Molecular phylogeny of the limacoid snail family Dyakiidae in Southeast Asia, with the description of a new genus and species

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Members of the terrestrial snail family Dyakiidae from Southeast Asia show a distinct geographical distribution pattern and possess different degrees of complexity in their amatorial organ gland. This study is the first molecular phylogeny of ten of the 12 genera in this family, performed to provide insights into the origin of Dyakiidae and the evolution of their shells and amatorial organ gland structure. A new genus and new species, ***Pseudoquantula lenticularis*** Jirapatrasilp & Panha **gen. & sp. nov.**, was uncovered based on its distinct morphological characters and molecular divergence. All other genera were retrieved as monophyletic except for *Dyakia*. Mainland Southeast Asia was inferred to be the ancestral range of the Dyakiidae, and the lineages then dispersed to and diversified in Borneo. Cladistic analysis showed that all 14 morphological characters used in this study were homoplastic. These results disagree with the previous amatorial organ transformation series, in which neither *Pseudoplecta* nor *Quantula* was ancestral to the other genera. The enigmatic genus *Pseudoplecta*, which lacks an amatorial organ gland, exhibited secondary loss.

ADDITIONAL KEYWORDS: biogeography – cladistic analysis – homoplasy – molecular systematics – phylogenetics – plesiomorphy – Southeast Asia.

INTRODUCTION

Terrestrial snails in the family Dyakiidae Gude & Woodward, 1921 belong to the infraorder Limacoidei ('limacoid clade'; Bouchet *et al*., 2017) or superfamily Limacoidea ('Limacacea') *s.l.* (Baker, 1941; Hausdorf, 1998, 2000). At present, the family contains 11 genera restricted to Southeast Asia, including mainland Indochina, the Malay Peninsula and the Indo-Malay Archipelago (Table 1). The members of Dyakiidae exhibit both dextral and sinistral forms and various shell shapes that range from lens-shaped, subglobose to trochiform. Accordingly, their classification based on only shell morphology might lead to confusion with other families in the same infraorder, such as Ariophantidae and Helicarionidae.

The family was first defined by Laidlaw (1931) based on the possession of an amatorial organ complex consisting of an amatorial organ (dart sac) furnished with accessory glands attached to its upper pole by one or more coiled tubules, a gametolytic sac attached to the amatorial organ, and the absence of shell lobes. Laidlaw (1931) included the four genera, *Dyakia* Godwin-Austen, 1891, *Everettia* Godwin-Austen,

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Table 1. An updated list of genera in the family Dyakiidae, its type species, diagnostic morphological characters, distributional range and number of species

Genera (type species)	Diagnostic morphological characters	Distributional range	Number of species	References*
Bertia Ancey, 1887	Shell: sinistral, semi-globose, well rounded	Cambodia and Vietnam	4	1, 2
(*Helix cambojiensis* Reeve, 1860)	Genitalia: **amg** four lobes, each lobe with thick **amd**; **go** attached to **am** without distinct division, slightly swollen near atrium, then tapering to small and cylindrical tube			
Dyakia Godwin-Austen, 1891	Shell: sinistral, turbinate, keeled	Peninsular Malaysia and Greater Sunda Islands	~20	1, 3, 4
(*Helix hugonis* Pfeiffer, 1863)	Genitalia: **amg** three or four lobes, each lobe with slender **amd** before fusion into common duct; **go** attached to **am**, with **gd** large and cylindrical and **gs** elongated and bulbous			
Everettia Godwin-Austen, 1891	Shell: dextral, depressed conical, well rounded	Endemic to Borneo	~30	1, 4, 5
(*Helix jucunda* Pfeiffer, 1863)	Genitalia: **amg** more than ten lobes, each lobe with slender **amd**; **go** attached to **am** without distinct division			
Asperitas Gude, 1911	Shell: dextral, subglobose to trochiform, well rounded to more or less angled	Lesser Sunda Islands, south-western Sulawesi and islands surrounding Banda Sea	~1–6	1, 4, 6
(*Xestina rugosissima* Möllendorff, 1903 (= Helix trochus Müller, 1774))	Genitalia: **amg** alveolar, three or four lobes, their upper parts integrated to tissue of vagina walls; each lobe with slender **amd**; **go** attached to **am** without distinct division			
Elaphroconcha Gude, 1911	Shell: amphidromous, depressed orbicular and well rounded	Sumatra, Java and Lesser Sunda Islands	~10	1, 4, 7
(*Ariophanta internota* Smith, 1898 (= *Nanina fruhstorferi* Martens, 1896))	Genitalia: **amg** three or four lobes, each lobe with slender **amd** before fusion into common duct; **go** attached shortly above atrium, with **gd** long and **gs** well defined, with stretched out tip			
Sasakina Rensch, 1930	Shell: dextral, conical trochiform and keeled	Lesser Sunda Islands	4	1, 4
(*Trochonanina oxyconus* Martens, 1896)	Genitalia: **amg** three lobes, with common **amd**; **go** attached to atrium without distinct division			
Kalamantania Laidlaw, 1931	Shell: dextral, depressed subglobose, well rounded and with limacisation	Endemic to Sabah in Borneo	1	1, 4
(*Helicarion*? *whiteheadi* Godwin-Austen, 1891)	Genitalia: **amg** about six or seven lobes, each lobe with slender **amd**; **go** attached to boundary between **am** and **fo** without distinct division; additional compact **gg** attached to lower half of **go** by several short ducts			

Table 1. Continued

Genera (type species)	Diagnostic morphological characters	Distributional range	Number of species	References*
Rhinocochlis Thiele, 1931 (*Helix nasuta* Metcalfe, 1852)	Shell: sinistral, lens shaped, keeled Genitalia: **amg** two lobes, each lobe with slender **amd**; **go** large attached to **am** without distinct division	Endemic to Borneo	1–2	1, 4
Pseudoplecta Laidlaw, 1932 (*Rotula bijuga* Stoliczka, 1873)	Shell: dextral, obesely lenticular, keeled Genitalia: **amg** and **amd** absent; **go** attached to tip of **am**, with **gd** cylindrical and **gs** elongated and bulbous	Peninsular Malaysia and Sumatra	1	1, 4
Quantula Baker, 1941 (*Nanina striata* Gray, 1834)	Shell: dextral, depressed to subglobose, more or less angled Genitalia: **amg** more than ten lobes, whose ducts enter long common **amd**; **go** small attached to **am**, with **gd** short and **gs** ovate	Indochina and introduced to Fiji and Line Archipelago	4	1, 4, 8
Phuphania Tumpeesuwan *et al*., 2007 (*Phuphania globosa* Tumpeesuwan *et al*., 2007)	Shell: dextral, semi-globose to globose and well rounded Genitalia: **amg** fused lobes, forms an ovate cap covering **am** and consists of two to six clusters of numerous **amd**; **go** attached to **am**, with **gd** cylindrical and **gs** gradually swollen to the end	Central and Northeastern Thailand	4	9, this study
Pseudoquantula (***Pseudoquantula lenticularis***)	Shell: dextral, depressed subglobose and keeled Genitalia: **amg** two lobes, each lobe with thick **amd**; **go** attached to **am**, with **gd** cylindrical and **gs** slightly swollen	Eastern Thailand	1	This study

The list of genera is given in chronological order. The term 'short' or 'long' is compared in relationship to the penis.
*1 = Schileyko (2003); 2 = Thach (2015); Hun *et al*. (2019); Sutcharit *et al*. (2019); 3 = Laidlaw (1963); Sutcharit *et al*. (2012); 4 = Hausdorf (1995);
5 = Liew *et al*. (2009); Hyman & Ponder (2010); 6 = Dharma (1999); Köhler *et al*. (2020); 7 = Dharma (1991); 8 = Abu-Bakar *et al*. (2014); BEDO (2017);
9 = Kongim & Panha (2013); Tumpeesuwan *et al*. (2007); Tumpeesuwan & Tumpeesuwan (2014).

1891, *Kalamantania* Laidlaw, 1931 and *Staffordia* Godwin-Austen, 1907. Later, eight additional genera were included in this family based on diagnostic characteristics identified by Laidlaw (1931) (Thiele, 1934; Baker, 1941; Schileyko, 2003; Tumpeesuwan *et al*., 2007). However, *Staffordia* was subsequently excluded from Dyakiidae and placed in its own family owing to the combined characteristics of both Ariophantidae and Dyakiidae, such as the presence of an amatorial organ complex and shell lobes, a gametolytic sac attached to the vagina, and the absence of caudal foss and horn (Schileyko, 2003). This present classification has followed Bouchet *et al*. (2017), excluding the tribe Vitrinulini Schileyko, 2003, which is now treated as a junior synonym of the subfamily Macrochlamydinae of Ariophantidae.

