Reassessment and systematic position of the sinistral snails of genus *Hemiplecta* from Thailand (Eupulmonata: Ariophantidae), with description of two new species

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Abstract

Indochina land snails of the family Ariophantidae are in need of thorough systematic revision. Here we comprehensively revise the systematics of the large-shelled, sinistral (counterclockwise) coiling snails from Thailand and Peninsular Malaysia. Molecular phylogeny based on mitochondrial (COI and 16S) and nuclear (28S) gene sequences demonstrates that these sinistral snails are not members of Dyakiidae as previously thought, but instead are more closely related to the genus *Hemiplecta* in the family Ariophantidae. Comparative morphology also reveals similarity of reproductive organ features (globular gametolytic organ, well-developed dart apparatus, and lack of amatorial organ complex). Based on this

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evidence, we propose to transfer these sinistral snails to the genus *Hemiplecta*. Molecular phylogenetic analyses further strongly support the monophyly of this sinistral lineage with respect to other members of *Hemiplecta*. This monophyletic clade consists of five members including three species that were previously classified as “*Dyakia*”, *H. lahatensis*, *H. retrorsa* and *H. salangana*, and two new species described herein, *H. ligorica* n. sp. and *H. thailandica* n. sp. This study also suggests that the anatomy of the gametolytic organ in the genus *Hemiplecta* corresponds well with the phylogenetic relationships and appears to be a taxonomically informative character, while the penial verge has little utility for generic recognition.

Keywords

Pulmonata – Dyakiidae – sinistral – endemic species – Indochina

Introduction

Southeast Asia has a diverse land snail fauna, and species vary greatly in size; shell diameter varies from half a millimeter (hypselostomatid; Schileyko, 1998; Páll-Gergely et al., 2015) to nearly seventy millimeters (i.e., ariophantids and dyakiids; Schileyko, 2002, 2003; Sutcharit et al., 2019). Traditionally, land snail classification has relied mainly on shell traits, and to a lesser extent has been based on reproductive anatomy. Several recent systematic studies have revealed considerable plasticity in morphological characteristics, and substantial incongruence between the morphology-based classification and molecular phylogenetic analyses. Such findings fuel the controversy over whether standard taxonomic methods are inadequate, and whether the distinct phylogenetic lineages derived from molecular data could facilitate the task of biological classification (Seberg et al., 2003; Tautz et al., 2003; Dunn, 2003; Hebert & Gregory, 2005; Hirano et al., 2014; Köhler & Criscione, 2015; Pholyotha et al., 2020).

In the present work, we revise the systematics of large-sized helicoid species assigned to the genera *Hemiplecta* Albers, 1850 and *Koratia* Godwin-Austen, 1919 (family Ariophantidae Godwin-Austen, 1883), as well as *Dyakia* Godwin-Austen, 1891 (family Dyakiidae Gude

and Woodward, 1921) from Indochina. The genus *Hemiplecta* is widely distributed from India to Southeast Asia. This genus is characterized by a large shell and by globular shape of the gametolytic sac (Blanford & Godwin-Austen, 1908; Schileyko, 2002, 2015). The genus *Koratia* was treated as a subgenus of *Hemiplecta* by Zilch (1959) and Solem (1966), but was later elevated to genus rank by Schileyko (2002, 2015) based on the absence of a penial verge in the reproductive organ. The genus *Dyakia*, which was described to include several Greater Sunda Islands species, is characterized by both sinistral (counterclockwise) shell and the unique genitalia characters of the amatorial organ complex (Godwin-Austen, 1898; Schileyko 2003; Sutcharit et al., 2012, 2019). Godwin-Austen (1898) was the first to revise the systematics of these snails and found that the sinistral species from the Malay Peninsula (Myanmar and Thailand) exhibit a distinct shape of the radula teeth. Laidlaw (1963) revised the taxonomy of *Dyakia*, but was uncertain about the Malay Peninsula species as they exhibited distinctive morphological character states (sculpturing as spiral wrinkles). Since then, the Southeast Asian helicoid snails with large and sinistral shells have consistently been attributed to the genus *Dyakia* s.l. (e.g., Panha, 1996; Maassen, 2001; Sutcharit et al., 2012).

However, this largely shell-based classification has never been tested in a phylogenetic context. Given that shell characteristics have repeatedly been found to evolve convergently in a wide range of land snail taxa, such a phylogenetic analysis is crucial in creating a natural classification. The recent morphological revision of so-called “*Dyakia*” from Peninsular Malaysia clearly revealed that this grouping was polyphyletic, with *Helix retrorsa* Gould, 1843 and *Nanina salangana* Martens, 1883 found to display genitalia similar to *Hemiplecta* (Sutcharit et al., 2012). This contradiction indicates that most of the shell characteristics vary considerably within the higher taxonomic categories and thus are unreliable for classification. In addition, a large proportion of Indochinese land snail taxa are still known exclusively from their shells. The high similarity of shell morphology does not always indicate a common ancestry, but rather it may frequently reflect convergent evolution related to adaptations to varying environmental conditions (Vermeij, 1993; Hirano et al., 2015; Köhler & Criscione, 2015), predation (Schilthuizen et al., 2006) or competition (Oheimb et al., 2018). Rather than shell features, the characters of the genital anatomy have been shown to be particularly informative for the recognition of taxa in many cases of the stylommatophoran groups, such as in the genera *Macrochlamys* Gray, 1847, *Sarika* Godwin-Austen, 1907 and *Traphospira* Blanford, 1905 (Pholyotha et al., 2018, 2020). Convergent shell features have also been found in many cases among the Australian camaenids (Köhler, 2010, 2011a, b, c, 2012; Köhler & Shea, 2012).

Land snail surveys from southern Thailand and Peninsular Malaysia have yielded a number of the sinistral snails that were preliminarily classified as the genus “*Dyakia*” based on their shell coiling. However, this classification has remained provisional. Better

sampling and more data are needed to determine whether these sinistral species are members of *Hemiplecta* or *Dyakia*. Therefore, the primary objective of this study is to test the correspondence between traditional morphology by means of comparative study of key morphological characters (i.e., shell and genital anatomy) and the monophyletic groups based on molecular phylogeny of these sinistral snails. The proposed taxonomic rearrangement of *Hemiplecta* and *Dyakia* and descriptions of two new species are described herein, along with re-descriptions of the other three nominal species.

Material and methods

Sampling and morphological examination

Snails were sampled throughout eastern to southern Thailand and Peninsular Malaysia (fig. 1). The details of each locality are listed in table 1. Animal use protocol in this study was approved by the Chulalongkorn University Animal Care and Use Committee (CU-ACUC) under the approval number 1723018. Living snails were euthanized by a two-step method following AVMA Guidelines for the Euthanasia of Animals (AVMA, 2013). Foot tissues were cut and stored in 95% ethanol before use for DNA extraction. Other remaining parts were preserved in 70% (v/v) ethanol for anatomical purposes. The genital organs of 3–5 specimens of each species were examined. Radulae were extracted, and examined under Scanning Electron Microscope (JEOL, JSM-5410 LV). The radula shape and teeth formula were analyzed.

Collection abbreviations

CUMZ: Chulalongkorn University Museum of Zoology, Bangkok

NHMUK: The Natural History Museum, London

FIGURE 1 Distribution of the sinistral *Hemiplecta* species examined in this study.

