

# Discovery of a New Helicarionoidean Land Snail Genus *Siamopotaxis* gen. nov. (Eupulmonata: Helicarionidae) from Thailand Based on Molecular Phylogenetic and Morphological Evidence

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Received: 10 April 2025; Accepted: 6 June 2025; Date of Publication: 14 October 2025

<https://zoobank.org/urn:lsid:zoobank.org:pub:048852E7-99F2-433F-B9EF-58339ADA1414>

**ABSTRACT.**— The new helicarionoidean land snail genus *Siamopotaxis* Pholyotha, gen. nov. is described for two new species, *Siamopotaxis principalis* Pholyotha, sp. nov. and *Siamopotaxis thailandensis* Pholyotha, sp. nov., both from Thailand. The new genus is characterised by a medium-sized, globose, high-spired, cream-coloured shell, with one or two supraplural bands, a rounded last whorl, a short epiphallid caecum, an elongated dart apparatus, and many radular teeth with pectiniform cusps. *Siamopotaxis principalis* sp. nov. differs from *S. thailandensis* sp. nov. by the presence of one spiral band, whereas the latter species has two spiral bands. A DNA sequence analysis of mitochondrial COI and 16S DNA, and nuclear 28S DNA gene fragments, supports the systematic placement of these new taxa and confirms that *Siamopotaxis* gen. nov. as a distinct clade within the Helicarionidae.

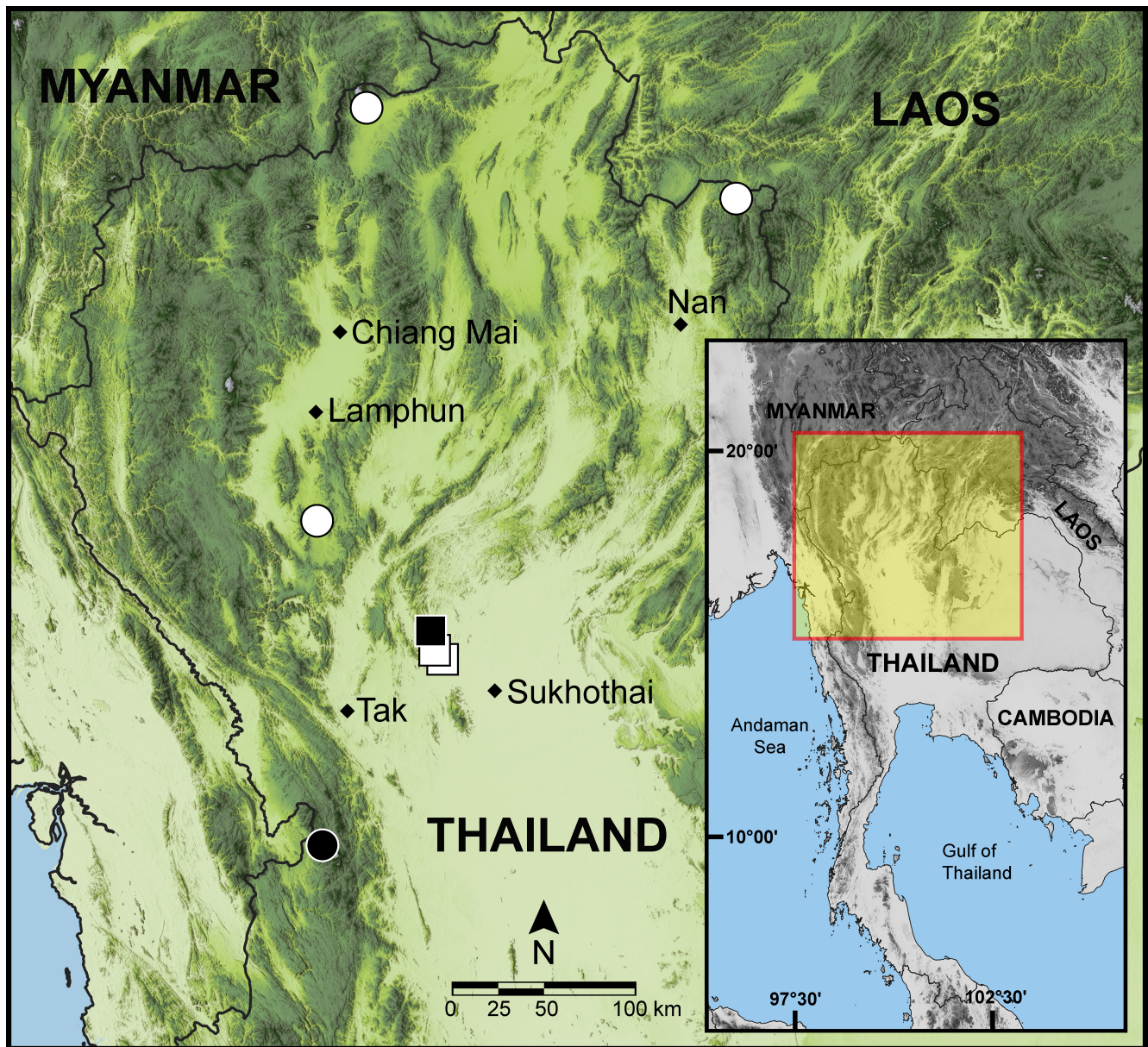
**KEYWORDS:** Diversity, Endemic, Indochina, Land snail, Limestone, Taxonomy

## INTRODUCTION

Thailand is one of the most biodiverse countries in mainland Southeast Asia and is particularly recognized for its terrestrial malacofauna. The country is home to nearly 100 species across 20 genera of helicarionoidean land snails (Blanford and Godwin-Austen 1908; Solem 1966; Panha 1996; Hemmen and Hemmen, 2001; Pholyotha et al., 2018, 2020, 2021a, b, c, 2022b, 2023b, c, 2024a, b; Sutcharit et al., 2021; Sutcharit and Pholyotha 2023). These snails are often locally endemic due to their narrow distribution ranges. This rich fauna is found on isolated hills and outcrops across various tropical forests covering extensive mountain ranges and limestone karst formations from north to south (Gupta, 2005; Naggs et al., 2006; Ridd et al., 2011). Previous studies have suggested that microhabitats within karst topography in tropical regions serve as hotspots for speciation, refugia, and areas of high endemism for karst-associated taxa (Clements et al., 2006, 2008; Grismer et al., 2018a, b; Foon et al., 2017). Recent years have seen several major land snail discoveries in Thai limestone karsts, leading to the description of enigmatic genera such as *Aenigmatoconcha* Tumpeesuwan & Tumpeesuwan, 2017, *Taphrenalla* Pholyotha & Panha, 2021, *Maelamaodiscus* Sutcharit & Pholyotha, 2023, *Siamochlamys* Pholyotha, 2023, and *Janbinmorma* Pholyotha & Panha, 2024. In particular, the limestone karsts of northern, western, and central Thailand are home to a remarkable diversity of land snails, with dozens of new species having been recently described (Jirapatrasilp et al., 2021a, b; Pholyotha et al., 2018, 2020, 2021a, b,

2022b, 2023b, c, 2024b; Sutcharit and Pholyotha, 2023).

Godwin-Austen (1882–1920), Blanford and Godwin-Austen (1908), and Solem (1966) produced the most significant revisionary works on various land snail groups, including the helicarionoidean snails, through the comparative studies of shell, radular and reproductive anatomy. Their works have long been considered the foundation of the systematic classification of the helicarionoidean snails, such as the highly diverse land snail fauna of the Oriental realm. Over the past decade, DNA sequence data have increasingly been used to refine systematic classifications and clarify the evolutionary relationships of various organisms, including helicarionoidean snails in Indochina (Sutcharit et al., 2020a, 2021; Pholyotha et al., 2020, 2021a, 2022b, 2024a). While these DNA data have enhanced our understanding of land snail diversity, they have also revealed discrepancies with traditional morphology-based classifications. These discrepancies may derive from the morphological conservatism or convergent evolution in land snails, highlighting the complexity of their evolutionary history (Criscione et al., 2012; Criscione and Köhler, 2013, 2014; Sutcharit et al., 2021; Pholyotha et al., 2022b, 2024a). For instance, a common garden snail that because of its ribbed or striated shell was hitherto classified in the Indian genus *Cryptozona* Mörch, 1872, was recently re-assigned to the Indochinese genus *Sarika* Godwin-Austen, 1907 based on DNA sequence data (Pholyotha et al., 2022b). Similarly, sinistral species from Thailand, previously classified in the trochomorphaeidean genus *Dyakia* Godwin-Austen, 1891, have now been reclassified into the helicarionoidean



**FIGURE 1.** Distribution of *Siamopotaxis principalis* sp. nov. (square) and *Siamopotaxis thailandensis* sp. nov. (circle) in Thailand. Black (solid) symbols indicate the type locality of each species. White symbols indicate other recorded localities.

dean genus *Hemiplecta* Albers, 1850 (Sutcharit et al., 2021). In another case, a species endemic to southern Thailand with a trochiform shell has long been thought to belong to either the trochomorpoidean genera *Trochomorpha* Albers, 1850 or *Videna* Adams & Adams, 1855. However, a DNA sequence study suggested that this species is better assigned to its own helicarioidean genus, *Janbinmorpha* Pholyotha & Panha, 2024 (Pholyotha et al., 2024a). These examples illustrate that taxonomic proposals based solely on morphological characters should be used with caution and need to be verified by DNA sequence data.

Recently, a helicarioidean specimen possessing a whitish shell with spiral band(s) was initially inter-

preted as a species of *Burmochlamys* Pholyotha & Panha, 2022, *Chalepotaxis* Ancey, 1887, or *Sophina* Benson, 1859, while its genitalia and radula more closely resemble the semi-slug genus *Durgella* Blanford, 1863, while its mantle extensions are very unique. However, DNA sequence data of mitochondrial 16S rRNA and cytochrome c oxidase subunit I (COI), and nuclear 28S rRNA, suggested that this specimen belongs to a unique helicarioidean lineage. Therefore, we propose a new genus including two new species based on integration of morphological characteristics and DNA sequence data. This discovery enhances our understanding of the diversity and evolution of helicarioidean land snails in Thailand.



**TABLE 1.** Information of specimens used for molecular phylogenetic analyses, including species name, specimen codes, museum registration numbers, GenBank accession numbers, locality name, and references.