Hausdorf (1995) was the first to propose a hypothesis of the evolutionary relationships of Dyakiidae based on a cladistic analysis of morphological data. Later, two species of *Asperitas* Gude, 1911 were sequenced as representatives from this family and added to a molecular phylogenetic and phylogenomic analyses of a higher-level classification (Wade *et al*., 2001, 2006; Teasdale, 2017). Those molecular phylogenetic studies confirmed the phylogenetic position of *Asperitas* within Limacoidei and that this genus represented a distinct clade closely related but not identical to the families Ariophantidae and Helicarionidae. Hausdorf (1995) claimed that the understanding of the relationships among dyakiid genera could provide insights into the evolution of Stylommatophora and Limacoidei, because dyakiid

genera exhibited a unique transformation series of an amatorial organ complex, which functions as a stimulator during copulation. In addition, the different distribution pattern of each genus could provide insights into the historical biogeography of Southeast Asia, an area that received attention from biogeographers for a long period of time (e.g. Wallace, 1860; Lohman *et al.*, 2011; de Bruyn *et al.*, 2014). However, since the discovery of *Phuphania* Tumpeesuwan, Naggs & Panha, 2007 (Tumpeesuwan *et al.*, 2007), there has been no further updated phylogeny and biogeographical analysis of Dyakiidae as a whole based on either morphological or molecular data. The molecular phylogenetic studies of Dyakiidae up to now were conducted only on the genus *Everettia* in northern Borneo owing to the endemism and high species diversity of the genus there (Liew *et al.*, 2009, 2020).

The present study is the first since the paper by Hausdorf (1995) to elucidate the relationships within Dyakiidae and the first to use a molecular phylogenetic analysis constructed from two mitochondrial [cytochrome *c* oxidase subunit I (*COI*) and 16S ribosomal (r)DNA] and one nuclear (28S rDNA) marker. We also test the hypotheses of Hausdorf (1995) by conducting a cladistic analysis of the morphological data and estimating the ancestral ranges of the genera in this family in order to reveal the evolution of morphological characters and biogeographical history of this family. In addition, one new genus and new species are described herein based on its distinct morpho-anatomical characters and its evolutionary distinctiveness as estimated by means of molecular phylogenetics.

MATERIAL AND METHODS

PREPARATION OF SPECIMENS AND MORPHOLOGICAL EXAMINATION

Voucher specimens of the family Dyakiidae collected from Thailand and surrounding countries in Southeast Asia since 2006 and deposited in Chulalongkorn University Museum of Zoology (CUMZ), Bangkok, Thailand, were examined. Additional Bornean specimens deposited in the BORNEENSIS mollusc collection at Universiti Malaysia Sabah (BOR/MOL) and *Bertia* Ancey, 1887 specimens deposited in the Natural History Museum, London (NHMUK) were also used in the molecular analyses. Two genera, *Inozonites* Pfeffer, 1883 and *Pliotropis* Möllendorff, 1899, which are presently classified in Dyakiidae (MolluscaBase, 2020), were not included in this study, because without any anatomical data their taxonomic positions remain dubious (Schileyko, 2003). In addition, two sinistral

taxa from southern Thailand, *Dyakia retrorsa* (Gould, 1844) and *Dyakia salangana* (Martens, 1883), which were excluded from Dyakiidae by Sutcharit *et al.* (2012), were also not included in the present study. Thus, a total of 51 specimens belonging to 29 morphospecies and ten genera of Dyakiidae sampled from mainland Southeast Asia, Peninsular Malaysia and Sabah were included in the molecular phylogenetic analysis (Fig. 1; Table 2). Genetic data were not obtained from two genera of Dyakiidae, namely, *Elaphroconcha* Gude, 1911 and *Sasakina* Rensch, 1930, and the outgroup *Staffordia* (Staffordiidae) in the study by Hausdorf (1995). Hence, these three genera were not included in the phylogenetic analysis. Four species of Ariophantidae, *Cryptozona siamensis* (Pfeiffer, 1856), *Hemiplecta distincta* (Pfeiffer, 1850), *Sarika resplendens* (Philippi, 1846) and *Sarika* sp., were used as the outgroup.

The living snails were photographed and killed by the two-step method for euthanasia (AVMA, 2013). Some specimens from each locality were fixed and preserved in 70% (v/v) ethanol for anatomical studies, and the remaining specimens were preserved in 95% (v/v) ethanol for molecular analyses. The handling of
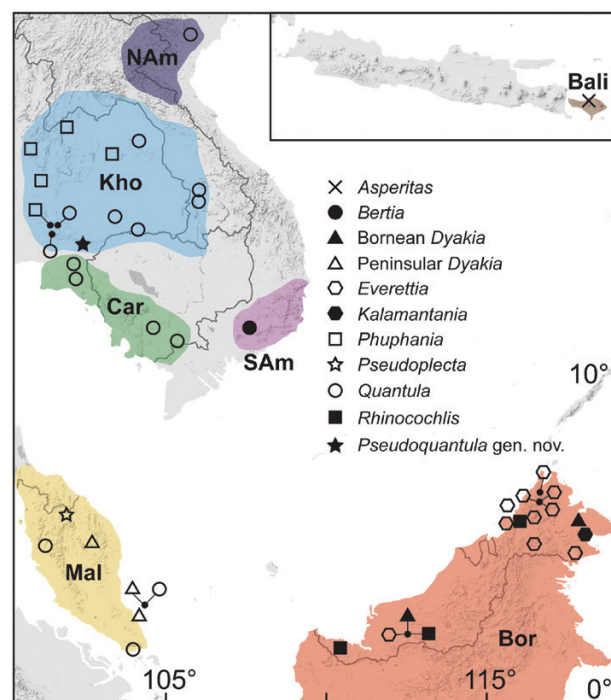

Figure 1. Distribution map of the samples in the family Dyakiidae used in this study. The shaded colours correspond to those in Figure 4. Abbreviations: Bali, Bali Island; Bor, Borneo Island; Car, Cardamom Range; Kho, Khorat Plateau; Mal, Malay Peninsula; NAm, northern Annamite Range; SAm, southern Annamite Range.

Table 2. List of specimens used in the molecular phylogenetic analysis with species name, locality details and GenBank accession numbers

No.	Specimen no.	Taxa	Area code	Latitude, longitude coordinates	Collection no.	Accession numbers		
						COI	16S rDNA	28S rDNA
1	H31	*Asperitas trochus* (Müller, 1774)	Bali	8°24′44.4″S, 115°35′12.3″E	CUMZ 5154	MT654630	MT651546	MT651601
2	H34	*Bertia cambojiensis* (Reeve, 1860)*	SAm	11°26′8.8″N, 107°25′38.6″E	NHMUK 20130833	MN296022	MN296390	–
3	H58	*Bertia cambojiensis* (Reeve, 1860)*	SAm	11°26′8.8″N, 107°25′38.6″E	NHMUK 20130833	MN296023	MN296391	MN296349
4	E13946	*Dyakia hugonis* (Pfeiffer, 1863)*	Bor	5°26′45.0″N, 117°3150.0′E	BOR/MOL 13946	MT803064	MT741748	MT741915
5	H9	*Dyakia janus* (Beck, 1837)	Mal	2°25′48.0″N, 103°59′00.6′E	CUMZ 4918	MT654622	MT651538	MT651593
6	H57	*Dyakia janus* (Beck, 1837)	Mal	2°48′36.9″N, 104°08′46.8″E	CUMZ 5180	MT654623	MT651539	MT651594
7	E126	*Dyakia* sp. 1	Bor	1°42′21.6″N, 112°32′55.9″E	BOR/MOL 5476	MT803065	MT741749	MT741916
8	E14362	*Dyakia* sp. 2	Mal	4°35′10.3″N, 102°28′14.4′E	BOR/MOL 14362	MT803066	MT741750	–
9	E16	*Everettia corrugata* (Laidlaw, 1937)	Bor	6°10′24.4″N, 116°29′29.3″E	BOR/MOL 12936	FJ160666	FJ160619	–
10	E14411	*Everettia dominiki* Liew *et al*., 2009	Bor	5°33′05.2″N, 116°3144.0′E	BOR/MOL 14411	MT803067	MT741751	MT741917
11	E26	*Everettia interior* Liew *et al*., 2009	Bor	4°38′17.3″N, 116°37′3.3″E	BOR/MOL 1137	FJ160684	FJ160637	.
12	E1	*Everettia jucunda* (Pfeiffer, 1863)*	Bor	5°19′29.9″N, 115°40′21.0′E	BOR/MOL 4261	FJ160682	FJ160635	–
13	E2	*Everettia jucunda* (Pfeiffer, 1863)*	Bor	5°43′33.3″N, 115°39′3.7′E	BOR/MOL 4237	FJ160683	FJ160636	–
14	E30	*Everettia jucundior* Liew *et al*., 2009	Bor	4°28′0″N, 117°55′0′E	BOR/MOL 1376	FJ160661	FJ160612	–

