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Phylogenetic and Morphological Evidence for Two New Species of Terrestrial Micro Snail Genus *Georissa* Blanford, 1864 (Neritimorpha: Hydrocenidae) from Central Thailand

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ABSTRACT.– This paper introduces two newly discovered endemic micro snails, *Georissa chatra* Buathanom & Pholyotha, sp. nov. and *G. principalis* Buathanom & Tongkerd, sp. nov., from limestone hills of Uthai Thani and Nakhon Sawan Provinces in central Thailand. These findings expand the number of *Georissa* species recorded in Thailand to seven. The taxonomic status and species boundaries of these new species were determined through a comprehensive analysis of comparative morphology and mitochondrial genetics. *Georissa chatra* sp. nov. is distinguished by a conical shell with tall and prominent carinas. *Georissa principalis* sp. nov. is characterized by an elongate conical or turreted shell with prominent cord-like spiral ridges, and an operculum with two layers. The cytochrome *c* oxidase subunit I (COI) phylogeny supports the monophyly of both lineages, but the relationships with other congeners remain unresolved. The analysis also revealed interspecific genetic distances among examined species ranging from 6.8% to 18.6%. Additionally, intraspecific genetic distances are surprisingly high, with 6.1% for *G. chatra* sp. nov. and 7.5% for *G. principalis* sp. nov. The observed high intraspecific genetic divergences are likely due to the significant endemism and fragmented distribution of populations within karst ecosystems. As a result, the discovery of these two new species significantly advances our understanding of micro snail diversity and represents a crucial first step in establishing a comprehensive DNA barcode reference library for micro snails in Thailand.

KEYWORDS: COI, Endemic, Limestone, Operculated snail, Morphology, Systematics, Taxonomy, Hydrocenoidea

INTRODUCTION

Georissa Blanford, 1864 is an operculate micro land snail belonging to the Hydrocenidae Troschel, 1857. The genus was proposed to be distinguished from *Hydrocena* Küster, 1844, with *Hydrocena pyxis* Benson, 1856 as the type species, by head morphology and operculum features (Blanford, 1864, 1869). *Georissa* is characterised by a small, conical and calcareous shell, a head with very blunt tentacles with almost hemispherical lobes, eyes located at outer base, and a calcareous and paucispiral operculum with a peg (Blanford, 1864, 1869; Thompson and Dance, 1983, Panha and Burch, 2005). In addition, this genus possesses a rhipidoglossan radula and respires through lungs rather than gills in the mantle cavity (Panha and Burch, 2005; Haase and Schilthuizen, 2007). These snails live in broad variety of microhabitats associated to the limestone karsts, and feeds on fragments of moss, algae, and lichens found on damp limestone surfaces (Thompson and Dance, 1983; Haase and Schilthuizen, 2007; Khalik et al., 2018, 2019a, b).

The genus *Georissa* is widely distributed across Asia to Africa, New Zealand, Australia, and the Pacific Islands, with more than a hundred species and subspecies described to date (Das and Aravind, 2021; Prieto et al., 2022; MolluscaBase, 2025). In mainland Southeast Asia, at least 24 nominal species and subspecies have been recorded, of which five species have been described from Thailand (Fischer and Dautzenberg, 1904; Preston, 1915; Hemmen and Hemmen, 2001; Panha and Burch, 2005; Inkhavilay et al., 2019; Sutcharit et al., 2020b; Preece et al., 2022; Klongklaew et al., 2024). In Thailand, no taxonomic revisions have been made for *Georissa* other than an overview of micro snails (including pupillids, diplommatinids, hydrocenids, etc.) by Panha and Burch (2005), an updated checklist of land snail for the country by BEDO (2017), and a recent molecular work of *Georissa* by Klongkaew et al. (2024).

During a malacological survey, a variety of *Georissa* specimens were collected from limestone hills and outcrops in central Thailand. Some specimens exhibited unique conchological traits not observed in any previously described taxa. Notably, shell variations were observed both within the same locality and across different regions, indicating that the shell-based taxonomy alone is inadequate for the systematic classification of the *Georissa*. To resolve these issues, DNA barcoding is essential. The mitochondrial cytochrome *c* oxidase subunit I (COI) gene has become a widely recognised barcoding marker in studies of land snail diversity, particularly for species recognition and delineation in Southeast Asian land snails (Sutcharit et

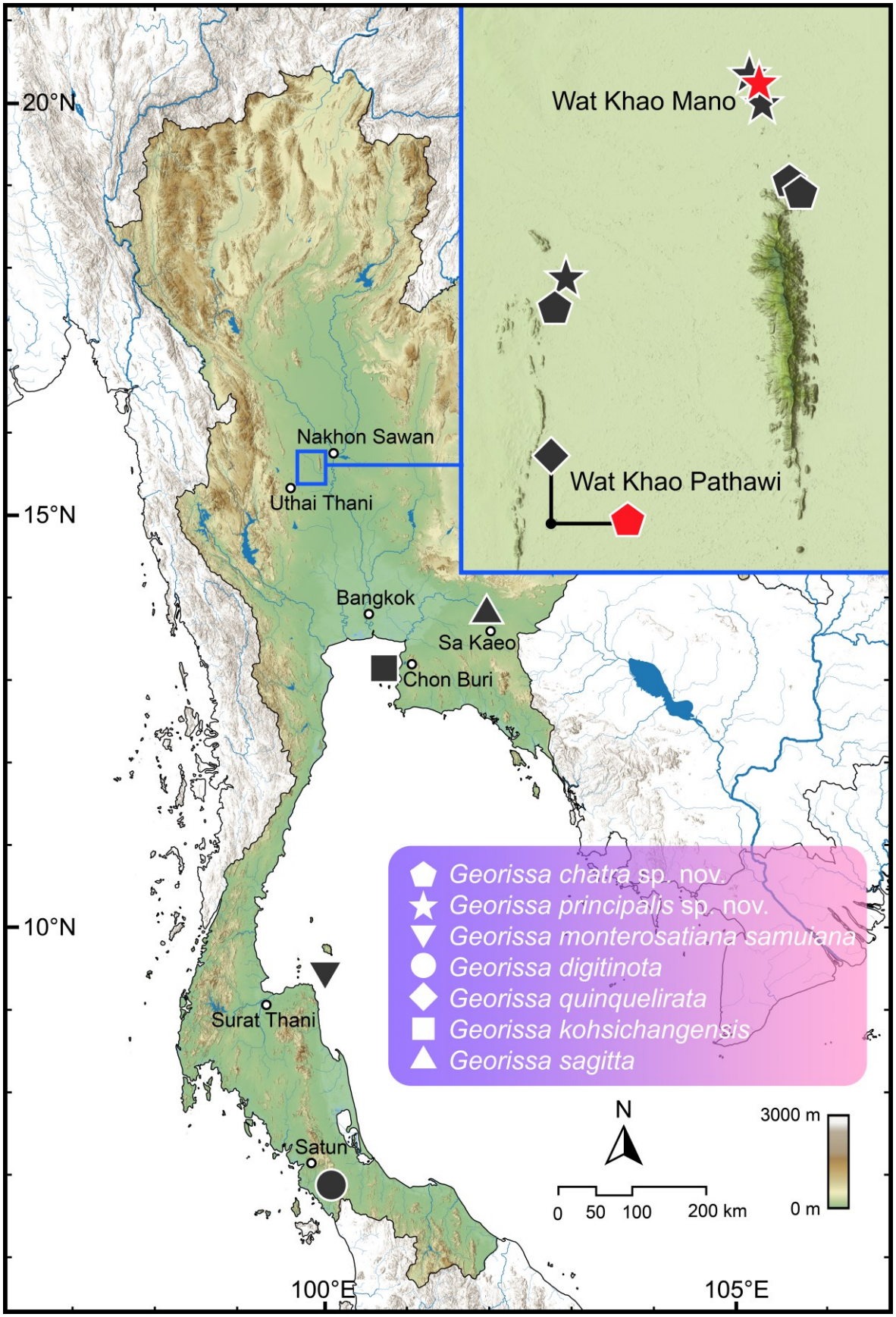

FIGURE 1. Distribution map of all *Georissa* species recorded from Thailand, with each symbol representing each distinct species. Red colour indicates the type localities of two new species described herein; black colour indicates other localities for the remaining species.

TABLE 1. List of samples used for phylogenetic analysis, with specimen codes, museum registration numbers, GenBank accession numbers, sampling localities, and references.