Taxon	Specimen codes	Museum registration	GenBank accession numbers			Locality name	References
			COI	16S	28S		
Infraorder Limacoidei							
Superfamily Helicarionoidea Bourguignat, 1877							
Family Helicarionidae Bourguignat, 1877							
Subfamily Durgellinae Godwin-Austen, 1888							
<i>Siamopotaxis principalis</i> sp. nov.*	N153-1	CUMZ 15257	PV719281	PV726227	-	Thailand: Sukhothai	This study
<i>Siamopotaxis principalis</i> sp. nov.*	N153-2	CUMZ 15257	PV719282	PV726228	-	Thailand: Sukhothai	This study
<i>Siamopotaxis principalis</i> sp. nov.*	N153-3	CUMZ 15257	PV719283	-	-	Thailand: Sukhothai	This study
<i>Siamopotaxis thailandensis</i> sp. nov.	N30	CUMZ 14924	PV719284	PV726229	-	Thailand: Lamphun	This study
<i>Siamopotaxis thailandensis</i> sp. nov.	N71-1	CUMZ 14923	PV719285	PV726230	-	Thailand: Chiang Mai	This study
<i>Siamopotaxis thailandensis</i> sp. nov.	N71-2	CUMZ 14923	PV719286	-	-	Thailand: Chiang Mai	This study
<i>Siamopotaxis thailandensis</i> sp. nov.	N71-3	CUMZ 14923	PV719287	PV726231	-	Thailand: Chiang Mai	This study
<i>Siamopotaxis thailandensis</i> sp. nov.	W71-1	CUMZ 14926	PV719288	-	-	Thailand: Tak	This study
<i>Siamopotaxis thailandensis</i> sp. nov.	W71-2	CUMZ 14926	PV719289	PV726232	PV733930	Thailand: Tak	This study
<i>Siamopotaxis thailandensis</i> sp. nov.	W71-3	CUMZ 14926	-	PV726233	PV733931	Thailand: Tak	This study
<i>Sakiella merguiensis</i> Godwin-Austen, 1910	MY19	CUMZ 14918	MN897081	MN888660	MN892711	Myanmar: Tanintharyi	Sutcharit et al. (2020a)
<i>Aenigmatoconcha clivicola</i> Tumpeesuwan & Tumpeesuwan, 2017*	NE68	CUMZ 7929	MW703614	PQ032747	PQ032738	Thailand: Loei	Pholyotha et al. (2021a, 2024a)
<i>Chalepotaxis infantilis</i> (Gredler, 1881)*	-	NHMW111548	KX027275	-	KX027276	China: Hunan	Páll-Gergely et al. (2017)
<i>Eurychlamys platychlamys</i> (Blanford, 1880)*	-	BNHS GAS 10	-	-	MW583029	India: Maharashtra	Bhosale et al. (2021)
<i>Satiella</i> sp.	-	BNHS GAS 69	-	-	MW583028	India: Maharashtra	Bhosale et al. (2021)
<i>Durgella siamensis</i> Möllendorff, 1902	C72	CUMZ 14232	PV719290	PV726234	PV733932	Thailand: Nakhon Nayok	This study
<i>Durgella erratica</i> (Godwin-Austen, 1888)	MY13	CUMZ 14234	PV719291	PV726235	PV733933	Myanmar: Mandalay	This study
<i>Durgella levicula</i> (Benson, 1859)*	W45	CUMZ 14245	PV719292	PV726236	PV733934	Thailand: Kanchanaburi	This study
<i>Sophina conjungens</i> Stoliczka, 1871	MY27	CUMZ 5196	MN897033	MN888612	MN892663	Myanmar: Mon	Sutcharit et al. (2020a)
<i>Sophina discoidalis</i> Stoliczka, 1871	MY32	CUMZ 5197	MN897041	MN888620	MN892671	Myanmar: Mon	Sutcharit et al. (2020a)
<i>Sophina schistostelis</i> (Benson, 1859)*	MY24	CUMZ 5195	MN897023	MN888602	MN892653	Myanmar: Mon	Sutcharit et al. (2020a)
<i>Sitala</i> sp. 1	E89	CUMZ 15298	PV719293	PV726237	PV733935	Thailand: Chonburi	This study
<i>Sitala</i> sp. 2	W111	CUMZ 15299	PV719294	PV726238	-	Thailand: Kanchanaburi	This study
<i>Sitala</i> sp. 3	S167	CUMZ 15300	PV719295	PV726239	-	Thailand: Chumphon	This study
Subfamily Helicarioninae Bourguignat, 1877							
<i>Fastosarion brazieri</i> (Cox, 1873)	-	-	-	-	AY014099	Australia: Queensland	Wade et al. (2001)
<i>Harmogenanina argentea</i> (Reeve, 1852)	-	-	-	-	AY014101	Réunion	Wade et al. (2001)
<i>Plegma caelatura</i> (Férussac, 1821)	-	-	-	-	AY014103	Réunion	Wade et al. (2001)
Family Ariophantidae Godwin-Austen, 1883							
<i>Macrochlamys tanymentula</i> Pholyotha & Panha, 2018	W16	CUMZ 7119	MT364985	MT365762	MT365706	Thailand: Kanchanaburi	Pholyotha et al. (2021b)
<i>Sarika resplendens</i> (Philippi, 1847)*	W4	CUMZ 7234	MT364982	MT365763	MT365707	Thailand: Ratchaburi	Pholyotha et al. (2021b)
<i>Taphrenalla diadema</i> (Dall, 1897)*	S46	CUMZ 7175	MT364940	MT365729	MT365673	Thailand: Phatthalung	Pholyotha et al. (2021b)

TABLE 1. Continued.

Taxon	Specimen codes	Museum registration	GenBank accession numbers			Locality name	References
			COI	16S	28S		
Superfamily Trochomorpoidea Mörch, 1864							
Family Chronidae Thiele, 1931							
<i>Trochochlamys</i> sp.	NE47	CUMZ 14869	OR075931	OR076722	OR076739	Thailand: Loei	Pholyotha et al. (2023a)
Family Euconulidae Baker, 1928							
<i>Parasitala</i> sp.	N123	CUMZ 14868	OR075930	-	OR076738	Thailand: Nan	Pholyotha et al. (2023a)
Family Trochomorphidae Möllendorff, 1890							
<i>Trochomorpha</i> sp.	NE74	CUMZ 14870	OR075932	OR076723	OR076740	Thailand: Sa Kao	Pholyotha et al. (2023a)
Family Dyakiidae Gude & Woodward, 1921							
<i>Khmerquantula leipo</i>	CA5	CUMZ 7940	MZ726377	MZ736661	MZ736666	Cambodia: Kampot	Pholyotha et al. (2021d)
Pholyotha & Panha, 2021*							
Family Geotrochidae Schileyko, 2002							
<i>Geotrochus haptoderma</i>	-	BORMOL 6349	MK779473	MK334189	OR076743	Malaysia: Sabah	Chang & Liew (2021), Pholyotha et al. (2023a)
(Vermeulen, Liew & Schilthuizen, 2015)							
Infraorder Arionoidei Gray, 1840							
Superfamily Arionoidea Gray, 1840							
Family Arionidae Gray, 1840							
<i>Arion hortensis</i> Férussac, 1819	-	-	MN022744	-	KU341315	UK	Saadi & Wade (2019)
Family Philomycidae Gray, 1847							
<i>Meghimatium bilineatum</i>	-	-	MN022745	-	MN022678	Mauritius	Saadi & Wade (2019)
(Benson, 1842)							

## MATERIALS AND METHODS

This study is based on dry shells and ethanol preserved samples collected from Thailand (Fig. 1) and deposited in the Malacological collection of the Chulalongkorn University Museum of Zoology (CUMZ), Bangkok. For the newly collected specimens, the animal use protocol in this study was approved by the Chulalongkorn University Animal Care and Use Committee (CU-ACUC) under approval numbers 2123023, 2423003, and 2523009. Specimens were hand-collected. Before preservation, photographs of shells, dissected genitalia and living individuals were taken using a Nikon camera (DSLR D850) with a Nikon 105 Macro lens (AF-S VR Micro-Nikkor 105mm f/2.8G IF-ED). Specimens were euthanised following the standard two-step protocol (American Veterinary Medical Association, 2020), and preserved in 95% (v/v) ethanol for anatomical studies and DNA analyses. Identification and classification were initially based on the literature (e.g., Godwin-Austen, 1882–1920; Blanford and Godwin-Austen, 1908; Solem, 1966; Schileyko, 2002, 2003; Inkhavilay et al., 2019; Jirapatrasilp et al., 2021a; Sutcharit et al., 2020a, b, 2021; Páll-Gergely et al., 2017; Preece et al., 2022; Pholyotha et al., 2018, 2020, 2021a, b, c, d, 2022a, b, 2023a, b, c, 2024a, b) and compared to the reference collections deposited in several natural history museums.

Morphological and anatomical descriptions focus on characters of the shell, genitalia, mantle lobes, and radula. Shell height and diameter were measured with a vernier caliper precise to 0.1 mm. The number of whorls, including the protoconch, was counted as described by Vermeulen and Liew (2022). Shell sculpture was imaged by scanning electron microscopy (SEM; JEOL, JSM-6610 LV). Specimens were dissected using an Olympus SZX2-TR30 stereoscopic light microscope. Anatomy was studied in three specimens per species in order to confirm that characters as described here are characteristic and consistent. Radula was extracted with 10% (w/v) sodium hydroxide solution, cleaned with distilled water, and imaged by scanning electron microscopy (SEM; JEOL, JSM-6610 LV).

Genomic DNA was extracted from small pieces of foot muscle by use of a NucleoSpin DNA extraction kit (Macherey-Nagel, Germany) for animal tissue following the standard procedure of the manual. Fragments of two mitochondrial genes, 16S rRNA (16S) and cytochrome c oxidase subunit I (COI), and a fragment of the nuclear 28S rRNA (28S) gene were amplified by PCR using the primer pair 16Sar and 16Sbr (Palumbi et al., 1991), the primer pair LCO1490 and HCO2198 (Folmer et al., 1994), and the primer pair LSU2 and LSU4 (Wade and Mordan 2000). 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 for 16S, at 51 °C



for COI, and at 60 °C for 28S, and 1 min at 72 °C, followed by a final extension step at 72 °C for 5 min. PCR products of COI, 16S, and 28S were sequenced at Bioneer Corporation, South Korea. Chromatograms were merged into one sequence contig using MEGA v. 7.0 (Kumar et al., 2016) and misreads were manually corrected where necessary. New sequences have been deposited in the GenBank database (Table 1).