Table 2. Continued

No.	Specimen no.	Taxa	Locality name	Area code	Latitude, longitude coordinates	Accession numbers		
						COI	16S rDNA	28S rDNA
15	E25	*Everettia lapidini* Liew et al., 2009	Mt Kinabalu south-western slope, ~1700 m, Sabah, Malaysia	Bor	6°0′20.9″N, 116°32′33.9″E	FJ160692	FJ160645	–
16	E20	*Everettia layanglayang* Liew et al., 2009	Mt Kinabalu north-western slope, S132, Sabah, Malaysia	Bor	6°8′20.3″N, 116°33′59.7″E	FJ160671	FJ160624	–
17	E3	*Everettia subconsul* (Smith, 1887)	Mt Tambuyukon eastern slope, 1100 m S114, Sabah, Malaysia	Bor	6°12′31.8″N, 116°41′55.2″E	FJ160676	FJ160629	–
18	E124	*Everettia* sp. 1	Lanjak Entimau, Sibu, Sarawak, Malaysia	Bor	1°42′21.6″N, 112°32′55.9″E	MT803068	MT741752	MT741918
19	K13849	*Kalamantania whiteheadi* (Godwin-Austen, 1891)*	Mt. Silam, Lahad Datu, Sabah, Malaysia	Bor	4°57′56.0″N, 118°10′25.0″E	MT803069	–	MT741919
20	H67	*Phuphania costata* Tumpeesuwan & Tumpeesuwan, 2014	Pha Phu, Loei, Thailand	Kho	17°34′39.9″N, 101°42′39.5″E	MT654625	MT651541	MT651596
21	H125	*Phuphania carinata* Kongim & Panha, 2013	Phu Kiew, Chiayaphum, Thailand	Kho	16°09′42.0″N, 101°39′36.0″E	MT803070	MT741753	–
22	H5	*Phuphania crossei* (Pfeiffer, 1862)	Jedkot Waterfall, Saraburi, Thailand	Kho	14°28′30.7″N, 101°09′29.0″E	MT654626	MT651542	MT651597
23	H8	*Phuphania crossei* (Pfeiffer, 1862)	Sakumotayan Waterfall, Phitsanulok, Thailand	Kho	16°50′11.9″N, 100°31′51.5″E	MT803071	MT741754	–
24	H61	*Phuphania crossei* (Pfeiffer, 1862)	Sap Chomphu Arboretum, Phetchabun, Thailand	Kho	15°55′43.5″N, 100°57′44.7″E	MT803072	MT741755	MT741920
25	H12	*Phuphania globosa* Tumpeesuwan et al., 2007*	Wat Tam Nam Pok, Khon Kaen, Thailand	Kho	16°49′01.5″N, 103°09′00.7″E	MT803073	–	MT741921
26	H42	*Phuphania globosa* Tumpeesuwan et al., 2007*	Nam Pung Reservoir, Sakon Nakhon, Thailand	Kho	16°57′21.5″N, 103°58′10.1″E	MT654624	MT651540	MT651595

Table 2. Continued

No.	Specimen no.	Taxa	Locality name	Area code	Latitude, longitude coordinates	Collection no.	Accession numbers		
							COI	16S rDNA	28S rDNA
27	H73	*Pseudoplecta bijuga* (Stoliczka, 1873)*	Air Bunum, Banding, Perak, Malaysia	Mal	5°38′13.4″N, 101°42′41.1″E	CUMZ 5150	MT654627	MT651543	MT651598
28	H21	**Pseudoquantula lenticularis** Jirapatrasilp & Panha, 2020	Khao Yai, Nakhon Nayok Province, Thailand	Kho	13°59′13.6″N, 102°12′18.3″E	CUMZ 5172	MT803074	MT741756	MT741922
29	H33	**Pseudoquantula lenticularis** Jirapatrasilp & Panha, 2020	Pang Srida Waterfall, Sa Kaeo, Thailand	Kho	13°59′13.6″N, 102°12′18.3″E	CUMZ 5152	MT803075	MT741757	MT741923
30	H72	**Pseudoquantula lenticularis** Jirapatrasilp & Panha, 2020	Pang Srida Waterfall, Sa Kaeo, Thailand	Kho	13°59′13.6″N, 102°12′18.3″E	CUMZ 5152	MT803076	–	MT741924
31	H30	*Quantula godwinausteni* (Laidlaw, 1931)	Wat Khao Sukim, Chanthaburi, Thailand	Car	12°45′48.9″N, 102°02′00.2″E	CUMZ 5171	MT803077	MT741758	MT741925
32	H17	*Quantula striata* (Gray, 1834)*	Yan Tao San, Ipoh, Perak, Malaysia	Mal	4°36′34.6″N, 101°6′49.9″E	CUMZ 5188	–	MT741759	MT741926
33	H23	*Quantula striata* (Gray, 1834)*	Singapore Botanic Gardens, Singapore	Mal	1°18′49.6″N, 103°48′56.6″E	CUMZ 5165	MT654628	MT651544	MT651599
34	H26	*Quantula striata* (Gray, 1834)*	Singapore Botanic Gardens, Singapore	Mal	1°18′49.6″N, 103°48′56.6″E	CUMZ 5165	MT803078	MT741760	MT741927
35	H56	*Quantula striata* (Gray, 1834)*	Pulau Tioman, Pahang, Malaysia	Mal	2°45′44.0″N, 104°07′24.7″E	CUMZ 5179	MT803079	–	MT741928
36	H18	*Quantula weinkauffiana* (Crosse & Fischer, 1863)	Khao Panom Sawai, Surin, Thailand	Kho	14°45′46.4″N, 103°22′10.6″E	CUMZ 5163	MT803080	MT741761	MT741929
37	H52	*Quantula weinkauffiana* (Crosse & Fischer, 1863)	Khong Sedon, Salavan, Laos	Kho	15°37′40.0″N, 105°47′38.7″E	CUMZ 5177	MT803081	–	MT741930
38	H53	*Quantula weinkauffiana* (Crosse & Fischer, 1863)	Tad Pha Suam, Champasak, Laos	Kho	15°16′36.8″N, 105°55′21.1″E	CUMZ 5178	MT803082	MT741762	MT741931

