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Reassessment and phylogenetic position of the overlooked limacoid land snail *Trochomorpha sculpticarina* Martens, 1883 (Eupulmonata, Ariophantidae), with the description of a new genus

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Abstract

The Malay Peninsula has traditionally been considered to harbour a diverse land-snail fauna, both in terms of a high species richness and a wide variety of conchological traits, especially within the limacoid land snails. A recent survey along the Malay Peninsula of southern Thailand discovered an overlooked limacoid taxon "*Trochomorpha*" *sculpticarina* Martens, 1883, previously assigned to genus *Trochomorpha* of the Trochomorphidae. This genus is herein described as *Janbinmorpha* **gen. nov.** based on comparative studies of shell morphology, external features, genital anatomy and radular morphology, as well as analyses of partial sequences of two mitochondrial markers, COI and 16S rRNA, and of one nuclear marker, 28S rRNA. This new genus is characterised by a combination of distinct morphological and anatomical features. The most distinguishing features are a depressed trochiform shell with a keeled last whorl, gametolytic organ without a duct, gametolytic sac with two lobes, and proximal epiphallus encircled with a thick sheath and attached by the penial retractor muscle. In addition, an analysis of the differentiation in mitochondrial and nuclear markers confirmed that this new genus, first recognised by morphology, is also genetically distinct. The molecular data also confirm that *J. sculpticarina* **comb. nov.** is a member of the Ariophantidae and has a close evolutionary relationship to *Hemiplecta* and *Maelamaodiscus*.

Key Words

Helicarionoidea, land snails, Malay Peninsula, phylogeny, systematics, taxonomy

Introduction

The Malay Peninsula, located in the Indo-Burma biodiversity hotspot in tropical Asia, is a significant hotspot of diversity and endemism of malacofauna, with various distribution patterns and speciation mechanisms (Myers et al. 2000; Clements et al. 2006; Foon et al. 2017; Pholyotha et al. 2021c). Southern Thailand is a part of the Malay Peninsula, representing 14% of the total land area of the country (Gardner et al. 2015). This region has a high species diversity and is also uniquely biologically complex, requiring further research to fully understand. The high species richness is associated with a variety of different factors. High relative humidity, a short dry season, a great amount of rainfall, and extensive ranges of limestone karsts and outcrops scattered along this area together with the impact of Quaternary climatic oscillations have significantly influenced the land snail diversification and speciation in this region (Gupta 2005; Clements et al. 2006; Naggs et al. 2006; Ridd et al. 2011; Gardner et al. 2015; Pholyotha et al. 2021c).

Basic data on land snail biodiversity in the southern peninsula of Thailand have been continuously collected and studied. However, information beyond the original description of many land-snail taxa is scarce. "*Trochomorpha*" *sculpticarina* Martens, 1883 is one such group of overlooked species in this region, and only a few taxonomic documents have mentioned this species. For example, in the comprehensive land snail checklists by Panha (1996) and Hemmen and Hemmen (2001), there is no record of this species from Thailand. Originally, Martens (1883) described this species based on specimens from Phuket Province in the South of Thailand and assigned it to *Trochomorpha* Albers, 1850 in the Trochomorphidae Möllendorff, 1890 because it has a depressed trochiform shell with a developed peripheral keel. Later, Maassen (2001) reported this species from Peninsular Malaysia under the trochomorphid genus *Videna* Adams & Adams, 1855. However, as known from several cases of conservatism and/or convergence in shell form, the general usefulness of the shell features as diagnostic characters has been challenged by studies of genital anatomy and molecular phylogeny (Hyman and Ponder 2010; Köhler and Shea 2012; Jirapatrasilp et al. 2021; Pholyotha et al. 2021a, b, 2022a; Sutcharit et al. 2021; Köhler et al. 2024).

During our field survey, many specimens identical to "*Trochomorpha*" *sculpticarina* were collected from southern Thailand and Myanmar. Its shell traits are similar to *Trochomorpha* or *Videna*, but the living snails resemble several species of the ariophantid genus *Hemiplecta* Albers, 1850. Moreover, its genital anatomy cannot be assigned to any known limacoid genera. Thus, we herein propose it as a new genus, *Janbinmorpha* gen. nov. for "*Trochomorpha*" *sculpticarina*. For proper taxonomic classification of this new genus, modern systematic study is needed. To ensure an accurate taxonomic assessment, we have generated DNA sequence data of this species for both mitochondrial and nuclear markers based on newly-collected samples and have analysed it with the current knowledge of the Asian limacoid snails (Jirapatrasilp et al. 2021; Bhosale et al. 2021; Pholyotha et al. 2021a, c, 2022a, 2023a; Sutcharit et al. 2021). The aims of the present study are to describe the new genus, *Janbinmorpha* gen. nov., based on a combination of morphological, anatomical and molecular information, and to understand the systematic position of the new genus within the limacoid clade.

Materials and methods

Preparation of specimens, species identification, and morphological studies

This study is based on dry shells and ethanol-preserved samples collected from Thailand since 2007 that are now deposited in the Malacological collections of the Chulalongkorn University Museum of Zoology (**CUMZ**), Bangkok, Thailand. Additional specimens from Myanmar were collected during the Myanmar land snail survey of the Forest Department, Ministry of Natural Resources and Environmental Conservation and Forestry, Myanmar, the Fauna & Flora International (**FFI**), and the Animal Systematics Research Unit, Department of Biology, Faculty of Science, Chulalongkorn University, Thailand (**ASRU**) in years 2016 and 2017. For the newly collected specimens, the animal use protocol was approved by the Chulalongkorn University Animal Care and Use Committee (**CU-ACUC**) under approval number 2123023. Before preservation, photographs of several 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). All living specimens were euthanised following the standard protocols for animal euthanasia (American Veterinary Medical Association 2020), and were subsequently preserved in 95% (v/v) ethanol for anatomical studies and DNA analyses.

Specimens were initially identified based on the literature describing Asian land snail taxonomy (e.g., Martens 1883; Blanford and Godwin-Austen 1908; Solem 1966; Schileyko 2002a, b, 2003; Liew et al. 2009; Pholyotha et al. 2023a; Inkhavilay et al. 2019; Jirapatrasilp et al. 2021; Sutcharit et al. 2021) and compared to the reference collections deposited in the Natural History Museum, London, UK (**NHM**; **NHMUK** when citing specimens deposited in the NHM), Forschungsinstitut und Naturmuseum Senckenberg, Frankfurt am Main, Germany (**SMF**), and Museum für Naturkunde, Humboldt University, Berlin, Germany (**ZMB**).

Adult shells were used to measure the shell height and shell width using a Vernier caliper, and to count the number of whorls. Photographs of shells were taken using a Nikon camera (DSLR D850) with Nikon 105 Macro lens. The shell sculpture was imaged by scanning electron microscopy (SEM; JEOL, JSM-6610 LV). Preserved snails were dissected using an Olympus SZX2-TR30 stereoscopic light microscope and were photographed using the Nikon camera (DSLR D850) with Nikon 105 Macro lens. The inner sculpture of genitalia was imaged by a stereo micro-scope with the Cell'D Imaging Software. Radulae were extracted with 10% (w/v) sodium hydroxide solution, cleaned with distilled water, and imaged by scanning electron microscopy (SEM; JEOL, JSM-6610 LV).

List of abbreviations used in the figures: **at** (atrium), **da** (dart apparatus), **e** (epiphallus), **ec** (epiphallic caecum), **es** (epiphallic sheath), **fo** (free oviduct), **gs** (gametolytic sac), **p** (penis), **prm** (penial retractor muscle), **v** (vagina), **vd** (vas deferens).

Molecular studies

We extracted genomic DNA 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, cytochrome c oxidase subunit 1 (COI) and 16S rRNA (16S), and of one nuclear gene, 28S rRNA (28S) were amplified by PCR using the universal primer pair LCO1490 and HCO2198 (Folmer et al. 1994), the primer pair 16Sar and 16Sbr (Palumbi et al. 1991), and the primer pair LSU2 and LSU4 (Wade and Mordan 2000), respectively. The PCR thermal cycling conditions for COI, 16S, and 28S were as follows: an initial cycle at 94 °C for 1 min; followed by 40 cycles of 10 s at 98 °C, 30 s at 51 °C for COI, 50 °C for 16S and 60 °C for 28S, and 2 min at 72 °C; and followed by a final extension step at 72 °C for 5 min. The amplified products were then sent for commercial sequencing at Bioneer Corporation, South Korea. Chromatograms were manually corrected for misreads, and forward and reverse strands were merged into one sequence file using MEGA v. 7.0 (Kumar et al. 2016). Sequences obtained in this study have been deposited in GenBank under accession numbers: PQ008991–PQ008998, PQ032739–PQ032747, and PQ032728–PQ032738 (Table 1).

Information regarding all sequences used in our molecular phylogenetic analyses is provided in Table 1. Sequence alignments of each gene fragment were generated separately using MAFFT v. 7 in the MAFFT online service (https://mafft.cbrc.jp/alignment/server/) with the default settings (Katoh et al. 2017). Uncorrected pairwise genetic distances (*P*-distances) were calculated using MEGA v. 7.0 (Kumar et al. 2016) under the option 'pairwise deletion of gaps'.

For phylogenetic analyses, sequences of the three genes 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). As suggested by the program Kakusan4, the concatenated dataset was divided into five partitions; the Felsenstein 1981 model with a gamma distribution was chosen for the first codon positions of COI, the Hasegawa, Kishino and Yano 1985 model with a gamma distribution was chosen for the second codon positions of COI, and the general time-reversible model with a gamma distribution was chosen for the third codon positions of COI, 16S and 28S. Phylogenetic relationships were estimated by employing the Maximum Likelihood (ML) and the Bayesian Inference (BI) methods through the online CIPRES Science Gateway (Miller et al. 2010). The ML analyses were performed by applying the GTRCAT model to the entire dataset at the default settings of RAxML-HPC2 on ACCESS v. 8.2.12 (Stamatakis 2014), as the program used did not allow for data partitioning. Branch support was estimated using 1000 bootstrap (BS) replicates. The BI analyses were performed 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 XSEDE v.3.2.7 (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 BI posterior probabilities (PP) were ≥ 0.95 and the ML bootstrap (BS) support values were ≥70% (Hillis and Bull 1993; Felsenstein 2004; Huelsenbeck and Rannala 2004; Mauro and Agorreta 2010).

Table 1. Information of specimens used in the molecular studies with species name, specimen codes, locality name, museum registration numbers, GenBank accession numbers, and references.