Taxa	Codes	Museum registration numbers	GenBank accession number (COI)	Localities	References
Order Cycloneritida					
Superfamily Hydrocenoidea Troschel, 1857					
Family Hydrocenidae Troschel, 1857					
Georissa chatra sp. nov.	NKS8C1-1	CUMZ 15270	PV631141	Limestone hill near Wat Si Uthum Phon, Mueang, Nakhon Sawan, Thailand	This study
Georissa chatra sp. nov.	NKS8C1-2	CUMZ 15270	PV631142	Limestone hill near Wat Si Uthum Phon, Mueang, Nakhon Sawan, Thailand	This study
Georissa chatra sp. nov.	NKS8C2-1	CUMZ 15270	PV631143	Limestone hill near Wat Si Uthum Phon, Mueang, Nakhon Sawan, Thailand	This study
Georissa chatra sp. nov.	NKS8C2-2	CUMZ 15270	PV631144	Limestone hill near Wat Si Uthum Phon, Mueang, Nakhon Sawan, Thailand	This study
Georissa chatra sp. nov.	NKS8C3	CUMZ 15270	PV631145	Limestone hill near Wat Si Uthum Phon, Mueang, Nakhon Sawan, Thailand	This study
Georissa chatra sp. nov.	NKS8C4	CUMZ 15270	PV631146	Limestone hill near Wat Si Uthum Phon, Mueang, Nakhon Sawan, Thailand	This study
Georissa chatra sp. nov.	UT1C	CUMZ 15267	PV631147	Wat Khao Pathawi, Thap Than, Uthai Thani, Thailand	This study
Georissa chatra sp. nov.	UT8C	CUMZ 15266	PV631148	Wat Khao Pathawi, Thap Than, Uthai Thani, Thailand	This study
Georissa chatra sp. nov.	UT2C	CUMZ 15269	PV631149	Tham Khao Kwang Thong, Sawang Arom, Uthai Thani, Thailand	This study
Georissa principalis sp. nov.	NKS6	CUMZ 15274	PV631150	Wat Tham Khao Noi, Mueang, Nakhon Sawan, Thailand	This study
Georissa principalis sp. nov.	NKS11J-1	CUMZ 15273	PV631151	Wat Khao Mano, Mueang, Nakhon Sawan, Thailand	This study
Georissa principalis sp. nov.	NKS11J-2	CUMZ 15273	PV631152	Wat Khao Mano, Mueang, Nakhon Sawan, Thailand	This study
Georissa quinquelirata Klongkaew et al., 2024	UT1R	CUMZ 15277	PV631153	Wat Khao Pathawi, Thap Than, Uthai Thani, Thailand	This study
Georissa quinquelirata Klongkaew et al., 2024	UT8	CUMZ 15278	PV631154	Wat Khao Pathawi, Thap Than, Uthai Thani, Thailand	This study
Georissa quinquelirata Klongkaew et al., 2024	-	ZRCBUU 0901	PP844569	Pathawi limestone hill, Thap Than, Uthai Thani, Thailand	Klongkaew et al. (2024)
Georissa quinquelirata Klongkaew et al., 2024	-	ZRCBUU 0901	PP844570	Pathawi limestone hill, Thap Than, Uthai Thani, Thailand	Klongkaew et al. (2024)
Georissa kohsichangensis Klongkaew et al., 2024	CB3	CUMZ 15279	PV631155	Area 1 in Koh Si Chang Island, Koh Sichang, Chonburi, Thailand	This study
Georissa kohsichangensis Klongkaew et al., 2024	CB4	CUMZ 15280	PV631156	Area 2 in Koh Si Chang Island, Koh Sichang, Chonburi, Thailand	This study
Georissa kohsichangensis Klongkaew et al., 2024	CB5	CUMZ 15281	PV631157	Area 3 in Koh Si Chang Island, Koh Sichang, Chonburi, Thailand	This study
Georissa kohsichangensis Klongkaew et al., 2024	-	ZRCBUU 0903	PP844571	Yai Man Cave, Koh Sichang, Chonburi, Thailand	Klongkaew et al. (2024)
Georissa kohsichangensis Klongkaew et al., 2024	-	ZRCBUU 0903	PP844572	Yai Man Cave, Koh Sichang, Chonburi, Thailand	Klongkaew et al. (2024)
Georissa sagitta Klongkaew et al., 2024	SK6N	CUMZ 15282	PV631158	Khao Maka Cave Temple, Mueang, Sakaeo, Thailand	This study
Georissa sagitta Klongkaew et al., 2024	-	ZRCBUU 0905	PP844573	Khao Maka Cave Temple, Mueang, Sakaeo, Thailand	Klongkaew et al. (2024)

TABLE 1. Continued.

Taxa	Codes	Museum registration numbers	GenBank accession number (COI)	Localities	References
Georissa sagitta Klongkaew et al., 2024	-	ZRCBUU 0905	PP844574	Khao Maka Cave Temple, Mueang, Sakaeo, Thailand	Klongkaew et al. (2024)
Georissa digitinota Klongkaew et al., 2024	-	ZRCBUU 0907	PP844575	Khao Noi Bodhiyan Temple, Mueang, Satun, Thailand	Klongkaew et al. (2024)
Georissa digitinota Klongkaew et al., 2024	-	ZRCBUU 0907	PP844576	Khao Noi Bodhiyan Temple, Mueang, Satun, Thailand	Klongkaew et al. (2024)
Georissa hadra Thompson & Dance, 1983	-	MZU/MOL 17.32	MH033897	Lang Cave, Mulu N.P., Mulu, Sarawak, Malaysia	Khalik et al. (2018)
Georissa muluensis Khalik et al., 2018	-	MZU/MOL 17.31	MH033893	Lagang Cave, Mulu National Park, Mulu, Sarawak, Malaysia	Khalik et al. (2018)
Georissa niahensis Godwin-Austen, 1889	-	MZU/MOL 17.25	MH033965	Painted Cave, Niah National Park, Niah, Sarawak, Malaysia	Khalik et al. (2018)
Georissa hosei Godwin-Austen, 1889	-	MZU/MOL 16.09	MH033907	Bukit Tongak, Bidi, Bau/Jambusan, Sarawak, Malaysia	Khalik et al. (2018)
Georissa anyiensis Khalik et al., 2018	-	MZU/MOL 17.60	MH033935	Bukit Anyi at Bukit Sarang, Bintulu, Sarawak, Malaysia	Khalik et al. (2018)
Georissa bauensis Khalik et al., 2018	-	MZU/MOL 16.03	MH033943	Gunung Podam, near Sungai Ayup, Kampung Bogag, Bau, Sarawak, Malaysia	Khalik et al. (2018)
Superfamily Neritoidea Rafinesque, 1815					
Family Neritidae Rafinesque, 1815					
Nerita planospira Anton, 1838	-	-	JX411675	The coasts of Malaysia	Chee and Mohd Nor (2014)
Nerita adenensis Mienis, 1978	-	-	MN461473	Iran	Cheshom (Unpublished)
Superfamily Helicinoidea Férussac, 1822					
Family Neritiliidae Schepman, 1908					
Neritilia cavernicola Kano & Kase, 2004	-	-	AB102709	Bantayan, Philippines	Kano and Kase (2004)

TABLE 2. Intra- and interspecific genetic differentiation among *Georissa* species by means of *p*-distances.

Taxa	1	2	3	4	5	6	7	8	9	10	11	12
1 *Georissa chatra* sp. nov.	0.061											
2 *Georissa principalis* sp. nov.	0.163	0.075										
3 *Georissa quinquelirata*	0.149	0.157	0.035									
4 *Georissa kohsichangensis*	0.160	0.145	0.137	0.053								
5 *Georissa sagitta*	0.165	0.140	0.129	0.115	0.008							
6 *Georissa digitinota*	0.164	0.152	0.162	0.152	0.139	0.000						
7 *Georissa anyiensis*	0.170	0.175	0.155	0.164	0.157	0.151	-					
8 *Georissa bauensis*	0.172	0.173	0.170	0.142	0.164	0.148	0.129	-				
9 *Georissa hadra*	0.174	0.164	0.168	0.157	0.156	0.158	0.119	0.138	-			
10 *Georissa hosei*	0.175	0.178	0.179	0.167	0.164	0.143	0.123	0.134	0.129	-		
11 *Georissa muluensis*	0.186	0.181	0.167	0.164	0.154	0.154	0.136	0.136	0.068	0.129	-	
12 *Georissa niahensis*	0.173	0.161	0.162	0.150	0.153	0.136	0.121	0.131	0.103	0.115	0.121	-

al., 2020a, 2021; Pholyotha et al., 2020, 2021, 2022b, 2024). Thus, this research aims to describe two newly identified *Georissa* species based on shell and operculum morphology, while confirming their taxonomic boundaries using mitochondrial COI phylogenetics.

MATERIALS AND METHODS

Georissa specimens were sampled from the limestone regions of Sa Kaeo, Uthai Thani, Nakhon Sawan, and Chonburi provinces in Thailand (Fig. 1). The micro snails were collected through direct visual searches and hand collection across various microsites, including cracks in rocks, moist surfaces of limestone walls, and beneath layers of ground litter. Before preservation, photographs of the living micro snails were taken using a Nikon DSLR D850 camera equipped with a Nikon 105mm Macro lens (AF-S VR Micro-Nikkor 105mm f/2.8G IF-ED). The micro snail specimens were then euthanized following the standard two-step protocol (American Veterinary Medical Association, 2020) and subsequently preserved in 95% (v/v) ethanol for further morphological and molecular studies. Most *Georissa* voucher specimens examined in this study have been deposited in the Chulalongkorn University Museum of Zoology (CUMZ), Bangkok, Thailand.

The collected *Georissa* specimens were identified by comparing their shell morphology with descriptions from the original literature and several related publiccations (Blanford, 1864, 1869; Möllendorff, 1894; Godwin-Austen and Nevill, 1879; Preston, 1915; Thompson and Dance 1983; Panha and Burch, 2005; Khalik et al., 2018, 2019a, b; Sutcharit et al., 2020b; Preece et al., 2022; Klongklaew et al., 2024), then compared with available type specimens and the reference collection. Prior to studying the shell morphology, adult shells were first washed in a Petri dish with water and detergent, and then were air-dried. Shells of *Georissa* were examined and imaged using a Leica M205C microscope equipped with fusion optics stereo and the Leica Application Suite Image System, and the scanning electron microscopy (SEM; JEOL, JSM-6610 LV). Some adult specimens were measured for size, and whorls were counted using a stereo microscope with the Cell'D Imaging Software.

Genomic DNA was extracted from the foot tissue by the use of the G-spin™ Genomic DNA Extraction Kit following the manufacturer's instructions. A fragment of the mitochondrial cytochrome *c* oxidase subunit I (COI) gene was amplified by PCR using the primer pairs LCO1490 and HCO2198 (Folmer et al., 1994). Reactions were performed under standard conditions with an initial cycle at 94 °C for 1 min, followed by 40 cycles of 10 s at 98 °C, 30 s at 50 °C, and 1 min at 72 °C, followed by a final extension step at 72 °C for 5 min. PCR products of COI were sequenced at Bioneer Corporation, South Korea. Forward and reverse strands were corrected for misreads and merged into one sequence file using MEGA v. 7.0 (Kumar et al., 2016). New sequences and sample data are provided in Table 1.