Table 2. Continued

No.	Specimen no.	Taxa	Locality name	Area code	Latitude, longitude coordinates	Collection no.	Accession numbers		
							COI	16S rDNA	28S rDNA
39	CA11	*Quantula weinkauffiana* (Crosse & Fischer, 1863)	Phnom Kampong Trach Cave Temple, Kampong Trach, Kampot, Cambodia	Car	10°34'1.77"N 104°28'6.13"E	CUMZ-CM215	MT803083	MT741763	MT741932
40	CA13	*Quantula weinkauffiana* (Crosse & Fischer, 1863)	Phnom Chhngok Cave, Tuek Chhou, Kampot, Cambodia	Car	10°38'34.91"N 104°16'4.07"E	CUMZ-CM216	MT803084	MT741764	MT741933
41	H122	*Quantula* sp. 1	Nang Rong Waterfall, Nakhon Nayok, Thailand	Kho	14°19'41.4"N, 101°19'05.2"E	CUMZ 5185	MT803085	MT741765	–
42	H24	*Quantula* sp. 1	Wang Ta Krai Waterfall, Nakhon Nayok, Thailand	Kho	14°19'58.9"N, 101°18'17.0"E	CUMZ 5170	MT803086	–	MT741934
43	H50	*Quantula* sp. 1	Khao Ang Rue Nai, Chacheongsao, Thailand	Car	13°25'08.0"N, 101°53'00.5"E	CUMZ 5175	MT803087	–	MT741935
44	H60	*Quantula* sp. 1	Wat Khao Sala, Surin, Thailand	Kho	14°25'09.5"N, 103°56'00.0"E	CUMZ 5181	MT803088	–	MT741936
45	H94	*Quantula* sp. 1	Wang Ta Krai Waterfall, Nakhon Nayok, Thailand	Kho	14°19'58.9"N, 101°18'17.0"E	CUMZ 5170	MT803089	MT741766	–
46	H97	*Quantula* sp. 1	Khao Ang Rue Nai, Chacheongsao, Thailand	Car	13°25'08.0"N, 101°53'00.5"E	CUMZ 5175	MT803090	MT741767	–
47	H51	*Quantula* sp. 2	Kam Hom Waterfall, Sakon Nakhon, Thailand	Kho	17°07'20.3"N, 104°01'07.4"E	CUMZ 5176	MT803091	MT741768	–
48	H124	*Quantula* sp. 3	Cuc Phuong, Nho Quan, Ninh Binh, Vietnam	NAm	20°15'04.0"N, 105°42'49.5"E	CUMZ 5186	MT803092	MT741769	–
49	E6297	*Rhinocochlis moluensis* (Godwin-Austen, 1891)	Crocker Range Park, Keningau, Sabah, Malaysia	Bor	5°20'14.6"N, 116°09'24.1"E	BOR/MOL 6297	MT803093	MT741770	MT741937
50	H19	*Rhinocochlis nasuta* (Metcalfe, 1852)*	Fairy Cave, Bau, Sarawak, Malaysia	Bor	1°22'52.4"N, 110°07'07.4"E	CUMZ 5162	MT654629	MT651545	MT651600
51	E127	*Rhinocochlis nasuta* (Metcalfe, 1852)*	Lanjak Entimau, Sibu, Sarawak, Malaysia	Bor	1°42'21.6"N, 112°32'55.9"E	BOR/MOL 5479	MT803094	MT741771	MT741938

Table 2. Continued

No.	Specimen no.	Taxa	Area code	Latitude, longitude coordinates	Locality name	Collection no.	Accession numbers		
							COI	16S rDNA	28S rDNA
52	H54	*Hemiplecta distincta* (Pfeiffer, 1850)	–	15°16′36.8″N, 105°55′21.1″E	Tad Pha Suam, Champasak, Laos	CUMZ 5267	MT654617	MT651532	MT651588
53	S129	*Cryptozona siamensis* (Pfeiffer, 1856)	–	10°29′49.5″N, 98°57′17.8″E	Wat Tha Mai Lai, Chumphon, Thailand	CUMZ 7240	MT364992	MT365774	MT365718
54	W4	*Sarika resplendens* (Philippi, 1846)	–	13°43′32.7″N 99°44′35.1″E	Khao Cha Ngum, Ratchaburi, Thailand	CUMZ 7234	MT364982	MT365763	MT365707
55	H48	*Sarika* sp.	–	4°54′54.9″N, 114°57′14.7″E	Bukit Sarang Helang, Bandar Seri Begawan, Brunei	CUMZ 5187	MT803095	MT741772	MT741939

Specimen numbers correspond to the numbers in Figure 2. Asterisk indicates the type species of its respective genus. Area codes follow those in Figure 1.

animals in this study was approved by Chulalongkorn University Animal Care and Use Committee (CU-ACUC) under the approval number 1723018. No material from BORNEENSIS was exported from Sabah, Malaysia, and all the sampling and laboratory procedures of the BOR/MOL specimen were performed by T.-S. Liew at Universiti Malaysia Sabah.

Intact adult shells were measured for whorl number, shell height (*h*) and maximum diameter or shell width (*d*) using a digital vernier calliper. The genitalia of three to ten specimens of each species were dissected and examined under an Olympus SZX2-TR30 stereoscopic light microscope. Shells and reproductive organs were imaged using a digital camera and a stereo microscope with Cell'D Imaging Software. Radulae were extracted, soaked in 10% (w/v) sodium hydroxide, cleaned with distilled water and then imaged by scanning electron microscopy (JEOL, JSM-6610 LV). Species identification and generic assignment followed Hausdorf (1995), Schileyko (2003), Tumpeesuwan *et al*. (2007), Liew *et al*. (2009) and Sutcharit *et al*. (2012, 2019), and specimens were compared with the relevant type specimens of the type species if possible. The morphological examination of the genera that could not be obtained in this study was done based on figures in the paper by Schileyko (2003).

Shell characters described refer to empty shells, whereas non-shell characters were derived from specimens preserved in ethanol. The general vouchers and type specimens were deposited in CUMZ and NHMUK.

ACQUISITION OF DNA SEQUENCE DATA

Whole genomic DNA was extracted from a small piece of foot muscle tissue using the NucleoSpin Tissue Kit (Macherey-Nagel, Germany) or DNeasy Blood & Tissue Kits (QIAGEN). Sequences of the two partial mitochondrial markers (*COI* and 16S rDNA) were amplified using the LCO1490 and HCO2198 (Folmer *et al*., 1994) and the 16Sar and 16Sbr (Palumbi *et al*., 1991) universal primers, respectively. Sequences of the large subunit of the nuclear rRNA gene (28S rDNA) were amplified using the 28SF4 and 28SR5 primers (Morgan *et al*., 2002). A nested polymerase chain reaction (PCR) was performed for unsuccessful amplifications by using the internal primers given in the Supporting Information (Table S1). The PCR thermal cycling conditions were as follows: 94 °C for 2 min, followed by 36 cycles of 94 °C for 30 s, the annealing temperature specific to each gene fragment (Supporting Information Table S1) for 2 min, and 72 °C for 2 min, and then a final extension step of 72 °C for 5 min. The PCR products were sent for commercial sequencing at Bioneer Co., Korea or Apical Scientific Sdn Bhd, Malaysia.

SEQUENCE ALIGNMENT AND MOLECULAR PHYLOGENETIC ANALYSES

Chromatograms were checked manually for misreads, and sequences were then trimmed in MEGA v.7.0 (Kumar *et al*., 2016). The sequence alignments of each gene fragment were performed separately using MAFFT v.7, which is available online (https://mafft. cbrc.jp/alignment/server/index.html), with default options (Katoh *et al*., 2017). The newly generated sequences have been deposited in the GenBank database with accession numbers given in Table 2.

The concatenated dataset was prepared in KAKUSAN4 (Tanabe, 2011) with the best-fitting model adjustment for maximum likelihood (ML) and Bayesian inference (BI) analyses. The ML analysis was performed by applying the best-fitting model (GTR+G for all gene fragments) to separate partitions for each gene at the default settings of RAxML-HPC2 on XSEDE v.8.2.10 (Stamatakis, 2014) in the CIPRES Science Gateway (Miller *et al*., 2010). Nodal support values of ML were assessed by performing 1000 bootstrap replicates and reported as bootstrap support (BS). The BI analysis was performed with the best-fitting models of each gene fragment (*COI* and 16S rDNA, GTR+G; 28S rDNA, HKY85+G) using MRBAYES on XSEDE v.3.2.6 (Ronquist *et al*., 2012) in the CIPRES Science Gateway. Two independent analyses were run simultaneously and consisted of four chains of 50 million generations. The sampling rate was 500 generations, and the first 50% of sampled trees were discarded as burn-in. For each node, BS values ≥ 70% were considered highly supported (Hillis & Bull, 1993) and BI posterior probability (PP) values ≥ 0.95 were considered statistically significant (San Mauro & Agorreta, 2010). Uncorrected pairwise genetic distances (*p*-distances) among different genera based on the *COI*, 16S and 28S sequences were calculated in MEGA v.7.

CLADISTIC ANALYSIS OF THE MORPHOLOGICAL DATA

The morphological characters and their states used for the cladistic analysis were modified from the study by Hausdorf (1995) (Table 3). The coding of each morphological character was compiled from the study by Hausdorf (1995) with the updated data of *Asperitas*, *Kalamantania*, *Quantula* Baker, 1941 and *Rhinocochlis* Thiele, 1931 from Schileyko (2003), *Phuphania* from Tumpeesuwan *et al*. (2007), *Everettia* from Liew *et al*. (2009), *Dyakia* from Sutcharit *et al*. (2012), *Bertia* from Sutcharit *et al*. (2019) and *Pseudoplecta* Laidlaw, 1932 and the new genus (*Pseudoquantula*, described below) from this study (Table 4). The maximum parsimony (MP) analysis of morphological data was conducted in PAUP* v.4.0a167 (Swofford, 2002) using *Staffordia* as the outgroup.