Taxa	Specimen Codes	Locality name	Museum registration number	GenBank accession numbers			References
				COI	16S	28S	
Infraorder Limacoidei							
Superfamily Helicarionoidea Bourguignat, 1877							
Family Ariophantidae Godwin-Austen, 1883							
Subfamily Ariophantinae Godwin-Austen, 1883							
Janbinmorpha sculpticarina (Martens, 1883), comb. nov.	S163-1	Anurak Community Lodge, Phanom, Surat Thani, Thailand	CUMZ 15076	–	PQ032739	PQ032728	This study
Janbinmorpha sculpticarina (Martens, 1883), comb. nov.	S163-2	Area near Anurak Community Lodge, Phanom, Surat Thani, Thailand	CUMZ 15076	PQ008991	PQ032740	PQ032729	This study
Janbinmorpha sculpticarina (Martens, 1883), comb. nov.	S208-2	Bang Pae Waterfall, Thalang, Phuket, Thailand	CUMZ 15077	PQ008992	–	–	This study
Janbinmorpha sculpticarina (Martens, 1883), comb. nov.	–	Tanintharyi, Myanmar	FLMNH 494197	MF983690	–	–	Slapcinsky and Mulcahy (Unpublished)
Janbinmorpha sculpticarina (Martens, 1883), comb. nov.	–	Tanintharyi, Myanmar	FLMNH 494198	MF983691	–	–	Slapcinsky and Mulcahy (Unpublished)
Ariophanta belangeri (Deshayes, 1832)	–	Kagal, Kolhapur, Maharashtra, India	BNHS GAS 73	–	–	MW583023	Bhosale et al. (2021)
Ariophanta intumescens (Blanford, 1866)	–	Mhalunge, Kolhapur, Maharashtra, India	BNHS GAS 74	–	–	MW583024	Bhosale et al. (2021)
Cryptozona bistrialis (Beck, 1837)	–	Nellore, Andhra Pradesh, India	–	KX514442	KT716352	KX378390	Ayyagari and Sreerama (2020)
Euplecta gardeneri (Pfeiffer, 1848)	–	Sri Lanka	–	–	–	AY841311	Wade et al. (2006)
Hemiplecta distincta (Pfeiffer, 1850)	H54	Tad Pha Suam, Paksong, Champasak, Laos	CUMZ 5267	MT654617	MT651533	MT651588	Sutcharit et al. (2021)
Hemiplecta humphreysiana (Lea, 1840)	H7	Botanic Garden, Singapore	CUMZ 5158	MT364994	MT365775	MT365719	Pholyotha et al. (2021c)
Hemiplecta pluto (Pfeiffer, 1863)	H63	Wat Pa Pha, Khamkeut, Bolikhamxay, Laos	CUMZ 5266	MT364995	MT365776	MT365720	Pholyotha et al. (2021c)
Khasiella pingoungensis (Godwin-Austen, 1888)	MY51-1	Pyinyaung, Mandalay, Myanmar	CUMZ 14560	PQ008993	PQ032741	PQ032730	This study

Taxa	Specimen Codes	Locality name	Museum registration number	GenBank accession numbers			References
				COI	16S	28S	
Khasiella pingoungensis (Godwin-Austen, 1888)	MY51-2	Pyinyaung, Mandalay, Myanmar	CUMZ 14560	PQ008994	PQ032742	PQ032731	This study
Mariaella dussumieri Pfeiffer, 1855	–	Ramling Temple, Kolhapur, Maharashtra, India	ZSI Moll 1789	–	–	MW583030	Bhosale et al. (2021)
Maelamaodiscus somsakpanhai Sutcharit & Pholyotha, 2023	W93-2	Phra Wor Shine, Mae Sod, Tak, Thailand	CUMZ 14295	–	–	PQ032732	This study
Maelamaodiscus somsakpanhai Sutcharit & Pholyotha, 2023	W109	Wat Phothikun, Mae Sod, Tak, Thailand	CUMZ 14296	–	–	PQ032733	This study
Megaustenia praestans Gould, 1843)	MY47	Golden valley near Bat Cave, Hpa-An, Myanmar (Burma)	CUMZ 14638	PQ008995	PQ032743	PQ032734	This study
***Megaustenia* sp.**	C19	Pa Ma-muang Bureau of Monks, Noen Maprang, Phitsanulok, Thailand	CUMZ 7241	MT364990	MT365778	MT365722	Pholyotha et al. (2021d)
***Ratnadvipia* sp.**	–	Sri Lanka	–	–	–	AY841312	Wade et al. (2006)
Subfamily Macrochlamydinae Godwin-Austen, 1888							
Macrochlamys aspides (Benson, 1863)	MY8	Lun Nya Mountain, Hpa An, Kayin, Myanmar	CUMZ 7135	MT364986	MT365761	MT365705	Pholyotha et al. (2021c)
Macrochlamys pedina (Benson, 1865)	–	Khandala,Maharashtra, India	BNHS GAS 146	–	–	MW583026	Bhosale et al. (2021)
Macrochlamys indica Godwin-Austen, 1883	–	Shivaji University, Kolhapur,Maharashtra, India	BNHS GAS 82	–	–	MW583025	Bhosale et al. (2021)
***Macrochlamys* sp.1**	L1	Laos	CUMZ 15262	PQ008996	PQ032744	PQ032735	This study
***Macrochlamys* sp.2**	MY4	Myanmar	CUMZ 15263	PQ008997	PQ032745	PQ032736	This study
Sarika resplendens (Philippi, 1847)	W4	Khao Cha Ngum, Photharam, Ratchaburi, Thailand	CUMZ 7234	MT364982	MT365763	MT365707	Pholyotha et al. (2021c)
Sarika obesior (Martens, 1867)	W65	Wat Nong Phlap, Hua Hin, Prachuap Khiri Khan, Thailand	CUMZ 7233	MT364977	MT365768	MT365712	Pholyotha et al. (2021c)
Taphrenalla diadema (Dall, 1897)	S46	Wat Tham Sumano, Srinagarindra, Phatthalung, Thailand	CUMZ 7175	MT364940	MT365729	MT365673	Pholyotha et al. (2021c)
Taphrenalla incilis Pholyotha & Panha, 2021	S69	Tham Khao Ting, Palian, Trang, Thailand	CUMZ 7209	MT364963	MT365746	MT365690	Pholyotha et al. (2021c)
Varadia amboliensis Bhosale, Thackeray, Muley & Raheem, 2021	–	Amboli, Maharashtra, India	BNHS GAS 129	–	–	MW583027	Bhosale et al. (2021)
Subfamily Ostracolethinae Simroth, 1901							
Parmarion martensi Simroth, 1893	NE100	Wat Tham Pha Khao, Si Wilai, Bueng Kan, Thailand	CUMZ 15264	PQ008998	PQ032746	PQ032737	This study
Family Helicarionidae Bourguignat, 1877							
Aenigmatoconcha clivicola Tumpeesuwan & Tumpeesuwan, 2017	NE68	Wat Tham Pha Lom, Mueang, Loei, Thailand	CUMZ 7929	MW703614	PQ032747	PQ032738	This study; Pholyotha et al. (2021d)
Chalepotaxis infantilis (Gredler, 1881)	Cha-inf-2	Guanyindong, Zhangjiajie Shi, Hunan, China	NHMW 111548	KX027275	–	KX027276	Pall-Gergely et al. (2016)
***Durgella* sp.**	N15	Tham Lom Tham Wang, Si Samrong, Sukhothai, Thailand	CUMZ 7242	MT364991	MT365777	MT365721	Pholyotha et al. (2021c)
Eurychlamys platychlamys (Blanford, 1880)	–	Sagar Upavan, Mumbai, Maharashtra, India	BNHS GAS 10	–	–	MW583029	Bhosale et al. (2021)
Fastosarion brazieri (Cox, 1873)	–	Mossman, Queensland, Australia	–	–	–	AY014099	Wade et al. (2001)
***Satiella* sp.**	–	Jawali, Kolhapur, Maharashtra, India	BNHS GAS 69	–	–	MW583028	Bhosale et al. (2021)
Sophina schistostelis (Benson, 1859)	MY24	Sanbel Cave, Mawlamyine, Mon, Myanmar	CUMZ 5195	MN897023	MN888602	MN892653	Sutcharit et al. (2020a)
Superfamily Trochomorphoidea Mörch, 1864							
Family Dyakiidae Gude & Woodward, 1921							
***Trochomorpha* sp.1**	NE74	Tham Khao Chakan, Khao Chakan, Sa Kaeo, Thailand	CUMZ 14870	OR075932	OR076723	OR076740	Pholyotha et al. (2023a)
***Trochomorpha* sp.2**	NE80	Wat Tham Pha Lom, Mueang, Loei, Thailand	CUMZ 14871	OR075933	OR076724	OR076741	Pholyotha et al. (2023a)
***Trochomorpha* sp.3**	S185-2	Talod Cave, Thung Song, Nakhon Si Thammarat, Thailand	CUMZ 14873	OR075934	OR076725	OR076742	Pholyotha et al. (2023a)
Trochomorpha froggatti (Iredale, 1941)	–	Batangan, Kinabatangan, Sabah, Malaysia	RMNH. 5005011.01	MK851194	MK851432	MK851503	Hendriks (2020)
Videna metcalfei (Pfeiffer, 1845)	–	Batangan, Kinabatangan, Sabah, Malaysia	RMNH. 5005031.01	MK851205	MK851445	MK851515	Hendriks (2020)
Family Geotrochidae Schileyko, 2002							
Geotrochus rhysa (Tillier & Bouchet, 1989)	–	Mount Kinabalu, Sabah, Malaysia	BORMOL 6347	MK779474	MK334188	OR076749	Chang and Liew (2021), Pholyotha et al. (2023a)
Geotrochus kitteli Vermeulen, Liew & Schilthuizen, 2015	–	Mount Kinabalu, Sabah, Malaysia	BORMOL 6406	MK779460	MK334194	OR076744	Chang and Liew (2021), Pholyotha et al. (2023a)