All COI sequences were aligned using MAFFT v. 7 with the default settings (Katoh et al., 2017) via the MAFFT online service (https://mafft.cbrc.jp/alignment/server/). Phylogenetic trees were constructed using maximum likelihood (ML) and Bayesian inference (BI) approaches through the online CIPRES Science Gateway (Miller et al., 2010). ML tree was inferred with RAxML-HPC2 on ACCESS v. 8.2.12 (Stamatakis, 2014) using a GTRCAT model and 1000 bootstrap replicates to assess branch support. For BI analysis, the partitioning and substitution model choice for the COI dataset were done in the program Kakusan4 (Tanabe 2011) by means of the Bayesian Information Criterion. As suggested by the Kakusan4 program, the COI dataset was divided into three partitions: the general time-reversible model with a gamma distribution for the first and the second codon positions, and the Felsenstein 1981 model with a gamma distribution for the third codon position. The analysis was conducted in MrBayes on ACCESS v. 3.2.7a (Ronquist et al., 2012) by running 20 million generations of Markov Chain Monte Carlo algorithms (MCMC). The sampling rate of the trees was 1000 generations, with the first 25% of obtained trees being discarded as burn-in. Both ML and BI trees were visualized and modified in FigTree v. 1.4.4. (Rambaut, 2018), then visually processed in Adobe Illustrator 2021. To assess the node robustness, a branch or clade was considered strongly supported or statistically significant if the ML bootstrap (BS) support values were ≥ 70% and the BI posterior probabilities (PP) were ≥ 0.95 (Hillis and Bull, 1993; Felsenstein, 2004; Huelsenbeck and Rannala, 2004; Mauro and Agorreta, 2010). Additionally, genetic *p*-distances were calculated using MEGA v. 7.0 (Kumar et al., 2016) with the 'pairwise deletion of gaps' option.

Institutional abbreviations

CUMZ Chulalongkorn University, Museum of Zoology, Bangkok, Thailand

NHM Natural History Museum, London, United Kingdom (**NHMUK** is used when citing specimens deposited in the NHM).

SMF Senckenberg Forschungsinstitut und Naturmuseum, Frankfurt am Main, Germany

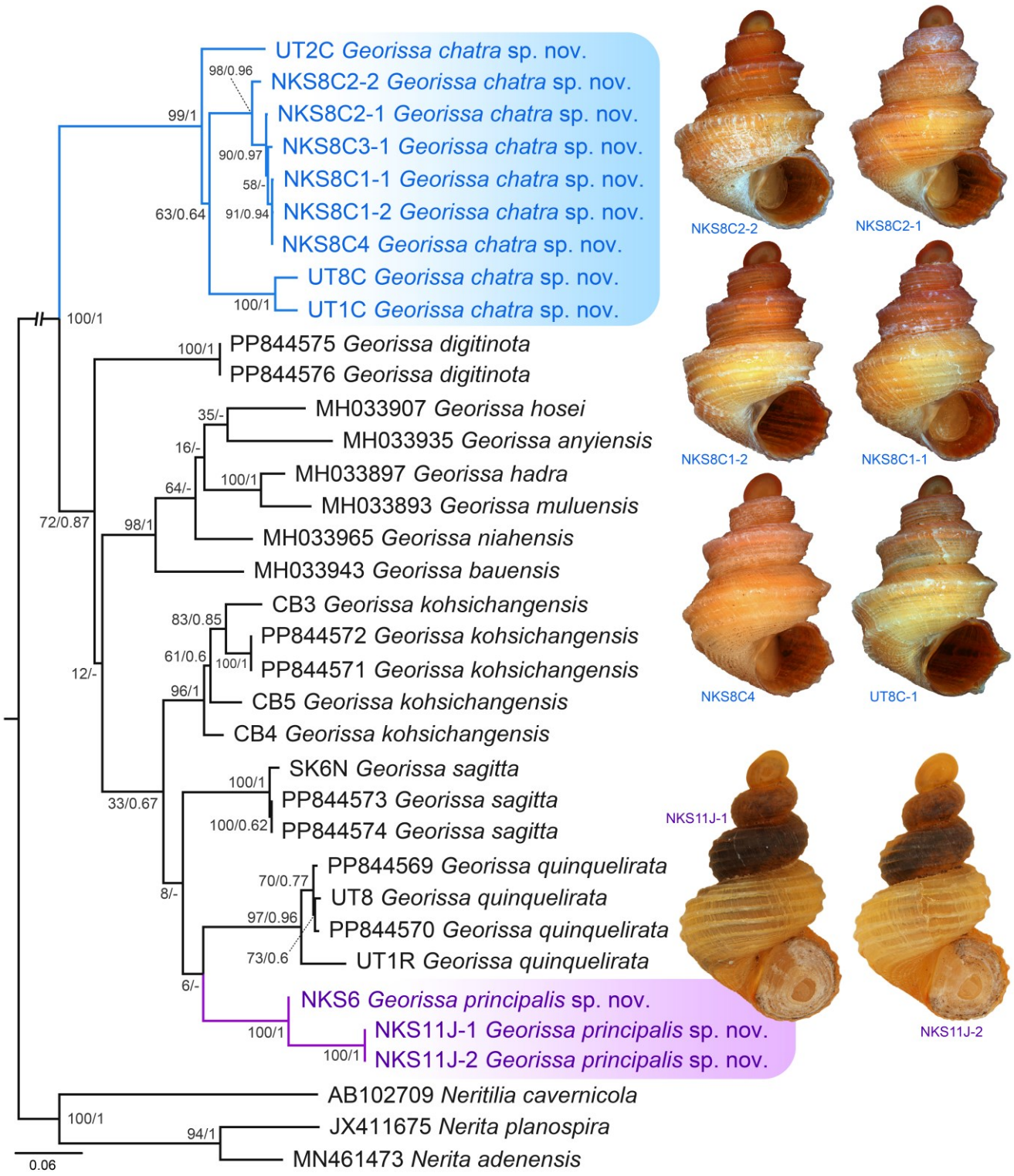

FIGURE 2. Maximum likelihood phylogeny based on analyses of mitochondrial cytochrome *c* oxidase subunit I (COI) sequences. Blue and purple boxes mark the two newly described species. Numbers on branches indicate nodal support by ML bootstrap (BS) and Bayesian posterior probabilities (PP). Representative shells of the newly described species are shown but not to scale.

RESULTS

COI phylogeny and genetic distances between species

Molecular phylogenetic trees were reconstructed based on the COI sequences obtained from 35 individuals, including 32 sequences from 12 *Georissa* species. Three sequences from two species of *Nerita* Linnaeus, 1758 and one species of *Neritilia* Martens, 1875 were used as outgroups. The final aligned COI sequences were composed of 658 base pairs, containing 266 variable sites, 392 conservative sites, and 241 parsimony-informative sites. The mean interspecific sequence divergence within *Georissa* varied between 6.8% (between *G. muluensis* Khalik et al., 2018 and *G. hadra* Thompson & Dance, 1983) to 18.6% (between *G. muluensis* and *G. chatra* sp. nov.) (Table 2). The intraspecific genetic distances within each lineage varied between 0% (*G. digitinota* Klongkaew et al., 2024) to 7.5% (*G. principalis* sp. nov.) (Table 2).

In this study, ML and BI analyses produced the phylogenetic trees with similar topologies that differed in some details. Therefore, only the tree topology from the ML analysis is presented in Figure 2. Both phylogenies confirmed the monophyly of *Georissa* with strong support [BB/PP: 100/1]. Both ML and BI analyses consistently showed that all currently recognized *Georissa* species from Thailand (*G. chatra* sp. nov., *G. principalis* sp. nov., *G. quinquelirata* Klongkaew et al., 2024, *G. kohsichangensis* Klongkaew et al., 2024, *G. sagitta* Klongkaew et al., 2024, and *G. digitinota*) were not retrieved together as a monophyletic group, whereas each species formed each well-supported clade. The phylogenetic relationships among species within the genus *Georissa* remain unresolved.

Taxonomy

Subclass Neritimorpha Koken, 1896
Order Cycloneritida Frýda, 1998
Superfamily Hydrocenoidea Troschel, 1857
Family Hydrocenidae Troschel, 1857

Genus *Georissa* Blanford, 1864

Georissa Blanford, 1864: 463. Blanford, 1869: 173. Pilsbry and Hirase, 1908: 38. Zilch, 1973: 263. Thompson and Dance, 1983: 112. Panha and Burch, 2005: 11. Haase and Schilthuizen, 2007: 215. Khalik et al., 2018: 1, 2019a: 1, 2019b: 35. Sutcharit et al., 2020b: 5. Das and Aravind, 2021: 93. Preece et al., 2022: 55. Klongklaew et al., 2024: 1347.
Chondrella Pease, 1871: 465.
Hydrocena (*Georissa*)—Preston, 1915: 1.
Omphalorissa Iredale, 1933: 57.

Type species.− *Hydrocena pyxis* Benson, 1856, by original designation.

Georissa chatra Buathanom & Pholyotha, sp. nov.

https://zoobank.org/urn:lsid:zoobank.org:act: 9294D056-C0A8-4287-8D26-C024582FD52E

(Figs 1–5)

Type material.− Holotype CUMZ 15265 (width 1.3 mm, height 1.8 mm; Fig. 3A). Paratypes CUMZ 15266 (18 preserved specimens; Figs 3B, C, 4A), 15267 (five preserved specimens), NHMUK (two shells) and SMF (two shells) from the type locality.

Type locality.− Wat Khao Pathawi, Thap Than District, Uthai Thani Province, Thailand (15°28'18.5"N 99°45'25.7"E).

Other material examined.− Tham Khao Kwang Thong, Sawang Arom District, Uthai Thani Province, Thailand (15°38'37.9"N 99°45'28.5"E): CUMZ 15268 (two preserved specimens), 15269 (one preserved specimen). Limestone hill near Wat Si Uthum Phon, Mueang District, Nakhon Sawan Province, Thailand (15°44'24.1"N 99°56'43.1"E): CUMZ 15270 (27 preserved specimens). Wat Tham Bo Ya, Mueang District, Nakhon Sawan Province, Thailand (15°43'48.1"N 99° 56'45.3"E): CUMZ 15271 (one preserved specimen).