For the phylogenetic analyses, we built a sequence dataset by incorporating the new sequences and some available GenBank sequences of limacoid snails (16S, COI and 28S), selected based on the recent phylogenetic trees presented by Pholyotha et al. (2023a, 2024a). The sequence dataset was derived from 37 individuals representing 29 species, including 30 individuals from 22 helicarionoidean species (comprising 19 helicarionid species and 3 ariophantid species), and 5 species of trochomorphaeids together with 2 species of arionoideans, included as distantly related outgroups to root the phylogenetic tree (Table 1). Sequences of each gene fragment were aligned by use of the on-line version of MAFFT (Katoh et al., 2017) available at <https://mafft.cbrc.jp/alignment/server/> with the default settings. Sequences of 16S, COI and 28S were concatenated into one partitioned dataset and the best-fit model of nucleotide substitution was identified for each gene partition by means of the Bayesian Information Criterion using the program Kakusan4 (Tanabe, 2011). The final concatenated sequence dataset contained 25 sequences of 16S, with an alignment length of 453 sites (227 conserved sites, 158 parsimony informative sites, and 213 variable sites), 31 sequences of COI, with an alignment length of 655 sites (370 conserved sites, 231 parsimony informative sites, and 285 variable sites), and 27 sequences of 28S, with an alignment length of 553 sites (403 conserved sites, 82 parsimony informative sites, and 144 variable sites).

As suggested by the program Kakusan4, the concatenated dataset was divided into five partitions; the Hasegawa, Kishino and Yano 1985 (HKY85) model with a gamma distribution was chosen for the first codon positions of COI, the Felsenstein 1981 (F81) model with a gamma distribution was chosen for the third codon positions of COI, and the general time-reversible (GTR) model with a gamma distribution was chosen for 16S, 28S, and the second codon positions of COI. A Maximum likelihood (ML) phylogeny was calculated through the online CIPRES Science Gateway (Miller et al., 2010) by applying the GTR+CAT model to the entire dataset with the default settings of RAxML-HP2 on ACCESS v. 8.2.12 (Stamatakis, 2014), as RAxML does not allow for data partitioning. Nodal support of the ML tree was inferred

by performing 1000 bootstrap replicates. Bayesian inference (BI) was performed through the online CIPRES Science Gateway (Miller et al., 2010) by running 50 million generations of Markov chain Monte Carlo (MCMC) methods (two simultaneous runs, each with four chains, of which one was heated), as implemented by MrBayes on ACCESS v.3.2.7a (Ronquist et al., 2012). The sampling rate of the trees was 1000 generations, with the first 25% of obtained trees being discarded as burn-in. A branch/clade was considered to be strongly/well supported or statistically significant if the ML bootstrap (BS) support value was  $\geq 70\%$  and the BI posterior probability (PP) was  $\geq 0.95$  (Hillis and Bull, 1993; Felsenstein, 2004; Huelsenbeck and Rannala, 2004; Mauro and Agorreta, 2010). Uncorrected pairwise genetic distances (*p*-distances) were calculated using MEGA v. 7.0 (Kumar et al., 2016) under the option ‘pairwise deletion of gaps’.

### Morphological and anatomical abbreviations

In this study, the term ‘proximal’ refers to the region closest to the genital opening, while ‘distal’ refers to the region furthest away from the genital opening. Abbreviations used in images: ant-ldl (anterior left dorsal lobe), at (atrium), ch (caudal horn), da (dart apparatus), e1 (portion of epiphallus nearer to penis), e2 (portion of epiphallus nearer to retractor muscle), ec (epiphallic caecum), fo (free oviduct), gd (gametolytic duct), gs (gametolytic sac), h (heart), k (kidney), lsl (left shell lobe), p (penis), post-ldl (posterior left dorsal lobe), prm (penial retractor muscle), puv (pulmonary vein), r (rectum), rdl (right dorsal lobe), rsl (right shell lobe), ur (ureter), v (vagina), vd (vas deferens).

### Institutional abbreviations

**CUMZ** Chulalongkorn University, Museum of Zoology, Bangkok, Thailand

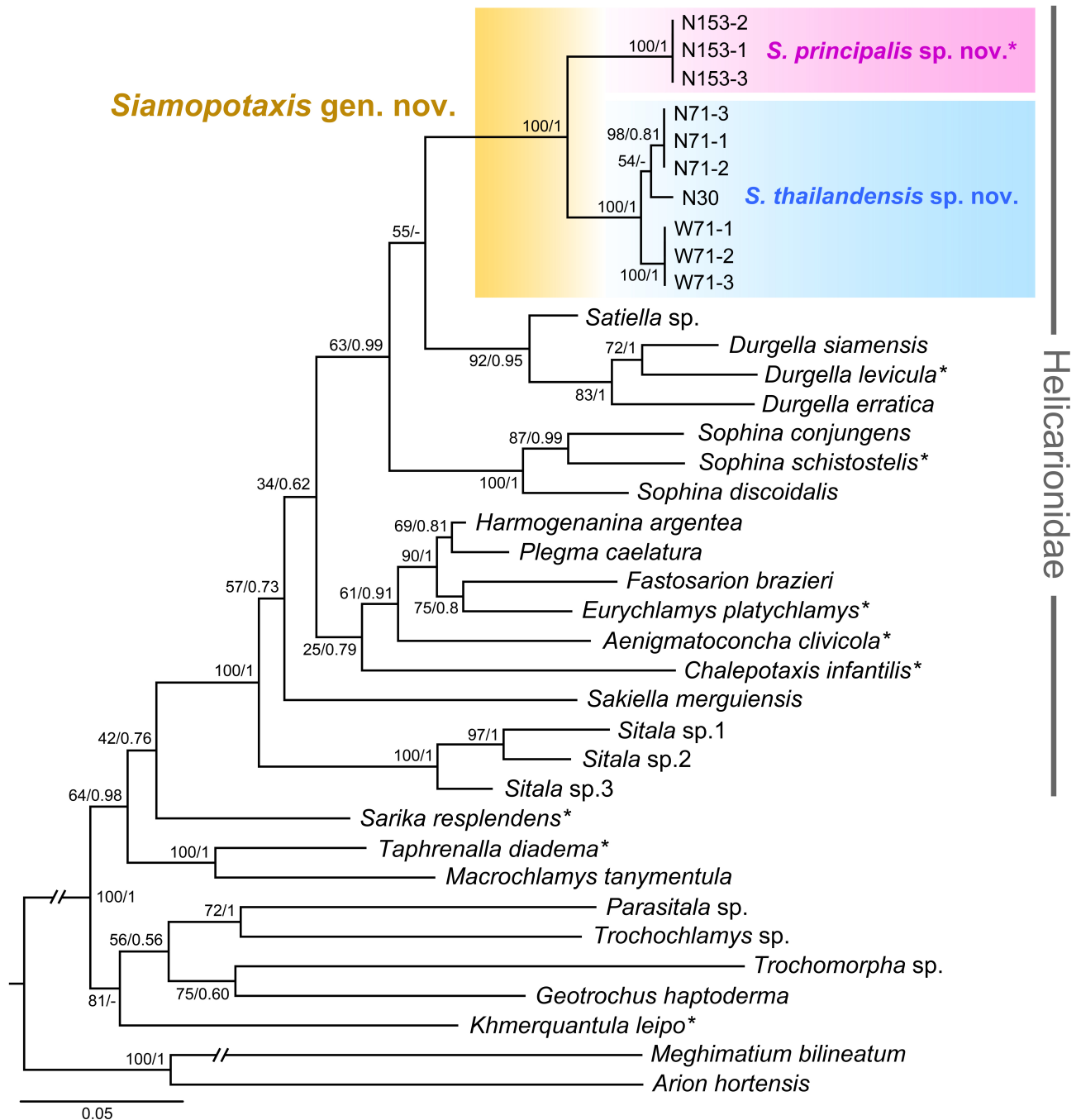
**NHM** Natural History Museum, London, United Kingdom (**NHMUK** is used when citing specimens deposited in the NHM).

**SMF** Senckenberg Forschungsinstitut und Naturmuseum, Frankfurt am Main, Germany

## RESULTS

### Molecular Phylogeny

The ML and BI trees revealed widely congruent topologies that differed only in minor aspects; therefore, only the tree topology from the ML analysis is presented in Figure 2. The Helicarionoidea (Ariophantidae + Helicarionidae) formed a well-supported clade in the BI tree, but a weakly supported clade in the ML



**FIGURE 2.** Maximum likelihood phylogram based on analyses of concatenated COI, 16S, and 28S sequences. Numbers on branches indicate nodal support by ML bootstrap (BS) and Bayesian posterior probabilities (PP) analyses. \* indicate the type species for each genus.

tree [BS/PP: 64/0.98]. Although these analyses revealed statistically significant support for the monophyly of the Helicarionidae [BS/PP: 100/1], the phylogenetic relationships within this family remain unresolved. Both trees supported the sister-group relationships of *Durgella* with *Satiella* Blanford & Godwin-Austen, 1908, while the *Durgella* + *Satiella* clade formed an unresolved trichotomy with the genera *Siamopotaxis* gen. nov. and *Sophina*. The two species

of *Siamopotaxis* gen. nov. formed a well-supported clade in both ML and BI analyses.

#### DNA Sequence Divergence

Terminal sequence clusters representing *Siamopotaxis principalis* sp. nov. differed from *Siamopotaxis thailandensis* sp. nov. by a mean uncorrected pairwise *p*-distances of 8.2% for COI and 3.0% for 16S. Comparing the *Siamopotaxis* gen. nov. with other



**TABLE 2.** Estimates of mitochondrial cytochrome c oxidase I (COI) gene sequence divergence (uncorrected *p*-distances) between *Siamopotaxis* gen. nov. and other genera.