Taxa	Specimen Codes	Locality name	Museum registration number	GenBank accession numbers			References
				COI	16S	28S	
Family Euconulidae Baker, 1928							
Siamoconus geotrochoides Pholyotha, 2023	NE46-1	Wat Tham Pha Lom, Mueang, Loei, Thailand	CUMZ 14298	OR075923	OR076716	OR076735	Pholyotha et al. (2023a)
Siamoconus boreas Pholyotha, 2023	N70-3	Ban Tha Si, Mae Mo, Lampang, Thailand	CUMZ 14310	OR075905	OR076701	OR076726	Pholyotha et al. (2023a)
Superfamily Gastrodontoidea Tryon, 1866							
Family Oxychilidae Hesse, 1927							
Oxychilus alliarius (Miller, 1822)	–	Deepdale, Derbyshire, UK	–	MN022739	–	MN022673	Saadi and Wade (2019)
Superfamily Limacoidea Batsch, 1789							
Family Vitrinidae Fitzinger, 1833							
Vitrina pellucida (Müller, 1774)	–	Kirkdale, Derbyshire, UK	–	MN022738	–	MN022672	Saadi and Wade (2019)
Infraorder Arionoidei Gray, 1840							
Superfamily Arionoidea Gray, 1840							
Family Philomycidae Gray, 1847							
Meghimatium bilineatum (Benson, 1842)	–	Mauritius	–	MN022745	–	MN022678	Saadi and Wade (2019)
Family Arionidae Gray, 1840							
Arion hortensis Férussac, 1819	–	Kirkdale, Derbyshire, UK	–	MN022744	–	KU341315	Saadi and Wade (2019)

Results

Molecular phylogeny

Molecular phylogenetic trees were reconstructed based on the concatenated mitochondrial COI and 16S sequences, and nuclear 28S sequences obtained from 53 individuals, including 31 ariophantids, 7 helicarionids, 5 trochomorphids, 2 dyakiids, 2 geotrochids, 2 euconulids, 1 oxychilid, and 1 vitrinid together with 2 species of arionoideans for the more distantly related outgroups to root the phylogenetic tree. The suitable outgroups in this study were selected based on the recent phylogenetic trees presented by Bhosale et al. (2021) and Pholyotha et al. (2023a). The final concatenated mtDNA + nDNA dataset contained 39 COI sequences, with an alignment length of 691 sites (377 conserved sites, 260 parsimony informative sites, and 305 variable sites), 32 sequences of 16S, with an alignment length of 522 sites (215 conserved sites, 204 parsimony informative sites, and 249 variable sites), and 50 sequences of 28S, with an alignment length of 557 sites (387 conserved sites, 117 parsimony informative sites, and 164 variable sites).

In this study, both Maximum Likelihood (ML) and Bayesian Inference (BI) analyses produced trees with identical topologies; therefore, only the tree topology from the ML analysis is presented in Fig. 1. Analyses of the combined COI + 16S + 28S dataset of about 31 sequences of at least 24 species representing all known ariophantid genera that have available DNA information from Asia have confirmed the monophyly of the *Janbinmorpha* gen. nov. as delineated herein. However, our results indicated that the phylogenetic relationships within the Limacoidei are still unresolved, especially a clade of the Helicarionoidea (including Ariophantidae and Helicarionidae; Fig. 1).

Although the phylogeny is not fully resolved, it highlights or identifies the phylogenetic positions of *Janbinmorpha* gen. nov. and some ariophantid genera (such as *Megaustenia*, *Khasiella*, *Parmarion*, and *Maelamaodiscus*) for the first time. The new genus was grouped together with the *Maelamaodiscus* + *Hemiplecta* clade with high support by BI (BS = 62%, PP = 0.97). However, the phylogenetic relationships within the *Janbinmorpha* + *Maelamaodiscus* + *Hemiplecta* clade could not be resolved in this study (Fig. 1). This clade was retrieved as the sister clade to the *Khasiella* + *Macrochlamys aspides* + *Sarika* + *Taphrenalla* clade with good support (BS = 71%, PP = 1). Relationships within the latter clade were resolved in this study (Fig. 1).

Pairwise comparisons of COI sequences showed that conspecific specimens of *Janbinmorpha sculpticarina* comb. nov. were differentiated by means of 0% to 4.4% uncorrected *p*-distances (Table 2), whereas 16S and 28S sequences of conspecific specimens differed by 0%. Comparing *Janbinmorpha* gen. nov. and other ariophantid genera, the uncorrected *p*-distances of the COI, 16S and 28S sequences ranged from 12.2% (between the new genus and *Taphrenalla*) to 14.8% (between the new genus and *Parmarion*) for COI (Table 3), from 11.8% (between the new genus and *Hemiplecta*) to 17.8% (between the new genus and *Cryptozona*) for 16S (Table 4), and from 2.7% (between the new genus and *Hemiplecta*) to 6.0% (between the new genus and *Cryptozona*) for 28S (Table 5).

Taxonomy and systematics

Superfamily Helicarionoidea Bourguignat, 1877
Family Ariophantidae Godwin-Austen, 1883
Subfamily Ariophantinae Godwin-Austen, 1883

Janbinmorpha **Pholyotha & Panha, gen. nov.**
https://zoobank.org/953A9F87-2E64-4A11-AFD6-061303E94409

Type species. *Trochomorpha sculpticarina* Martens, 1883; here designated.

Etymology. The name combines "*Janbin*" in reference to the shape of an unidentified flying object (UFO) in the Thai language, and similar to the shell shape of

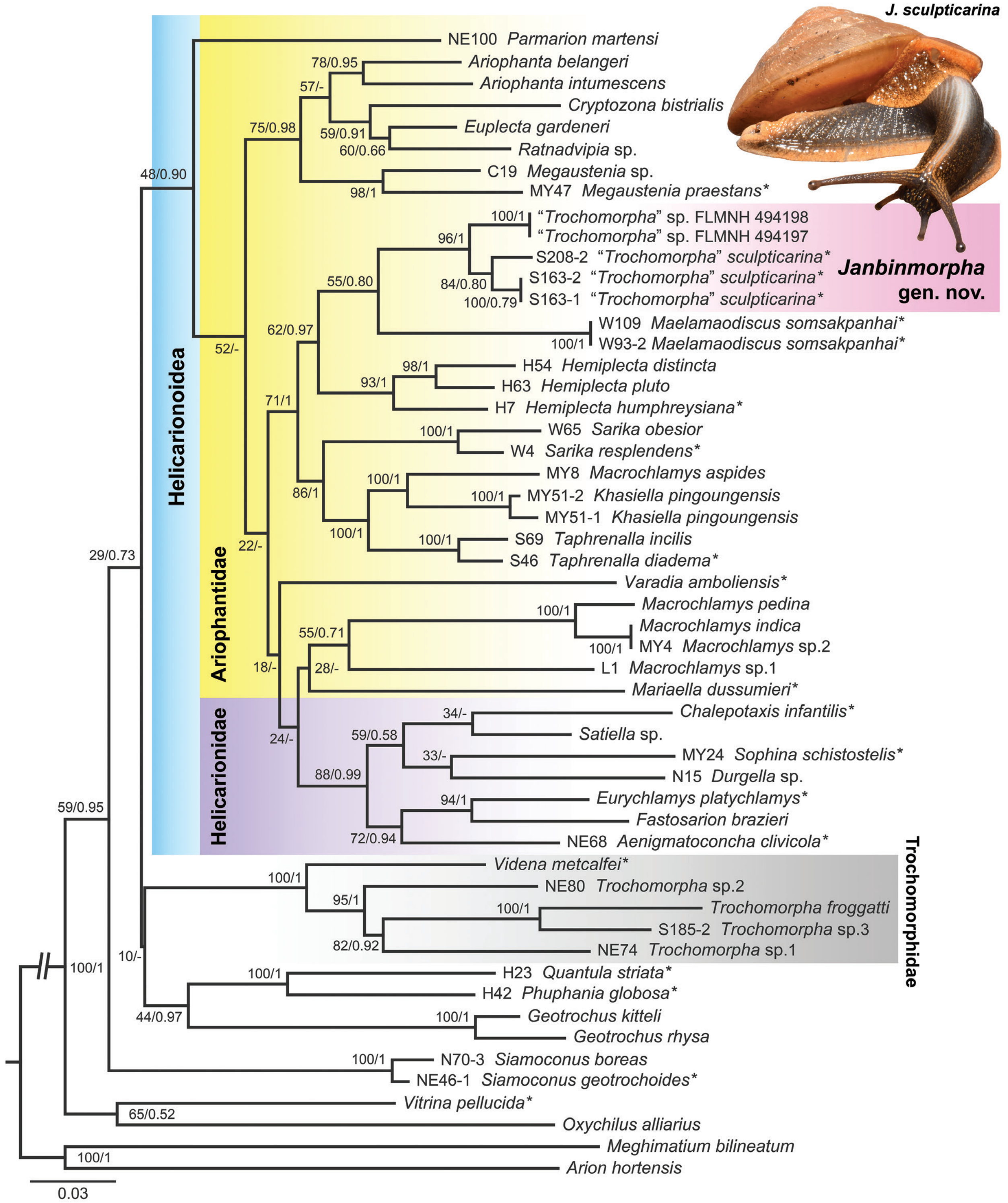

Figure 1. Maximum likelihood phylogram based on analyses of concatenated COI, 16S, and 28S sequences. Numbers on branches indicate nodal support by ML bootstrap (BS) and Bayesian posterior probabilities (PP) analyses. Asterisk indicates the type species of its corresponding genus. The sample code in front of species name indicates voucher samples as shown in Table 1. Living specimen of *Janbinmorpha sculpticarina* (Martens, 1883), comb. nov. from Phang-nga Province, not to scale.

this new genus, and "*morpha*" in reference to the similarity of shell morphology between this new genus and the genus *Trochomorpha*.

Diagnosis. Shell dextral, umbilicated, depressed, lenticular, ribbed, with keeled last whorl. Animal with three dorsal lobes; foot tripartite; caudal foss present; caudal horn very reduced. Genitalia having epiphallic caecum, flagellum and dart apparatus; proximal epiphallus encircled with thickened muscular epiphallic sheath; gametolytic organ without duct and gametolytic sac consisting of two bulbs. Radula with tricuspid central tooth; unicuspid or bicuspid lateral teeth; unicuspid marginal teeth.

Table 2. Estimates of cytochrome c oxidase I (COI) sequence divergence (uncorrected *p*-distances) within *Janbinmorpha sculpticarina* comb. nov.

Sequences of *Janbinmorpha sculpticarina*	*J. sculpticarina* S163-2	*J. sculpticarina* S208-2	*J. sculpticarina* FLMNH 494197	*J. sculpticarina* FLMNH 494198
J. sculpticarina S163-2				
J. sculpticarina S208-2	0.027			
J. sculpticarina FLMNH 494197	0.044	0.043		
J. sculpticarina FLMNH 494198	0.044	0.043	0.000	

Description. See below under the type species.