Etymology.− The specific epithet "*chatra*" refers to a dome or umbrella-like structure sometimes with multiple tiers or layers, which is used in several Asian royal or state ceremonies, reflecting the distinctive shell shape of this new species.

Diagnosis.− Shell minute, conical, dark orange, with tall and prominent carinas: one on upper periphery and one on below periphery.

Description.− Shell (Figs 2, 3A–F, 4). Shell solid, dextral, minute (width up to 1.4 mm, height up to 2.0 mm), conical, semi-translucent to opaque, and monochrome reddish to dark orange in colour. Whorls 4–4⅛, increasing regularly, convex; spire elevated-conical with rounded apex; suture narrowly impressed and deep. Protoconch about 1¼ whorl, globular, and sculptured with partly concatenated shallow pits or rugulose (Fig. 3B). Teleoconch with irregular growth lines, and sculptured with two carinas: upper one above periphery, tall and prominent and slightly curved upwards (towards apex), and bears a groove on its upper side;

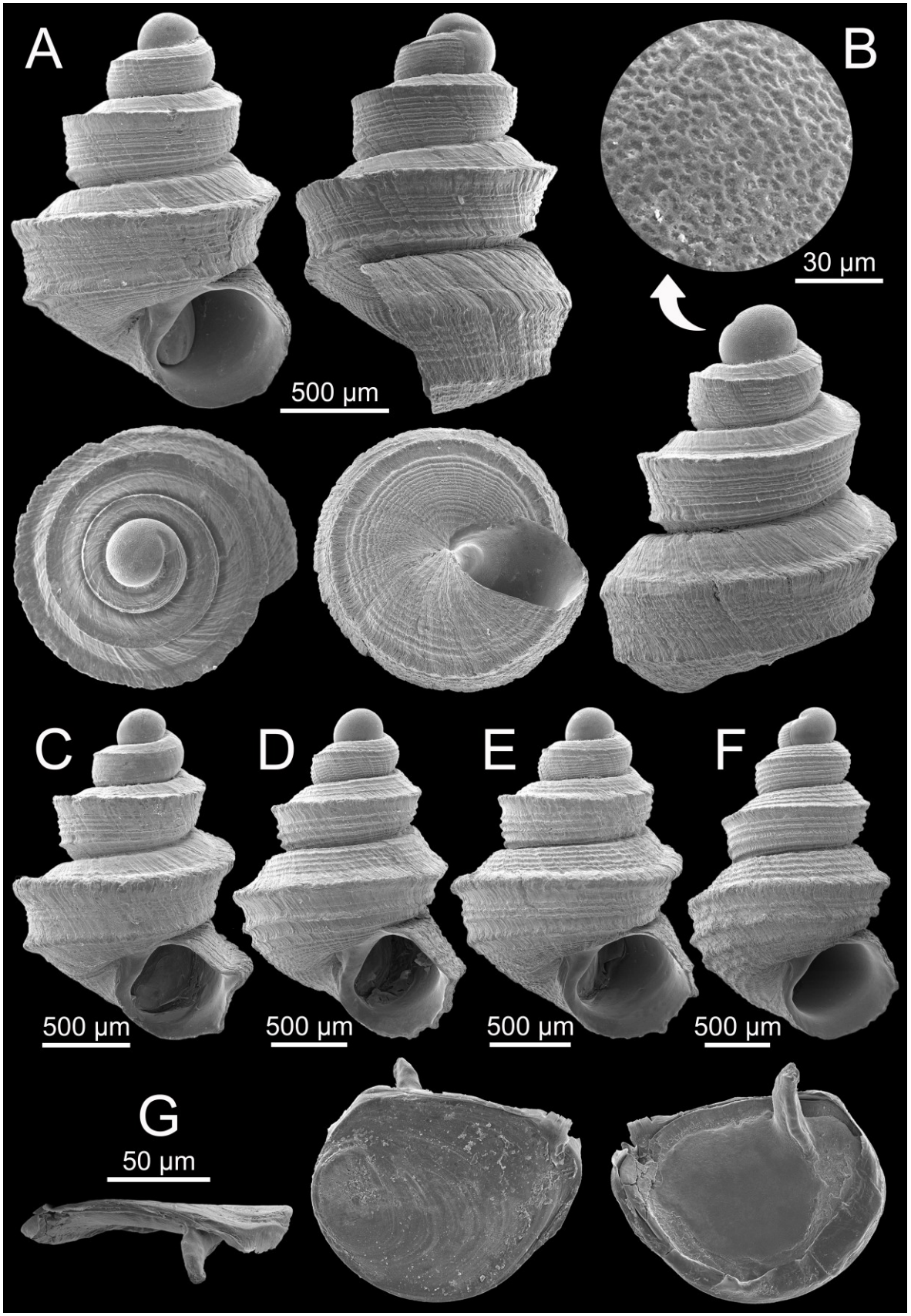

FIGURE 3. Scanning electron micrographs of *Georissa chatra* sp. nov. **A.** holotype CUMZ 15265 from Wat Khao Pathawi, Uthai Thani. **B, C.** paratype CUMZ 15266 from the type locality, (**B**) close-up view of protoconch and (**C**) entire shell in apertural view. **D–G** specimen CUMZ 15270 from limestone hill near Wat Si Uthum Phon, Nakhon Sawan, (**D–F**) entire shells in apertural view and (**G**) operculum with lateral view, and outer and inner surface views, respectively.

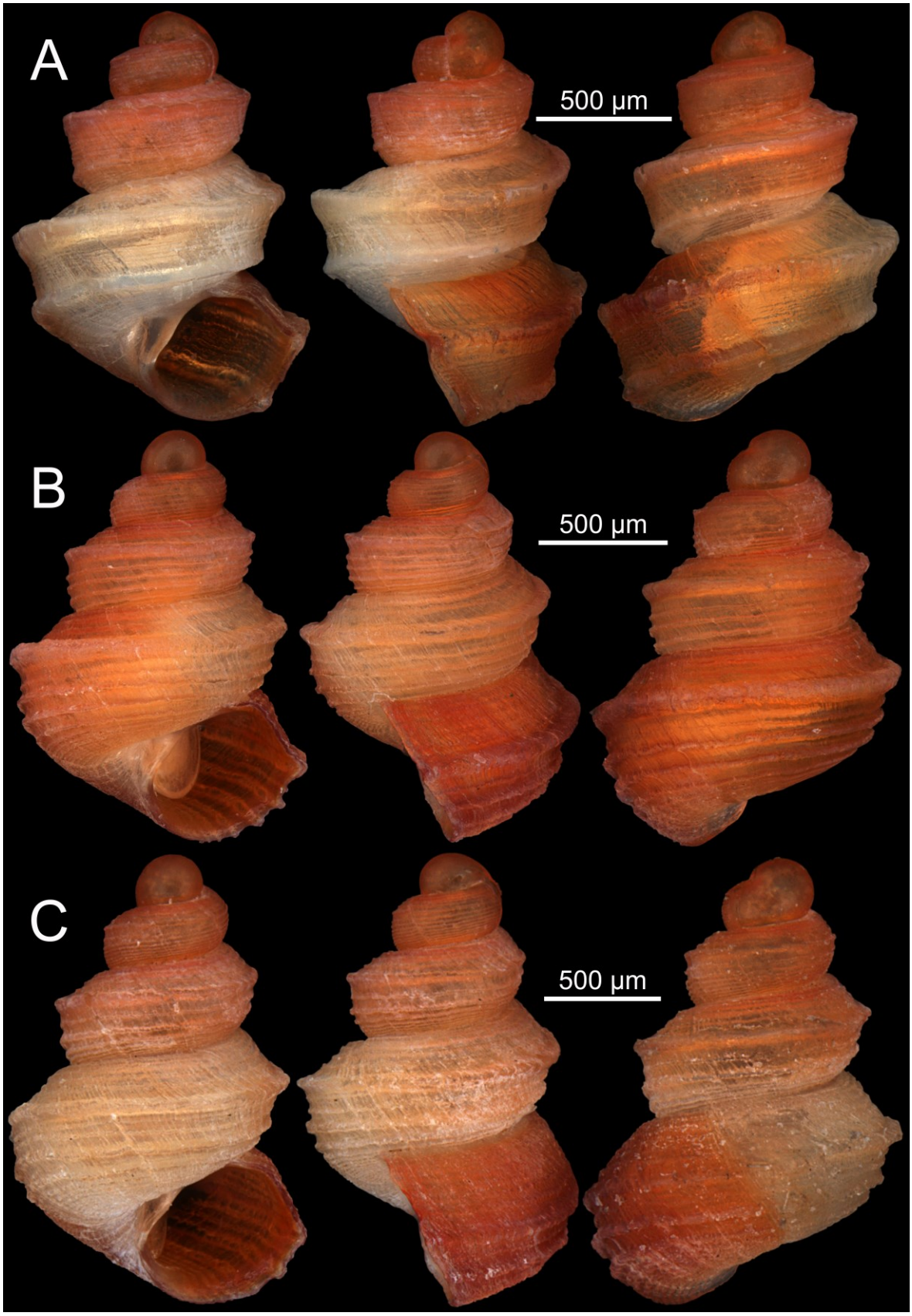

FIGURE 4. Shells of *Georissa chatra* sp. nov. **A.** paratype CUMZ 15266 from Wat Khao Pathawi, Uthai Thani. **B, C.** specimens CUMZ 15270 from limestone hill near Wat Si Uthum Phon, Nakhon Sawan.