The first unconstrained analysis recovered either a polytomy of all genera (strict consensus) or some intergeneric relationships (majority-rule consensus; Supporting Information, Fig. S1). Therefore, we used the generic relationship based on the Bayesian tree, in which the nodes with PP values < 0.95 decayed into polytomy, as the constraint for the cladistic analysis of the morphological data. *Elaphroconcha*, *Sasakina* and *Staffordia* were excluded from the constrained topology because they were not analysed in the molecular phylogenetic analyses.

ANCESTRAL RANGE RECONSTRUCTION

An ultrametric tree was constructed in BEAST v.1.8.4 (Drummond *et al*., 2012), with a relative rate of 1.0, on XSEDE in the CIPRES Science Gateway. All the dyakiid taxa were grouped as the 'ingroup' and enforced to be monophyletic. Two runs of 20 million generations were executed using an uncorrelated lognormal relaxed-clock model and coalescent (constant size) model for a tree prior with a random starting tree. The appropriate substitution models for each gene partition were selected with JMODELTEST 2 v.2.1.6 on XSEDE (Darriba *et al*., 2012) in the CIPRES Science Gateway (GTR+I+G for all gene fragments). We sampled parameters every 1000 generations and assessed the convergence (ESS ≥ 200) in TRACER v.1.6 (Rambaut *et al*., 2014). LOGCOMBINER v.1.8.4 (Drummond & Rambaut, 2007) was used to combine the two runs, and TREEANNOTATOR v.1.8.4 (Drummond & Rambaut, 2007) was used to construct a single maximum clade credibility tree using median heights as node heights after tree files from both runs were combined, discarding the first 10% of trees as burn-in and rechecking the effective sample size. For each node, PP values of ≥ 0.95 were considered statistically significant (Drummond & Rambaut, 2007).

The division of the geographical area in this study follows Gupta (2005), yielding a total of seven areas (Fig. 1). The resulting ultrametric tree, excluding the outgroup, together with geographical area information (Table 2), was subjected to an ancestral range reconstruction in RASP v.4.2 (Yu *et al*., 2019). The R package BIOGEOBEARS (Matzke, 2014) was implemented in the program, and DEC+J was selected as the best model indicated by the highest Akaike information criterion (with a correction for small sample sizes) weight (AICc_wt) value (Supporting Information, Table S2). In addition, the dispersal–extinction–cladogenesis (DEC) (Ree & Smith, 2008) module, which is also implemented in the program, was applied for comparison. The maximum number of areas that could be occupied at each node was set as seven areas. Because DIVALIKE and BAYAREALIKE

Table 3. List of morphological characters and their states modified from the study by Hausdorf (1995)

Character	State
1. Number of major lobes of the amatorial organ gland	0 = l 1 = 2 2 = 3–5 3 = ~6–7 4 = > 10 5 = absent
2. Length of the amatorial organ duct(s)	0 = longer than the terminal amatorial organ section 1 = ½ to the same length as the terminal amatorial organ section 2 = ¼–½ of the length of the terminal amatorial organ section 3 = < ¼ of the length of the terminal amatorial organ section 4 = amatorial organ duct absent
3. Type of amatorial organ duct	0 = common 1 = multiple 2 = absent
4. Terminal amatorial organ section (from insertion point of **go** to terminal end of **am**)	0 = < ½ of the penis length 1 = ½ to the same length as the penis 2 = longer than penis
5. Insertion of site of the amatorial organ	0 = atrium 1 = penis 2 = vagina
6. Insertion site of the gametolytic sac	0 = vagina l = near the opening of the amatorial organ 2 = near the terminal end of the amatorial organ
7. Gametolytic sac	0 = longer than free oviduct l = shorter than free oviduct
8. Insertion site of the penial retractor	0 = near the junction between penis and epiphallus l = near the insertion point of vas deferens to epiphallus
9. Ectocone of radular marginals	0 = very small or absent l = almost as long as mesocone

Table 3. Continued

Character	State
10. Number of radular teeth per row	0 = < 200 l = > 200
11. Coiling	0 = mostly dextral l = mostly sinistral
12. Number of whorls	0 = > 4 l = < 4
13. Last whorl	0 = mostly rounded or angled l = mostly keeled
14. Shell width	0 = usually < 25 mm l = usually > 25 mm

models were retrieved as less fit in BioGeoBEARS, S-DIVA (Yu *et al*., 2010) and BayesArea (Landis *et al*., 2013) modules which are similar to DIVALIKE and BAYAREALIKE models, respectively, were not applied further.

DESCRIPTIONS OF GENERA AND SPECIES

The genital terminology and abbreviations were used as defined by Godwin-Austen (1891), Tumpeesuwan *et al*. (2007) and Sutcharit *et al*. (2012): **am**, amatorial organ; **amd**, amatorial organ duct; **amg**, amatorial organ gland; **amp**, amatorial organ pilaster; **ap**, amatorial organ papilla; **at**, atrium; **e**, epiphallus; **fo**, free oviduct; **gd**, gametolytic duct; **gg**, gametolytic gland; **go**, gametolytic organ; **gs**, gametolytic sac; **ov**, oviduct; **p**, penis; **pp**, penial pilaster; **pr**, penial retractor muscle; **ps**, penial sheath; **v**, vagina; **vd**, vas deferens; **vp**, vaginal pilaster. Some of the characters of the genitalia that were named differently in studies by other authors are given in the Supporting Information (Table S3).

Institutional abbreviations: BOR/MOL, BORNEENSIS mollusc collection, Universiti Malaysia Sabah; CUMZ, Chulalongkorn University, Museum of Zoology, Bangkok; MNHN, Muséum national d'Histoire naturelle, Paris; NHMUK, The Natural History Museum, London.

RESULTS

The total number of sequences, sequence and alignment length, and the number of variable and parsimony-informative sites for each of the three partial gene fragments (*COI*, 16S and 28S) are reported in the Supporting Information (Table S4). The uncorrected intrageneric and pairwise intergeneric distances

Table 4. Character matrix used for the cladistic analysis

Taxon	Character													
	1	2	3	4	5	6	7	8	9	10	11	12	13	14
Asperitas	2	3	1	2	1	1	0	0	1	1	0	0	0	1
Bertia	2	1	1	2	2	1	0	0	0	1	1	0	0	1
Bornean *Dyakia*	2	3	0	2	1	1	0	0	0	0	1	0	1	1
Peninsular *Dyakia*	2	1	0	2	0	1	0	0	0	0	1	0	1	1
Elaphroconcha	2	2	0	2	0	1	0	1	0	0	0	0	0	1
Everettia	4	2	1	2	1	1	1	0	0	0	0	0	0	0
Kalamantania	3	2	1	2	2	1	0	0	0	0	0	1	0	1
Phuphania	2	1	1	2	1	1	0	0	0	0	0	0	0	1
Pseudoplecta	5	4	2	0	1	2	0	0	1	0	0	0	1	0
Pseudoquantula	1	1	1	1	2	1	0	0	1	0	0	0	1	0
Quantula	4	0	0	2	2	1	1	0	0	0	0	0	0	1
Rhinocochlis	1	2	1	2	0	1	0	0	1	0	1	0	1	1
Sasakina	2	2	0	2	0	1	0	1	1	1	0	0	1	0
Staffordia	0	0	0	0	0	0	0	0	0	0	0	0	0	0

within the Dyakiidae for the partial *COI* gene fragment ranged between 0.18 and 13.41% and between 9.14 and 17.38%, respectively. For the partial 16S rRNA gene fragment, the uncorrected intrageneric and pairwise intergeneric distances ranged between 0.28 and 11.74% and between 10.06 and 23.66%, respectively (Supporting Information, Table S5). For the partial 28S rRNA, the uncorrected intrageneric and pairwise intergeneric distances ranged between 0.00 and 2.64% and between 1.09 and 15.34%, respectively (Supporting Information, Table S6).