Constituent species. This new genus contains only the type species, *J. sculpticarina* comb. nov.

Distribution. Currently known only from the Malay Peninsula.

Remarks. *Janbinmorpha* gen. nov. is clearly discriminated from all other Southeast Asian limacoid genera (e.g., *Hemiplecta*, *Holkeion* Godwin-Austen, 1908, *Siamoconus* Pholyotha in Pholyotha et al. 2023a, *Videna* and *Trochomorpha*) by the shape of the gametolytic sac and by the attachment of the penial retractor muscle. This new genus has no gametolytic duct and the gametolytic sac is divided into two lobes, while the gametolytic sac of all other limacoid genera is not divided into two lobes and most of them have a gametolytic duct. The penial retractor muscle of this new genus is attached to two regions (epiphallic caecum and epiphallic sheath), while all other limacoid genera have the retractor muscle attached to either the epiphallic caecum or epiphallus (Blanford and Godwin-Austen 1908; Solem 1966; Schileyko 2002a, b, 2003; Sutcharit et al. 2020a, 2021; Sutcharit and Panha 2021; Pholyotha et al. 2021b, c, 2022a, b, 2023b, c).

Janbinmorpha gen. nov. also differs from *Videna* in having a long dart apparatus and the position of gametolytic organ on female side, while the latter genus has no dart apparatus and gametolytic duct opening into the base of the penis (Schileyko 2002a).

Janbinmorpha gen. nov. is conchologically very similar to the Indian helicarionoidean genus *Sivella* Blanford, 1863. However, this new genus differs by having a long dart apparatus, a straight epiphallic caecum, and no gametolytic duct. In comparison, *Sivella* has a relatively short gametolytic duct and a subglobular gametolytic sac, and does not have a dart apparatus or epiphallic caecum (Godwin-Austen 1918; Schileyko 2003).

In addition, the molecular phylogeny (Fig. 1) supports a distinct lineage of the monotypic *Janbinmorpha* gen. nov. from genera *Hemiplecta*, *Siamoconus*, *Videna* and *Trochomorpha*. Currently, genetic sequences of *Holkeion* and *Sivella* are not available in the online GenBank sequence database for phylogenetic analysis.

Janbinmorpha sculpticarina (Martens, 1883), comb. nov.

Figs 1–5, 6A

Trochomorpha sculpticarina Martens, 1883: 136, pl. 25, figs 13–16.
Type locality: "insulam Salanga" [Phuket Province, Thailand].

Videna sculpticarina–Basch and Solem 1971: 95. Maassen 2001: 116.

Type material examined. Syntype ZMB/Moll 58132 (1 shell; Fig. 2A) ex. Paetel collection from Salanga [Phuket Province, Thailand]. Syntypes ZMB/Moll 34164 (2 shells; Fig. 2B) ex. Weber collection from Salanga [Phuket Province, Thailand].

Other material examined. Myanmar-Southern. Buddha Cave, Lenya City, Tanintharyi Region, 11°13'46.2"N, 99°10'34.3"E: CUMZ 15254 (1 preserved specimen). **Thailand. Salanga** [Phuket Province, Thailand]: ZMB/Moll 75765 (1 shell) ex. Webb collection, ZMB/Moll 88249 (1 shell) ex. Kammaun collection, SMF 179828/2 (2 shells; Fig. 2C), SMF 179829/2 (2 shells) ex. Möllendorff collection, NHMUK 1883.3.27.4 (1 shell). **Phuket:** Bang Pae Waterfall, Thalang District, 8°02'21.9"N, 98°23'27.8"E: CUMZ 15077 (4 shells and 4 preserved specimens; Fig. 2D), 15161 (3 shells). **Chumphon:** Tham Nam Lod Thepnimit Bureau of Monks, Sawi District, 10°22'37.8"N, 99°00'41.2"E: CUMZ 15157 (2 shells). Wat Tham Sanook, Mueang District, 10°28'51.4"N, 99°04'28.3"E: CUMZ 15156 (1 shell). Area in Pak Song, Phato District, 9°46'10.8"N, 98°40'42.9"E: CUMZ 15255 (1 preserved specimen). **Ranong:** Near Wat Pa Thung Rong, Kapoe District, 9°37'00.2"N, 98°37'52.3"E: CUMZ 15256 (2 preserved specimens). **Phang-nga:** Wat Khiriwong (Tham Kob), Thap Put District, 8°31'55.9"N, 98°34'38.4"E: CUMZ 15163 (1 shell). Wat Pa Dok Daeng, Takua Pa District, 8°44'28.6"N, 98°18'24.3"E: CUMZ 15151 (3 shells and 3 preserved specimens; Fig. 2F). Ton Phrai Waterfall, Thai Mueang District, 8°26'10.4"N, 98°18'33.3"E: CUMZ 15150 (1 shell and 2 preserved specimens). Nature study route 1 in Ko Surin Nuea, Khura Buri District, 9°27'01.1"N, 97°52'39.1"E: CUMZ 15164 (1 shell). Nature study route 4 in Ko Surin Nuea, Khura Buri District, 9°25'46.3"N, 97°52'14.0"E: CUMZ 15152 (2 preserved specimens). Nature study route 3 in Ko Surin Tai, Khura Buri District, 9°23'48.2"N, 97°52'02.8"E: CUMZ 15162 (2 shells). **Surat Thani:** Nature trail at Ratchaprapha Dam, Ban Ta Khun District, 8°58'19.1"N, 98°48'16.7"E: CUMZ 15154 (29 shells). Area in Khiri Rat Nikhom District, 9°04'13.1"N, 98°59'45.6"E: CUMZ 15153 (8 shells; Fig. 2E). Area near Anurak Community Lodge, Klong Sok, Phanom District, 8°53'05.6"N, 98°41'12.6"E: CUMZ 15076 (2 preserved specimens). **Nakhon Si Thammarat:** Area in Khao Noi, Sichon District, 8°56'17.3"N, 99°48'54.7"E: CUMZ 15155 (1 shell). **Krabi:** Toh Chong Toh Yuan Shrine, Ao Luek District, 8°22'25.5"N, 98°44'09.7"E: CUMZ 15160 (1 shell). **Trang:** Khao Ting Cave, Palian District, 7°09'32.3"N, 99°48'10.3"E: CUMZ 15158 (1 shell).

Table 3. Estimates of evolutionary divergence between *Janbinmorpha* gen. nov. and other genera based on uncorrected *p*-distance of COI gene fragment sequences.

Genera	01	02	03	04	05	06	07	08	09	10	11	12	13	14	15	16	17	18	19	20	21	22	23
01 *Janbinmorpha*	–																						
02 *Cryptozona*	0.138	–																					
03 *Hemiplecta*	0.126	0.118	0.080																				
04 *Megaustenia*	0.145	0.124	0.136	0.098																			
05 *khasiella*	0.128	0.115	0.112	0.133	–																		
06 *Macrochlamys*	0.141	0.129	0.131	0.136	0.113	0.133																	
07 *Sarika*	0.130	0.134	0.122	0.137	0.102	0.121	0.05																
08 *Taphrenalla*	0.122	0.116	0.110	0.134	0.094	0.118	0.116	0.05															
09 *Parmarion*	0.148	0.146	0.136	0.142	0.123	0.135	0.128	0.124	–														
10 *Aenigmatoconcha*	0.131	0.128	0.139	0.143	0.130	0.133	0.124	0.125	0.139	–													
11 *Chalepotaxis*	0.156	0.148	0.150	0.159	0.118	0.145	0.145	0.144	0.145	0.127	–												
12 *Durgella*	0.148	0.161	0.134	0.159	0.131	0.138	0.133	0.136	0.142	0.147	0.157	–											
13 *Sophina*	0.157	0.141	0.139	0.155	0.126	0.153	0.132	0.137	0.127	0.142	0.142	0.144	-										
14 *Quantula*	0.147	0.141	0.137	0.138	0.140	0.144	0.147	0.133	0.137	0.145	0.150	0.157	0.150	–									
15 *Phuphania*	0.144	0.144	0.134	0.143	0.133	0.141	0.136	0.133	0.142	0.145	0.147	0.140	0.166	0.125	–								
16 *Geotrochus*	0.170	0.172	0.167	0.179	0.159	0.170	0.156	0.161	0.171	0.143	0.165	0.163	0.165	0.185	0.179	0.049							
17 *Siamoconus*	0.129	0.124	0.134	0.139	0.134	0.137	0.143	0.126	0.134	0.131	0.147	0.143	0.163	0.146	0.150	0.147	0.031						
18 *Trochomorpha*	0.168	0.161	0.151	0.151	0.146	0.155	0.152	0.146	0.152	0.154	0.149	0.159	0.174	0.161	0.157	0.171	0.136	0.128					
19 *Videna*	0.153	0.140	0.131	0.135	0.124	0.133	0.129	0.118	0.151	0.141	0.135	0.153	0.157	0.138	0.138	0.174	0.135	0.121	–				
20 *Oxychilus*	0.173	0.146	0.155	0.167	0.159	0.175	0.169	0.153	0.156	0.157	0.171	0.171	0.151	0.168	0.174	0.195	0.175	0.173	0.171	–			
21 *Vitrina*	0.160	0.149	0.151	0.158	0.144	0.168	0.147	0.148	0.153	0.144	0.166	0.151	0.153	0.166	0.160	0.173	0.151	0.162	0.168	0.156	–		
22 *Meghimatium*	0.215	0.218	0.202	0.215	0.202	0.217	0.195	0.205	0.214	0.189	0.221	0.214	0.214	0.232	0.208	0.210	0.203	0.218	0.225	0.214	0.191	–	
23 *Arion*	0.223	0.205	0.219	0.222	0.205	0.207	0.185	0.202	0.215	0.194	0.211	0.203	0.198	0.218	0.212	0.199	0.208	0.207	0.214	0.234	0.224	0.214	–

Table 4. Estimates of evolutionary divergence between *Janbinmorpha* gen. nov. and other genera based on uncorrected *p*-distance of 16S gene fragment sequences.