Genera	01	02	03	04	05	06	07	08	09	10	11	12	13	14	15	16	17
1 <i>Siamopotaxis</i> gen. nov.	0.046																
2 <i>Durgella</i>	0.149	0.091															
3 <i>Sophina</i>	0.129	0.152	0.098														
4 <i>Aenigmatoconcha</i>	0.138	0.158	0.135	-													
5 <i>Chalepotaxis</i>	0.156	0.162	0.142	0.127	-												
6 <i>Sakiella</i>	0.144	0.146	0.142	0.136	0.142	-											
7 <i>Sitala</i>	0.137	0.158	0.133	0.127	0.148	0.127	0.058										
8 <i>Macrochlamys</i>	0.145	0.158	0.157	0.140	0.154	0.142	0.132	-									
9 <i>Sarika</i>	0.131	0.133	0.127	0.121	0.139	0.124	0.117	0.115	-								
10 <i>Taphrenalla</i>	0.134	0.146	0.139	0.124	0.145	0.119	0.116	0.104	0.118	-							
11 <i>Trochochlamys</i>	0.168	0.167	0.163	0.153	0.153	0.137	0.161	0.144	0.144	0.139	-						
12 <i>Parasitala</i>	0.146	0.160	0.153	0.125	0.157	0.136	0.137	0.133	0.118	0.122	0.140	-					
13 <i>Trochomorpha</i>	0.158	0.177	0.163	0.147	0.148	0.148	0.149	0.147	0.139	0.150	0.142	0.142	-				
14 <i>Khmerquantula</i>	0.144	0.156	0.149	0.133	0.157	0.131	0.138	0.128	0.128	0.127	0.131	0.133	0.145	-			
15 <i>Geotrochus</i>	0.159	0.169	0.159	0.156	0.156	0.150	0.142	0.148	0.151	0.142	0.156	0.154	0.145	0.144	-		
16 <i>Arion</i>	0.203	0.215	0.205	0.194	0.211	0.208	0.198	0.217	0.180	0.200	0.226	0.203	0.202	0.200	0.195	-	
17 <i>Meghimatium</i>	0.216	0.218	0.204	0.189	0.221	0.206	0.205	0.227	0.192	0.209	0.202	0.203	0.215	0.209	0.215	0.214	-

**TABLE 3.** Estimates of mitochondrial 16S rRNA gene sequence divergence (uncorrected *p*-distances) between *Siamopotaxis* gen. nov. and other genera.

Genera	01	02	03	04	05	06	07	08	09	10	11	12	13
1 <i>Siamopotaxis</i> gen. nov.	0.015												
2 <i>Durgella</i>	0.119	0.044											
3 <i>Sophina</i>	0.113	0.111	0.045										
4 <i>Aenigmatoconcha</i>	0.141	0.156	0.148	-									
5 <i>Sakiella</i>	0.140	0.130	0.143	0.133	-								
6 <i>Sitala</i>	0.138	0.144	0.107	0.135	0.134	0.056							
7 <i>Macrochlamys</i>	0.170	0.171	0.161	0.144	0.149	0.149	-						
8 <i>Sarika</i>	0.139	0.147	0.149	0.147	0.131	0.145	0.131	-					
9 <i>Taphrenalla</i>	0.181	0.192	0.171	0.149	0.165	0.145	0.101	0.109	-				
10 <i>Trochochlamys</i>	0.219	0.245	0.232	0.208	0.227	0.210	0.187	0.197	0.192	-			
11 <i>Khmerquantula</i>	0.195	0.204	0.196	0.184	0.203	0.183	0.157	0.179	0.176	0.205	-		
12 <i>Trochomorpha</i>	0.269	0.278	0.255	0.232	0.261	0.241	0.216	0.248	0.232	0.235	0.269	-	
13 <i>Geotrochus</i>	0.210	0.219	0.203	0.197	0.197	0.207	0.171	0.181	0.171	0.189	0.181	0.203	-

helicarionid genera, the uncorrected *p*-distance ranged from 12.9% (between *Siamopotaxis* gen. nov. and *Sophina*) to 15.6% (between *Siamopotaxis* gen. nov. and *Chalepotaxis*) in COI (Table 2), 11.3% (between *Siamopotaxis* gen. nov. and *Sophina*) to 14.1% (between *Siamopotaxis* gen. nov. and *Aenigmatoconcha*) in 16S (Table 3), and 2.2% (between *Siamopotaxis* gen. nov. and *Satiella*) to 6.0% (between *Siamopotaxis* gen. nov. and *Sitala*) in 28S (Table 4).

## Systematic Descriptions

### Superfamily Helicarionoidea Bourguignat, 1877

#### Family Helicarionidae Bourguignat, 1877

#### Subfamily Durgellinae Godwin-Austen, 1888

#### Genus *Siamopotaxis* Pholyotha gen. nov.

<https://zoobank.org/urn:lsid:zoobank.org:act:1236F7D2-87A5-4BFB-9704-D83974358039>

**Type species.**— *Siamopotaxis principalis* sp. nov.

**Etymology.**— The name combines ‘*Siam*’, which is a former name of Thailand, chosen because this snail is restricted to the country as far as we know, and ‘*potaxis*’ in reference to the similarity between this new genus and the genus *Chalepotaxis* with respect to shell colour and the presence of suprapерipheral bands.

**Diagnosis.**— Shell dextral, small to medium-sized, subglobose to globose, perforate, milky-white to cream colour, and suprapерipheral band present. Animal with five mantle extensions, foot tripartite, and caudal horn present. Genitalia with epiphallic caecum and dart apparatus, and without flagellum. Radula many, pectiniform cusps.

**Description.**— Shell dextral, small to medium-sized, subglobose to globose, thin, polished, milky-white to cream, with one or two orange-brown suprapерipheral

**TABLE 4.** Estimates of nuclear 28S rRNA gene sequence divergence (uncorrected *p*-distances) between *Siamopotaxis* gen. nov. and other genera.

Genera	01	02	03	04	05	06	07	08	09	10	11	12	13
1 <i>Siamopotaxis</i> gen. nov.	0.000												
2 <i>Durgella</i>	0.026	0.014											
3 <i>Satiella</i>	0.022	0.020	-										
4 <i>Sophina</i>	0.025	0.034	0.033	0.007									
5 <i>Aenigmatococoncha</i>	0.033	0.046	0.040	0.047	-								
6 <i>Chalepotaxis</i>	0.027	0.035	0.029	0.041	0.040	-							
7 <i>Eurychlamys</i>	0.042	0.049	0.047	0.050	0.044	0.053	-						
8 <i>Fastosarion</i>	0.049	0.052	0.053	0.055	0.047	0.051	0.038	-					
9 <i>Harmogenanina</i>	0.031	0.038	0.035	0.038	0.033	0.038	0.024	0.031	-				
10 <i>Plegma</i>	0.033	0.041	0.042	0.041	0.040	0.044	0.027	0.038	0.011	-			
11 <i>Sakiella</i>	0.029	0.043	0.038	0.042	0.040	0.040	0.051	0.060	0.042	0.049	-		
12 <i>Sitala</i>	0.060	0.058	0.060	0.059	0.075	0.067	0.071	0.080	0.067	0.071	0.069	-	
13 <i>Macrochlamys</i>	0.055	0.060	0.064	0.057	0.067	0.078	0.082	0.078	0.067	0.064	0.075	0.071	-
14 <i>Sarika</i>	0.067	0.066	0.069	0.058	0.071	0.075	0.080	0.078	0.062	0.060	0.078	0.075	0.038
15 <i>Taphrenalla</i>	0.047	0.051	0.060	0.047	0.067	0.067	0.069	0.067	0.051	0.049	0.071	0.062	0.022
16 <i>Trochochlamys</i>	0.067	0.076	0.075	0.067	0.082	0.078	0.082	0.089	0.067	0.069	0.086	0.091	0.075
17 <i>Parasitala</i>	0.091	0.092	0.095	0.096	0.098	0.098	0.098	0.098	0.091	0.086	0.102	0.104	0.082
18 <i>Trochomorpha</i>	0.095	0.084	0.084	0.094	0.100	0.091	0.100	0.100	0.082	0.091	0.098	0.095	0.089
19 <i>Khmerquantula</i>	0.064	0.072	0.067	0.067	0.078	0.073	0.080	0.082	0.064	0.069	0.078	0.082	0.064
20 <i>Geotrochus</i>	0.075	0.072	0.075	0.081	0.089	0.086	0.089	0.082	0.075	0.080	0.091	0.086	0.069
21 <i>Arion</i>	0.093	0.090	0.095	0.086	0.106	0.095	0.095	0.102	0.078	0.086	0.095	0.093	0.091
22 <i>Meghimatium</i>	0.104	0.103	0.113	0.110	0.115	0.111	0.113	0.115	0.095	0.104	0.113	0.106	0.109

**TABLE 4.** Continued.

Genera	14	15	16	17	18	19	20	21	22
1 <i>Siamopotaxis</i> gen. nov.									
2 <i>Durgella</i>									
3 <i>Satiella</i>									
4 <i>Sophina</i>									
5 <i>Aenigmatococoncha</i>									
6 <i>Chalepotaxis</i>									
7 <i>Eurychlamys</i>									
8 <i>Fastosarion</i>									
9 <i>Harmogenanina</i>									
10 <i>Plegma</i>									
11 <i>Sakiella</i>									
12 <i>Sitala</i>									
13 <i>Macrochlamys</i>									
14 <i>Sarika</i>	-								
15 <i>Taphrenalla</i>	0.038	-							
16 <i>Trochochlamys</i>	0.080	0.073	-						
17 <i>Parasitala</i>	0.084	0.084	0.082	-					
18 <i>Trochomorpha</i>	0.080	0.082	0.098	0.122	-				
19 <i>Khmerquantula</i>	0.071	0.060	0.071	0.086	0.091	-			
20 <i>Geotrochus</i>	0.071	0.060	0.086	0.095	0.082	0.049	-		
21 <i>Arion</i>	0.080	0.084	0.091	0.106	0.098	0.089	0.086	-	
22 <i>Meghimatium</i>	0.104	0.100	0.102	0.113	0.124	0.104	0.104	0.060	-

bands, 5–5¼ whorls, high conical spire, whorls rounded, and umbilicus narrow.

Animal (Fig. 3) pale colour and well-developed mantle edges with five lobes: two shell lobes and three dorsal lobes. Pedal groove aulacopod type and foot sole tripartite. Lateral foot margin, caudal foss and caudal horn present. Pallial anatomy typically sigmurethrous (Fig. 3C).