The phylogenetic trees (Fig. 2, showing the MRBAYES topology) based on the concatenated datasets using both ML and BI methods (MRBAYES and BEAST) yielded largely consistent phylogenies that differed in the position of *Pseudoplecta bijuga* (Stoliczka, 1873) and *Kalamantania whiteheadi* (Godwin-Austen, 1891). In addition, all dyakiid taxa in this study clustered together as monophyletic (BS = 100%, PP = 1). All multispecies genera were recovered as reciprocally monophyletic, except for *Dyakia* (BS = 94–100%, PP = 1). For the genera that consisted of only a single species, a statement on their monophyly is not possible. *Dyakia* was retrieved as polyphyletic, with the studied species divided over two clades (one clade in the Malay Peninsula and one clade in Borneo), with highly supported values (BS = 100%, PP = 1). The genera with sinistral coiling (*Bertia*, *Dyakia* and *Rhinocochlis*) did not form a monophyletic group.

Regarding the relationships among genera, the new genus has been retrieved as the sister taxon to all other genera (BS = 97%, PP = 1), whereas *Bertia* was the sister clade to the remaining genera (BS = 98%,

PP = 1). The other genera have mainly been grouped into three clades, two of which were highly supported, namely the *Phuphania* + *Quantula* (BS = 88%, PP = 1) and *Asperitas* + *Dyakia* + *Rhinocochlis* (BS = 92%, PP ≥ 0.99) clades. The Bornean species of *Dyakia* were sister to *Rhinocochlis*, with significant support in the MRBAYES analysis (PP = 0.96), but not in the ML (BS = 59%) and BEAST (PP = 0.65) analyses. *Pseudoplecta* was the sister clade to *Everettia* with low support values from the Bayesian analyses (BS < 50%, MRBAYES PP = 0.87, BEAST PP = 0.91). The relationship between *Kalamantania* and the other larger clades could not be resolved. Within the *Quantula* clade, *Quantula striata* (Gray, 1834) and *Quantula weinkauffiana* (Crosse & Fischer, 1863) were sister clades, each with high support (BS = 100%, PP = 1). In contrast, the sister relationships of the other species were not supported by the analyses. There was high variability in shell form, in terms of the shell dimension and the keel at the shell periphery, within each of the *Quantula* clades (Fig. 3).

The results of the cladistic analysis were superimposed on the most parsimonious tree constrained with the Bayesian tree topology (Fig. 4) because the fit measures of the most parsimonious trees from unconstrained analysis indicated homoplasy from the dataset (Supporting Information, Table S7). This tree topology revealed *Asperitas* as the sister taxon to the polyphyletic *Dyakia* + *Rhinocochlis* clade. In addition, the analysis recovered the clade *Everettia* + *Pseudoplecta*, which was not supported by the molecular phylogeny, and *Elaphroconcha* + *Sasakina*, which was not included in the molecular analysis.
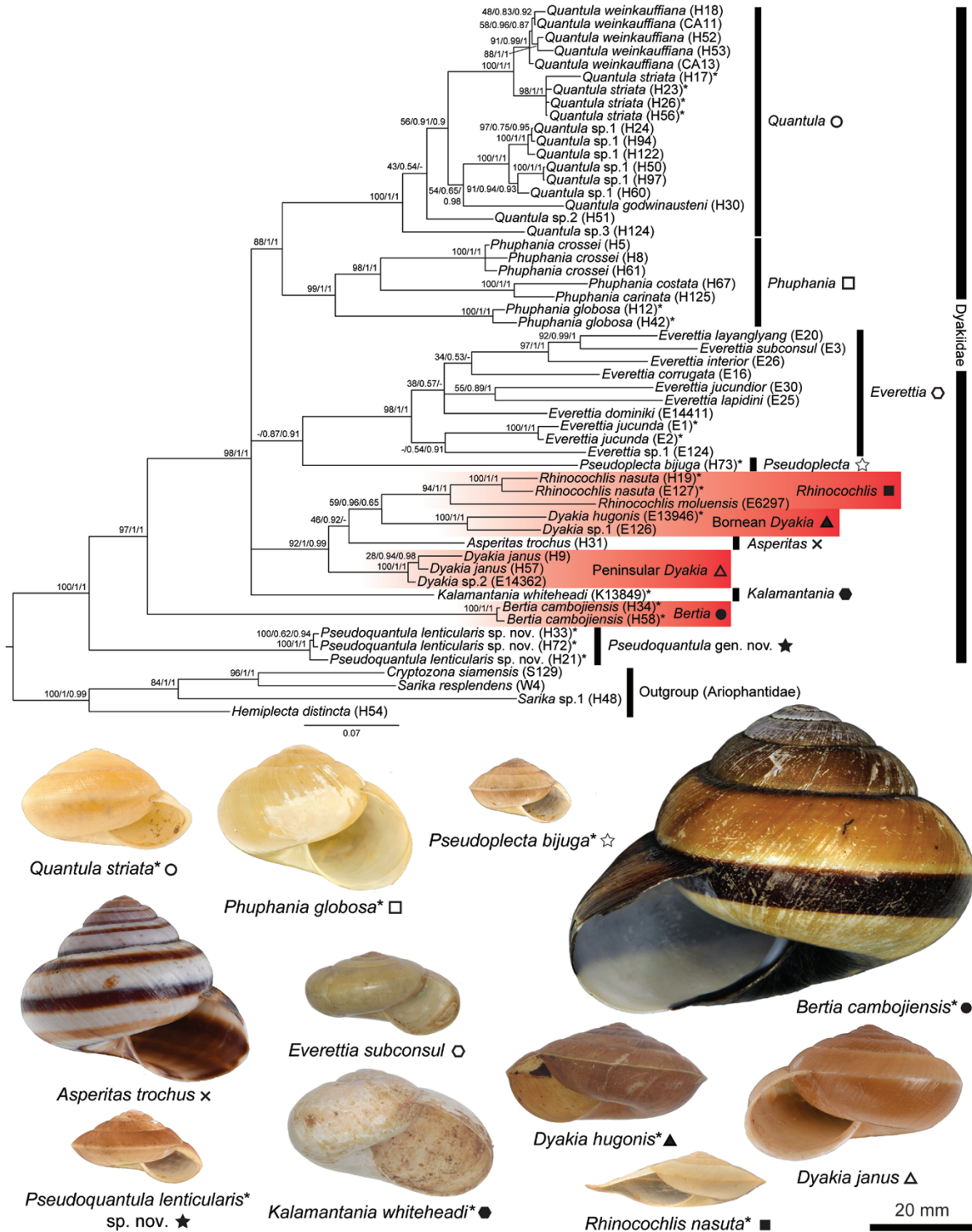
Figure 2. Phylogenetic tree based on the MRBAYES analysis. Nodal support values are given as bootstrap support (maximum likelihood)/posterior probability (MRBAYES)/posterior probability (BEAST). The symbols correspond to those in Figure 1. An asterisk indicates the type species of its corresponding genus. Red gradient bars indicate the genera with sinistral shell coiling. Representative shells of all genera in this study are shown below.
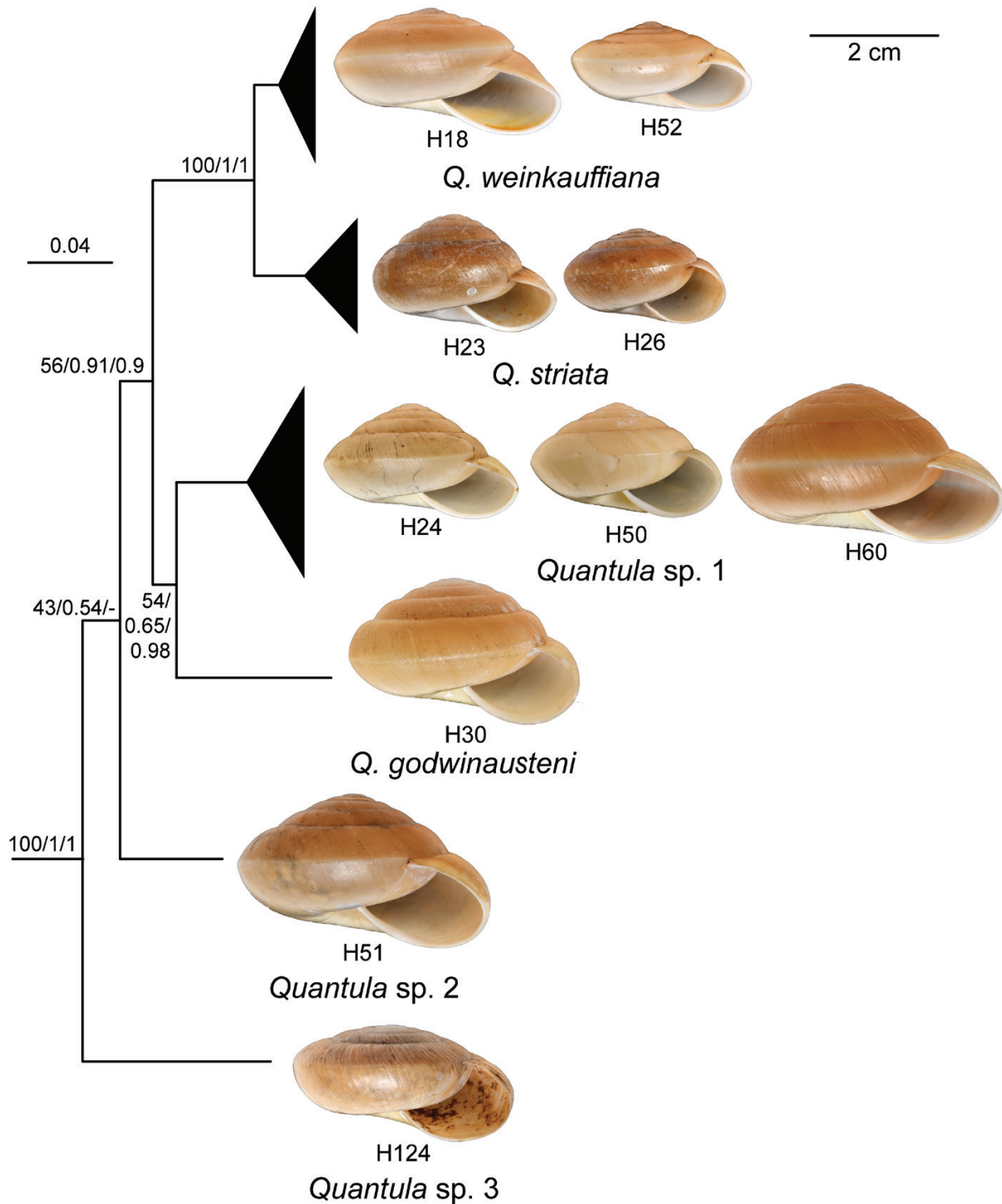
Figure 3. The phylogenetic relationships in the *Quantula* clade with its respective representative shell morphology. The specimen numbers correspond to those in Table 2. Nodal support values are given as bootstrap support (maximum likelihood)/posterior probability (MRBAYES)/posterior probability (BEAST).