TABLE 1 Samples and GenBank accession numbers for all sequences in the study

Species and localities	Specimen code	Voucher code	Co-ordinates	Accession nos.		
				COI	16S	28S
Ariophantidae						
<i>Hemiplecta ligorica</i> n. sp.						
Tam Lord, Nop Phitam, Nakhon Si Thammarat, Thailand	H28	CUMZ5088	8°47'18.0"N 99°38'39.8"E	MT654596	MT651512	MT651567
Krung Ching Waterfall, Nop Phitam, Nakhon Si Thammarat, Thailand	H59	CUMZ5092	8°43'34.8"N 99°39'58.4"E	MT654597	MT651513	MT651568
Tam Khao Lek, Nop Phitam, Nakhon Si Thammarat, Thailand	H91	CUMZ5087	8°46'08.1"N 99°48'14.7"E	MT654598	MT651514	MT651569
Si Khid Waterfall, Nakhon Si Thammarat, Thailand	H101	CUMZ5254	9°00'52.9"N 99°46'19.6"E	MT654599	MT651515	MT651570
<i>Hemiplecta retrorsa</i> (Gould, 1843)						
Ngao Waterfall, Muang, Ranong, Thailand	H10	CUMZ5255	9°51'21.5"N 98°37'41.8"E	MT654600	MT651516	MT651571
Wat Sathit Khirirom, Khiriat Nikhom, Suratthani, Thailand	H85	CUMZ5020	9°01'48.5"N 98°59'11.9"E	MT654601	MT651517	MT651572
Hot Spring, Muang, Ranong, Thailand	H117	CUMZ5099	9°57'27.9"N 98°39'07.5"E	MT654602	MT651518	MT651573
<i>Hemiplecta salangana</i> (Martens, 1883)						
Bukit Chuping, Perlis, Malaysia	H3	CUMZ5076	6°29'41.5"N 100°16'01.9"E	MT654603	MT651519	MT651574
Sra Morakot, Klong Thom, Krabi, Thailand	H88	CUMZ4980	7°55'32.4"N 99°16'11.4"E	MT654604	MT651520	MT651575
Kaki Bukit, Perlis, Malaysia	H96	CUMZ5256	6°39'46.7"N 100°12'01.1"E	MT654605	MT651521	MT651576
Klong Jak, Koh Lanta, Krabi, Thailand	H109	CUMZ5011	6°42'06.5"N 99°38'46.8"E	MT654606	MT651522	MT651577
Khao Sai, Donsak, Suratthani, Thailand	H115	CUMZ5257	9°12'52.7"N 99°40'09.6"E	MT654607	MT651523	MT651578
<i>Hemiplecta lahatensis</i> (Morgan, 1885)						
Gua Bewah, Kenyir Lake, Terrengganu, Malaysia	H78	CUMZ5258	4°50'43.7"N 102°43'14.6"E	MT654608	MT651524	MT651579

TABLE 1 Samples and GenBank accession numbers for all sequences in the study (Cont.)

Species and localities	Specimen code	Voucher code	Co-ordinates	Accession nos.		
				COI	16S	28S
Gua Matu Madu, Gua Musang, Kelantan, Malaysia	H8o	CUMZ5259/1	4°50'13.4"N 101°56'56.3"E	MT654609	MT651525	MT65158o
<i>Hemiplecta thailandica</i> n. sp.						
Wat Khao Sukim, Tha Mai, Chanthaburi, Thailand	H68	CUMZ5o5o	12°45'48.5"N 102°o1'58.2"E	MT65461o	MT651526	MT651581
Soidao Waterfall, Soidao, Chanthaburi, Thailand	H82	CUMZ5o47	13°o4'48.3"N 102°1o'15.7"E	MT654611	MT651527	MT651582
Klong Narai Waterfall, Chanthaburi, Thailand	H99	CUMZ526o	12°34'59.1"N 102°1o'2o.9"E	MT654612	MT651528	MT651583
Sib-ha Chan Waterfall, Kaeng Hang Maeo, Chanthaburi, Thailand	H1o3	CUMZ5o79	12°53'54.8"N 101°49'oo.8"E	MT654613	MT651529	MT651584
Khao Soi Dao, Chanthaburi, Thailand	H1o6	CUMZ5o49	12°55'19.6"N 102°14'41.8"E	MT654614	MT65153o	MT651585
Makok Waterfall, Khlung, Chanthaburi, Thailand	H112	CUMZ5o51	12°35'15.1"N 102°15'22.3"E	MT654615	MT65153	MT651586
<i>Hemiplecta cymatium</i> (Pfeiffer, 1856)						
Perak, Malaysia	H62	CUMZ5261	5°38'13.4"N 101°42'41.1"E	MT654616	MT651531	MT651587
<i>Hemiplecta distincta</i> (Pfeiffer, 185o)						
Tad Pha Suam, Paksong, Champasak, Laos	H54	CUMZ5267	15°16'35.9"N 1o5°55'21.4"E	MT654617	MT651532	MT651588
<i>Hemiplecta esculenta</i> Maassen, 2oo6						
Tam Chiang Dao, Chiang Dao, Chiang Mai, Thailand	H2	CUMZ5157	19°23'4o.7"N 98°55'41.8"E	MT654618	MT651533	MT651589
<i>Hemiplecta funerea</i> (Smith, 1896)						
Ton Tong Waterfall, Pua, Nan, Thailand	H16	CUMZ4575	19°12'33.4"N 101°o4'14.2"E	MT654619	MT651534	MT65159o
<i>Hemiplecta humphreysiana</i> (Lea, 184o)						
Botanic Garden, Singapore	H7	CUMZ5158	1°18'49.6"N 1o3°48'56.6"E	MT65462o	MT651535	MT651591

Species and localities	Specimen code	Voucher code	Co-ordinates	Accession nos.		
				COI	16S	28S
<i>Hemiplecta pluto</i> (Pfeiffer, 1863)						
Wat Pa Pha, Khamkeut, Bolikhamxay, Laos	H63	CUMZ5266	18°11'16.8"N 104°56'25.5"E	MT654621	MT651536	MT651592
<i>Cryptozona siamensis</i> (Pfeiffer, 1856)						
Wat Tha Mai Lai, Chumphon, Thailand	S129	CUMZ7240	10°29'54.0"N 98°57'16.2"E	MT364992	MT365774	MT365718
<i>Sarika resplendens</i> (Philippi, 1846)						
Khao Cha Ngum, Ratchaburi, Thailand	W4	CUMZ7234	13°43'39.1"N 99°44'38.6"E	MT364982	MT365763	MT365707
<i>Macrochlamys caverna</i> Polyotha & Panha, 2018						
Wat Tham Chang Pueak, Tha Wung, Lopburi, Thailand	C16	CUMZ7111	14°54'05.8"N 100°30'16.6"E	MT364987	MT365760	MT365704
Dyakidae						
<i>Dyakia janus</i> (Beck, 1837)						
Pulau Besar, Johor, Malaysia	H9	CUMZ4918	2°25'48.0"N 103°59'00.6"E	MT654622	MT651538	MT651593
Tioman Island, Malaysia	H57	CUMZ5180	2°48'36.9"N 104°08'46.8"E	MT654623	MT651539	MT651594
<i>Bertia cambojiensis</i> (Reeve, 1860)						
Near Lake, Cat Tien National Park, Dong Nai, Vietnam	H58	NHMK 20130833		MN296023	MN296391	MN296349
<i>Phuphanian globosa</i> Tumpeesuwan et al., 2007						
Nam Pung Reservoir, Sakon Nakhon, Thailand	H42	CUMZ5173	17°17'06.7"N 103°43'36.8"E	MT654624	MT651540	MT651595
<i>Phuphanian costata</i> Tumpeesuwan & Tumpeesuwan, 2014						
Tham Pha Phu, Muang, Loei, Thailand	H67	CUMZ5182	17°34'39.9"N 101°42'39.5"E	MT654625	MT651541	MT651596
<i>Phuphanian crosseii</i> (Pfeiffer, 1862)						
Jedkot Waterfall, Kaeng Khoi, Saraburi, Thailand	H5	CUMZ5147	14°28'20.7"N 101°09'29.0"E	MT654626	MT651542	MT651597

TABLE 1 Samples and GenBank accession numbers for all sequences in the study (Cont.)

Species and localities	Specimen code	Voucher code	Co-ordinates	Accession nos.		
				COI	16S	28S
<i>Pseudoplecta bijuga</i> (Stoliczka, 1873) Air Bunum, Banding, Perak, Malaysia	H73	CUMZ5150	5°38'13.4"N 101°42'41.1"E	MT654627	MT651543	MT651598
<i>Quantula striata</i> (Gray, 1834) Botanic Garden, Singapore	H23	CUMZ5165	1°18'49.6"N 103°48'56.6"E	MT654628	MT651544	MT651599
<i>Rhinocochlis nasuta</i> (Metcalfe, 1852) Fairly Cave, Sarawak, Malaysia	H19	CUMZ5162	1°22'52.4"N 110°07'07.4"E	MT654629	MT651545	MT651600
<i>Asperitas trochus</i> (Müller, 1774) Taman Tirtagangga, Bali, Indonesia	H31	CUMZ5154		MT654630	MT651546	MT651601
Out group						
<i>Helix pomatia</i> Linnaeus, 1758 Copenhagen, Denmark	H44	CUMZ5265	–	MT654631	MT651547	MT651602
<i>Camaena suprafusca</i> Möllendorff, 1898 Tad Moang Waterfall, Khamkeut, Bolikhamxay, Laos	H46	CUMZ5263	18°12'20.8"N 104°33'32.1"E	MT654632	MT651548	MT651603
<i>Chloritis diplochone</i> Möllendorff, 1898 Wat Khao Sukim, Tha Mai, Chanthaburi, Thailand	H39	CUMZ5264	12°45'48.5"N 102°01'58.2"E	MT654633	MT651549	MT651604
<i>Amphidromus glaucolarynx</i> (Dohrn, 1861) Sai Yok, Kanchanaburi, Thailand	H38	–		MT654634	MT651550	MT651605