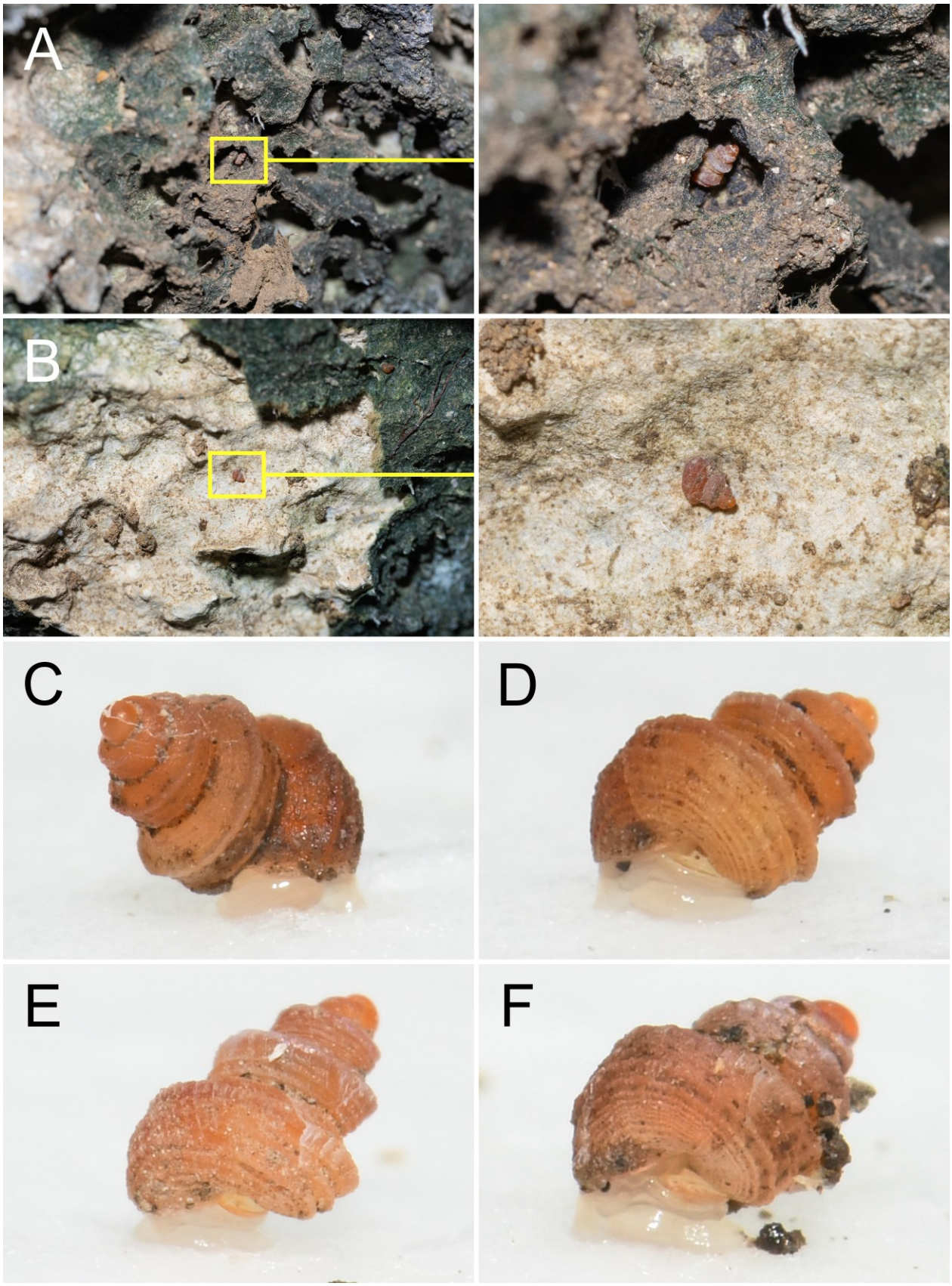

FIGURE 5. Living *Georissa chatra* sp. nov. from a limestone hill near Wat Si Uthum Phon, Nakhon Sawan. **A, B.** snails in microhabitats on the limestone wall; insets showing close-up views of (**A**) a snail hiding in a small crevice and (**B**) a snail on a bare wall. **C–F.** four different individuals while climbing slowly on moist tissue paper.

lower one less prominent and locate above suture. Area between two carinas with more or less strong, equally spaced and uneven ridges interrupted by irregular growth lines. Below periphery generally with densely packed sculpture arranged into equally spaced spiral threads encircled umbilicus. Aperture D-shaped; peristome simple; lip rather thicken and slightly bulging at palatal and basal sides. Umbilicus closed.

Operculum (Fig. 3G). Operculum calcareous, yellowish-orange, semi-translucent, broadly ovate or D-shaped, nucleus submarginal, concentric growth lines, and apophysis short. Operculum relatively smaller than aperture and can be retracted into shell.

External body (Fig. 5C–F). Animal with short body, foot rounded off and broader in front, nearly colorless to cream, large and dark eye spot.

Distribution, habitat and occurrence.− *Georissa chatra* sp. nov. could be found on limestone hills of central Thailand in Uthai Thani and Nakhon Sawan provinces (Fig. 1) with low abundance across all known locations. Living snails were found attached on limestone rocks covered with algae and lichen, on bare rock, and in rock crevices (Fig. 5A, B). *Georissa quinquelirata* also coexists with this new species at Wat Khao Pathawi (Fig. 1).

Differential diagnosis.− *Georissa chatra* sp. nov. differs from all *Georissa* species known from Indochina, i.e., *G. illex* (Benson, 1856), *G. blanfordiana* Stoliczka, 1871 and *G. liratula* Stoliczka, 1871 from Myanmar, *G. semisculpta* Godwin-Austen & Nevill, 1879, and *G. monterosatiana monterosatiana* Godwin-Austen & Nevill, 1879 from Peninsular Malaysia, *G. monterosatiana samuiana* Möllendorff, 1894, *G. quinquelirata*, *G. kohsichangensis*, *G. sagitta*, and *G. digitinota* from Thailand by the presence of tall and prominent carinas (upper and below) on the last whorl. In contrast, *G. blanfordiana* and *G. digitinota* have much nearly smooth shell surface; *G. kohsichangensis*, *G. ilex, G. monterosatiana monterosatiana*, *G. monterosatiana samuiana*, and *G. semisculpta* have weak spiral ridges on the shell surface; and *G. liratula*, *G. quinquelirata* and *G. sagitta* have strong and prominent spiral ridges on the shell surface (Blanford, 1864; Godwin-Austen and Nevill, 1879; Möllendorff, 1894; Preston, 1915; Zilch, 1973; Thompson and Dance, 1983; Panha and Burch, 2005; BEDO, 2017; Khalik et al., 2018, 2019a, b; Sutcharit et al., 2020b; Preece et al., 2022; Klongklaew et al., 2024).

Remarks.− *Georissa chatra* sp. nov. has variable shell sculptures ranging from very tall and prominent carinas with weak to less prominent spiral ridges (Figs 3A, C, E, 4A) to relatively low carinas with strong and prominent spiral ridges (Figs 3D, F, 4B, C). However, the shell variations in a single land snail species have often been reported and shown to be correlated with variation in habitats (Khalik et al., 2019a, b; Pholyotha et al., 2020, 2022b). In addition, the ML and BI analyses revealed that these shell variations grouped together with strong support within the clade of *G. chatra* sp. nov. (Fig. 2). Additionally, the *p*-distance analysis also revealed the divergence of this new species from all previously described species (Fig. 2).

Georissa principalis Buathanom & Tongkerd, sp. nov.

https://zoobank.org/urn:lsid:zoobank.org:act: F9A2770C-E7ED-42C6-BF35-55898BD71D4B

(Figs 1, 2, 6–8)

Type material.− Holotype CUMZ 15272 (width 1.4 mm, height 2.5 mm; Fig. 6A). Paratypes CUMZ 15273 (24 preserved specimens; Figs 6B–D, 7), NHMUK (two shells) and SMF (two shells) from the type locality.

Type locality.− Wat Khao Mano, Mueang District, Nakhon Sawan Province, Thailand (15°48'38.6"N 99°54'52.3"E).

Other material examined.− Wat Tham Khao Noi, Mueang District, Nakhon Sawan Province, Thailand (15°49'02.7"N 99°54'35.9"E): CUMZ 15274 (30 preserved specimens). Wat Khao Ruea, Mueang District, Nakhon Sawan Province, Thailand (15°47'50.2"N 99° 55'09.1"E): CUMZ 15275 (43 preserved specimens). Tham Khao Kaji, Sawang Arom District, Thani Province, Thailand (15°39'15.1"N 99°45'34.9"E): CUMZ 15276 (two preserved specimens).

Etymology.− The name "*principalis*" is derived from the Latin word meaning "chief" or "leader" and is chosen to honor Her Royal Highness Princess Maha Chakri Sirindhorn for her outstanding leadership in biodiversity conservation in Thailand.

Diagnosis.− Shell minute, elongate, turreted, yellow-orange to light brownish, with about six to seven prominent spiral ridges at the periphery, and operculum with 2 layers.

Description.− Shell (Figs 2, 6A, B, 7). Shell solid, dextral, minute (width up to 1.4 mm, height up to 2.5 mm), elongate conical to turreted and semi-translucent to opaque. Whorls 4⅛–4¼, increasing regularly, convex, evenly rounded; spire highly elevated-conical with blunt apex; suture widely impressed and deep.

Surface dull; shell colour yellowish orange to light brownish. Protoconch about 1¼ whorl, globular, and sculptured with partly concatenated shallow pits or rugulose (Fig. 6B). Teleoconch with irregular growth lines; and sculptured with strong and equally spaced cord-like spiral ridges (six to seven ridges from upper corner of peristome to suture seen in apertural view), and a spiral series of low, small, scale-like structures situated deep within the suture. Area between ridges smooth or with fine spiral threads. Below periphery equally spaced and dull ridges encircled umbilicus. Aperture broadly ovate or D-shaped; peristome simple; lip rather evenly thicken throughout. Umbilicus closed.

Operculum (Fig. 6C, D). Operculum D-shaped, concentric, nucleus submarginal and composed of 2 layers. Inner layer (white arrowheads in Fig. 6C, D) calcareous, yellowish orange, concentric, nucleus submarginal, and with short apophysis. Outer layer is a calcium-accumulated layer (yellow arrowhead in Fig. 6C), thickened, irregular surface, similar shape with inner layer, separatable, and usually with large hole at nucleus of operculum. Operculum relatively large, fit with aperture, and cannot be retracted into shell.