Two morphological characters, the insertion site of the gametolytic sac (character 6) and the number of whorls (character 12), were uninformative and thus not shown. There were no synapomorphies for the clades *Asperitas* + *Dyakia* + *Rhinocochlis*, *Phuphania* + *Quantula* and *Everrettia* + *Pseudoplecta*,
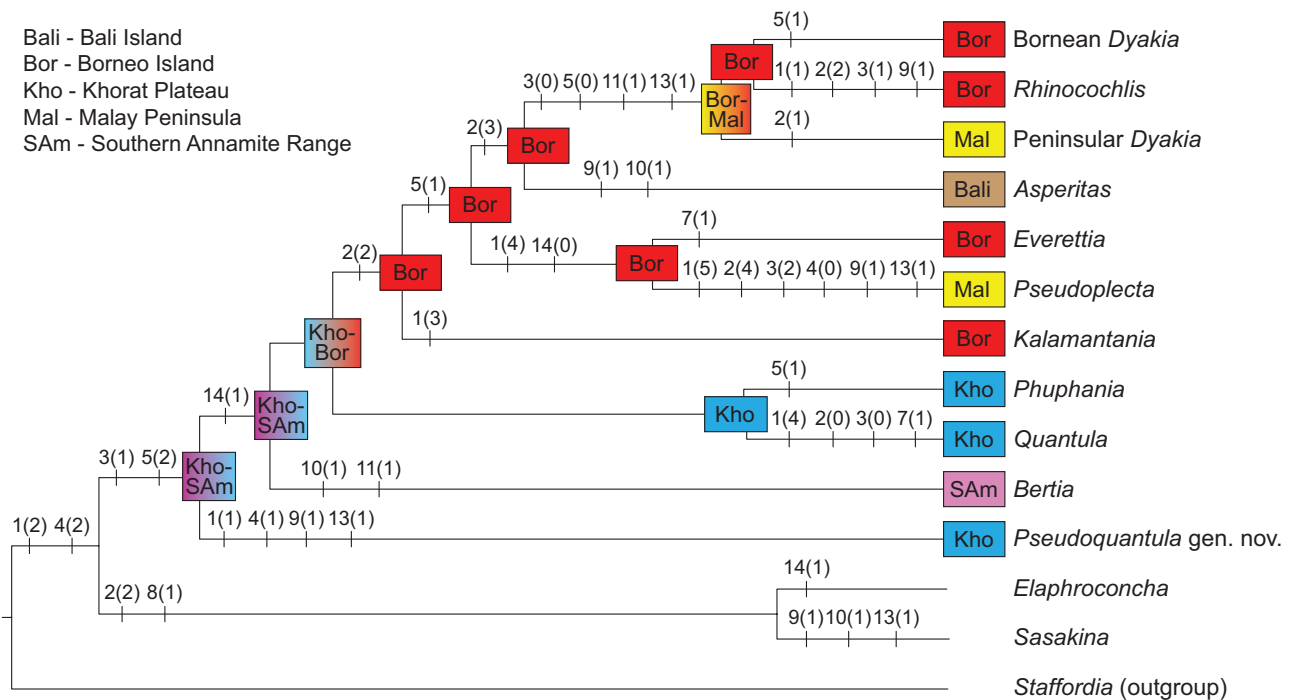
Figure 4. The most parsimonious tree superimposed with character state changes and the results from the ancestral range reconstructions. The character states correspond to those in Table 3. The area codes and colours correspond to those in Table 2 and Figure 1.

whereas one synapomorphy [insertion site of the penial retractor muscle (character 8) near the junction between the penis and epiphallus] supported the *Elaphroconcha* + *Sasakina* clade. The greatest number of autapomorphies (three) and character state changes (six) was found in *Pseudoplecta*.

The ancestral range estimations based on both the DEC module and the DEC+J model applied in BioGeoBEARS recovered the same ancestral ranges of all nodes (Supporting Information, Fig. S2). The results of ancestral ranges of each major node leading to each genus were superimposed on the most parsimonious tree (Fig. 4). The southern Annamite Range and Khorat Plateau, both located in mainland Southeast Asia, have been retrieved as the ancestral range of Dyakiidae. In addition, the ancestral ranges of the clade excluding *Bertia* and the new genus *Pseudoquantula* have been retrieved as the Khorat Plateau in BioGeoBEARS and the Khorat Plateau and Borneo Island in DEC. Lastly, Borneo Island has been retrieved as the ancestral range of the remaining taxa from the Malay Peninsula, Borneo and Bali. The full result of the ancestral range reconstruction is shown in the Supporting Information (Fig. S2).

Helix crossei Pfeiffer, 1862, for which the systematic relationships have until now remained unclear, is now confirmed as belonging to this family and assigned to the genus *Phuphania* based on the results of the

phylogenetic analyses (BS = 98%, PP = 1) and the occurrence of fused lobes of the amatorial organ gland forming a cap covering the amatorial organ (Fig. 5C). The updated description of *Phuphania* has been provided because the boundary of this genus was extended by the addition of *Phuphania crossei*. Furthermore, the internal anatomical details of *Pseudoplecta bijuga*, the type and only species of this genus, were updated, and the external body features and radula are reported here for the first time based on recently collected material.

SYSTEMATICS

FAMILY DYAKIIDAE GUDE & WOODWARD, 1921

GENUS *PSEUDOQUANTULA* JIRAPATRASILP & PANHA **GEN. NOV.**

Zoobank registration: urn:lsid:zoobank. org:act:B3250796-CC74-4E5E-A8EE-38E50885DA5D

Type species: Pseudoquantula lenticularis Jirapatrasilp & Panha, sp. nov.