Genera	01	02	03	04	05	06	07	08	09	10	11	12	13	14	15	16	17	18
01 *Janbinmorpha*	–																	
02 *Cryptozona*	0.178	–																
03 *Hemiplecta*	0.118	0.164	0.068															
04 *Megaustenia*	0.140	0.176	0.136	0.089														
05 *khasiella*	0.126	0.193	0.139	0.156	–													
06 *Macrochlamys*	0.153	0.188	0.158	0.173	0.149	0.167												
07 *Sarika*	0.145	0.199	0.136	0.132	0.141	0.166	0.069											
08 *Taphrenalla*	0.132	0.171	0.127	0.168	0.123	0.151	0.138	0.026										
09 *Parmarion*	0.149	0.184	0.165	0.173	0.192	0.187	0.165	0.173	–									
10 *Aenigmatoconcha*	0.126	0.183	0.146	0.142	0.149	0.159	0.155	0.162	0.175	–								
11 *Durgella*	0.177	0.201	0.156	0.165	0.185	0.189	0.161	0.197	0.187	0.163	–							
12 *Sophina*	0.184	0.202	0.155	0.165	0.176	0.197	0.171	0.196	0.182	0.145	0.122	–						
13 *Quantula*	0.183	0.180	0.170	0.206	0.183	0.209	0.206	0.169	0.170	0.208	0.211	0.208	–					
14 *Phuphania*	0.187	0.162	0.182	0.206	0.187	0.190	0.207	0.184	0.178	0.203	0.234	0.206	0.128	–				
15 *Geotrochus*	0.191	0.227	0.200	0.207	0.218	0.206	0.208	0.201	0.210	0.200	0.249	0.225	0.189	0.176	0.082			
16 *Siamoconus*	0.216	0.218	0.232	0.227	0.227	0.222	0.225	0.223	0.211	0.216	0.228	0.236	0.188	0.206	0.217	0.024		
17 *Trochomorpha*	0.240	0.272	0.242	0.250	0.247	0.242	0.245	0.231	0.249	0.249	0.268	0.256	0.258	0.236	0.212	0.252	0.179	
18 *Videna*	0.196	0.223	0.207	0.222	0.209	0.215	0.219	0.204	0.222	0.222	0.255	0.237	0.189	0.174	0.201	0.206	0.212	–

Table 5. Estimates of evolutionary divergence between *Janbinmorpha* gen. nov. and other genera based on uncorrected *p*-distance of 28S gene fragment sequences.

Genera	01	02	03	04	05	06	07	08	09	10	11	12	13	14	15	16
01 *Janbinmorpha*	–															
02 *Ariophanta*	0.041	0.022														
03 *Cryptozona*	0.060	0.048	–													
04 *Euplecta*	0.044	0.027	0.034	–												
05 *Hemiplecta*	0.027	0.053	0.070	0.059	0.005											
06 *Maelamaodiscus*	0.030	0.046	0.065	0.054	0.042	–										
07 *Mariaella*	0.058	0.057	0.068	0.057	0.061	0.061	–									
08 *Megaustenia*	0.040	0.031	0.047	0.028	0.049	0.046	0.053	0.006								
09 *Ratnadvipia*	0.047	0.030	0.038	0.021	0.058	0.051	0.053	0.029	–							
10 *khasiella*	0.047	0.053	0.064	0.055	0.056	0.045	0.064	0.046	0.058	-						
11 *Macrochlamys*	0.057	0.061	0.073	0.064	0.071	0.058	0.067	0.056	0.065	0.059	0.049					
12 *Sarika*	0.038	0.055	0.069	0.058	0.045	0.046	0.063	0.051	0.057	0.036	0.058	0.002				
13 *Taphrenalla*	0.033	0.042	0.055	0.047	0.040	0.041	0.056	0.034	0.048	0.018	0.050	0.032	0.006			
14 *Varadia*	0.051	0.053	0.060	0.057	0.056	0.054	0.062	0.053	0.058	0.066	0.065	0.063	0.055	–		
15 *Parmarion*	0.041	0.050	0.062	0.050	0.042	0.053	0.049	0.046	0.052	0.054	0.062	0.044	0.042	0.056	–	
16 *Aenigmatoconcha*	0.060	0.058	0.076	0.061	0.074	0.061	0.058	0.055	0.058	0.058	0.059	0.059	0.053	0.066	0.054	–
17 *Chalepotaxis*	0.060	0.059	0.064	0.053	0.072	0.057	0.051	0.052	0.043	0.064	0.061	0.065	0.057	0.056	0.060	0.036
18 *Durgella*	0.047	0.044	0.056	0.044	0.063	0.049	0.053	0.035	0.041	0.051	0.064	0.059	0.046	0.051	0.054	0.038
19 *Eurychlamys*	0.058	0.062	0.072	0.057	0.063	0.061	0.058	0.055	0.058	0.060	0.069	0.067	0.057	0.066	0.054	0.038
20 *Fastosarion*	0.062	0.069	0.082	0.069	0.075	0.067	0.060	0.061	0.062	0.068	0.067	0.068	0.059	0.073	0.053	0.039
21 *Satiella*	0.054	0.053	0.060	0.048	0.061	0.049	0.051	0.042	0.049	0.053	0.056	0.057	0.050	0.051	0.053	0.034
22 *Sophina*	0.047	0.048	0.052	0.044	0.058	0.049	0.062	0.042	0.045	0.049	0.058	0.053	0.044	0.047	0.054	0.039
23 *Quantula*	0.082	0.077	0.103	0.084	0.082	0.093	0.094	0.078	0.084	0.082	0.098	0.090	0.076	0.091	0.083	0.087
24 *Phuphania*	0.075	0.075	0.087	0.076	0.077	0.080	0.087	0.075	0.082	0.072	0.090	0.071	0.061	0.082	0.071	0.084
25 *Geotrochus*	0.054	0.062	0.078	0.059	0.075	0.068	0.077	0.063	0.067	0.069	0.082	0.067	0.057	0.073	0.056	0.081
26 *Siamoconus*	0.054	0.049	0.066	0.040	0.068	0.067	0.060	0.048	0.049	0.056	0.069	0.061	0.053	0.069	0.050	0.068
27 *Trochomorpha*	0.064	0.063	0.073	0.058	0.089	0.076	0.079	0.056	0.064	0.073	0.084	0.071	0.069	0.070	0.070	0.078
28 *Videna*	0.074	0.074	0.084	0.063	0.084	0.088	0.095	0.058	0.074	0.086	0.100	0.087	0.080	0.084	0.085	0.096
29 *Oxychilus*	0.058	0.060	0.076	0.059	0.075	0.056	0.075	0.055	0.060	0.066	0.069	0.065	0.057	0.069	0.060	0.077
30 *Vitrina*	0.060	0.051	0.058	0.044	0.075	0.069	0.065	0.057	0.056	0.069	0.075	0.070	0.061	0.064	0.054	0.073
31 *Meghimatium*	0.086	0.077	0.094	0.084	0.106	0.099	0.090	0.089	0.088	0.092	0.101	0.093	0.088	0.083	0.088	0.105
32 *Arion*	0.064	0.073	0.082	0.071	0.080	0.079	0.083	0.068	0.077	0.072	0.085	0.069	0.071	0.070	0.080	0.092

Table 5. Continued.

Genera	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32
01 *Janbinmorpha*																
02 *Ariophanta*																
03 *Cryptozona*																
04 *Euplecta*																
05 *Hemiplecta*																
06 *Maelamaodiscus*																
07 *Mariaella*																
08 *Megaustenia*																
09 *Ratnadvipia*																
10 *khasiella*																
11 *Macrochlamys*																
12 *Sarika*																
13 *Taphrenalla*																
14 *Varadia*																
15 *Parmarion*																
16 *Aenigmatoconcha*																
17 *Chalepotaxis*	–															
18 *Durgella*	0.028	–														
19 *Eurychlamys*	0.047	0.043	–													
20 *Fastosarion*	0.045	0.051	0.032	–												
21 *Satiella*	0.026	0.026	0.039	0.045	–											
22 *Sophina*	0.038	0.034	0.043	0.049	0.030	–										
23 *Quantula*	0.094	0.089	0.104	0.099	0.082	0.087	–									
24 *Phuphania*	0.084	0.084	0.099	0.092	0.084	0.077	0.043	–								
25 *Geotrochus*	0.081	0.075	0.083	0.077	0.073	0.077	0.061	0.057	0							
26 *Siamoconus*	0.069	0.062	0.069	0.073	0.064	0.068	0.093	0.084	0.071	0						
27 *Trochomorpha*	0.073	0.063	0.081	0.082	0.070	0.080	0.105	0.095	0.074	0.066	0.026					
28 *Videna*	0.089	0.079	0.098	0.100	0.084	0.093	0.093	0.088	0.087	0.078	0.036	–				
29 *Oxychilus*	0.073	0.064	0.077	0.081	0.071	0.062	0.091	0.077	0.071	0.064	0.078	0.093	–			
30 *Vitrina*	0.071	0.064	0.066	0.079	0.064	0.054	0.098	0.094	0.069	0.065	0.083	0.097	0.064	–		
31 *Meghimatium*	0.100	0.092	0.100	0.103	0.100	0.094	0.139	0.124	0.099	0.089	0.102	0.116	0.099	0.077	–	
32 *Arion*	0.085	0.079	0.085	0.089	0.085	0.073	0.121	0.107	0.085	0.076	0.088	0.102	0.079	0.071	0.063	–

Diagnosis. Shell depressed and lenticular; body whorl keeled on periphery; surface with prominent radial ribs and reticulated microsculptures; whorls 6 and increasing regularly; aperture obliquely crescent-shaped with simple peristome; umbilicus open and funnel shaped. Animal dark gray with pigmentation of yellow to orange dots or patches; one stripe at middle of body running from anterior to posterior; three dorsal lobes present; foot tripartite; caudal foss present; caudal horn very reduced. Genitalia having very short flagellum; two bundles of penial retractor muscle; epiphallic sheath thickened and entirely covering proximal epiphallus; gametolytic duct absent; gametolytic sac having two lobes; dart apparatus present.