SMF: Forschungsinstitut und Naturmuseum
Senckenberg, Frankfurt am Main
ZMB: Museum für Naturkunde, Humboldt
University, Berlin

Molecular studies

Up to three specimens from each population and each recognizable morph were selected for DNA sequencing, with priority given to dissected individuals. Genomic DNA was extracted from the foot or mantle tissue using a NucleoSpin Tissue kit (MACHEREY-NAGEL), following the manufacturer's protocol. The mitochondrial cytochrome c oxidase subunit I gene (*COI*) was amplified using the universal primers LCO1490 – GGTC AACAAATCATAAAGATATTGG and HCO2198 – TAAACTTCAGGGTGACCAAAAAATCA (Folmer et al., 1994), while the 16S ribosomal RNA gene (*16S*) was amplified by primers 16SsinF – GCCGCAGTACCTTGACTGTGCT or 16Sar – CGCCTGTTTATCAAAAACAT with 16sbr – CCGGTCTGAACTCAGATCACGT (Kessing et al., 1989), and the nuclear 28S ribosomal RNA gene (*28S*) was amplified by primers 28SF4 – AGTACCGTGAGGGAAAGTTG and 28SR5 – ACGGGACGGGCGGTGGTGC (Morgan et al., 2002). The PCR amplification was conducted in a final volume of 20 µl containing 1 µl of each primer (10 mM), 2 µl of the extracted genomic DNA (25 ng), 7 µl of distilled water, and 10 µl of EmeraldAmp PCR Master Mix (TAKARA BIO INC.). Thermal cycling was performed at 94°C for 3 min, followed by 35 cycles of 94°C for 30 s, 51–60°C (depending on samples and gene) for 60 s, extension at 72°C for 1 min, and then the final extension at 72°C for 5 min. All PCR products were purified by PEG precipitation and then commercially sequenced by an automated sequencer (ABI prism 3730XL) with the same primers in both directions. Newly obtained nucleotide sequences were deposited in the

GenBank database (see table 1 for accession numbers).

Phylogenetic analysis

Sequences were edited and aligned using ClustalW, implemented in MEGA7 (Kumar et al., 2016). The final concatenated alignment used in phylogenetic tree construction contained 1576 bp: 655 bp of *COI*, 369 bp of *16S*, and 552 bp of *28S*. These sequences came from 43 specimens representing seven genera of Dyakiidae and four recognized genera of Ariophantidae occurring in Thailand, along with specimens of the non-limacoid taxa Camaenidae and Helicidae as outgroups. The details of taxon sampling used in phylogenetic analysis are shown in table 1. Most of the sequences in this study were newly obtained from 42 specimens, but some sequences were retrieved from previous studies (i.e., Sutcharit et al., 2019 and Pholyotha et al., 2020).

The best-fit model of nucleotide substitution and the best partitioning scheme were identified by PartitionFinder2 v.2.3.4 (Lanfear et al., 2016), by using a heuristic search algorithm under the Akaike Information Criterion (AIC). The partitioned concatenated dataset was then used to infer the phylogenetic relationship by using Bayesian inference (BI) and maximum likelihood (ML) analyses, implemented in CIPRES Science Gateway (Miller et al., 2010). The ML analysis was performed using RAXML v.8.2.10 (Stamatakis, 2014). The GTRGAMMA was set as the model for all gene partitions. One thousand ML bootstrap replicates were performed to assess topology support. The BI trees were estimated by running a 10 million generation Metropolis-coupled Markov chain Monte Carlo (MC-MCMC) as implemented in MrBayes 3.2.6 (Ronquist et al., 2012). The best-fit models for each partition followed the PartitionFinder2 results. Each MCMC consisted of two runs with four chains, one chain of which was heated. A data

partition was applied that allowed parameters to be estimated separately for each partition. Sampling rate of the trees was once every 1000 generations. Stationarity was considered to have been reached when the average standard deviation of split frequencies shown in MrBayes was less than 0.01 and the log likelihood of sampled trees reached a stationary distribution. The first 25% of obtained trees were discarded as burn-in. The remaining trees were used to estimate the consensus tree topology, bipartition posterior probability (bpp) and branch lengths. Nodes with bipartition posterior probabilities (bpp) greater than 0.95 of BI analysis supported and/or bootstrap support values larger than 70 of ML analysis were considered as supported nodes (Huelsenbeck & Hillis, 1993; Larget & Simon, 1999). Genetic divergence based on *COI* sequences among pairwise OTUs was also calculated using uncorrected p-distances as implemented in MEGA7 (Kumar et al., 2016).

Results

Molecular phylogenetic trees were reconstructed based on the concatenated mitochondrial *COI* and *16S* genes, and as well as nuclear *28S* sequences obtained from 43 individuals. This concatenated dataset was divided into five partitions, consisting of partitions for *16S* and *28S* genes, and for each of three codon positions of the *COI* gene. The best-fit models for each partition were GTR+G for the first codon position of *COI* and *16S*, GTR+I+G for the second codon position of *COI* and *28S*, and GTR+I for the third codon position of *COI* genes. Both maximum likelihood (ML) and Bayesian inference (BI) analyses produced trees with identical topologies, and with all major clades relatively well supported. Therefore, only the tree topology from BI is presented in fig. 2. Overall, our phylogeny

is largely congruent with the current generic and familial classification with the notable exception that some sinistral species currently treated as members of the genus *Dyakia* (Dyakiidae) cluster closely together with species of the genus *Hemiplecta* (Ariophantidae). However, these two families are distinctly recognized by the comparative morphology of shells and genitalia.

All nominal genera that were placed in the Dyakiidae based on their morphology are recovered as one major clade in our tree. However, *Dyakia*, as presently delineated, is non-monophyletic. While *D. janus* (Beck, 1837) is nested with the dyakiid clade, five other species assigned to this genus are placed among the Ariophantidae, and more specifically, within the genus *Hemiplecta*. The relationships among other dyakiid genera, mostly represented by the type species, are well supported in both BI and ML analyses. Three sinistral genera, *Dyakia*, *Rhinocochlis* Thiele, 1931 and *Bertia* Ancey, 1887 are not recovered as monophyletic. All three species of the *Phuphania* Tumpeesuwan et al., 2007 form the sister group to *Quantula striata* (Gray, 1834). The clade containing the ariophantid genera, *Cryptozona* Mörch, 1872, *Macrochlamys* and *Sarika* forms a sister group to Dyakiidae, with strong support from both ML and BI analyses.

The other major clade consists of the remaining ariophantids, including the genera *Hemiplecta* and *Koratia*, and the five sinistral snails that were provisionally classified as “*Dyakia*” species from southern Thailand and Peninsular Malaysia. Three of these have previously been identified as nominal species, “*Dyakia*” *retrorsa*, “*Dyakia*” *salangana*, and “*Dyakia*” *lahatensis* (Morgan, 1885a), whereas the other two represent putative newly discovered species. The phylogenetic tree also reveals that all these five sinistral species form a monophyletic clade and that

FIGURE 2 Bayesian inference tree based on 1576 bp concatenated alignment dataset of COI + 16S + 28S genes. Numbers on nodes indicate bootstrap values from maximum likelihood (ML) and bpp from Bayesian inference analysis (BI), and are shown as BI/ML. Images of living specimens are not to scale.

this clade is sister to the other members of the genus *Hemiplecta* and *Koratia*. Within this clade, "*Dyakia*" *retrorsa* is most closely related to "*Dyakia*" sp. 1 from Nakhon Si Thammarat, Thailand. "*Dyakia*" *salangana* is sister to "*Dyakia*" *lahatensis*, while "*Dyakia*" sp. 2 from

eastern Thailand is the sister lineage of the above four species.

The genus *Koratia* (type species: *Helix distincta* Pfeiffer, 1850) does not form a monophyletic clade based on the present analysis. "*Koratia*" *distincta* and "*Koratia*" *pluto* (Pfeiffer,

1863) is clustered with *H. esculenta*, *H. cymatium*, and *H. humphreysiana* (the type species of *Hemiplecta*), while “*Koratia*” *funerea* (Smith, 1896) is placed as a basal taxon to other *Hemiplecta* species.

