora). *Invertebrate Systematics*, 32: 1171–1205. doi.org/10.1071/IS18015
- Hyman, I.T., Lamborena, I. de la I. and Köhler, F. 2017. Molecular phylogenetics and systematic revision of the south-eastern Australian Helicarionidae (Gastropoda, Stylommatophora). *Contributions to Zoology*, 86: 51–95. doi.org/10.1163/18759866-08601004
- Jirapatrasilp, P., Sutcharit, C and Panha, S. 2022. Annotated checklist of the operculated land snails from Thailand (Mollusca, Gastropoda, Caenogastropoda): the family Pupinidae, with descriptions of several new species and subspecies, and notes on classification of *Pupina* Vignard, 1829 and *Pupinella* Gray, 1850 from mainland Southeast Asia. *ZooKeys*, 1119: 1–115. <https://doi.org/10.3897/zookeys.1119.85400>
- Johnson, R.I. 1969. Pfeiffer's Novitates Conchologicae, Series I, Land Mollusca, 1854–1879, and Dunker's Novitates Conchologicae, Series II, Marine Mollusca, 1862–1882. A complete collation. *Journal of the Society for Bibliography of Natural History*, 5: 236–239.

- Jordaens, K., Dillen, L. and Backeljau, T. 2009 Shell shape and mating behaviour in pulmonate gastropods (Mollusca). *Biological Journal of the Linnean Society*, 96: 306–321.
- Laudee, P. and Malicky, H. 2018. Five new species of caddisflies (Trichoptera: Insecta) from Upper Tenasserim Range, Thailand and Myanmar. *Zootaxa*, 4524: 351–358. doi.org/10.11646/zootaxa.4524.3.4
- Möllendorff, O.F. von. 1900. Zur Binnenmollusken-Fauna Annams III. *Nachrichtsblatt der Deutschen Malakozoologischen Gesellschaft*, 32: 117–121.
- MolluscaBase 2022. MolluscaBase. Accessed at <https://www.molluscabase.org> on 2022-03-06. doi:10.14284/448
- Morse, E.S. 1864. Observations on the terrestrial Pulmonifera of Maine, including a catalogue of all the species of terrestrial and fluviatile Mollusca known to inhabit the state. *Journal of the Portland Society of Natural History*, 1: 1–63.
- Myers, N., Mittermeier, R.A., Mittermeier, C.G., da Fonseca, G.A. B. and Kent, J. 2000. Biodiversity hotspots for conservation priorities. *Nature*, 403: 853–858. doi.org/10.1038/35002501
- Nantararat, N., Sutcharit, C., Tongkerd, P., Ablett, J., Naggs, F. and Panha, S. 2014. An annotated catalogue of type specimens of the land snail genus *Cyclophorus* Monfort, 1810 (Caenogastropoda, Cyclophoridae) in the Natural History Museum, London. *ZooKeys*, 411: 1–56. doi.org/10.3897/zookeys.411.7258
- Neubert, E. 1998. Annotated checklist of the terrestrial and freshwater molluscs of the Arabian Peninsula with descriptions of new species. *Fauna of Arabia*, 17: 333–461.
- Nevill, G. 1878. *Hand List of Mollusca in the Indian Museum, Calcutta*. Calcutta, Trustees. Volume 1, 338 pp.
- Páll-Gergely, B., Fehér, Z., Otani, J.U. and Asami, T. 2016. An integrative taxonomic approach to infer the systematic position of *Chalepotaxis* Ancy, 1887 (Gastropoda: Stylommatophora: Helicarionidae). *Molluscan Research*, 37: 113–119. doi.org/10.1080/13235818.2016.1234996
- Pfeiffer, L. 1842. Description de deux mollusques nouveaux, découverts par M. Perrot sur le plateau des Ncelgherries. *Revue Zoologique*, 1842: 304–305.
- Pfeiffer, L. 1859. *Monographiae Heliceorum Viventium Supplementum Secundum*. Lipsiae, F.A. Brockhaus, 920 pp.