Description. ***Shell*** (Figs 2, 3A–D). Shell dextral, depressed, lenticular, medium-sized (shell width up to 19.8 mm, shell height up to 9.3 mm), thickened, rather opaque, yellowish brown to dark brownish. Embryonic shell about 2½ whorls, with raised growth lines forming riblet-like textures (Fig. 3A, B). Whorls 6, convex, regularly increasing, separated by shallow suture. Later

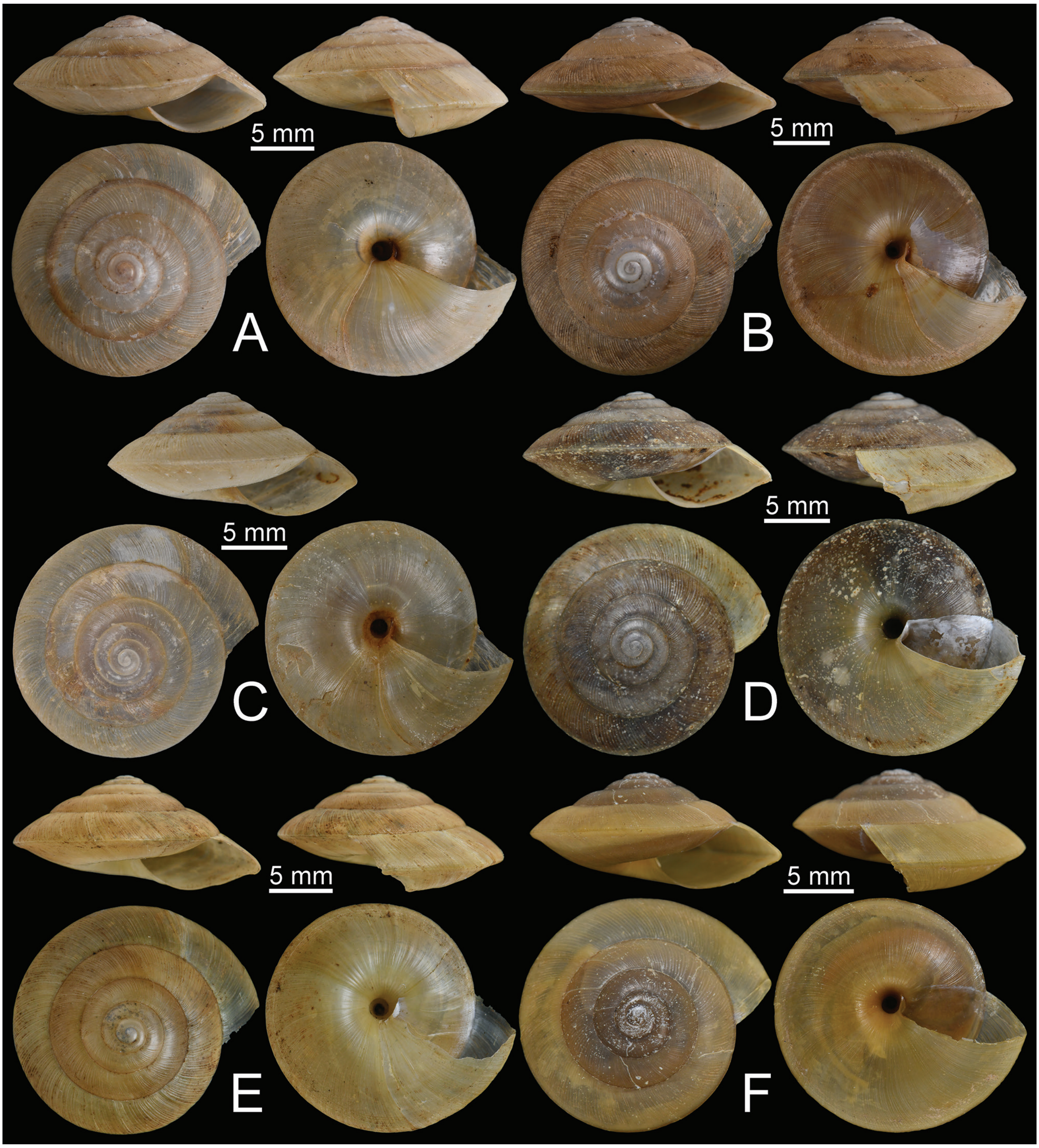

Figure 2. Shell of *Janbinmorpha sculpticarina* (Martens, 1883), comb. nov. **A.** Syntype from Salanga [Phuket Province]: ZMB/Moll 58132; **B.** Syntypes from Salanga [Phuket Province]: ZMB/Moll 34164; **C.** Specimen from Salanga I., Malaysia [Phuket Island, Phuket Province, Thailand]: NHMUK 1888.3.27.4; **D.** Specimen from Phuket Province: CUMZ 15077; **E.** Specimen from Surat Thani Province: CUMZ 15153; **F.** Specimen from Phang-nga Province: CUMZ 15151 using for SEM imaging.

whorls distinct, regular, curved radial ribs, with fine, widely regularly spaced radial ribs, with reticulated microsculptures; and 4–5 distinct spiral threads close to the periphery, positioned above the radial ribs (Fig. 3C, D). Last whorl distinctly angular, compressed at periphery, and moderately convex below periphery. Spire rather elevated. Aperture obliquely crescent-shaped; peristome simple; columellar margin simple and slightly reflected near umbilicus. Umbilicus opened, deep, slightly less than one-third the width of the last whorl from the bottom view of the shell.

Genitalia (Fig. 4). Atrium (at) enlarged and short. Penis (p) enlarged and short cylindrical. Inner wall sculptured with small, curly and closely packed oblique penial pilasters extending through entire penis chamber; penial verge absent; junction between penis and epiphallus thickened (Fig. 4B). Epiphallus (e) long cylindrical tube: proximal epiphallus longer than penis and vagi-

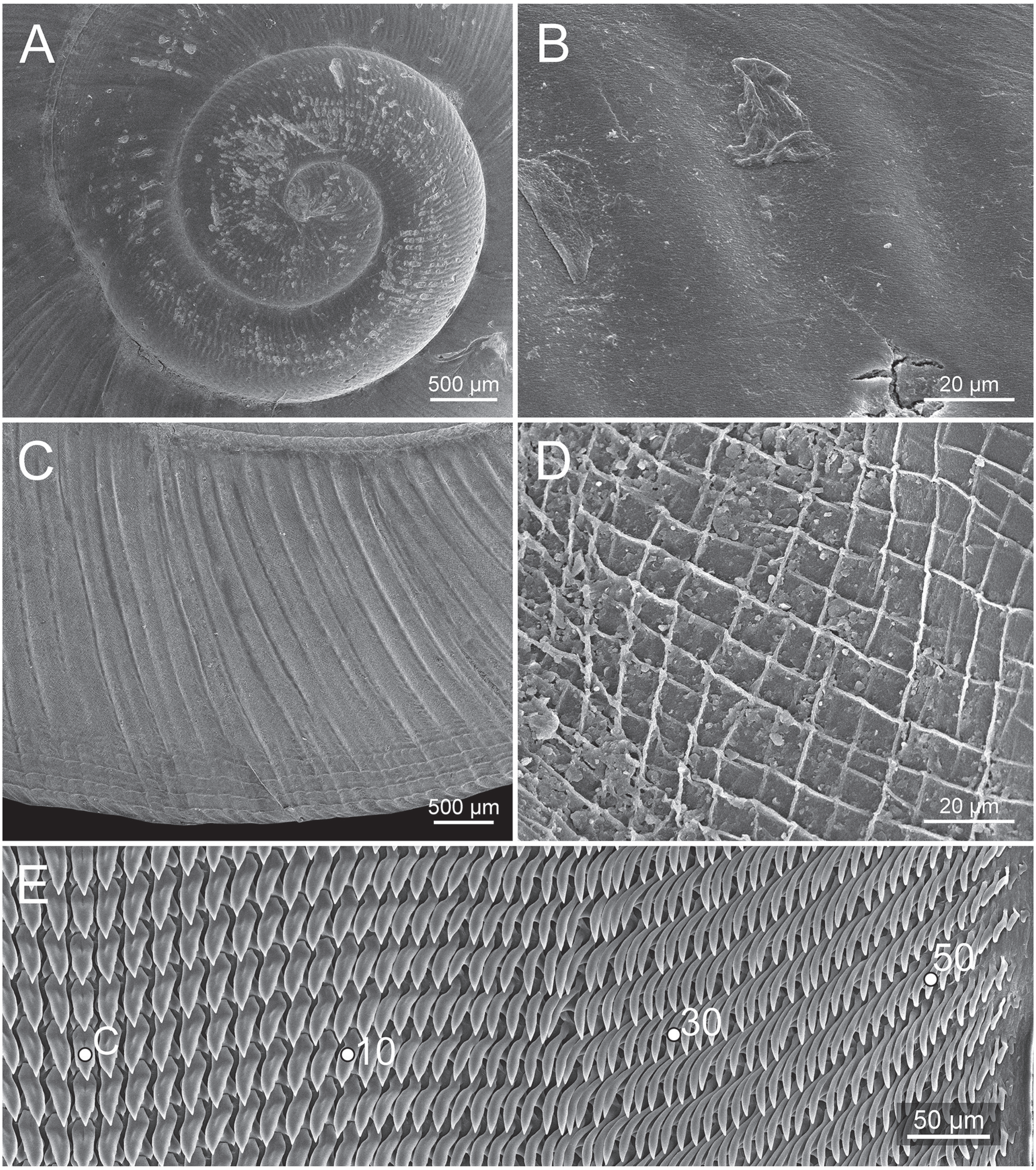

Figure 3. Scanning electron microscope (SEM) images of shell surface and radula of *Janbinmorpha sculpticarina* (Martens, 1883), comb. nov. **A–D.** Specimen CUMZ 15151, showing shell surface; **A.** Protoconch viewed from above; **B.** Zoomed-in view of protoconch; **C.** Body whorl viewed from above; **D.** Zoomed-in view of body whorl; **E.** Specimen CUMZ 15077, showing radula; central tooth indicated by 'C'.