External body (Fig. 8B–E). Animal morphology generally similar the previous species; but differs by pale grey around cephalic area and snout.

Distribution, habitat and occurrence.− *Georissa principalis* sp. nov. was found from few limestone hills in Nakhon Sawan and Uthai Thani provinces (Fig. 1). They occur in low densities and are usually found attached on shaded limestone walls or rocks, in rock crevices and mossy limestone wall (Fig. 8A). The snails may probably feed on algae, moss fragments and lichens.

Differential diagnosis.− *Georissa principalis* sp. nov. is easy to distinguish from all known *Georissa* species known from Thailand, Myanmar and Peninsular Malaysia by its more elongated shell with strongly prominent spiral cord-like ridges, and a unique operculum with two layers, while all other *Georissa* species have an ovate conic to conical shell, a less prominent spiral ridge, and a simple operculum with only one layer (Blanford, 1864; Möllendorff, 1894; Godwin-Austen and Nevill, 1879; Preston, 1915; Zilch, 1973; Thompson and Dance, 1983; Panha and Burch, 2005; Khalik et al., 2018, 2019a, b; Sutcharit et al., 2020b; Preece et al., 2022; Klongklaew et al., 2024). This new species can be distinguished from *G. liratula* and *G. chatra* sp. nov. by having an elongate conical shape, with six to seven cord-like ridges on upper periphery, while *G. liratula* has an ovate conical shape, and *G. chatra* sp. nov. has a conical shape with tall and prominent carinas. *Georissa principalis* sp. nov. closely resembles *G. heudei* Pilsbry & Hirase, 1908 and *G. sinensis* (Heude, 1882) from China in its operculum, but this new species differs in the shell surface with strongly prominent spiral cord-like ridges, while the latter two species have a much nearly smooth shell surface (Pilsbry and Hirase, 1908).

Remarks.− Both ML and BI analyses confirm the monophyly of *G. principalis* sp. nov. and indicate that this new species represents a distinct lineage, separated from all other *Georissa* species.

In most *Georissa* species, the operculum is relatively smaller than the aperture and can be retracted into the shell. However, the operculum of *G. principalis* sp. nov., *G. heudei* and *G. sinensis* is a thick, calcareous, white plate that fits securely within the aperture and cannot be retracted (Heude, 1882; Pilsbry and Hirase, 1908; Yen, 1939). Based on these distinct operculum characteristics, Pilsbry and Hirase (1908) proposed the subgenus *Georissopsis*, designating *Georissa heudei* as the type species. However, the phylogenetic analysis in this study remains inconclusive in determining whether *Georissopsis* constitutes a distinct lineage within *Georissa*.

DISCUSSION

Our results contribute to a deeper understanding of species diversity among operculate micro snails in mainland Southeast Asia, with a particular focus on Thailand. Historical records show that *G. monterosatiana samuiana* is the only species of this genus described in Thailand (Hemmen and Hemmen 2001; Panha and Burch, 2005). While Panha and Burch (2005) reported additional three species from Thailand, they have not been formally described. In the checklist of molluscan biodiversity in Thailand by BEDO (2017), additional six *Georissa* species and subspecies were listed. These are three Burmese species (*G. blanfordiana*, *G. ilex* and *G. liratula*), two Malaysian species (*G. monterosatiana monterosatiana* and *G. semisculpta*), and one Borneo species (*G. williamsi*). However, there is still no evidence to support the occurrence of all these species in Thailand. Therefore, the total number of *Georissa* species remained unchanged from 1894 to 2024. Later, four species (*G. quinquelirata*, *G. kohsichangensis*, *G. sagitta*, and *G. digitinota*) described by Klongklaew et al. (2024) as well as two new species described herein (*G. chatra* sp. nov. and *G. principalis* sp. nov.) are among the first terrestrial micro snails in the genus *Georissa* to be described from Thailand in this century.

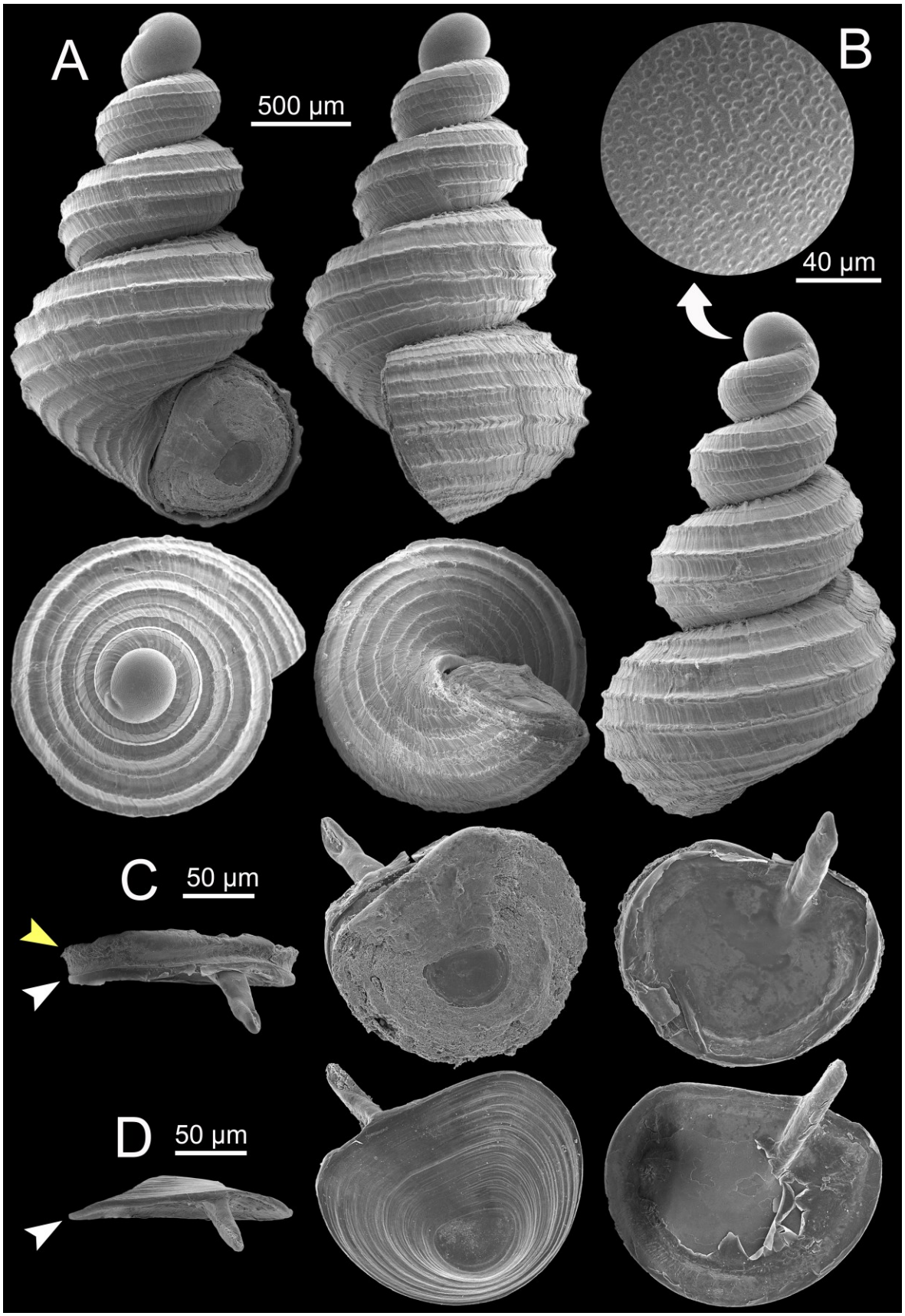

FIGURE 6. Scanning electron micrographs of *Georissa principalis* sp. nov. **A.** holotype CUMZ 15272 from Wat Khao Mano, Nakhon Sawan. **B–D.** paratype CUMZ 15273 from the type locality. **B**. close-up view of protoconch. **C, D.** operculum with lateral view, and outer and inner surface view, respectively, (**C**) with two layers (outer and inner layers), and (**D**) outermost layer was removed. Yellow arrowhead indicates the outer layer; arrowheads indicate the inner layer.