Within the genus *Hemiplecta*, the average genetic distance was estimated to be 8.14% (table 2). The minimum divergence is 2.92% between the pair of *H. cymatium* (Pfeiffer, 1856) and *H. humphreysiana*, while the maximum divergence is 9.75% between “*Dyakia*” *salangana* and *H. humphreysiana*. Among the five sinistral “*Dyakia*” snails, the average genetic distance ranges from 5.83% to 7.46%. The intraspecific genetic distances for these species are relatively low, except in “*Dyakia*” *salangana*, where the structured subclades show a considerable divergence of 3.03% between Thai and Malaysian populations.

All systematic descriptions and related remarks are presented as Appendix.

Discussion

Evolution of the sinistral clade within the dextral-dominated genus

Current systematic classification of the Dyakiidae and Ariophantidae is still heavily influenced by traditional shell-based characters, and is sometimes incongruent with molecular phylogeny (Hyman et al., 2007, 2017; Köhler et al., 2020). Diagnostic characters of reproductive organs in Dyakiidae are the presence of amatorial organ complex (amatorial organ gland and duct) and the connection of the gametolytic organ to the amatorial organ (Laidlaw, 1931; Hausdorf, 1995; Sutcharit et al., 2012). However, unique characters of the Ariophantidae are still equivocal. Most of the known taxa are described based solely on their shells, and without genitalia characters. Moreover, a conclusive phylogeny

is still far from complete. Nevertheless, the currently accepted defining character states of the Ariophantidae include the presence of shell lobes, caudal foss, and well-developed caudal horn, either absence or presence of amatorial organ (but if present, without accessory organs), and a gametolytic organ that is attached to the vagina (Hausdorf, 1998; Schileyko, 2002; Hyman & Ponder, 2010). The present phylogeny reveals that five sinistral species are clustered with the dextrally-coiled genus *Hemiplecta* (Ariophantidae), although sinistrality has long been considered as a diagnostic character of *Dyakia* s.s. (Godwin-Austen, 1891; Laidlaw, 1931; Schileyko, 2003). This phylogenetic grouping is supported by the anatomy of reproductive organs. The genitalia of sinistral clade resembled those of *Hemiplecta* instead of the *Dyakia*. Only the reversed genital opening on the body side was detected between opposite coiling snails (Sutcharit et al., 2012; this study). Normally, the reproductive anatomy in stylommatophorans is highly asymmetric, and the sinistral individuals have identical genital structure as a mirror-image to other dextral individuals of the same taxa (Gittenberger, 1988).

From our multi-locus phylogeny, sinistrality thus is not a trait unique to *Dyakia* but has convergently evolved in *Hemiplecta* as well. Sinistrality has sporadically evolved and has occurred independently among different stylommatophoran clades (Asami et al., 1998; Sutcharit et al., 2007; Hoso et al., 2010; Jirapatrasilp et al., 2020). In our results, the sinistral shell coiling has become fixed within this *Hemiplecta* clade, similar to the Japanese endemic genus *Euhadra* Pilsbry, 1890, of which four out of about 20 species are sinistral and all are derived from a single sinistral ancestor (Ueshima and Asami, 2003; Davison et al., 2005). In other cases, dextral and sinistral individuals co-occur in the same population (chirally dimorphic). For example, in

TABLE 2 Genetic divergence based on uncorrected p-distance of 655 bp *COI* gene fragment sequences of *Hemiplecta* species (%±S.E.). Average interspecific distances between pairwise taxa are shown below diagonal. Average intraspecific distances for each taxon are shown in bold

Taxa	1.	2.	3.	4.	5.	6.	7.	8.	9.	10.	11.
1. <i>H. retrorsa</i>	1.23 ± 0.32										
2. <i>H. ligorica</i> n. sp.	6.41 ± 0.86	1.18 ± 0.31									
3. <i>H. salangana</i>	7.18 ± 0.87	6.66 ± 0.82	3.03 ± 0.47								
4. <i>H. lahatensis</i>	6.90 ± 0.87	7.46 ± 0.89	5.83 ± 0.74	1.85 ± 0.47							
5. <i>H. thailandica</i> n. sp.	6.56 ± 0.93	6.74 ± 0.88	6.17 ± 0.82	6.74 ± 0.90	0.37 ± 0.16						
6. <i>H. esculenta</i>	9.03 ± 0.99	8.35 ± 0.99	8.12 ± 0.91	8.62 ± 0.99	8.36 ± 1.06	N/A					
7. <i>H. distincta</i>	8.77 ± 0.98	9.15 ± 1.05	8.34 ± 0.98	8.69 ± 1.01	8.67 ± 1.07	5.23 ± 0.81	N/A				
8. <i>H. pluto</i>	8.46 ± 1.03	9.04 ± 1.04	9.38 ± 0.98	9.15 ± 1.04	8.21 ± 1.00	6.31 ± 0.87	6.62 ± 0.89	N/A			
9. <i>H. cymatium</i>	9.44 ± 1.08	9.54 ± 1.07	9.35 ± 1.01	8.54 ± 0.98	8.92 ± 1.11	8.46 ± 1.00	8.77 ± 1.02	8.46 ± 1.02	N/A		
10. <i>H. humphreysiana</i>	9.90 ± 1.12	9.62 ± 1.08	9.75 ± 1.03	9.31 ± 1.02	9.59 ± 1.14	8.62 ± 1.00	9.08 ± 1.06	8.31 ± 1.03	2.92 ± 0.65	N/A	
11. <i>H. funerea</i>	8.87 ± 1.06	9.46 ± 1.05	7.97 ± 0.91	8.46 ± 1.04	7.44 ± 1.02	8.00 ± 1.05	8.15 ± 1.07	8.31 ± 1.10	8.92 ± 1.10	8.31 ± 1.05	N/A

the Southeast Asian endemic tree snail genus *Amphidromus* Albers, 1850, which comprises two subgenera. One subgenus, *Amphidromus*, includes chirally dimorphic species, while another subgenus, *Syndromus* Pilsbry, 1900, includes only sinistral species. Phylogenetic analysis has shown that sinistrality has persisted as the ancestral state of the sinistral *Syndromus* clade (Sutcharit et al., 2007), which is similar to the case of the sinistral *Hemiplecta* clade in this study.

It is interesting to consider how sinistrality has evolved independently within the genus *Hemiplecta*, where dextrality is the dominant or more common morphology. One of the likely explanations is predation pressure. A comparative survey of the diversity of the sinistral snails as potential prey (i.e., those with lower-spired shells) showed that the sinistral taxa occur more commonly within the distribution range of a snail-eating snake (genus *Pareas*) (Hoso et al., 2010). In feeding experiments, snail-eating snakes tended to prey on dextral over sinistral individuals. This survival advantage of sinistral individuals is more likely to enhance the chance of population fixation by complete premating isolation (Hoso et al., 2007, 2010; Danaisawadi et al., 2016). Another predation experiment revealed that snail-eating snakes avoided approaching or striking at a sinistral snail ("*Dyakia*" *salangana*), suggesting it was more difficult and costlier to handle than dextral snails (Danaisawadi et al., 2016). The adult *Hemiplecta* spp. have much greater shell size than the predation threshold size; however, these large snails can be small enough to be preyed upon when they are young. The factor of snake predation may counterbalance the disadvantage in copulation, and if the sinistral phenotype exceeds 50% under selective advantage, this phenotype would become fixed for the population (Gittenberger, 1988; Johnson et al., 1990; Asami et al., 1998; Ueshima and Asami, 2003;

Davison et al., 2005; Gittenberger et al., 2012). Moreover, many studies have shown that interchiral mating (copulation between individuals with opposite coiling direction) is almost impossible in low-spired snails (shell width greater than shell height) that generally perform simultaneous reciprocal copulation. Thus, reverse coiling populations would become isolated rapidly and give rise to a single-origin sinistral clade through a complete premating isolation mechanism (Batenburg & Gittenberger, 1996; Gittenberger, 1988; Asami et al., 1998; Reise et al., 2002; Gittenberger et al., 2012).

Taxonomic implications in Hemiplecta

The genus *Hemiplecta* currently comprises at least twenty nominal species, with most known by shell characteristics only (Schileyko, 2002). The anatomy of the type species, *H. humphreysiana*, was described by Collinge (1902) and Blanford & Godwin-Austen (1908), and that of *H. cymatium* and *H. distincta* was described by Stoliczka (1873), Godwin-Austen (1900, 1919), and Schileyko (2002). The conic to depressed-conic shell, globular gametolytic sac with undifferentiated gametolytic duct, very short flagellum, and short to long epiphallic caecum have been recognized as characters unique to the genus (Schileyko, 2002, 2015). The function of the epiphallus and epiphallic flagellum is thought to produce the spermatophore, the tail-pipe forming in the flagellum, and the capsule in the epiphallus. The epiphallic caecum is believed to function in turning the spermatophore so that the tail-pipe is moved into the penis first (Gómez, 2001).