- Pfeiffer, L. 1860 [1854–1860]. *Novitates Conchologicae. Series prima*. Mollusca extramarina. Descriptions et figures de coquilles, extramarines nouvelles, ou peu connues. Beschreibung und Abbildung neuer oder kritischer Land- und Süßwasser Mollusken. Tome 1, Lief. 12: 121–138, pls 34–46. [Published in parts, dates follow Johnson (1969)]
- 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. doi.org/10.5852/ejt.2020.674
- Pholyotha, A., Sutcharit, C., Tongkerd, P. and Panha, S. 2020b. 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. doi.org/10.3897/zookeys.976.53859
- Pholyotha, A., Sutcharit, C., Tongkerd, P. and Panha, S. 2021a. 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. doi.org/10.5852/ejt.2021.767.1487
- 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. doi.org/10.1163/18759866-bja10013
- Pholyotha, A., Sutcharit, C., Tongkerd, P., Lin, A. and Panha, S. 2020c. 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. doi.org/10.1080/13235818.2020.1723041
- 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 *Burmochlamys* (Eupulmonata, Helicarionidae). *ZooKeys*, 1110: 1–37. <https://doi.org/10.3897/zookeys.1110.82461>
- Pilsbry, H.A. 1894 [1893–1895]. *Manual of Conchology. Second Series: Pulmonata (Helicidae, Volume 7). Volume 9*. Academy of Natural Sciences Philadelphia, Philadelphia, 336 pp. [pp. 49–160 (1894)]
- Poyarkov, N.A., Nguyen, T.V., Pawangkhanant, P., Yushchenko, P.V., Brakels, P., Nguyen, L.H., Nguyen, H.N., Suwannapoom, C., Orlov, N. and Vogel, G. 2022. An integrative taxonomic revision of slug-eating snakes (Squamata: Pareidae: Pareinae) reveals unprecedented diversity in Indochina. *PeerJ*, 10: e12713. doi.org/10.7717/peerj.12713
- Poyarkov, N.A., Pawangkhanant, P., Gorin, V.A., Juthong, W. and Suwannapoom, C. 2018. A new species of miniaturised narrow-mouth frog of the genus *Microhyla* Tschudi, 1838 (Amphibia: Anura: Microhylidae) from northern Tenasserim, Thailand. *Journal of Natural History*, 54: 1525–1558. doi.org/10.1080/00222933.2020.1804005
- Prashad, B. 1927. On the dates of publication of Hanley and Theobald's "Conchologica Indica". *Journal and Proceedings of the Asiatic Society of Bengal, new series* 22: 129–130.
- Preece, R.C., White, T.S., Raheem, D.C., Ketchum, H., Ablett, J., Taylor, H., Webb, K. and Naggs, F. 2022. William Benson and the origins of the golden age of malacology in British India: Biography, illustrated catalogue and evaluation of his molluscan types. *Tropical Natural History, Supplement* 6: 1–434.
- Schileyko, A.A. 2001. *Treatise on recent terrestrial pulmonated mollusks. Part 7. Endodontidae, Thyrophorellidae, Charopidae. Ruthenica, Supplement 2*: 881–1034.
- Schileyko, A.A. 2002. *Treatise on recent terrestrial pulmonated mollusks. Part 9. Helicarionidae, Gymnarionidae, Rhysotinae, Ariophantidae. Ruthenica, Supplement 2*: 1167–1307.
- Schileyko, A.A. 2003. *Treatise on recent terrestrial pulmonate mollusks. Part 10. Ariophantidae, Ostracolethidae, Rysosotidae, Milacidae, Dyakiidae, Staffordiidae, Gastrodondidae, Zonitidae, Daubebardiidae, Parmacellidae. Ruthenica, Supplement 2*: 1309–1466.
- Solem, A. 1966. Some non-marine mollusks from Thailand. *Spolia Zoologica Musei Hauniensis*, 24: 1–110.