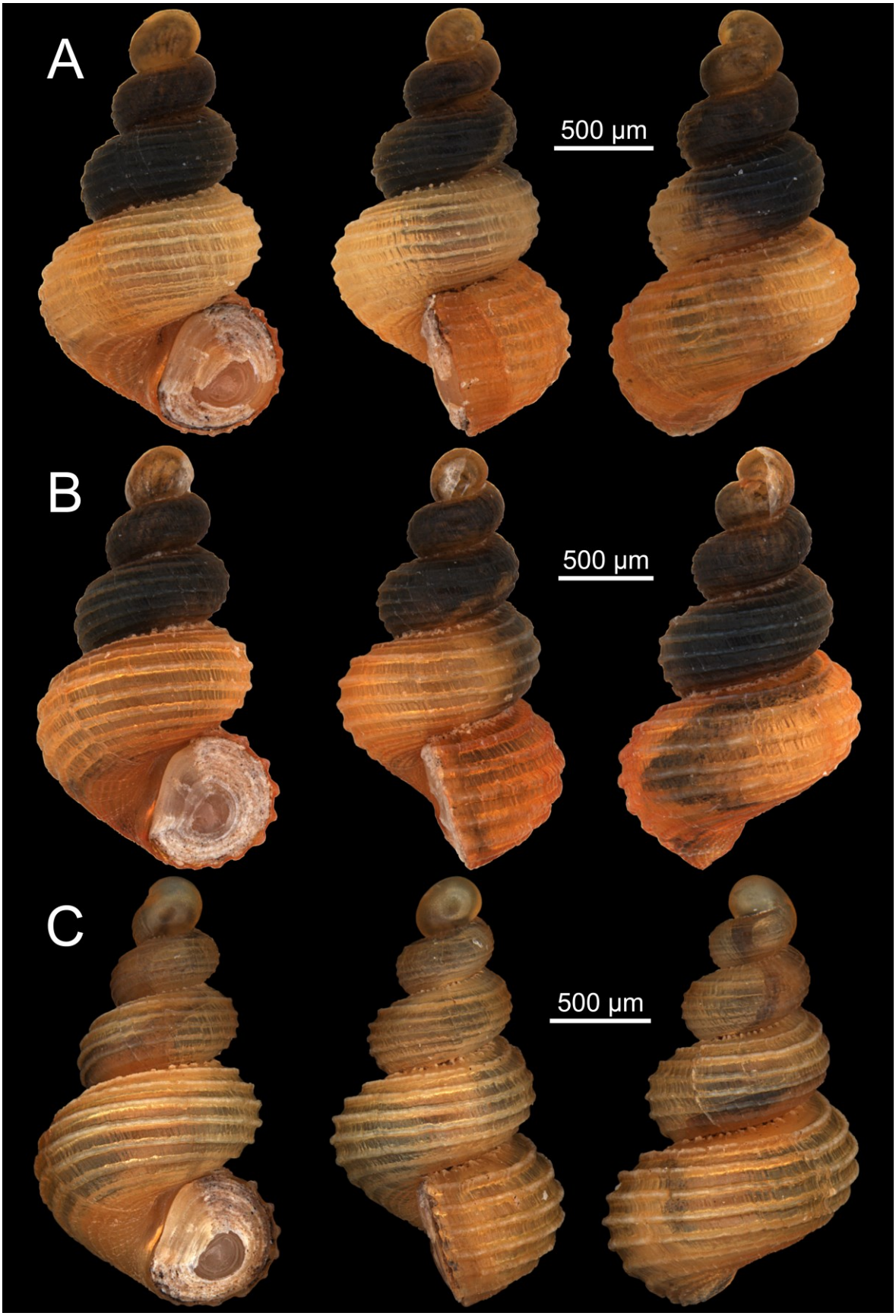

FIGURE 7. Shells of *Georissa principalis* sp. nov. **A–C.** paratype CUMZ 15273 from Wat Khao Mano, Nakhon Sawan.

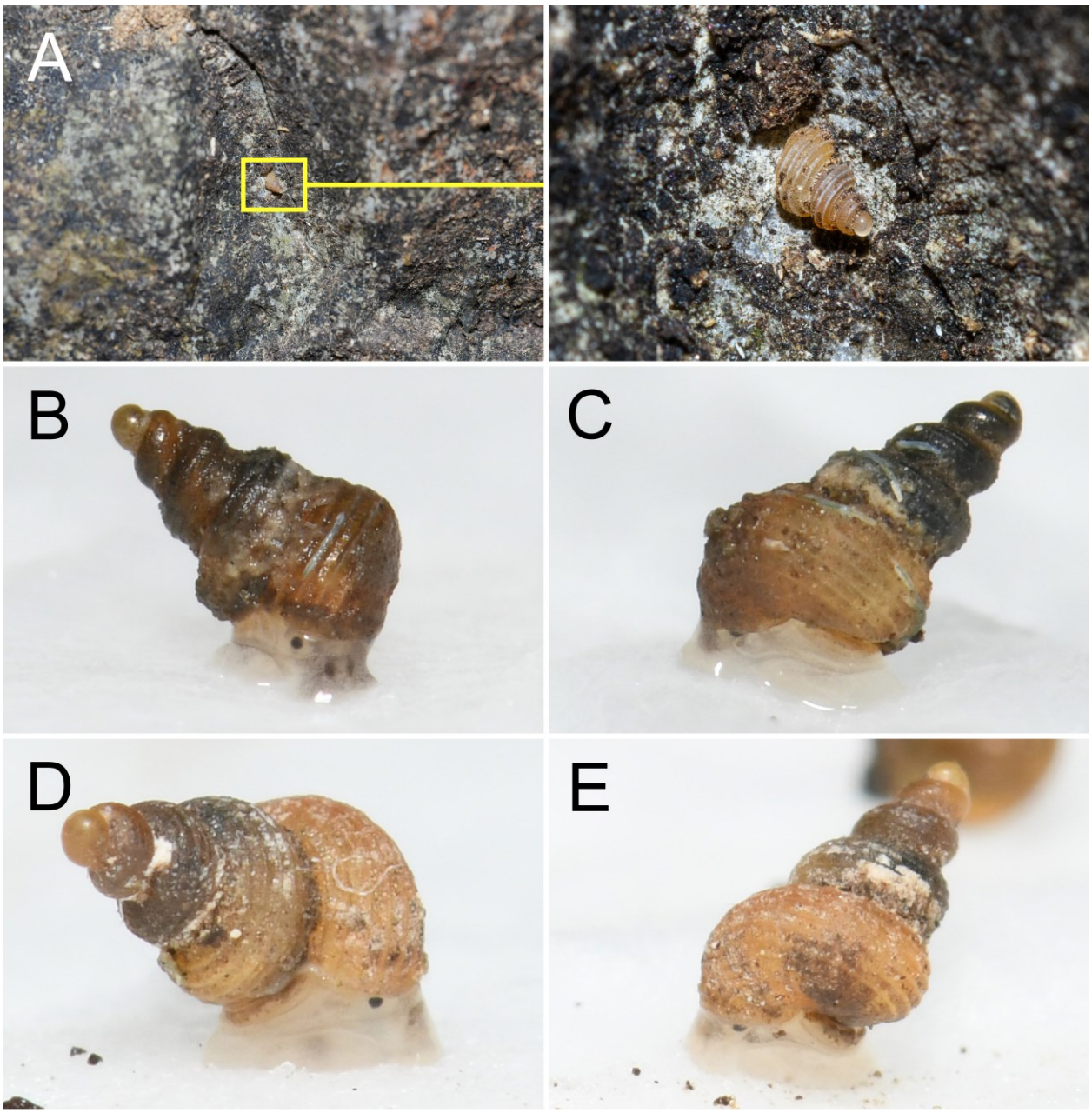

FIGURE 8. Living *Georissa principalis* sp. nov. **A.** snail in a microhabitat on the limestone wall at Tham Khao Kaji, Uthai Thani; an inset showing a close-up view of a snail among lichen on a bare wall. **B–E.** four different individuals while climbing slowly on moist tissue paper, (**B, C**) from Wat Khao Ruea, Nakhon Sawan and (**D, E**) from Wat Khao Mano, Nakhon Sawan.

In this study, two newly described *Georissa* species increase the total number of species recorded in Thailand to seven. Both *G. chatra* sp. nov. and *G. principalis* sp. nov. are limestone karst-restricted species, occurring in only isolated limestone hills in central Thailand. In addition, our phylogenetic results also reveal a high genetic divergence in the mitochondrial COI fragment both between and within *Georissa* lineages from Thailand, which is comparable to the divergence observed in the karst-restricted pulmonated genera *Aenigmatoconcha* Tumpeesuwan & Tumpeesuwan, 2017 and *Sophina* Benson, 1859 (Sutcharit et al., 2020a; Pholyotha et al., 2021). The high genetic divergence in the karst-restricted animals can generally be attributed to a combination of factors, including a high degree of endemism, a disjunct distribution of populations, fragmented habitats, a prolonged isolation, and varying edaphic conditions within karst ecosystems. These factors have driven their evolutionary diversification and the development of remarkably different lifestyles (Sutcharit et al., 2020a; Pholyotha et al., 2021, 2022a, 2023). Thailand contains many unique limestone regions (Naggs et al., 2006; Ridd et al., 2011; Latinne et al., 2013), but they remain insufficiently explored. Therefore, an extensive survey of the limestone hills and outcrops in the

country could uncover more intriguing malacofauna, as well as a possible discovery of numerous new species of *Georissa*.

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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-Euthana- sia-Final-1-17-20.pdf [accessed 12 Feb 2020]

BEDO [Biodiversity-Based Economy Development Office]. 2017. Land snails: checklist of molluscan biodiversity in Thailand. BEDO, Bangkok, 300 pp. [in Thai]

Blanford, W.T. 1864. On the classification of the Cyclostomacea of eastern Asia. Annals and Magazine of Natural History, Series 3, Volume 13(78): 441–465.

Blanford, W.T. 1869. On the animal and operculum of *Georissa*, W. Blanf., and on its relations to *Hydrocena*, Parreyss; with a note on *Hydrocena tersa*, Bens., and *H. milium*, Bens. Annals and Magazine of Natural History, Series 4, Volume 3(13–18): 173–179.

Chee, S.Y. and Mohd Nor, S.A. 2014. DNA barcoding reveals neritid diversity (Mollusca: Gastropoda) diversity in Malaysian waters. Mitochondrial DNA Part A, 27(3): 2282–2284. https://doi.org/10.3109/19401736.2014.987237

Das, N.K. and Aravind, N.A. 2021. A new species from the genus *Georissa* Blandford, 1864 (Gastropoda, Neritimorpha, Hyrdrocenidae) from a limestone cave of Meghalaya, northeast India. Journal of Conchology, 44(2): 93–101.

Felsenstein, J. 2004. Inferring phylogenies. Sinauer Associates, Massachusetts, Sunderland, 580 pp.

Fischer, H. and Dautzenberg, P. 1904. Catalogue des mollusques terrestres et fluviatiles de l'Indo-Chine orientale cites jusqu' à ce jour. In: Mission Pavie, Indo-Chine 1879–1895, Études diverses III. Recherches sur l'Histoire Naturelle de l'Indo-Chine orientale. Ernest Leroux, Éditeur, Paris, 390–450.

Folmer, O., Black, M., Hoeh, W., Lutz, R. and Vrijenhoek, R. 1994. DNA primers for amplification of mitochondrial cytochrome c oxidase subunit I from diverse metazoan invertebrates. Molecular Marine Biology and Biotechnology, 3: 294–299.