The nominal genus *Koratia* was previously treated as a distinct genus based on the absence of a penial verge inside the penis (table 3; Godwin-Austen, 1919; Schileyko, 2002). However, our phylogenetic analysis indicates that three nominal species

TABLE 3 Shell lobe and genitalia variation among species classified into the genus *Hemiplecta*

Taxa	Shell coiling	Penial verge	Epiphallic caecum	Gametolytic organ shape	References
<i>H. humphreysiana</i> (Lea, 1840)	dextral	present	straight	globular	Godwin-Austen (1898), Collinge (1902), this study
<i>H. cymatium</i> (Pfeiffer, 1856)	dextral	present	straight	globular	Stoliczka (1873), this study
<i>H. esculenta</i> Maassen, 2006	dextral	present	straight	globular	This study
<i>H. retrorsa</i> (Gould, 1843)	sinistral	absent	straight	globular	This study
<i>H. salangana</i> (Martens, 1883)	sinistral	absent	straight	globular	This study
<i>H. thailandica</i> n. sp.	sinistral	absent	straight	globular	This study
<i>H. ligorica</i> n. sp.	sinistral	absent	straight	globular	This study
<i>H. distincta</i> (Pfeiffer, 1850)	dextral	absent	straight	globular	This study
<i>H. pluto</i> (Pfeiffer, 1862)	dextral	absent	straight	globular	Godwin-Austen (1900, 1919), Schileyko (2002), this study
<i>H. funerea</i> (Smith, 1896)	dextral	absent	coiled	globular	This study
					This study

previously assigned to the *Koratia* do not form a monophyletic group but instead are nested with other *Hemiplecta* (fig. 2). Therefore, absence of a penial verge may be attributed to the reproductive plasticity in *Hemiplecta* s.l. Our analysis also emphasizes the importance of describing genitalia along with other characters when defining these diverse taxonomic groups. In view of our molecular results, *Koratia* should no longer be considered as a separate genus.

Within the sinistral clade, this study elucidates the presence of five genetically distinct and morphologically divergent lineages, which we recognize here as distinct species, namely *H. retrorsa*, *H. salangana*, *H. lahatensis*, and two newly proposed species: *H. ligorica* n. sp. and *H. thailandica* n. sp. The divergence values among them are high (5.83–7.46%) when compared with the approximately 4% of the optimum intra/interspecific threshold value in stylommatophoran land snails (Davison et al., 2009). The deep divergence detected here is similar in order of magnitude to that in other land snails reported elsewhere; for example, about 6–12 % among Australian camaenid species (Criscione et al., 2012). Furthermore, the molecular phylogenetic results also confirm the validity of *H. funerea* as a genetically distinct species and undoubtedly support the specific validity of *H. pluto*. Traditionally, these two species have been recognized as a subspecific entity or a synonym, respectively, of *H. distincta* (Fischer & Dautzenberg, 1904; Schileyko, 2011). Only the recent treatment by Inkhavilay et al. (2019) has raised them to a specific level, but without clear supporting evidence.

Currently, the sinistral clade comprises five nominal species, four of which were anatomically examined, with the exception of *H. lahatensis*. This species possesses a sinistral shell with a wrinkled shell surface, and its distribution covers the northern part of Peninsular Malaysia; it likely belongs to the *Hemiplecta*.

Further examination of newly-collected adult specimens are necessary to confirm this species' generic position and morphological relationship with other sinistral-shelled taxa.

In terms of distribution, four of the species range from the southern Tenasserim Range through the Malay Peninsula. The exception is *H. thailandica* n. sp., which is restricted to Indochina (Eastern Thailand) and probably in Cambodia (Sutcharit et al., 2020); this could be attributed to allopatric speciation. This close relationship between the Malay Peninsula and Indochina populations has been similarly reported in various land snail groups and also in other animals, including butterflies and centipedes (Muadsub & Pinkaew, 2014; Siriwtut et al., 2015). These repeated disjunct distribution patterns are indicative of a cause that is linked to the geographical history of Sundaland. The fluctuation of sea level in the South China Sea contributed to the exposure of rainforest connection between Indochina and the Malay Peninsula (Voris, 2000; Woodruff, 2010; Lukoschek et al., 2011).

The most consistent and reliable character for species delimitation in every species of land snail is the internal anatomy of the penis, along with other genital characters relating to the penis and epiphallus, whereas the gametolytic organ was informative at the genus level (Hyman et al., 2017; Jirapatrasilp et al., 2020; Pholyotha et al., 2020; Siriboon et al., 2020). For example, reproductive organs are highly consistent in the dark shell and yellow shell forms (C. Sutcharit, unpublished data) of *H. funerea*, (i.e., coiled epiphallal caecum and penial verge absent; table 3). This supports the hypothesis that reproductive anatomy is an important factor in species recognition during copulation. In contrast, when delineating species by their shell morphology, the shape and coiling are of little value. The shell banding patterns are readily recognizable in some living species, e.g., *H. ligorica* n. sp., by its small

and banded shell. However, this feature may be more difficult to distinguish in bleached, dead shells. Another pair of species that co-occur, *H. pluto* and *H. distincta*, can reliably be distinguished in life by their red or brownish body color, respectively (see Inkhavilay et al., 2019: fig. 56c, d), although the colors are faded in alcohol-preserved specimens.

Conclusion

Based on phylogenetic results and morphological information in the present study, we have transferred the sinistral species previously and incorrectly assigned to *Dyakia* (family Dyakiidae) to the genus *Hemiplecta* (family Ariophantidae). Two previously unrecognised species are described based on consistent differentiation in molecular, shell, and genitalia characters. Our data also provide further support for three other sinistral *Hemiplecta* species, which are also re-described herein. The results also suggest the synonymization of the formerly recognized as (sub)genus *Koratia* under the *Hemiplecta*. Finally, the results indicate the evolutionary instability of shell traits that are often used for land snail classification, while genital characters are highlighted as reliable taxonomic markers for delimiting species and at least some higher taxa. The integration of multiple independent characters including molecular evidence is crucial for delimiting higher systematic levels.

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APPENDIX

Systematics

Family Ariophantidae Godwin-Austen, 1888

Genus *Hemiplecta* Albers, 1850

Hemiplecta Albers, 1850: 60, 61. Albers, 1860: 52, 53. Zilch, 1959: 317. Schileyko, 2002: 1282, 1283.

Koratia Godwin-Austen, 1919: 202. Zilch, 1959: Schileyko, 2002: 1281, 1282. **New synonym**

Ariophanta (*Semperia*) Godwin-Austen, 1898: 82 [non Crosse, 1867: 74, 75].

New synonym

Semperia: Blanford & Godwin-Austen, 1908: 299. Zilch, 1959: 313.

Dyakia (*Semperia*): Baker, 1941: 267. Schileyko, 2003: 1363.

Type species. Helix humphreysiana Lea, 1840; subsequent designation by Martens in Albers, 1860: 52.

Description

Shell. Shell medium to large, conic to depressed conic and dextral or sinistral. Shell color monochrome brownish or whitish

and with or without spiral band. Last whorl rounded to keeled and little descending near aperture. Apertural lip simple to slightly thickened in adult snails. Umbilicus narrowly open.

Genitalia. Genitalia with long cylindrical tubular penis, thin penial sheath, and penial verge may be present or absent. Penial retractor muscle attached at tip of a straight or coiled epiphallic caecum; flagellum short. Dart apparatus well developed. Gametolytic organ (without distinct duct) with globular or bulbous sac.

Radula. Radula with symmetric unicuspid central tooth; asymmetric unicuspid lateral teeth. Marginal teeth curved and bicuspid. Jaw smooth (without vertical ribs), crescentic, with anteriorly convex cutting margin.

External features (fig. 2). Living snail with long and brownish to dark brown tentacles. Skin reticulated brown with dark brown reticulations over the entire body. Mantle with well-developed dorsal lobes; short and finger-shaped shell lobes may be absent or present. Foot unipartite and pedal groove typical of aulacopods. Caudal horn not overhanging; caudal foss, short vertical slit in tail above sole margin and well defined.

Distribution. The range of this genus is from Southeast Asia to New Guinea. The records from India and Maldives are ambiguous and need further study (Blanford & Godwin-Austen, 1908; Schileyko, 2002).