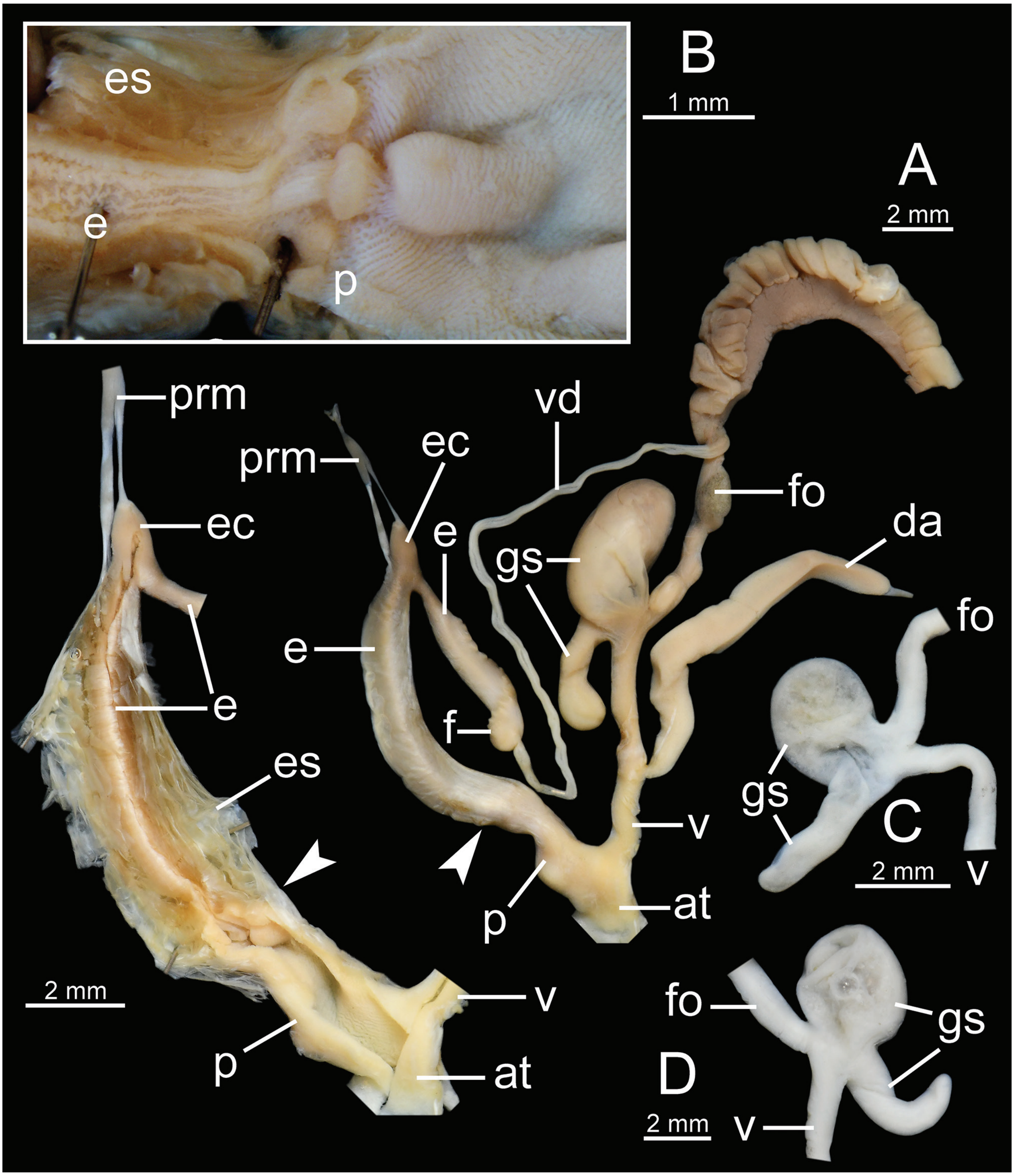

Figure 4. Genitalia of *Janbinmorpha sculpticarina* (Martens, 1883), comb. nov. **A.** Specimen from Surat Thani Province: CUMZ 15076, showing general view of genital system; **B.** Specimen from Phang-nga Province: CUMZ 15150, showing internal structure of penis and epiphallus; **C.** Specimen from Phuket Province: CUMZ 15077, showing gametolytic organ; **D.** Specimen from Phang-nga Province: CUMZ 15150, showing gametolytic organ. White arrowhead indicates the end of the penis.

na, and encircled with thickened epiphallic sheath (es); distal epiphallus smaller diameter than proximal part. Epiphallic caecum (ec) large, straight, and located near middle of epiphallus. Penial retractor muscle (prm) rather thickened and divided into two bundles: one bundle attached to tip of epiphallic caecum and another bundle attached to distal end of epiphallic sheath (Fig. 4A). Flagellum (f) very short or nearly absent. Vas deferens (vd) small tube continuing from free oviduct to near distal tip of epiphallus.

Vagina (v) long cylindrical tube, about two times penis length. Dart apparatus slender, long and located on mid-vaginal length. Gametolytic organ with undistinguished duct; gametolytic sac (gs) divided into two lobes separated at base: one large and bulbous shape, and another small and long-slender tube (Fig. 4A, C, D). Free

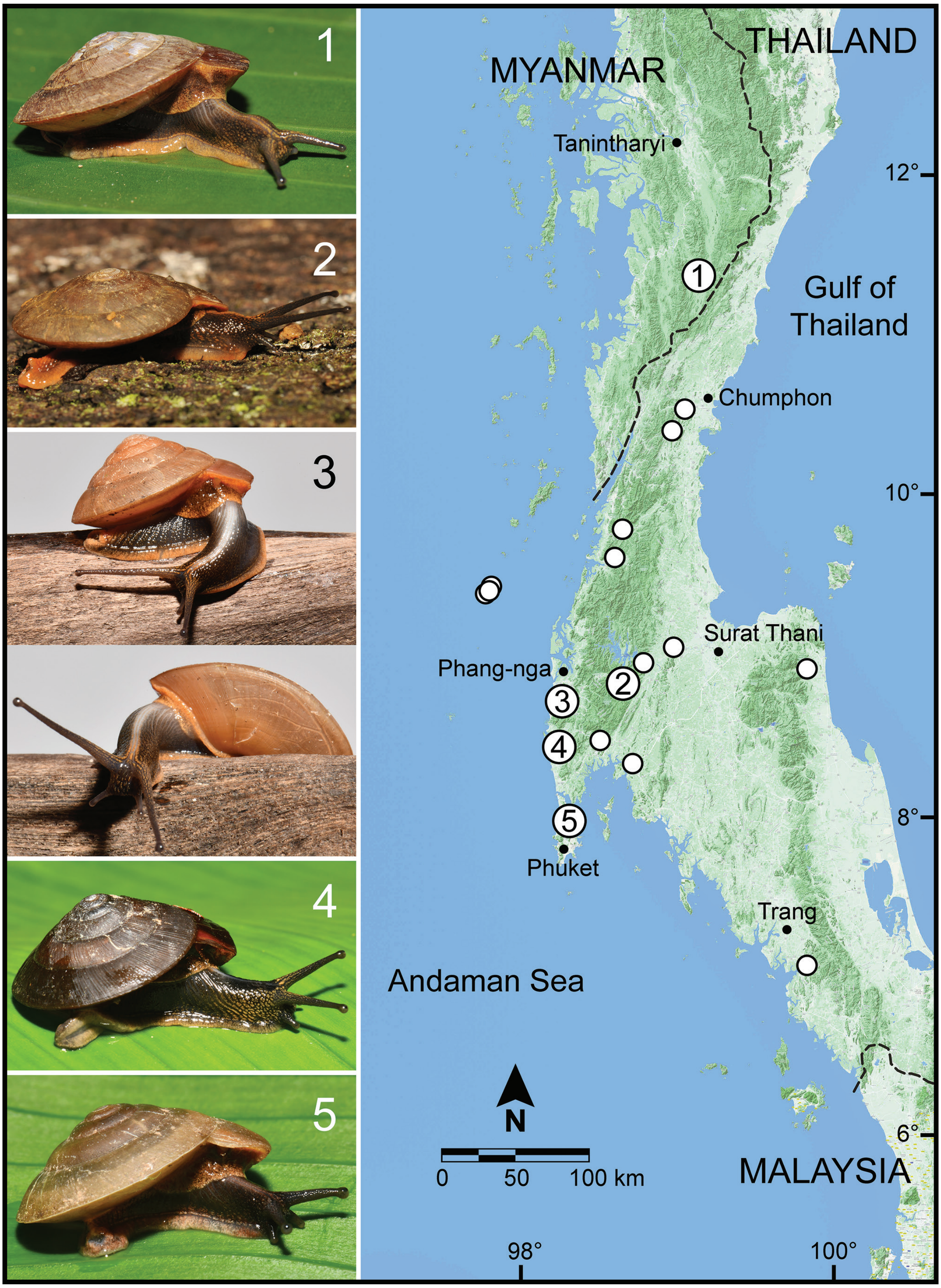

Figure 5. Map of the Malay Peninsula in southern Thailand and the southernmost tip of Myanmar showing the sampling sites. Localities where the living specimens were collected are indicated by numbers on map, not to scale.

oviduct (fo) long cylindrical, approximately as long as vagina length. Oviduct enlarged with lobules; prostate gland bound to oviduct.

Radula (Fig. 3E). Teeth arranged in a wide-angle U-shape with half-row formula: 1–(11–15)–56. Central tooth relatively symmetrical tricuspid; mesocone large and triangular shape with pointed cusp; ectocones very small with dull cusp. Lateral teeth unicuspid or asymmetrical bicuspid with mesocone large with pointed cusp and ectocone nearly wanting with dull cusp. Lateral teeth larger than marginal teeth. Marginal teeth starting at approximately row number 11 to 15 with obliquely elongate unicuspid form; outermost teeth narrower and shorter than inner teeth.