Godwin-Austen, H.H. and Nevill, G. 1879. Descriptions of shells from Perak and the Nicobar Islands. Proceedings of the Zoological Society of London, 47: 734–740. https://biodiversity library.org/page/28521906

Haase, M. and Schilthuizen, M. 2007. A new *Georissa* (Gastropoda: Neritopsina: Hydrocenidae) from a limestone cave in Malaysian Borneo. Journal of Molluscan Studies, 73(3): 215–221. https://doi.org/10.1093/mollus/eym020

Hemmen, J. and Hemmen, C. 2001. Aktualisierte Liste der terrestrischen Gastropoden Thailands. Schriften zur Malakozoologie aus dem Haus der Natur-Cismar, 18: 35–70.

Heude, P.M. 1882. Notes sur les mollusques terrestres de la vallée du Fleuve Bleu. Mémoires concernant l'histoire naturelle de l'Empire chinois, 1(2): 1–87. https://www.biodiversitylibrary. org/page/34061405

Hillis, D.M. and Bull, J.J. 1993. An empirical test of bootstrapping as a method for assessing confidence in phylogenetic analysis. Systematic Biology, 42: 182–192. https://doi.org/10.1093/ sysbio/ 42.2.182

Huelsenbeck, J.P. and Rannala, B. 2004. Frequentist properties of Bayesian posterior probabilities of phylogenetic trees under simple and complex substitution models. Systematic Biology, 53: 904–913. https://doi.org/10.1080/10635150490522629

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

Iredale, T. 1933. Systematic notes on Australian land shells. Records of the Australian Museum, 19(1): 37–59. https://doi. org/10.3853/j.0067-1975.19.1933.690

Kano, Y. and Kase, T. 2004. Genetic exchange between anchialine cave populations by means of larval dispersal: the case of a new gastropod species *Neritilia cavernicola*. Zoologica Scripta, 33: 423–437.

Katoh, K., Rozewicki, J. and Yamada, K.D. 2017. MAFFT online service: multiple sequence alignment, interactive sequence choice and visualization. Briefings in Bioinformatics, 20: 1160–1166.

Khalik, M.Z., Hendriks, K., Vermeulen, J.J. and Schilthuizen, M. 2018. A molecular and conchological dissection of the "scaly" *Georissa* of Malaysian Borneo (Gastropoda, Neritimorpha, Hydrocenidae). ZooKeys, 773: 1–55. https://doi.org/10.3897/ zookeys.773.24878

Khalik, M.Z., Bozkurt, E. and Schilthuizen, M. 2019a. 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, 53(8): 1–14. https://doi.org/10. 1111/jzs.12352

Khalik, M.Z., Hendriks, K., Vermeulen, J.J. and Schilthuizen, M. 2019b. Conchological and molecular analysis of the "non-scaly" Bornean *Georissa* with descriptions of three new species (Gastropoda, Neritimorpha, Hydrocenidae). ZooKeys, 840: 35–86. https://doi.org/10.3897/zookeys.840.33326

Klongklaew, K., Poeaim, S. and Dumrongrojwattana, P. 2024. Four new species of *Georissa* W. Blanford, 1864 (Gastropoda, Hydrocenidae) from Thailand. Zoosystematics and Evolution, 100(4): 1347–1360. https://doi.org/10.3897/zse.100.128717

Kumar, S., Stecher, G. and Tamura, K. 2016. MEGA7: Molecular

Evolutionary Genetics Analysis version 7.0 for bigger datasets. Molecular Biology and Evolution, 33: 1870–1874.

Latinne, A., Waengsothorn, S., Rojanadilok, P., Eiamampai, K., Sribuarod, K. and Michaux, J.R. 2013. Diversity and endemism of Murinae rodents in Thai limestone karsts. Systematics and Biodiversity, 11(3): 323–344. https://doi.org /10.1080/14772000.2013.818587

Mauro, D.S. and Agorreta, A. 2010. Molecular systematics: a synthesis of the common methods and the state of knowledge. Cellular and Molecular Biology Letters, 15: 311–341. https://doi.org/10.2478/s11658-010-0010-8

Miller, M.A., Pfeiffer, W. and Schwartz, T. 2010. Creating the CIPRES Science Gateway for inference of large phylogenetic trees. Proceedings of the Gateway Computing Environments Workshop (GCE), 14 Nov. 2010, New Orleans, LA, 1–8.

Möllendorff, O.F. von. 1894. On a collection of land-shells from the Samui Islands, Gulf of Siam. Proceedings of the Zoological Society of London, 62: 146–156.

MolluscaBase, 2025. MolluscaBase. *Georissa* W.T. Blanford, 1864. Available from https://www.molluscabase.org/aphia.php?p=taxdetails&id=818273 [Accessed 20 March 2025].

Naggs, F., Panha, S. and Raheem, D. 2006. Developing land snail expertise in South and Southeast Asia, a new Darwin Initiative Project. The Natural History Journal of Chulalongkorn University, 6: 43–46.

Panha, S. and Burch, J.B. 2005. An introduction to the microsnails of Thailand. Malacological Review, 37/38: 1–155.

Pease, W.H. 1871. Catalogue of the land-shells inhabiting Polynesia, with remarks on their synonymy, distribution, and variation, and descriptions of new genera and species. Proceedings of the Zoological Society of London, 39: 449–477. https://www.biodiversitylibrary.org/page/28554313

Pholyotha, A., Sutcharit, C., Tongkerd, P. and Panha, S. 2020. 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., Tongkerd, P. and Panha, S. 2021. 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. 2022a. 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

Pholyotha, A., Sutcharit, C., Lin, A. and Panha, S. 2022b. Multigene phylogeny reveals the ribbed shell morphotypes in the land snail genus *Sarika* (Eupulmonata: Ariophantidae), with description of two new species from Thailand and Myanmar. Contributions to Zoology, 91: 97–132. https://doi.org/10.1163/18759866-bja10027

Pholyotha, A., Panha, S., Sutcharit, C., Jirapatrasilp, P., Seesamut, T., Liew, T.-S. and Tongkerd, P. 2023. Molecular phylogeny of the land snail family Euconulidae in Thailand and its position in the superfamily Trochomorphoidea (Stylommato-phora: Limacoidei), with description of a new genus. Invertebrate Systematics, 37(8): 571–605. https://doi.org/10. 1071 /is23012

Pholyotha, A., Sutcharit, C., Panha, S. and Tongkerd, P. 2024. Reassessment and phylogenetic position of the overlooked limacoid land snail *Trochomorpha sculpticarina* Martens, 1883 (Eupulmonata, Ariophantidae), with the description of a new genus. Zoosystematics and Evolution, 100(3): 1135–1154. https://doi.org/10.3897/zse.100.129455

Pilsbry, H.A. and Hirase, Y. 1908. New land shells of the Chinese Empire-I. Proceedings of the Academy of Natural Sciences of Philadelphia, 60: 37–43.

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 golden age of malacology in British India: Biography, illustrated catalogue and evaluation of his molluscan types. Tropical Natural History, Supplement 6: 1–434.

Preston, H.B. 1915. Mollusca: Freshwater Gastropoda & Pelecypoda. The Fauna of British India, including Ceylon and Burma. Taylor and Francis, London. 244 pp.

Prieto, C.E., Quinonero-Salgado, S., Ruiz-Cobo, J. and Alonso, A. 2022. The first cave-dwelling Hydrocenidae (Gastropoda: Cicloneritida) in Europe, *Hydrocena canttabrica* sp. nov., lives in the Cantabrian Region (Spain). Spira, 8: 47–59.

Rambaut A. 2018. FigTree v.1.4.4. [accessed 20 December 2024]. https://tree.bio.ed.ac.uk/software/figtree/.

Ridd, M.F., Barber, A.J. and Crow, M.J. 2011. Introduction to the geology of Thailand. In: Ridd, M.F., Barber, A.J. and Crow, M.J. (Eds). The geology of Thailand. Geological Society, London.

Ronquist, F., Teslenko, M., van der Mark, P., Ayres, D.L., Darling, A., Höhna, S., Larget, B., Liu, L., Suchard, M.A. and Huelsenbeck, J.P. 2012. MrBayes 3.2: efficient Bayesian phylogenetic inference and model choice across a large model space. Systematic Biology, 61: 539–542.

Stamatakis, A. 2014. RAxML version 8: a tool for phylogenetic analysis and post-analysis of large phylogenies. Bioinformatics (Oxford, England), 30: 1312–1313.

Sutcharit, C., Jeratthitikul, E., Pholyotha, A., Lin, A. and Panha, S. 2020a. Molecular phylogeny reveals high diversity and endemism in the limestone karst-restricted land snail genus *Sophina* Benson, 1859 from Myanmar (Eupulmonata: Helicarionidae), 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., Thach, P., Chhuoy, S., Ngor, P.B., Jeratthitikul, E., Siriwut, W., Srisonchai, R., Ng, T.H., Pholyotha, A., Jirapatrasilp, P. and Panha, S. 2020b. Annotated checklist of the land snail fauna from southern Cambodia (Mollusca, Gastropoda). ZooKeys, 948: 1–46. https://doi.org/10.3897/zookeys.948.51671

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

Tanabe, A.S. 2011. Kakusan4 and Aminosan: two programs for comparing nonpartitioned, proportional and separate models for combined molecular phylogenetic analyses of multilocus sequence data. Molecular Ecology Resources, 11: 914–921.

Thompson, F.G. and Dance, S.P. 1983. Non-marine mollusks of Borneo. II Pulmonata: Pupillidae, Clausiliidae. III Prosobranchia: Hydrocenidae, Helicinidae. Bulletin of the Florida State Museum Biological Science, 29(3): 101–152. https://ufdc.ufl.edu/UF00095805/00001

Yen, T.-C. 1939. Die chinesischen Land- und Süßwasser-Gastropoden des Natur-Museums Senckenberg. Abhandlungen der Senckenbergischen Naturforschenden Gesellschaft, 444: 1–233.

Zilch, A. 1973. Die Typen und Typoide des Natur-Museums Senckenberg, 52. Mollusca: Hydrocenidae. Archiv für Molluskenkunde, 103(4/6): 263–272.