Remarks. Historically, Godwin-Austen (1898) revised the systematics of the ariophantid snails in British India and Burma (today in South Asia and part of Southeast Asia). He found that the sinistral species, especially from Burma [Myanmar] tended to have radula teeth

distinctly different from the typical *Ariophanta* from India. This character agrees with some Sumatra and Sulawesi species as reported by Semper (1870). Later, Laidlaw (1931) revised the genus of sinistral species and reported similar results, suggesting that the taxonomic position of sinistral species from Myanmar and Thailand needed revision. Then, Godwin-Austen (1898: 82) proposed the name "*Semperia*" as a subgeneric division of *Ariophanta* with *Helix retrorsa* Gould, 1843 as the type species. Unfortunately, this genus-group name was preoccupied by Crosse (1867) for fissurellid limpets. In addition, this nominal subgenus has not been widely accepted as valid.

1 *Hemiplecta retrorsa* (Gould, 1843)

(figs 1, 3A, B, 5A, B, 6A–C)

Helix retrorsa Gould, 1843: 139. Type locality: Tavoy, British Burma. Pfeiffer, 1848: 76. Pfeiffer, 1876: 128. Hanley and Theobald, 1876: pl. 25, fig. 6.

Helix (Caracolla) retrorsa: Gould, 1844: 455, pl. 24, fig. 5.

Ariophanta retrorsa: Godwin-Austen, 1883: 133, 136, 137, pl. 34, figs 4, 5, 7, 8.

Ariophanta (Semperia) retrorsa: Godwin-Austen, 1898: 82.

Dyakia retrorsa: Blanford & Godwin-Austen, 1908: 300. Laidlaw, 1931: 191. Laidlaw, 1963: 145.

Material examined. Type material: syntype MCZ 169330 (1 shell; fig. 3A) from Tavoy British Burma [Dawei District, Tanintharyi Region, Myanmar]. Non-type material: **THAILAND:** Ta Kien Thong Waterfall, Sangkhlaburi District, Kanchanaburi Province: CUMZ 5096. Kaeng Kracharn National Park, Phetchaburi Province: CUMZ 5021, 5025. Kui Buri National Park, Prachuapkhirikhan Province: CUMZ 5039. Pala-U Waterfall, Hua Hin District,

FIGURE 3 Shell characters. A, B. *Hemiplecta retrorsa*, (A) syntype MCZ 169330 and (B) specimen CUMZ 5099 from Ranong Province. C, D. *Hemiplecta salangana*, (C) syntype ZMB/Moll 32578 and (D) specimen CUMZ 4967 from Phuket Province. E. *Hemiplecta lahatensis*, syntype MNHN-IM-2000-22834.

Prachuapkhirikhan Province: CUMZ 5036, 5044, 5046. Tam Phu Ta-kien, Tha Sae District, Chumporn Province: CUMZ 5032. Boonya Bann Waterfall, Muang District, Ranong Province: CUMZ 5045. Hot Spring, Muang District, Ranong Province: CUMZ 5024, 5094, 5099 (fig. 3B). Khao Narai, Kapoe District, Ranong Province: CUMZ 5081. Tone Phet

Waterfall, Muang District, Ranong Province: CUMZ 5028. Khao Lak National Park, Thai Mueang District, Phang Nga Province: CUMZ 5019, 5038. Tam Nam Put, Thap Put District, Phang Nga Province: CUMZ 5035, 5091. Tao Thong Waterfall, Thap Put District, Phang Nga Province: CUMZ 5030, 5033, 5042. Wat Khiriwong, Thap Put District, Phang Nga

FIGURE 4 Shell characters. A. *Hemiplecta lahatensis*, specimen CUMZ 5259/2. B, C, *Hemiplecta thailandica* n. sp., (B) holotype CUMZ 5095/1 and (C) specimen CUMZ 5098 from Chanthaburi Province. D, E. *Hemiplecta ligorica* n. sp., (D) holotype CUMZ 5093/1 and (E) paratype CUMZ 5087 from the type locality.

Province: CUMZ 5022, 5023, 5082. Khao Sok National Park, Suratthani Province: CUMZ 5034, 5041, 5043. Wat Sathit Khirirom, Khiriratnikhom District, Suratthani Province: CUMZ 5020, 5027, 5040. Klong Saeng Wildlife Sanctuary, Suratthani Province: 5029. Rajjaprabha Reservoir, Ban Takhun District, Suratthani Province: CUMZ 5026, 5031, 5037.

Description

Shell (fig. 3A, B). Shell relatively large (width up to 50.0 mm, height up to 25.0 mm), depressed conic, thickened and sinistral. Whorls 6–7, increasing regularly, nearly flattened, with shallow suture. Spire convex; apex acute; embryonic shell smooth; following whorls with thin growth lines

FIGURE 5 Genital characters. A, B. *Hemiplecta retrorsa*, CUMZ 5094 from Ranong Province. C, D. *Hemiplecta thailandica* n. sp., holotype CUMZ 5095/1 from the type locality. E, F. *Hemiplecta ligorica* n. sp., paratype CUMZ 5087 from the type locality. A, E, C. Male and female genital organs. B, D, F. Internal wall sculpture of penis, vagina and dart apparatus chamber. Abbreviations: at, atrium; da, dart apparatus; dp, dart papilla; e, epiphallus; ec, epiphallic caecum; fl, flagellum; fo, free oviduct; go, gametolytic organ; p, penis; ps, penial sculpture; pr, penial retractor muscle; v, vagina; vd, vas deferens; vs, vaginal sculpture.

and spirally undulated surface sculpture. Periostracum thin corneous. Shell color monochrome brownish to yellowish-brown. Last whorl angular with strong and sharp peripheral keel that diminishes close to aperture. Aperture little descending, broadly ovate-lunate; lip simple to thickened in adult specimens. Columella slightly dilated; parietal callus thin and translucent. Umbilicus narrowly open and deep.

Genitalia (fig. 5A, B). Atrium very short. Penis a long, slender, cylindrical tube and enclosed by a thin penial sheath. Epiphallus about as long as penis length. Epiphallic caecum short, straight; penial retractor muscle thin and attached to the tip. Flagellum short and little curved. Vas deferens a narrow tube connecting free oviduct and epiphallic-flagellum junction. Internal wall of penis exhibits closely packed papillae over nearly entire penis length; penial verge absent.

FIGURE 6 SEM images of radula. A–C. *Hemiplecta retrorsa*, CUMZ 5094 from Ranong Province, (A) central and inner lateral teeth, (B) outer lateral teeth, and (C) outer marginal teeth. D, E. *Hemiplecta thailandica* n. sp., holotype CUMZ 5095/1 from the type locality, (D) central and lateral teeth, and (E) lateral teeth and marginal teeth. F. *Hemiplecta ligorica* n. sp., paratype CUMZ 5087 from the type locality. Central tooth indicated by 'C'. Numbers indicate the tooth order from lateral to marginal end.

Vagina long, about same length as penis, cylindrical and similar diameter to penis. Internal wall of vagina possesses irregular vaginal pilasters. Dart apparatus a long muscular cylinder; dart papilla short, conic, with a smooth surface. Gametolytic organ small, globular. Free oviduct short and surrounded by thickened blackish muscular tissue (pinkish in fresh specimens) at distal end.

Radula (fig. 6A–C). Teeth arranged in V-shaped rows with approximately 391 (195–(60–70)–1–(60–70)–195) teeth. Central tooth symmetric unicuspid and sword-shaped with dull head. Lateral teeth asymmetric unicuspid, sword-shaped, and inclined towards central tooth. Marginal teeth start from tooth 60–70, elongate sword-shaped, apically bicuspid;

endocone and ectocone small with pointed cusp. Outermost teeth shorter and smaller than inner teeth.

Remarks. This species was originally described from southeastern Myanmar, with large shell and strong peripheral keel. The specimens from southwestern peninsular Thailand agree well with the type specimens of this species. In Thailand, this species is known mainly from the western region along the Tenasserim Range in Kanchanaburi, Prachuap Khirikhan, Chumphorn, Ranong, Phang Nga and Suratthani Provinces. This species can be distinguished from *H. salangana* by its angular last whorl with strong keel on periphery, and without a spiral band. In contrast, *H. salangana* tends to have a

rounded last whorl, and usually has a narrow brownish spiral band on periphery.

2 *Hemiplecta salangana* (Martens, 1883)

(figs 1, 3C, D)

Nanina salangana Martens, 1883: 134–136, pl. 25, figs 8–12. Type locality: insulam Salanga (Junk Ceilon) ad oram occidentalem peninsulae Malaccanae [Phuket Province, Thailand and Peninsular Malaysia].

Dyakia salangana: Laidlaw, 1931: 191. Laidlaw, 1933: 226. Benthem Jutting, 1960: 17, 20. Berry, 1963: 14, pl. 9, fig. 61. Laidlaw, 1963: 145, 146. Chang, 1996: 4, fig. 1.