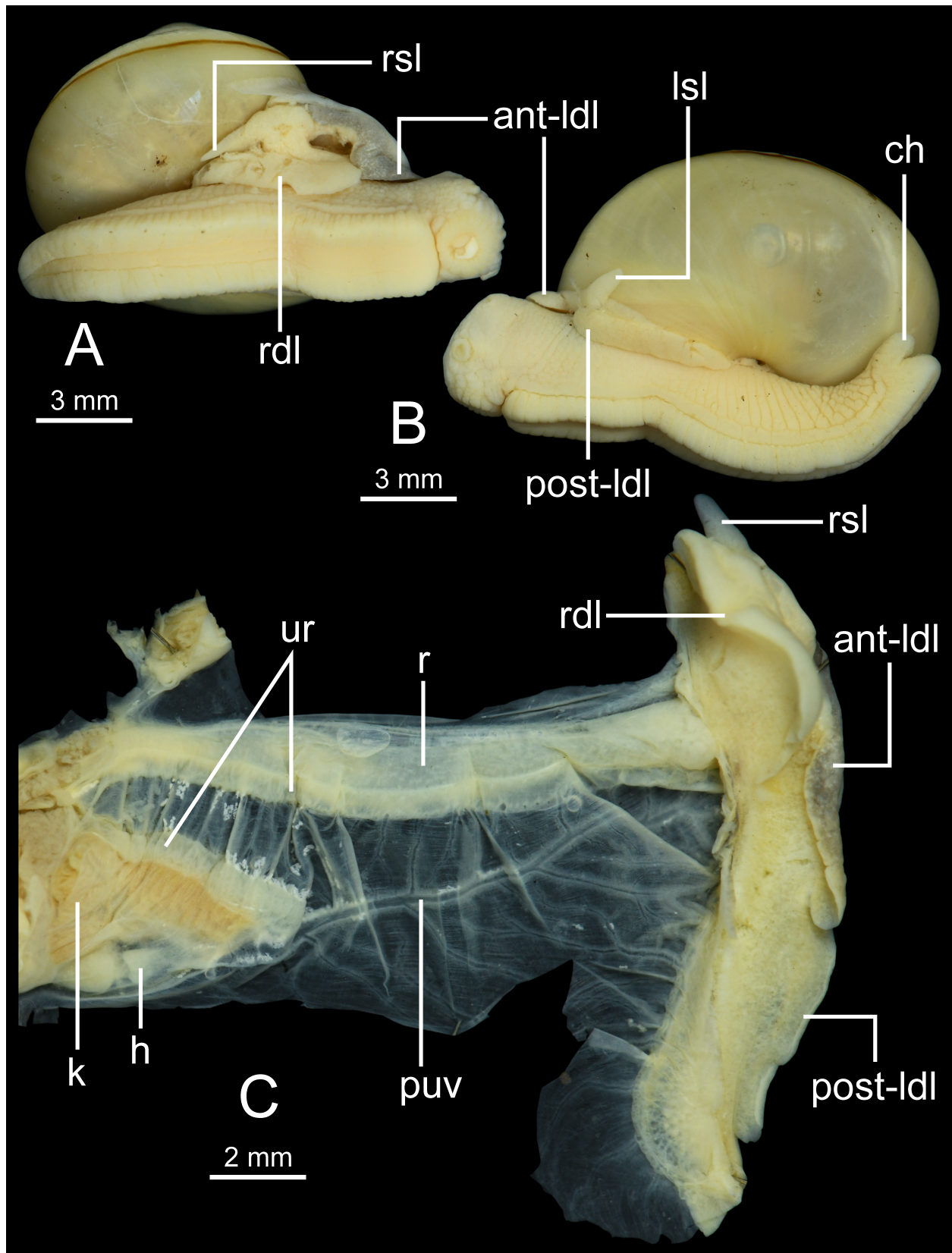
Genitalia with long penis embedded in penial sheath, penial retractor muscle attached to epiphallic caecum, and flagellum absent. Gametolytic duct and sac bulbous and well-developed dart apparatus.

Radula arranged in nearly straight line and gradually developing curved edge. Central tooth reduced to small and asymmetrically multicuspid; lateral and marginal teeth undifferentiated with pectiniform, excessively numerous, elongated bicuspid with several small accessory ectoconal cusps on outer edge.

**Constituent species.**— This new genus contains two species, *Siamopotaxis principalis* sp. nov. and *Siamopotaxis thailandensis* sp. nov.

**Distribution.**— Currently known only from Thailand.





**FIGURE 3.** Synoptic illustration of mantle extensions and pallial system of *Siamopotaxis principalis* sp. nov. (CUMZ 15257). **A** right side of an ethanol preserved specimen showing mantle lobes (shell lobes and dorsal lobes), pneumostome and tripartite foot sole. **B** left side of an ethanol preserved specimen showing mantle lobes and caudal horn. **C** pallial system.

**Remarks.**— *Siamopotaxis* gen. nov. clearly differs from other Southeast Asian helicarionoidean genera such as *Aenigmatoconcha*, *Burmochlamys*, *Chalepotaxis*, *Cryptaustenia*, *Durgella*, *Sakiella*, *Satiella*, *Siamochlamys*, *Sitala*, and *Sophina* by a unique combination of shell, mantle, genital, and radular traits. The new genus has a rather globose, thin, high-spired, milky-white to cream-coloured shell with one to two orange-brown supra-peripheral bands and last whorl rounded at periphery. The two shell lobes are rather small and do not cover the entire shell when fully extended. The genitalia have a small and straight epiphallic caecum, a large dart apparatus, but do not have a flagellum. The radular teeth have many, pectiniform cusps.

In contrast, the genera *Aenigmatoconcha*, *Burmochlamys*, *Chalepotaxis*, and *Sophina* have monocuspid and spatula-shaped radula (Páll-Gergely et al., 2017; Sutcharit et al., 2020a; Pholyotha et al., 2021a, 2022a).

The semislug genera *Cryptaustenia*, *Durgella*, and *Satiella* have a vitrinoid, globose and low-spired shell, pale to dark yellowish colour, without any spiral bands, and well-developed shell lobes that extend over the shell (Blanford and Godwin-Austen, 1908; Schileyko, 2002, 2003; Pholyotha et al., 2024b).

*Sakiella* has a depressed, conical and low-spired shell, yellowish to light-corneous in colour, and lacking any spiral bands. The animal has a dark line on the dorsal side and three to four prominent blackish spots along the lateral side and above the peripodial grooves (Blanford and Godwin-Austen, 1908; Schileyko, 2003).

*Siamochlamys* has a depressed shell, umbilicus narrowly perforate, brownish shell without any spiral bands; shell lobes well-developed and extending over the shell; radula with tricuspid central and lateral teeth, and bicuspid marginal teeth (Pholyotha et al., 2023b).

*Sitala* and the chronid genus *Kaliella* have more or less trochiform and horny shells, usually with a ribbed or striated spiral sculpture, without spiral bands, and last whorl with rounded to keeled periphery (Blanford and Godwin-Austen, 1908; Schileyko, 2002; Vermeulen and Liew, 2022).

The molecular phylogeny (Fig. 2) shows that the new genus forms a distinct, well-supported clade within the Limacoidei. However, it is not yet possible to compare the new genus with the genera *Burmochlamys*, *Cryptaustenia*, and *Siamochlamys* as there are currently no comparative DNA sequence data of these genera.

***Siamopotaxis principalis* Pholyotha, sp. nov.**

<https://zoobank.org/urn:lsid:zoobank.org:act:14B2B3B2-070C-4095-959D-2447C7416C5A>

(Figs 1–3, 4A–D, 5A, B, 6A, 7A, B, 8A, B)

**Type locality.**— Wat Choeng Pha, Thung Saliang District, Sukhothai Province, Thailand (17°19'14.0"N, 99°30'35.0"E).

**Material examined.**— Holotype: CUMZ 15186 (Fig. 4A) and paratypes CUMZ 15257 (Fig. 4B–D; 85 shells and 29 ethanol-preserved specimens), NHMUK (two shells) and SMF (two shells) from the type locality. Paratypes: CUMZ 15258 (one shell) from Tham Lom-Tham Wang, Si Samrong District, Sukhothai Province, Thailand (17°13'39.5"N, 99°31'56.8"E); CUMZ 15187 (three shells) from Wat Tham Rakhang, Si Samrong District, Sukhothai Province, Thailand (17°09'58.8"N, 99°33'38.3"E).

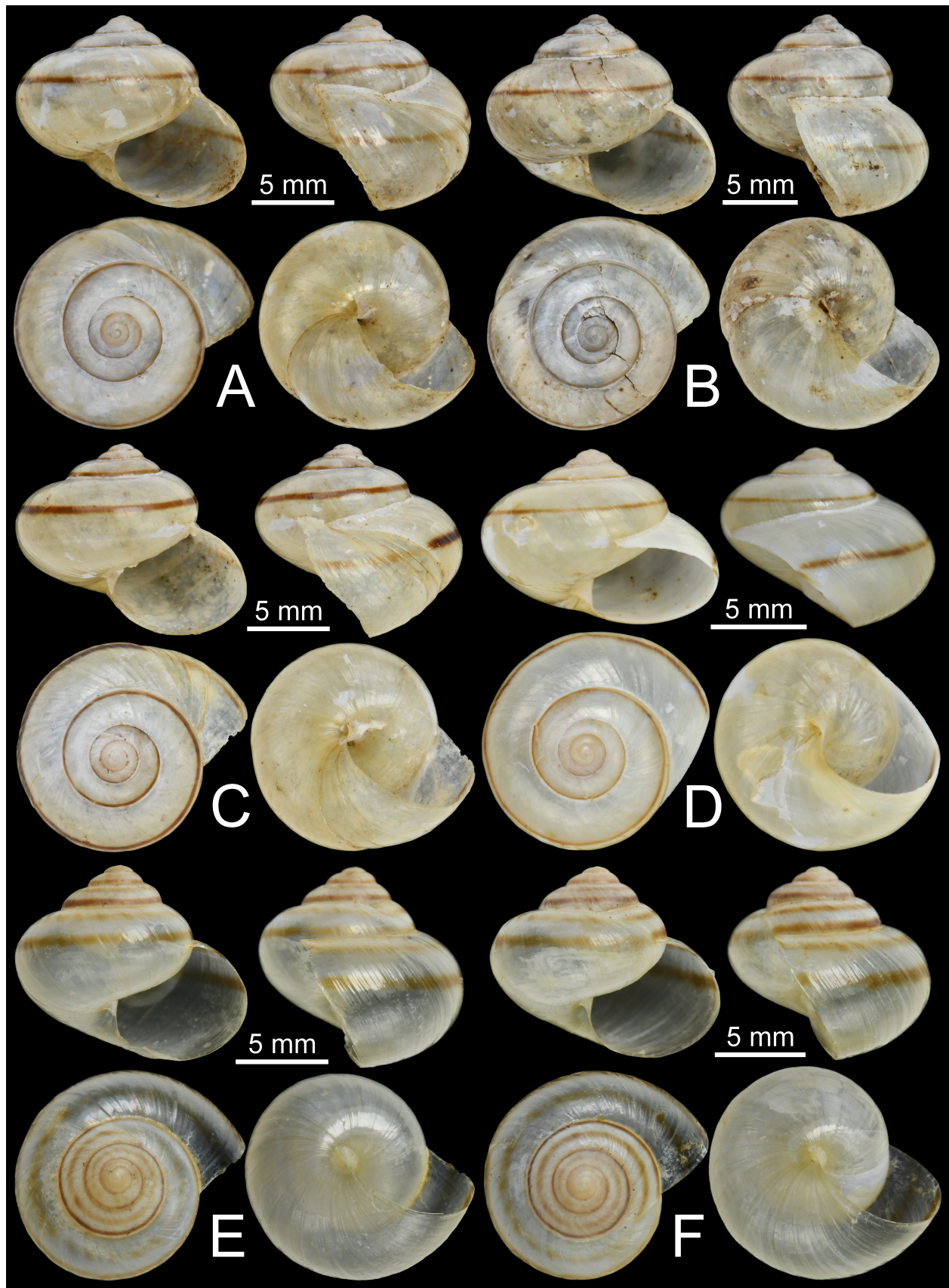
**Etymology.**— The specific name '*principalis*' is derived from the Latin word meaning 'first', 'chief', or 'leader'. It honors Her Royal Highness Princess Maha Chakri Sirindhorn, in recognition of her dedicated efforts to support the conservation of Thailand's biodiversity.