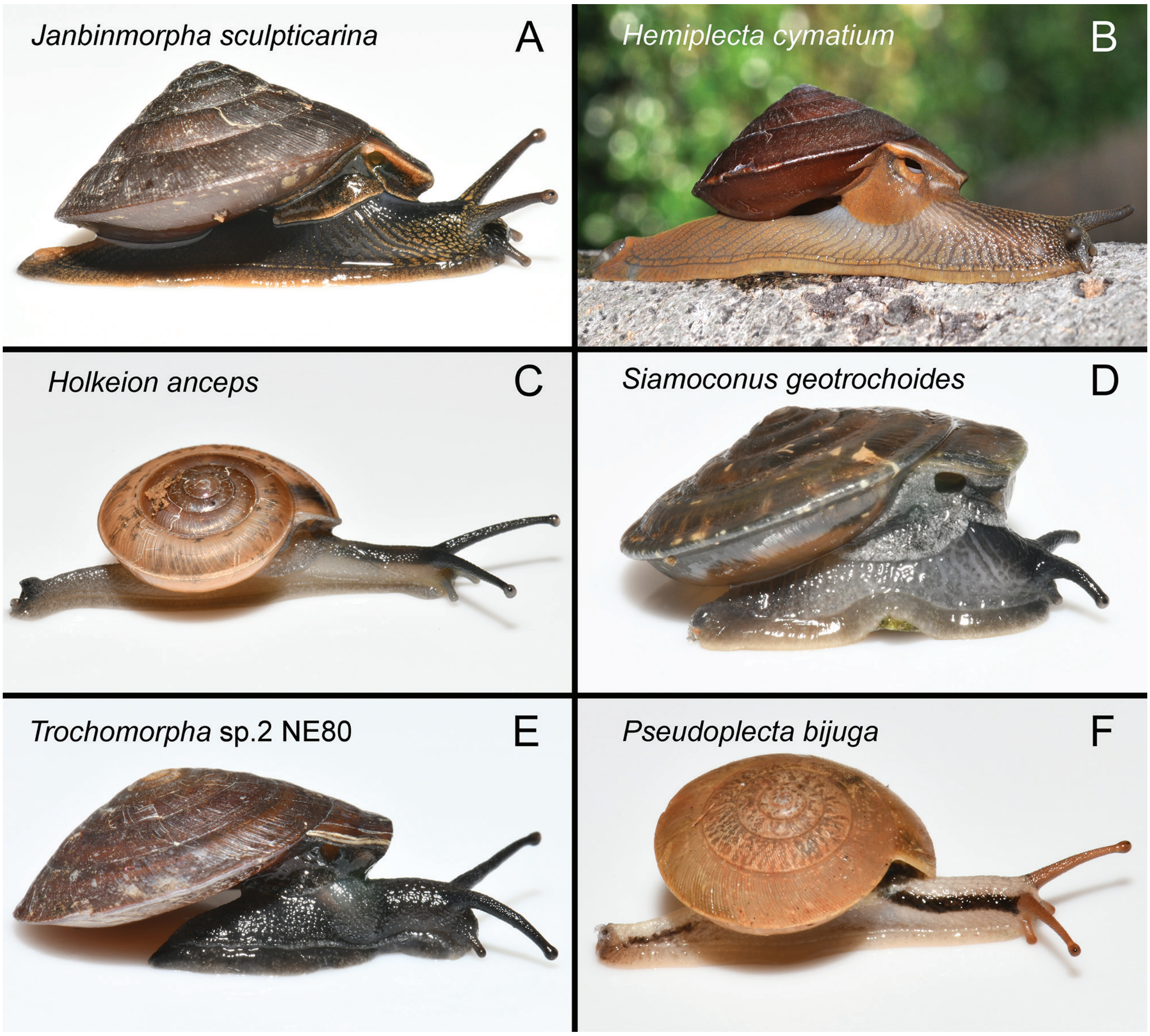

Figure 6. Representative living limacoid snails with a depressed trochiform shell from Thailand and the Malay Peninsula. **A.** *Janbinmorpha sculpticarina* (Martens, 1883), comb. nov. in the Ariophantidae; **B.** *Hemiplecta cymatium* (Pfeiffer, 1856) in the Ariophantidae; **C.** *Holkeion anceps* (Gould, 1843) in the Ariophantidae; **D.** *Siamoconus geotrochoides* Pholyotha, 2023 in the Euconulidae; **E.** *Trochomorpha* sp.2 in the Trochomorphidae; **F.** *Pseudoplecta bijuga* (Stoliczka, 1873) in the Dyakiidae.

External features (Figs 1, 5, 6A). Living snails with dark gray body and more or less distinct pale milky or yellow to orange stripe running from head to caudal horn; entire animal with pigmentation of yellow to orange dots or patches. Eye stalks long and pale blackish; lower tentacles shorter and paler in colour. Mantle lobes or mantle extensions well developed, crescent-shaped, yellow to orange, divided into three dorsal lobes, and somewhat thickened near their margins. Right dorsal lobe prominent, broadly crescent-shaped, and larger than both anterior and posterior left dorsal lobes. Anterior left dorsal lobe broadly crescent-shaped; posterior left dorsal lobe relatively long crescent-shaped. Sole evenly tripartite, pedal groove very strong. Foot margin yellow to orange. Caudal foss cup-shaped; caudal horn very reduced, short, not overhung, and yellow to orange.

Distribution. (Fig. 5). This species is apparently restricted to the southern peninsula of Thailand. Major populations of *J. sculpticarina* comb. nov. occur in the Phuket Range, while a few populations can be found in Nakhon Si Thammarat and the southern part of the Tenasserim ranges. This species was also recorded from the Pulau Aur Island, Malaysia (Basch and Solem 1971), but this record needs to be confirmed with the newly collected specimens.

Remarks. According to the limacoid snails with a depressed trochiform shell from Thailand and the Malay Peninsula, *Janbinmorpha sculpticarina* comb. nov. (Fig. 6A) is conchologically similar to some helicarionoidean species, for example *Hemiplecta cymatium* (Pfeiffer, 1856) (Fig. 6B) and *Holkeion anceps* (Gould, 1843) (Fig. 6C), and is also similar to some trochomorphoidean species, such as *Siamoconus geotrochoides* Pholyotha in Pholyotha et al. 2023a (Fig. 6D), *Trochomorpha* sp.2 (Fig. 6E), and *Pseudoplecta bijuga* (Stoliczka, 1873) (Fig. 6F). However, *J. sculpticarina* comb. nov. can be distinguished by its genitalia in having two lobes of the gametolytic sac, no gametolytic duct, and a penial retractor muscle attached to the epiphallic caecum and epiphallic sheath. In comparison, *Hemiplecta cymatium* possesses a bulbous gametolytic sac, no gametolytic duct, and a penial retractor muscle attached to epiphallic caecum only (Sutcharit and Panha, unpublished data), while *Holkeion anceps* has an elongate gametolytic duct and a penial retractor muscle attached to the epiphallic caecum (Pholyotha et al. 2023b). The trochomorphoideans, *S. geotrochoides* and *Trochomorpha* sp.2 differ by having a long gametolytic duct and a penial retractor muscle attached to the epiphallus (Pholyotha et al. 2023a; Pholyotha and Panha, unpublished data). In addition, *P. bijuga* possesses a gametolytic organ located on the amatorial organ and a penial retractor muscle attached to the epiphallus (Jirapatrasilp et al. 2021).

Compared with other taxa having a depressed trochiform shell, and regardless of genitalia data, *J. sculpticarina* comb. nov. differs from *Trochomorpha* species and *Videna* species recorded from mainland Southeast Asia by a combination of no spiral band, larger shell size, relatively narrower umbilicus, and strong radial striations with reticulated microsculptures (Möllendorff 1902; Preece et al. 2022; Inkhavilay et al. 2023).

Trochomorpha benigna (Pfeiffer, 1863), *T. vinhensis* Thach, 2018 and *T. buotia* Inkhavilay et al., 2023 are very similar to *J. sculpticarina* comb. nov. in terms of shell shape and size. For comparison, *J. sculpticarina* comb. nov. has a narrower funnel-shaped umbilicus, while *T. benigna* and *T. vinhensis* have a wider funnel-shaped umbilicus and showing all preceding whorls (Inkhavilay et al. 2023). Compared with *T. buotia*, *J. sculpticarina* comb. nov. has radial striations and reticulated microsculptures on shell surface, depressed shell, a strong peripheral keel, and last whorl convex below periphery, while *T. buotia* has radial and spiral striations on the shell surface, a dome-shaped shell, distinctly sharpened peripheral keel, and last whorl flattened below periphery (Inkhavilay et al. 2023).

Discussion

Mainland Southeast Asia harbours a taxonomically diverse, overwhelmingly endemic fauna of limacoid snails, especially in the Helicarionoidea (e.g., Ariophantidae and Helicarionidae) and Trochomorphoidea (e.g., Dyakiidae, Euconulidae, and Trochomorphidae). Confusion in classification and identification of these limacoid snails has happened multiple times because there is a morphological convergence of shell shape; previously, most taxonomists or other researchers based their decisions only on shell morphology (Panha 1996; Hemmen and Hemmen 2001; Maassen 2001; Inkhavilay et al. 2019; Pholyotha et al. 2020, 2021a, c, 2022a, 2023c; Sutcharit et al. 2020b; Sutcharit and Panha 2021). The present study is an example of the long-standing taxonomic confusion that has existed since the works of Martens (1883) and Maassen (2001) were published. Prior to this study, *J. sculpticarina* comb. nov. had been assigned to either *Trochomorpha* or *Videna* in the Trochomorphidae. However, in this study, we have considered that general characters of *J. sculpticarina* comb. nov. are similar to those of *Hemiplecta* species in the Ariophantidae. The similarities include shell with an opened and deep umbilicus, animal with a reduced caudal horn and no shell lobe, genitalia with an absence of gametolytic duct and the presence of long dart apparatus and short flagellum (Sutcharit and Panha 2021).

The close relationship of *Janbinmorpha* gen. nov. and *Hemiplecta* is not only evident from their closely similar body features and reproductive anatomy, but also is evident from the molecular data. However, the significant differences in some genital traits and the amount of genetic variation among mitochondrial and nuclear gene sequences are indicative of the distinct lineages within the Ariophantidae. Our molecular phylogenetic analysis confirms that *Janbinmorpha* gen. nov. is a genetically well-supported clade that is grouped together with the ariophantid genera *Hemiplecta* and *Maelamaodiscus*, but the relationships among them remain only partially resolved. However, the genitalia of *Maelamaodiscus* are rather distinct from *Janbinmorpha* gen. nov. and *Hemiplecta* by the presence of a long flagellum and long gametolytic duct (Sutcharit and Pholyotha 2023). Although the relationships within the limacoid snails, especially the Ariophantidae, are not resolved, *Janbinmorpha* gen. nov. is not grouped with the Trochomorphidae. In this study, the monophyly of the Trochomorphidae is confirmed and includes both genera *Trochomorpha* and *Videna*. Therefore, we conclude that molecular and morphological data support *J. sculpticarina* comb. nov. as a member of the Ariophantidae instead of the Trochomorphidae.

Regarding the helicarionoidean snails, we also have pointed out unresolved aspects of molecular phylogenetics of the mainland Southeast Asian taxa, which are currently being studied and will continue as a goal moving forward. Our molecular phylogeny reveals that although the phylogenetic relationships within the Helicarionoidea are not resolved, all taxa assigned to the Helicarionidae always form a monophyletic clade. For the ariophantid lineages, despite the completely unresolved evolutionary relationships, we have found that there are at least two major clades of the Ariophantidae. The first major group includes the Indian taxa of *Ariophanta*, *Cryptozona*, *Euplecta*, *Ratnadvipia* and the Southeast Asian taxa of *Megaustenia*, while the second major group includes the Southeast Asian taxa of *Sarika*, *Khasiella*, *Taphrenalla*, *Macrochlamys*, *Hemiplecta*, *Maelamaodiscus*, and *Janbinmorpha* gen. nov. However, understanding phylogenetic relationships within this group is beyond the scope of this paper, and we suggest that more molecular data, especially the data of the type taxa of each genus from Asia as well as Australia and Africa, are needed to resolve the relationships within the Helicarionoidea.

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