Hemiplecta salangana var. *martensi* Collinge, 1903: 209. Type locality: Bukit Bersa.

Dyakia salangana salangana: Maassen, 2001: 106, 107.

Dyakia salangana martensi: Maassen, 2001: 107.

Ariophanta trangensis Thach and Huber in Thach, 2020: 36, 37, figs 446–447. Type locality: Suburb of Trang City, Trang Province, Thailand. **New Synonym**

Material examined. Type material: syntype of *Nanina salangana* ZMB/Moll 32578 (2 shells; fig. 3C) from Salanga; possible syntype ZMB/Moll 57522 (1 shell) from Salanga Hinterindien; possible syntype SMF 165021 (1 shell) from Salanga; syntype of *Hemiplecta salangana* var. *martensi* Collinge, 1903, NHMUK 1904.5.26.18–19 (2 shells) from Bukit Bersa. Non-type material: **MALAYSIA**: Bukit Chuping, Perlis (6°29'41.1"N, 100°16'01.0"E): CUMZ 5006, 5076, 5097. Gunung Kilian, Perlis: CUMZ 4958. Kampung Wang Kelian, Perlis (6°40'55.1"N, 100°11'15.2"E): CUMZ 4994. Pulau Langgun Island, Langkawi, Kedah: CUMZ 4992. Langkawi Island, Kedah: CUMZ 4962, 4968, 4981, 4999, 5001. **THAILAND**: Kathu waterfall, Kathu District, Phuket Province: CUMZ 4967 (fig. 3D), 4973. Tone Sai

Waterfall, Thalang District, Phuket Province: CUMZ 4952. Koh Lanta, Krabi Province: CUMZ 5008, 5011, 5015. Sra Morakot, Khlong Thom District, Krabi Province: CUMZ 4980, 5007. Tam Tab Prik, Krabi Province: CUMZ 4970. Wat Tam Sue, Muang District, Krabi Province: CUMZ 4951, 4997, 5017, 5077. Botanic Garden, Trang Province: CUMZ 4957, 4965, 4985. Khao Huay Haeng, Huai Yot District, Trang Province: CUMZ 4982, 4995. Khao Pra Yod, Huai Yot District, Trang Province: CUMZ 4979. Sai Rung Waterfall, Pa-lian District, Trang Province: CUMZ 5016. Tam Chang Hai, Na Young District, Trang Province: CUMZ 4971. Khao Auk Taru, Muang District, Phatthalung Province: CUMZ 4998, 5010, 5018. Khao Poo-Chao, Srinagarindra District, Patthalung Province: CUMZ 4977, 4984, 4991. Budha Kodome, Srinagarindra District, Patthalung Province: CUMZ 5005, 5009. Tam Malai, Muang District, Patthalung Province: CUMZ 5012. Tam Praya Hong, Kong Ra District, Patthalung Province: CUMZ 4950, 4974. Tam Su-mano, Srinagarindra District, Patthalung Province: CUMZ 4996. Tam Wang Thong, Khuan Khanun District, Phatthalung Province: CUMZ 4953, 4955, 4964, 5013. Khuan Kaloung District, Satun Province: CUMZ 4989. La-ngu District, Satun Province: CUMZ 4966, 4978. Tale Bann National Park, Khuan Don District, Satun Province: CUMZ 4972, 4976, 4983. Tam Khantiphol, Thung Wa District, Satun Province: CUMZ 4959. Tam Tone Din, Khuan Don District, Satun Province: CUMZ 4947, 4969. Tarutao, La-ngu District, Satun Province: CUMZ 4946, 4949, 4956, 4963, 4993, 5003, 5004. Tone Pariphat Waterfall, Rattaphum District, Songkhla Province: CUMZ 5014. Tam Sri Kesorn, Rattaphum District, Songkhla Province: CUMZ 4954. Wat Charoen Pu-pha, Rattaphum District, Songkhla Province: CUMZ 4975, 5000. Khao Loop Chang, Sadao District, Songkhla Province: CUMZ 4920.

Description

Shell (fig. 3C, D). Shell relatively large (width up to 45.0 mm, height up to 24.0 mm), depressed conic, thickened and sinistral. Whorls 6–7, increasing regularly, convex, with wide and depressed suture. Spire convex; apex acute; embryonic shell smooth; following whorls with very thin growth lines and spirally undulated sculpture. Periostracum thin corneous to brownish. Shell color monochrome brownish to yellowish-brown, a narrow brown peripheral band usually present. Last whorl well-rounded. Aperture little descending, broadly ovate-lunate; lip simple to thickened in adult specimens. Columella slightly dilated; parietal callus thin and translucent. Umbilicus narrow and deep.

Genitalia. The external genital organs were described in Sutcharit et al. (2012: fig. 2a, b). Internal wall of penis exhibits closely packed papillae distally that abruptly cease proximally, close to atrium; penial verge absent. Internal sculpture of vagina with thin and smooth longitudinal sculpture; internal surface of amatorial organ smooth.

Radula. The radula morphology was briefly described by Sutcharit et al. (2012: fig. 2d, e). The distinct characters are each row with about 360 teeth (181–(15–20)–1–(15–20)–185). Central tooth unicuspid triangular. Lateral teeth unicuspid, oblique, triangular and inclined towards central tooth. Marginal teeth start from tooth 15–20, elongate bicuspid, endocone and ectocone small with round head. Outermost teeth shorter and smaller than inner teeth.

Remarks. *Hemiplecta salangana* is known from several localities in the southern part of peninsular Thailand and in the north of Malaysia. This species can be distinguished from *H. retrorsa* by its relatively smaller and more depressed shell, last whorl well-rounded

to weakly angular, and usually with narrow dark brown spiral band on periphery. External features of soft body are similar to those of *H. retrorsa*, only with paler brownish color over entire body compared to *H. retrorsa*.

The “*Ariophanta trangensis* Thach and Huber, 2020” was recently described from southern Thailand based solely on shell features. The holotype of this species shows no essential differences from the syntype of *H. salangana* and specimens recorded from the western coast of southern Thailand. In addition, the type localities are within the same geographical ranges, and the phylogenetic result shows no genetic subdivision within the wide geographical range of *H. salangana*. Therefore, we have synonymized “*Ariophanta trangensis*” as a junior synonym of *H. salangana*.

3 *Hemiplecta lahatensis* (Morgan, 1885) (figs 1, 3E, 4A)

Helix lahatensis Morgan, 1885b: 68. Type locality: forêt située entre Lahat et Ipoh.

Ariophanta lahatensis: Morgan, 1885a: 382, pl. 6, fig. 4.

Dyakia lahatensis: Laidlaw, 1931: 193. Laidlaw, 1963: 142. Chang, 1996: 5 with text figure.

Material examined. Type material: syntype MNHN-IM-2000-22834 (3 shells; fig. 3E) from Royaume de Pérak, vallée de Kinta [Kinta District, Perak State, Malaysia]. Non-type material: **MALAYSIA:** Gua Bewah, Kenyir Lake, Terengganu (4°50'43.7"N, 102°43'14.6"E), CUMZ 5258. Gua Matu Madu, Gua Musang, Kelantan (4°50'13.4"N, 101°56'56.3"E) CUMZ 5259/1, 5259/2 (fig. 4A).

Description

Shell (figs 3E, 4A). Shell small (width up to 40 mm, height up to 24 mm), depressed conic, thickened and sinistral. Whorls 5–6, increasing

regularly, nearly flattened, with very wide and shallow suture. Spire convex; apex acute; embryonic shell smooth; following whorls with thin growth lines and spirally undulated sculpture. Periostracum thin corneous. Shell color brownish to yellowish-brown, with thin, brown peripheral band. Last whorl rounded, with very weak peripheral keel that weakens close to aperture. Aperture straight, broadly ovate-lunate; lip simple to thickened in adult specimens. Columella slightly dilated; parietal callus thin and translucent. Umbilicus relatively wide and deep.

Remarks. Morgan (1885b) seems to have described *H. lahatensis* based on juvenile specimens, where the syntype (fig. 3E) has a very thin shell and pale brown shell color, strong peripheral keel, and very thin and sharp apertural lip. These traits appear in both *H. retrorsa* and *H. salangana* at similar growth stages. The phylogenetic tree shows a distinct clade of two specimens from Kelantan (H80) and Terengganu (H78), with high support. This clade is recovered as a sister group to the *H. salangana* clade with fairly high support. The average genetic divergence of this clade from *H. salangana* is about 5.83%, which is comparable to that of interspecific genetic divergence of 6.67% within this sinistral *Hemiplecta* clade (table 2). Therefore, we propose this clade as a distinct species and recognize it as *H. lahatensis*. Although *H. lahatensis* tends to have a very similar shell morphology to *H. salangana*; the main distinguishing character states are the slightly smaller size, with prominent irregular growth lines both above and below the periphery. Unfortunately, we lack reproductively mature specimens, and therefore refrain to re-describe the genitalia of this species. Additional topotypic and mature specimens are necessary to clarify the status and the unique characters of this species.