**Diagnosis.**— Shell medium-sized, subglobose to globose, thin, milky-white with one orange-brown supra-peripheral band, and varix present. Protoconch sculptured with shallow pits. Animal with five mantle extensions; genitalia with very long and coiled penis, small epiphallic caecum, and very large dart apparatus.

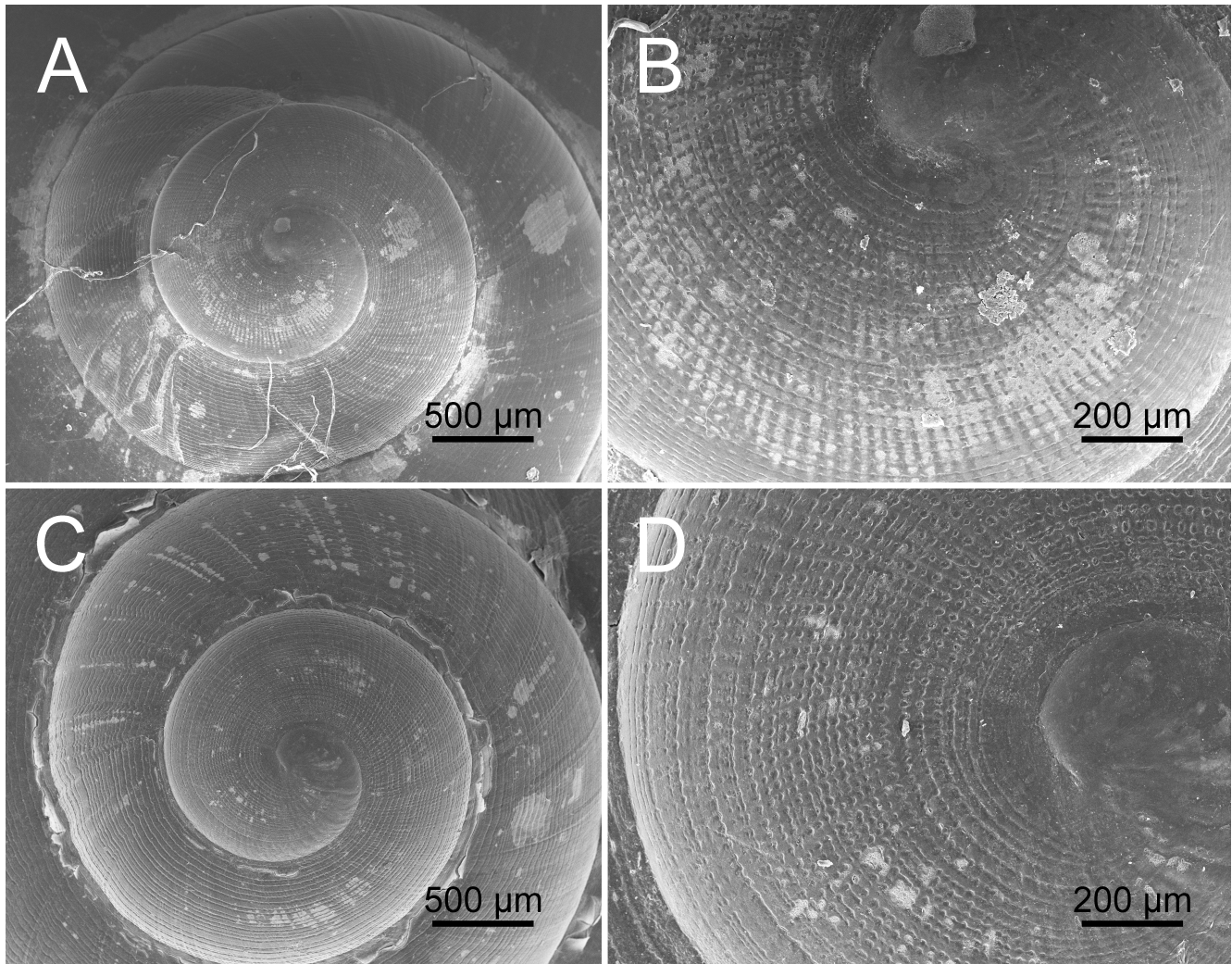
**Description.**— Shell (Figs 4A–D, 5A, B). Shell medium-sized (width up to 12.2 mm, height up to 9.7 mm), subglobose to globose, dextral, thin, transparent, polished. Colour milky-white to pale cream with one narrow orange-brown band located above periphery. Protoconch with fine, equally and densely spaced spiral striations consisting of rows of minute pits arranged in reticulate pattern towards teleoconch (Fig. 5A, B). Teleoconch with distinct to inconspicuous, equally and densely placed shallow spiral grooves, and inconspicuous growth lines (Fig. 5A). Spire little elevated; suture wide and slightly impressed. Whorls 5–5¼, convex, regularly increasing. Last whorl enlarged, well-rounded, and little descending (Fig. 4A–D). Aperture oblique, diagonal, roundly lunate, width greater than height; peristome simple, thin and not expanded. Columellar margin thin and little expanded near umbilicus. Umbilicus minutely opened.

Reproductive anatomy (Fig. 6A). Atrium (at) enlarged and very short. Penis (p) very long, coiled or convoluted, cylindrical, and embedded in thin semi-transparent penial sheath. Epiphallus (e1 + e2) much shorter and narrower than penis; e1 cylindrical; e2





**FIGURE 4.** A–D *Siamopotaxis principalis* sp. nov., A holotype CUMZ 15186, and B–D paratypes CUMZ 15257 from the type locality. E, F *Siamopotaxis thailandensis* sp. nov., E holotype CUMZ 15116 and F paratype CUMZ 15117 from the type locality.



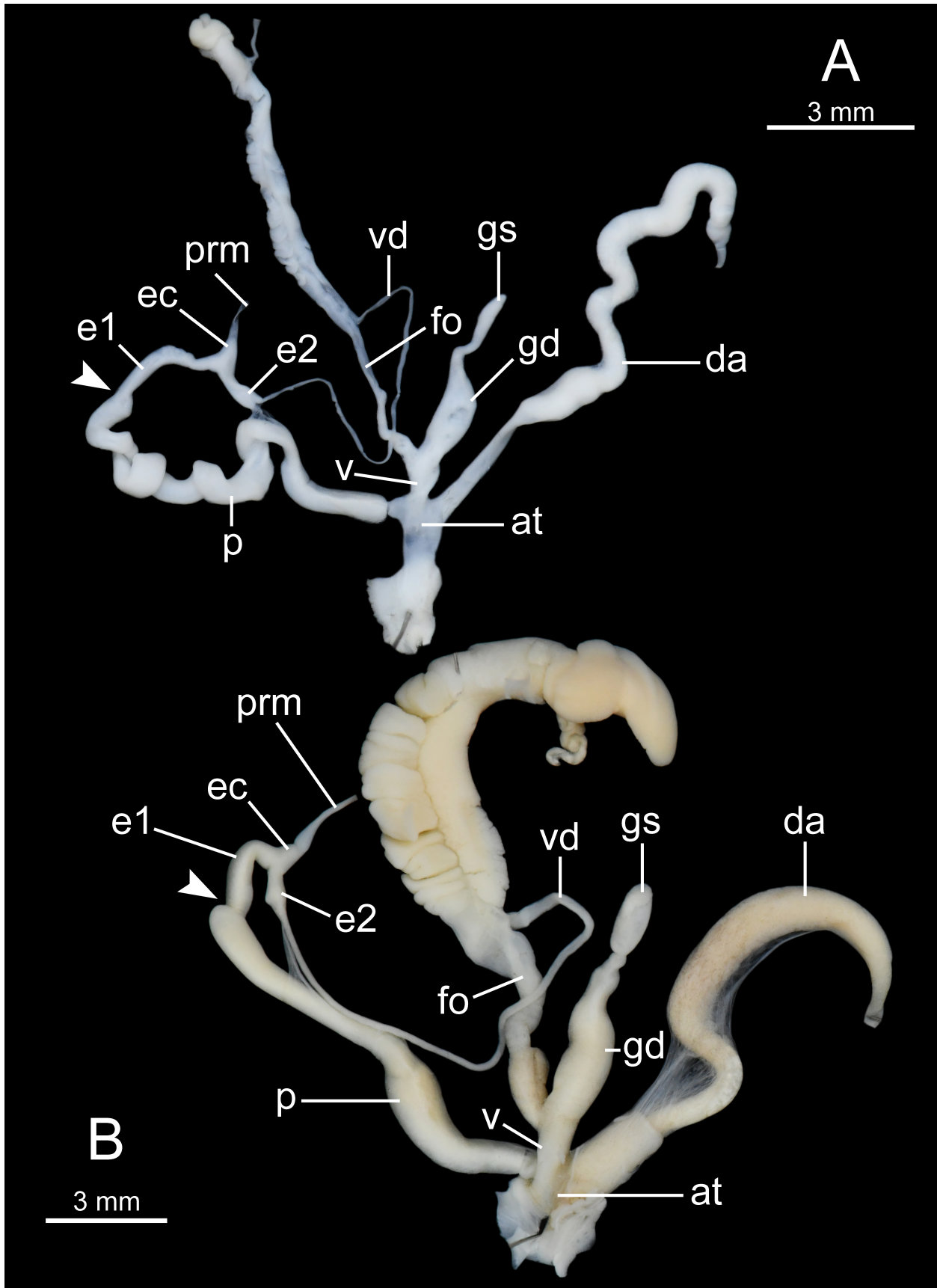
**FIGURE 5.** Microsculpture of protoconch. **A, B** *Siamopotaxis principalis* sp. nov., paratype CUMZ 15257, **A** protoconch and early teleconch, **B** close-up view of protoconch. **C, D** *Siamopotaxis thailandensis* sp. nov., paratype CUMZ 15117, **C** protoconch and early teleconch, **D** close-up view of protoconch.

bulbous shaped and about half of e1 length. Epiphallic caecum (ec) short, small, and bulbous; penial retractor muscle (prm) thick and attached at tip of epiphallic caecum. Vas deferens (vd) very long and slender. Vagina (v) very short. Dart apparatus (da) large, long cylindrical, and located on atrium at vagina and penis junction. Gametolytic duct (gd) bulbous, proximally enlarged and then tapering to smaller and slender tube, slightly shorter than epiphallus (e1 + e2). Gametolytic sac (gs) enlarged and bulbous. Free oviduct (fo) much shorter than penis; proximally enlarged and bulbous; distal part longer and cylindrical. Oviduct enlarged lobules; prostate gland running alongside oviduct.