- 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. doi.org/10.3897/zookeys.1047.65735
- Sutcharit, C., Ablett, J., Tongkerd, P., Naggs, F. and Panha, S. 2015. Illustrated type catalogue of *Amphidromus* Albers, 1850 in the Natural History Museum, London, and descriptions of two new species. *ZooKeys*, 492: 49–105. doi.org/10.3897/zookeys.492.8641
- Sutcharit, C., Ablett, J.D. and Panha, S. 2019. An annotated type catalogue of seven genera of operculate land snails (Caenogastropoda, Cyclophoridae) in the Natural History Museum, London. *ZooKeys*, 842: 1–65. doi.org/10.3897/zookeys.842.29243

- Sutcharit, C., Jeratthitikul, E., Pholyotha, A., Lin, A. and Panha, S. 2020. Molecular phylogeny reveals high diversity and endemism in the limestone karst-restricted land snail genus *Sophina* Benson, 1859 from Myanmar (Eupulmonata: Helicariionidae), with description of four new species. *Journal of Zoological Systematics and Evolutionary Research*, 58: 957–981. doi.org/10.1111/jzs.12420
- 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. doi.org/10.1163/18759866-BJA10016
- Tanmuangpak, K., Tumpeesuwan, C. and Tumpeesuwan, S. 2017. A new species of *Sesara* Albers, 1860 from northeastern Thailand (Stylommatophora: Helicariionidae). *Molluscan Research*, 37: 1–7. doi.org/10.1080/13235818.2016.1155431
- Theobald, W. 1857. Notes on the distribution of some the land and freshwater shells of India: Part I. Birmah and the Tenasserim Provinces. *Journal of the Asiatic Society of Bengal*, 26: 245–254.
- Theobald, W. 1859. Descriptions of some new Burmese and Indian Helicidae with remarks on some previously described species. *The Journal of the Asiatic Society of Bengal*, 28: 305–309.
- Theobald, W. 1876a. Catalogue of the Land and Fresh-water Shells of British India. Thacker, Spink and Co., Calcutta. 65 pp.
- Theobald, W. 1876b. Descriptions of some new land and freshwater shells from India and Burmah. *Journal of the Asiatic Society of Bengal*, 45:184–189.
- Thiele, J. 1929 [1929–1935]. *Handbuch der Systematischen Weichtierkunde*. Fischer, Jena. Volume 1 [part 1, pp. 1–376 (1929), part 2, pp.377–778 (1931)], Volume 2 [part 3, pp. 1–376 (1934), part 4, pp. 1023–1154 (1935)].
- Tryon Jr, G.W. 1887. *Manual of Conchology, Structure and Systematic, with Illustrations of the Species, Volume III (Helicidae: volume I)*. The Academy of Natural Science Philadelphia, Philadelphia. 313 pp.
- Tryon Jr., G.W. 1888 [1888–1889]. *Manual of Conchology, Structure and Systematic, with Illustrations of the Species, Volume 4 (Helicidae: volume II)*. The Academy of Natural Science of Philadelphia, 296 pp.
- Vermeulen, J.J. and Liew, T.-S. 2022. Land snails and slugs of Sabah and Labuan (Malaysia). Institute for Tropical Biology and Conservation, Universiti Malaysia Sabah, Kota Kinabalu, Malaysia. Pp iii–x, 1–432. doi.org/10.6084/m9.figshare.17156255
- Wade, C.M., Mordan, P.B. and Clarke, B. 2001. A phylogeny of the land snails (Gastropoda: Pulmonata). *Proceedings of the Royal Society of London. Series B: Biological Sciences*, 268: 413–422.
- Wade, C.M., Mordan, P.B. and Naggs, F. 2006. Evolutionary relationships among the pulmonate land snails and slugs (Pulmonata, Stylommatophora). *Biological Journal of the Linnean Society*, 87: 593–610.
- Wu, M. and Liu, Z. 2019. The first proven oxychilid land snail endemic to China (Eupulmonata, Gastrodontoidea). *ZooKeys*, 870: 33–50. doi.org/10.3897/zookeys.870.32903
- Zilch, A. 1959. Gastropoda, Euthyneura. In: OH Schindewolf (ed.) *Handbuch der Paläozoologie*, 6: 1–400. Gebrüder Borntraeger, Berlin.
-