4 *Hemiplecta thailandica* Sutcharit and Panha, n. sp.

Zoobank: urn:lsid:zoobank.org:pub:C102ECB3-9CFC-4AE1-91Bo-2AD7AF7C06CC
(figs 1, 4B, C, 5C, D, 6D, E)

Type material examined. Holotype CUMZ 5095/1 (width 50.1 mm, height 29.1 mm; fig. 4B). Paratypes. Same data as holotype: CUMZ 5047 (1 shell), 5049 (1 shell), 5052 (4 shells), 5057 (1 shell), 5063 (3 (shells), 5071 (11 shells), 5072 (13 shells), 5073 (10 shells), 5095/2 (3 specimens in ethanol), NHMUK (2 shells), SMF (2 shells).

Other material examined. THAILAND: Klong Keaw Waterfall, Bo Rai District, Trat Province: CUMZ 5048. Wat Khao Sukim, Tha Mai District, Chanthaburi Province: CUMZ 5050, 5053, 5054, 5056, 5060, 5064, 5067, 5069. Makok Waterfall, Khlung District, Chanthaburi Province: CUMZ 5051, 5055, 5059, 5062, 5066, 5068, 5075, 5078, 5080. Aow-Beng Waterfall, Makham District, Chanthaburi Province: CUMZ 5058. Hin Dard Waterfall, Pong Namron District, Chanthaburi Province: CUMZ 5061. Plieu Waterfall, Chanthaburi Province: CUMZ 5098 (fig. 4C). Sib-ha Chan Waterfall, Kaeng Hang Maeo District, Chanthaburi Province: CUMZ 5065, 5079. Boy Scout Camping area, Khao Khitchakut District, Chanthaburi Province: CUMZ 5074.

Type locality. The primary evergreen forest at Khao Soidao, Soidao District, Chanthaburi Province (12°55'19.2"N 102°14'51.6"E).

Etymology. The species name "*thailandica*" refers to the type locality of this new species in Chanthaburi Province, Thailand.

Diagnosis. Large and low conic shell with brown to brownish yellow shell color, rounded last whorl with narrow dark brown spiral band

on periphery. Penial sculpture with small penial papillae arranged over nearly entire penis length.

Description

Shell (fig. 4B, C). Shell large (width up to 55.0 mm, height up to 35.0 mm), low conic, thickened and sinistral. Whorls 6–7, increasing regularly, convex, with depressed suture. Spire convex; apex acute; embryonic shell smooth; following whorls with irregular growth lines and spirally undulated sculpture. Periostracum thin corneous to brownish. Shell color brownish to yellowish brown, and with dark brown band on periphery. Last whorl with rounded to weak peripheral keel. Aperture descending; broadly ovate-lunate; lip simple to thickened in adult specimens. Columella slightly dilated; parietal callus thin and translucent. Umbilicus narrow and deep.

Genitalia (fig. 5C, D). Atrium short. Penis a long, slender and cylindrical tube. Epiphallus about same length as penis. Epiphallic caecum short, straight; penial retractor muscle thin and attached at the tip. Flagellum very short and enlarged. Vas deferens a narrow tube connecting the free oviduct and epiphallic-flagellum junction. Internal wall of penis exhibits closely packed papillae over nearly entire penis length; penial verge absent.

Vagina long, about same length as penis, cylindrical and with a similar diameter as the penis. Internal wall of vagina corrugated, forming a thin and smooth longitudinal pilasters. Dart apparatus a very long and enlarged muscular cylinder; dart papilla short, conic with smooth surface. Gametolytic organ large, of globular shape. Free oviduct long and surrounded by thickened blackish (pinkish in fresh specimens) tissue around the middle.

Radula (fig. 6D, E). Each row with about 250+ teeth (+120–(70–80)–1–(70–80)–130+). Central tooth unicuspid triangular with pointed head. Lateral teeth unicuspid, oblique and inclined towards central tooth; inner teeth with triangular shape; outer teeth much elongated and similar to marginal teeth. Marginal teeth start from tooth 70–80, elongate bicuspid; endocone large and ectocone small with pointed head.

Remarks. This new species is mainly distributed in the eastern part of Thailand in Chanthaburi and Trat Provinces, and probably in the Cardamom Mountains of Cambodia (Sutcharit et al., 2020). *Hemiplecta thailandica* n. sp. can be distinguished from *H. retrorsa* and *H. salangana* in having a relatively larger shell, more elevated spire, more depressed suture, a well-rounded last whorl, with dark brown spiral band on periphery, which is only slightly descending near aperture.

5 *Hemiplecta ligorica* Sutcharit and Panha, n. sp.

Zoobank: urn:lsid:zoobank.org:act:13C3CF0F-033A-4B45-9474-0ABE79A6FF66 (figs 1, 4D, E, 5E, F, 6F)

Type material examined. Holotype CUMZ 5093/1 (width 31.8 mm, height 19.3 mm; fig. 4D). Paratypes. Same data as holotype: CUMZ 5087 (1 specimen in ethanol; fig. 4E), 5090 (6 shells), 5093/2 (2 shells), NHMUK (1 shell), SMF (1 shell).

Other material examined. THAILAND: Khao Phanom Wang, Kanchanadit District, Suratthani Province: CUMZ 5089. Krung Ching Waterfall, Nop Phitam District, Nakhon Si Thammarat Province: CUMZ 5083, 5084, 5085, 5092. Tam Lord, Nop Phitam District, Nakhon Si Thammarat Province: CUMZ 5086, 5088.

Type locality. The limestone hills at Tam Khao Lek, Nop Phitam District, Nakhon Si Thammarat Province, Thailand (8°46'05.6"N, 99°43'38.5"E).

Etymology. For the historical name of Nakhon Si Thammarat Province, where the type locality is situated.

Diagnosis. Small, sinistral helicoid shell with whitish color, rounded last whorl with dark brown to brownish spiral band on periphery and upper shell surface. Penial sculpture with small papillae arranged over about half of penis length.

Description

Shell (fig. 4D, E). Shell small (width up to 32.0 mm, height up to 20.0 mm), depressed conic, thickened and sinistral. Whorls 5–6, increasing regularly, little convex, with very wide and depressed suture. Spire convex; apex acute; embryonic shell smooth; following whorls with thin growth lines and spirally undulated sculpture. Periostracum thin and transparent. Shell color whitish to pale brown, usually with wide blackish to dark brown peripheral band just below periphery, and narrow brown spiral band on upper part of last whorl. Last whorl usually well-rounded to little angular. Aperture little descending, ovate-lunate; lip simple to thickened in adult specimens. Columella slightly dilated; parietal callus thin and translucent. Umbilicus narrowly open and deep.

Genitalia (fig. 5E, F). Atrium very short. Penis a short, slender and cylindrical tube. Epiphallus long, about three times the penis length. Epiphallic caecum short, straight; penial retractor muscle thin and attached to the tip. Flagellum very short. Vas deferens a narrow tube connecting the free oviduct and epiphallic-flagellum junction. Internal wall of penis exhibits closely packed papillae over about

half of penis length that abruptly cease close to atrium; penial verge absent.

Vagina long, about two times the length of penis, cylindrical and its diameter similar to that of penis. Internally vagina possesses few corrugated pilasters, which are thin and smooth longitudinal pilasters. Dart apparatus a long muscular cylinder; dart papilla long, conic, with a smooth surface. Gametolytic organ large, of globular shape. Free oviduct long and surrounded by thickened blackish tissue (pinkish in fresh specimens) at distal end.

Radula (fig. 6F). Each row with 240+ teeth (+120–(15–20)–1–(15–20)–120+). Central tooth unicuspid triangular with rounded head. Lateral teeth unicuspid, oblique, triangular and inclined towards central tooth. Marginal teeth start from tooth 15–20, bicuspid, endocone and ectocone small with round head.

Remarks. *Hemiplecta ligorica* n. sp. is known from several localities in limestones outcrops in Suratthani and Nakhon Sri Thammarat Provinces. They tend to be distributed along the Khao Luang range in moist to dry evergreen forest. This new species differs from all other sinistral species in having a relatively smaller, pale brownish to whitish shell with two dark brown spiral bands: one on the periphery and another below the periphery.

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