Radula (Fig. 7A, B). Teeth pectiniform and numerous with half row around 330 teeth. Central tooth asymmetrical, and very reduced to tiny multicuspid. Lateromarginal teeth narrowly elongate bicuspid, outer edge serrated with three to five pointed cusps, and diminishing gradually in size outwards.

Pallial anatomy (Fig. 3C). Pulmonary cavity typically sigmurethrous (sigmoid-shaped ureter); heart (h; auricle and ventricle) located to the left of kidney (k); pulmonary cavity approximately two times longer than wide. Pulmonary vein (puv) and venation on lung roof well-developed; kidney (k) elongate, located posterior of mantle cavity; ureter (ur) large, 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 edges among right shell lobe (rsl), right dorsal lobe (rdl) and anterior left dorsal lobe (ant-ldl).

External appearance (Figs 3, 8A, B). Body colour cream with head and eye tentacles pale grey. Five mantle extensions developed and mostly cream colour. Both right- (rsl) and left- (lsl) shell lobes small, narrow and finger-shaped (Fig. 3). Right dorsal lobe (rdl) large and broad crescent shaped (Fig. 3A, C). Left dorsal lobe divided into anterior and posterior lobes. Anterior



**FIGURE 6.** Genitalia. **A** *Siamopotaxis principalis* sp. nov., paratype CUMZ 15257. **B** *Siamopotaxis thailandensis* sp. nov., paratype CUMZ 15117. White arrowhead indicates the approximate end of the penis.



left dorsal lobe (ant-ldl), large and broad crescent shaped (Fig. 3A, B). Posterior left dorsal lobe (post-ldl) long, large and crescent shaped (Fig. 3B, C). Caudal foss and caudal horn (ch) present with similar colour to body (Figs 3B, 8A, B).

**Distribution, habitat and occurrence.**— The new species is known from limestone hills in Sukhothai Province, central Thailand (Fig. 1). Living snails live on vertical rock faces, and favor hiding or sheltering in small rock crevices during drought periods.

**DNA sequence analyses.**— The ML and BI analyses indicated that the samples of *Siamopotaxis principalis* sp. nov. (n = 3) formed a monophyletic group with high support (Fig. 2; BS = 100%, PP = 1). The three specimens had identical COI and 16S sequences.

**Remarks.**— *Siamopotaxis principalis* sp. nov. is easy to distinguish by its unique milky-white shell with an orange-brown suprapерipheral band.

Among the Southeast Asian helicarionid species that possess a whitish shell with spiral band, this new species clearly differs from *Burmochlamys cassidula* (Benson, 1859), *B. fasciola* Pholyotha & Panha, 2022, *Sophina pisinna* Sutcharit & Panha, 2020, *Sophina furfuracea* Sutcharit & Panha, 2020, and *Chalepotaxis infantilis* (Gredler, 1881) by having many radular teeth with pectiniform cusps. In contrast, these five latter species have monocuspid and spatulate-shaped radulae (Páll-Gergely et al., 2017; Sutcharit et al., 2020a; Pholyotha et al., 2022a).

***Siamopotaxis thailandensis* Pholyotha, sp. nov.**

<https://zoobank.org/urn:lsid:zoobank.org:act:43B34C34-88B1-4EF4-A5EA-B9AE96D48B47>

(Figs 1, 2, 4E, F, 5C, D, 6B, 7C, D, 8C, D)

**Type locality.**— Wat Mae Klong Kee, Umphang District, Tak Province, Thailand (16°13'41.5"N, 98°55'08.6"E).

**Material examined.**— Holotype: CUMZ 15116 (Fig. 4E) and paratypes: CUMZ 15117 (Fig. 4F; five shells and 16 ethanol-preserved specimens), NHMUK (two shells) and SMF (two shells) from the type locality. Paratypes: CUMZ 15118 (six ethanol-preserved specimens) from area near Huai Kon, Chaloem Phra Kiat District, Nan Province, Thailand (19°34'43.3"N, 101°04'54.7"E); CUMZ 14923 (four ethanol-preserved specimens) from Wat Tham Huai Bon, Fang District, Chiang Mai Province, Thailand (19°59'00.1"N, 99°11'05.1"E); CUMZ 14924 (four ethanol-preserved specimens) from Tham Pa Phai, Li District, Lamphun Province, Thailand (17°52'35.2"N, 98°55'00.4"E).

**Etymology.**— The species name refers to Thailand, the country of the type locality.

**Diagnosis.**— Shell medium-sized, globose, thin, milky-white with two orange-brown suprapерipheral bands, and varix inconspicuous. Protoconch sculptured with shallow pits. Animal with five mantle extensions; genitalia with long penis, small epiphallic caecum, and large dart apparatus.

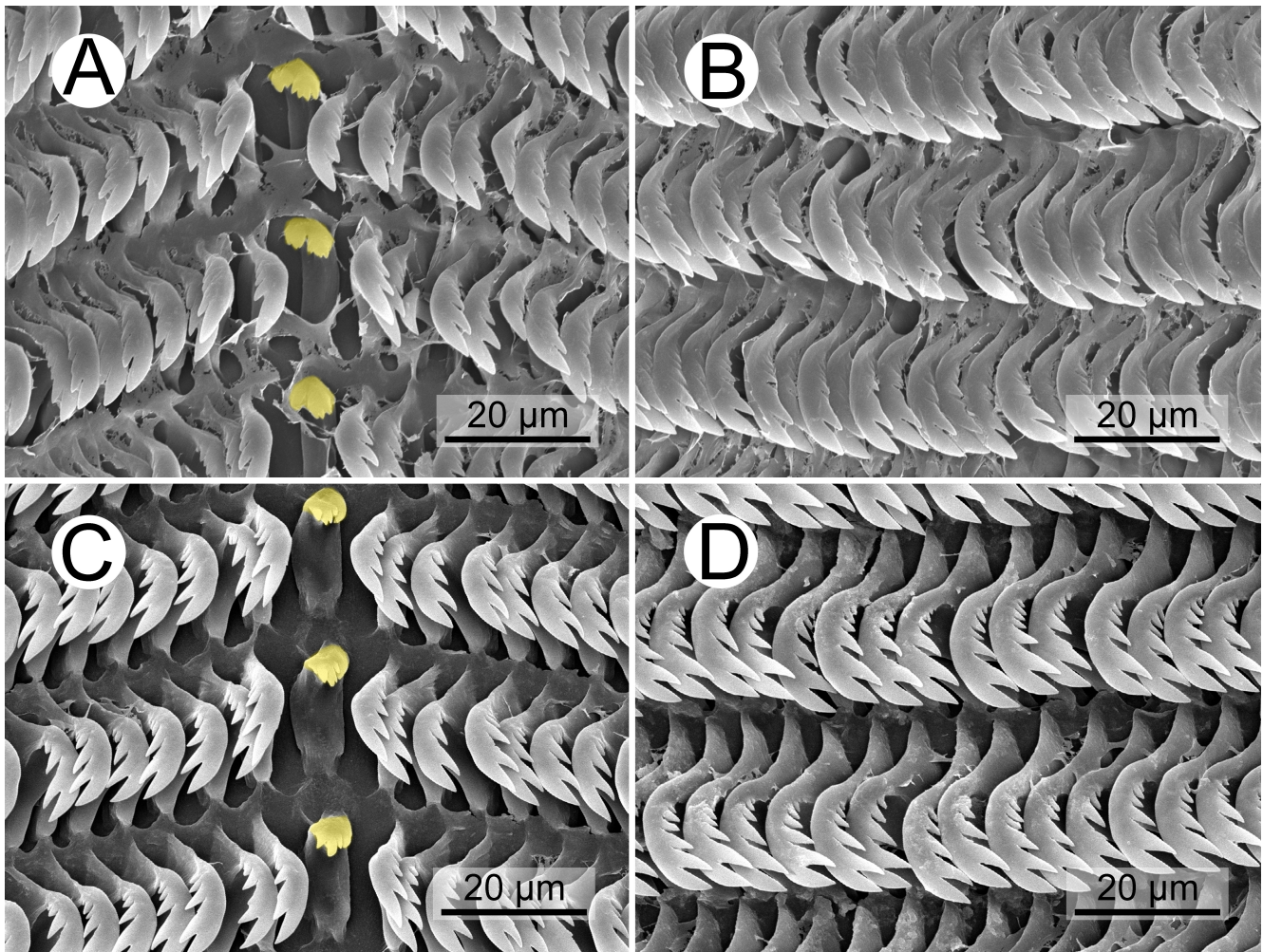
**Description.**— Shell (Figs 4E, F, 5C, D). Shell medium-sized (width up to 12.4 mm, height up to 10.0 mm), globose, dextral, rather thin, transparent, glossy. Colour milky-white with two narrow orange-brown bands located below suture and above periphery. Protoconch with fine, densely spaced spiral striations consisting of rows of minute, rather sharply outlined pits arranged in reticulate pattern towards teleoconch (Fig. 5C, D). Teleoconch with distinct to inconspicuous, equally and densely spaced shallow spiral grooves, and inconspicuous growth lines (Fig. 5C). Spire little elevated; suture slightly impressed. Whorls 5–5¼, convex, regularly increasing; last whorl enlarged, well-rounded; varix rather inconspicuous (Fig. 4E, F). Aperture oblique, diagonal, roundly lunate, width greater than height; peristome simple, thin and not expanded. Columellar edge thin and little expanded near umbilicus. Umbilicus minute.

Reproductive anatomy (Fig. 6B). Atrium (at) enlarged and very short. Penis (p) long, cylindrical, and embedded in thin semi-transparent penial sheath. Epiphallus (e1 + e2) much shorter and narrower than penis; e1 cylindrical and larger than e2; e2 bulbous and about half of e1 length. Epiphallic caecum (ec) short, small, and bulbous; penial retractor muscle (prm) thick and attached at tip of epiphallic caecum. Vas deferens (vd) very long and thin tube. Vagina (v) short. Dart apparatus (da) large, long cylindrical, and connected to atrium chamber. Gametolytic sac (gs) bulbous; gametolytic duct (gd) long and bulbous or large and cylindrical, longer than epiphallus (e1 + e2). Free oviduct as long as gametolytic organ (gs + gd); proximally enlarged and bulbous; distal part longer and cylindrical. Oviduct enlarged lobules; prostate gland running alongside oviduct.

Radula (Fig. 7C, D). Teeth pectiniform with half row about 175 teeth. Central tooth small and multicuspid. Lateromarginal teeth narrowly elongate bicuspid, outer edge serrated with three to five pointed cusps. Outermost teeth shorter and smaller than inner teeth.

External appearance (Fig. 8C, D). Body colour cream with upper part of body pale grey on tail. Head and eye tentacles pale grey to dark grey. Mantle lobes similar to those of *Siamopotaxis principalis* sp. nov. in





**FIGURE 7** SEM images of the radula. **A, B** *Siamopotaxis principalis* sp. nov., paratype CUMZ 15257, **A** middle area with central tooth, **B** lateromarginal area. **C, D** *Siamopotaxis thailandensis* sp. nov., paratype CUMZ 14923, **C** middle area with central tooth, **D** lateromarginal area. Yellow colour indicates the central tooth.

number, shape and colour. Caudal horn raised and cream colour; caudal foss present.

**Distribution, habitat and occurrence.**— This new species is widely distributed from northern to western Thailand (Fig. 1). The snail lives in limestone forests and it is most easily observed after rain, when crawling on the leaves of plants, the trunks or branches of bamboo, or even wet rock faces, but very inconspicuous at other times. When disturbed, snails flick their tail and may either drop to the ground or suspend themselves in the air, using a long strand of sticky mucus attached to nearby leaves or branches. This behavior seems to serve as an anti-predator adaptation, similar to those observed in several helicarionoidean snails and semislugs (Blanford and Godwin-Austen, 1908; Pholyotha et al., 2021a, c, 2024b).

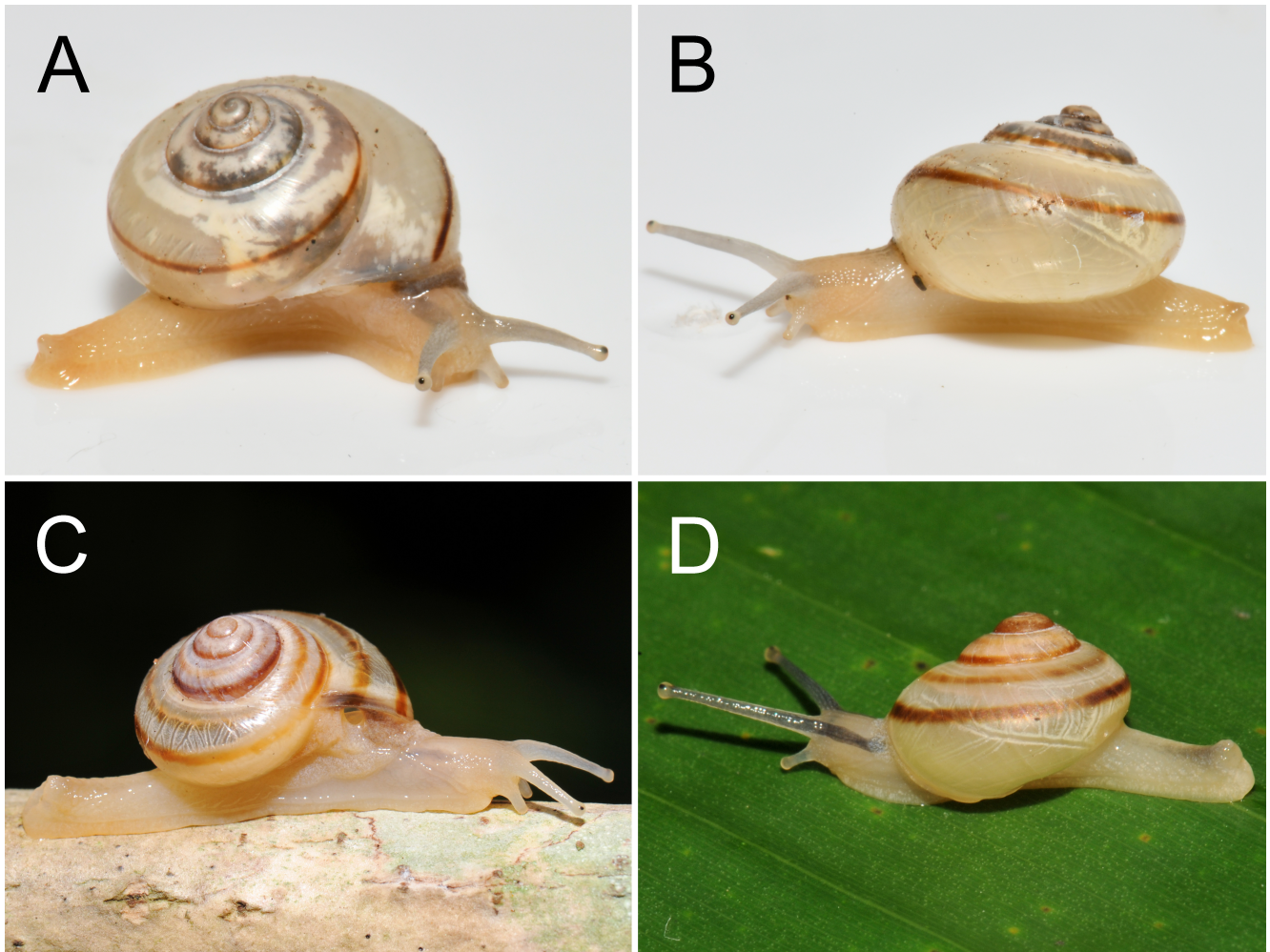
**DNA sequence analyses.**— The ML and BI analyses revealed that the individuals of *Siamopotaxis thailandensis* sp. nov. ( $n = 7$ ) formed a monophyletic group

with high support (Fig. 2; BS = 100%, PP = 1). The mean intraspecific genetic distance of this new species was 1.2% for both COI and 16S.

**Remarks.**— The milky-white shell with two orange-brown suprapерipheral bands distinguish *Siamopotaxis thailandensis* sp. nov. from the other known Southeast Asian helicarionid taxa including *Burmochlamys cassidula*, *B. fasciola*, *Sophina pisinna*, *Sophina furfuracea*, and *Chalepotaxis infantilis*. In comparison, these five latter species have monochrome pale cream shells with one brownish band (Blanford and Godwin-Austen, 1908; Páll-Gergely et al., 2017; Sutcharit et al., 2020a; Pholyotha et al., 2022a).

*Siamopotaxis thailandensis* sp. nov. differs from its sister species, *Siamopotaxis principalis* sp. nov., by having two spiral bands on the shell periphery and an uncoiled penis, whereas the latter new species has one spiral band on periphery and a convoluted penis. Furthermore, the two new species are also genetically distinct. The average genetic distances between them





**FIGURE 8.** Photographs of living snails. **A, B** *Siamopotaxis principalis* sp. nov., paratype CUMZ 15257, **A** right side, **B** left side. **C, D** *Siamopotaxis thailandensis* sp. nov., **C** right side of paratype CUMZ 15117, **D** left side of paratype CUMZ 14924.

based on the COI and 16S genes were 8.2% and 3.0%, respectively.

Regardless of shell colour and suprapерipheral bands, *Siamopotaxis thailandensis* sp. nov. and *Siamopotaxis principalis* sp. nov. share the characters of small to medium-sized, globose to trochiform shells, and regularly expanding whorls with *Sitala attegaia* (Benson, 1859), *Sitala infula* (Benson, 1848), *Sitala liricincta* (Stoliczka, 1871), and *Sitala arx* (Benson, 1859) from Myanmar. However, the two new species have a globose shell with a well-rounded last whorl, whereas the four *Sitala* species possess a conical to trochiform shell that is angular to acutely keeled at periphery of the last whorl (Blanford and Godwin-Austen, 1908).

### CONCLUSION

*Siamopotaxis* gen. nov. is identified as a new helicarionoidean genus by means of comparative morphology, anatomy, and phylogeny. It consists of

two new species (*Siamopotaxis thailandensis* sp. nov. and *Siamopotaxis principalis* sp. nov.), both endemic to Thailand. Both species exhibit shells (globose shape, milky-white colour, with brownish band(s)), radulae (pectiniform and numerous teeth), and genitalia (epiphallallic caecum and dart apparatus present, and without flagellum) that are very different from most other known helicarionoidean taxa. However, morphological and anatomical features alone are not always reliable taxonomic markers. It has been shown that shell traits as well as radular features (e.g., spatulate shape in *Aenigmatoncha*, *Sophina*, and *Chalepotaxis*), or genital appearances (e.g., presence or absence of dart apparatus in *Durgella*) may not reflect phylogenetic relationships, revealing widespread constructional conservatism and potentially even convergence (Criscione et al., 2012; Criscione and Köhler 2013, 2014; Pholyotha et al., 2024a).

The distinctiveness of *Siamopotaxis* gen. nov. is not only based on comparison of their shells, mantle lobes, radulae, and genitalia, but is also confirmed by their

position in the phylogenetic tree. Our molecular phylogeny affirms that it is a member of the Helicarionidae. In addition, our results indicate that the Helicarionidae is formed as a monophyletic group, in agreement with a previous analysis (Pholyotha et al., 2024a). However, the sister group of *Siamopotaxis* gen. nov. cannot be inferred from the phylogenetic tree in this study because it is part of a pan-helicarionid polytomy together with *Durgella*, *Sophina*, and *Satiella*. *Siamopotaxis* gen. nov. differs from all these genera in several key morpho-anatomical characters and exhibits high genetic divergence, which warrant its recognition as a distinct genus.

### ACKNOWLEDGEMENTS

We are grateful to all of our colleagues and research staff members of the Animal Systematics Research Unit (ASRU), Department of Biology, Faculty of Science, Chulalongkorn University for their assistance in collecting materials. We also express our gratitude to anonymous reviewers for their constructive comments, which helped to improve the quality of this article. This research project is supported by grants for development of new faculty staff, the Ratchadaphiseksomphot Fund, Chulalongkorn University to A. Pholyotha. Additionally, this research is funded by the Ratchadaphiseksomphot Fund Chulalongkorn University, the Thailand Science Research and Innovation Fund Chulalongkorn University, the NSRF via the Program Management Unit for Human Resources & Institutional Development, Research and Innovation [grant number B42G670038].

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