Etymology

Compound word formed from the Greek prefix ψευδο-, false, and the genus *Quantula* [in turn from Latin
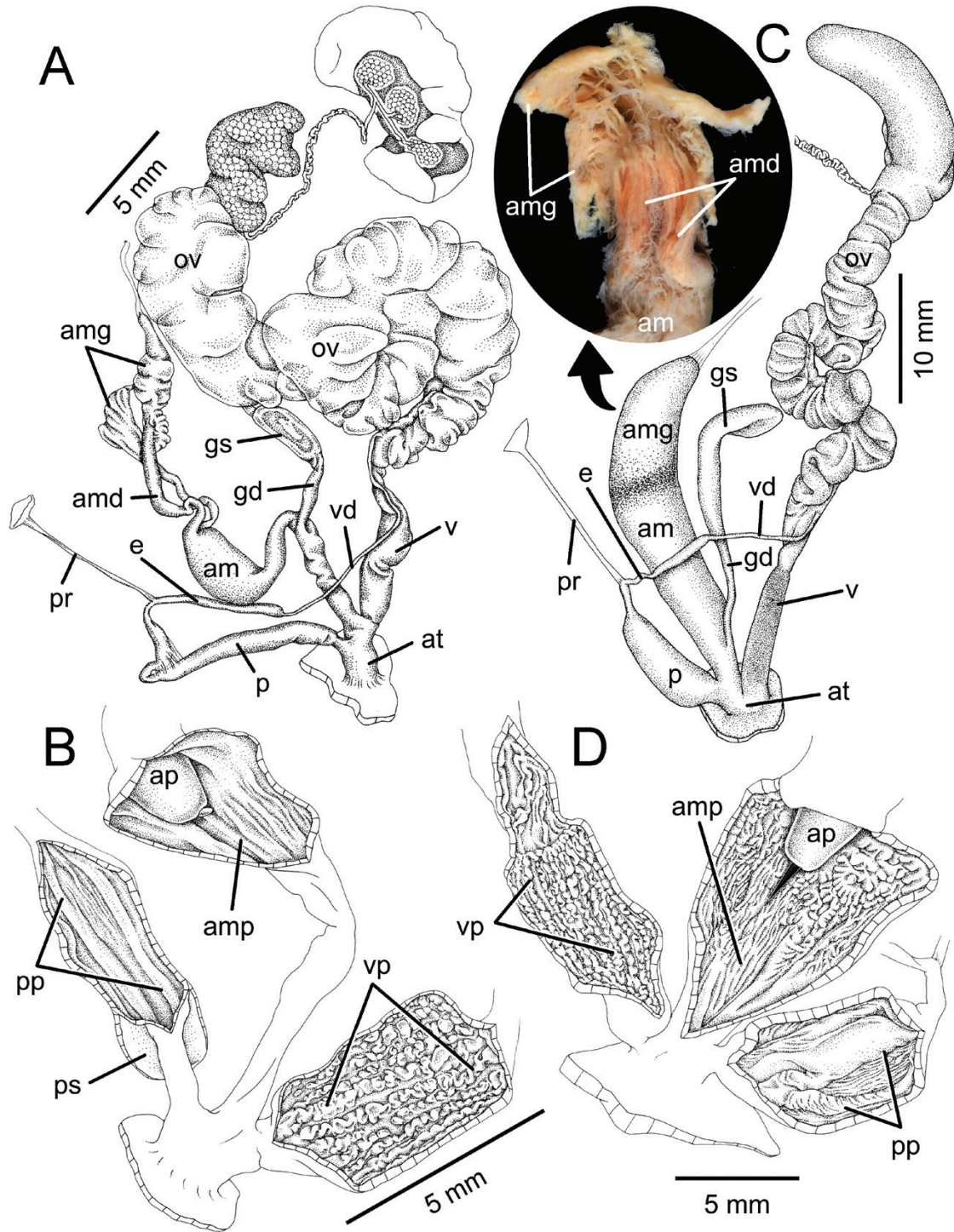
Figure 5. A, B, *Pseudoquantula lenticularis*, paratype CUMZ 5152: A, whole genitalia; and B, internal wall sculpture of penis, vagina and amatorial organ chamber. C, D, *Phuphania crossei*, specimen CUMZ 5147: C, whole genitalia, with inset showing amatorial organ glands and ducts; and D, internal wall sculpture of penis, vagina and amatorial organ chamber with the corneous spike.
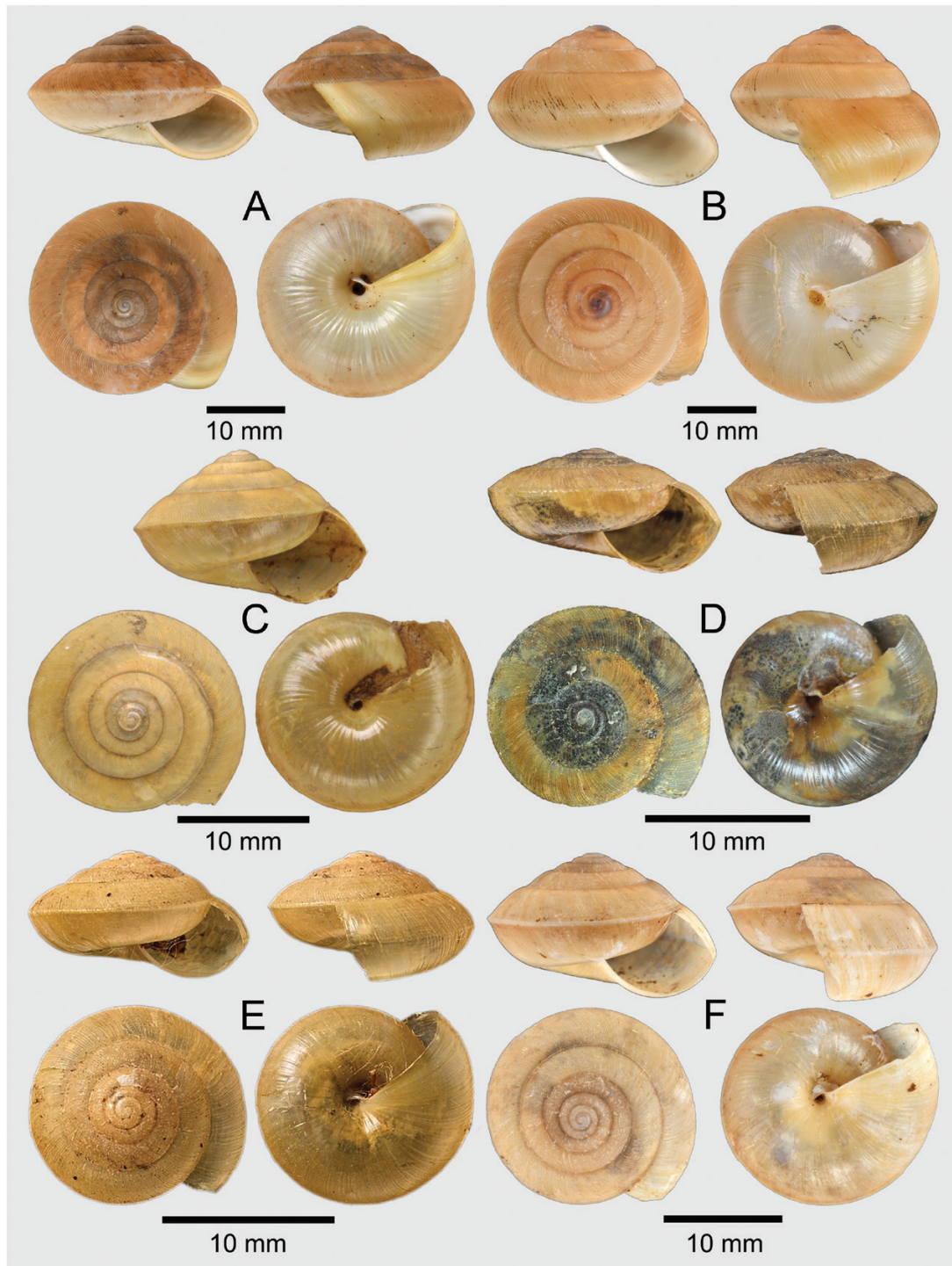
Figure 6. A, ***Pseudoquantula lenticularis***, holotype CUMZ 5153. B, *Phuphania crossei*, specimen CUMZ 5147. C, possible syntype of *Rotula bijuga* Stoliczka, 1873, NHMUK 20200203. D, syntype of *Macrochlamys pataniensis* Morgan, 1885, MNHN-IM-2000-34171. E, *Pseudoplecta bijuga*, labelled as a paratype of *Pseudoplecta cameroni* n. gen.? n. sp. MSS, NHMUK 1933.3.24.2-3. F, *Pseudoplecta bijuga*, specimen CUMZ 5151.
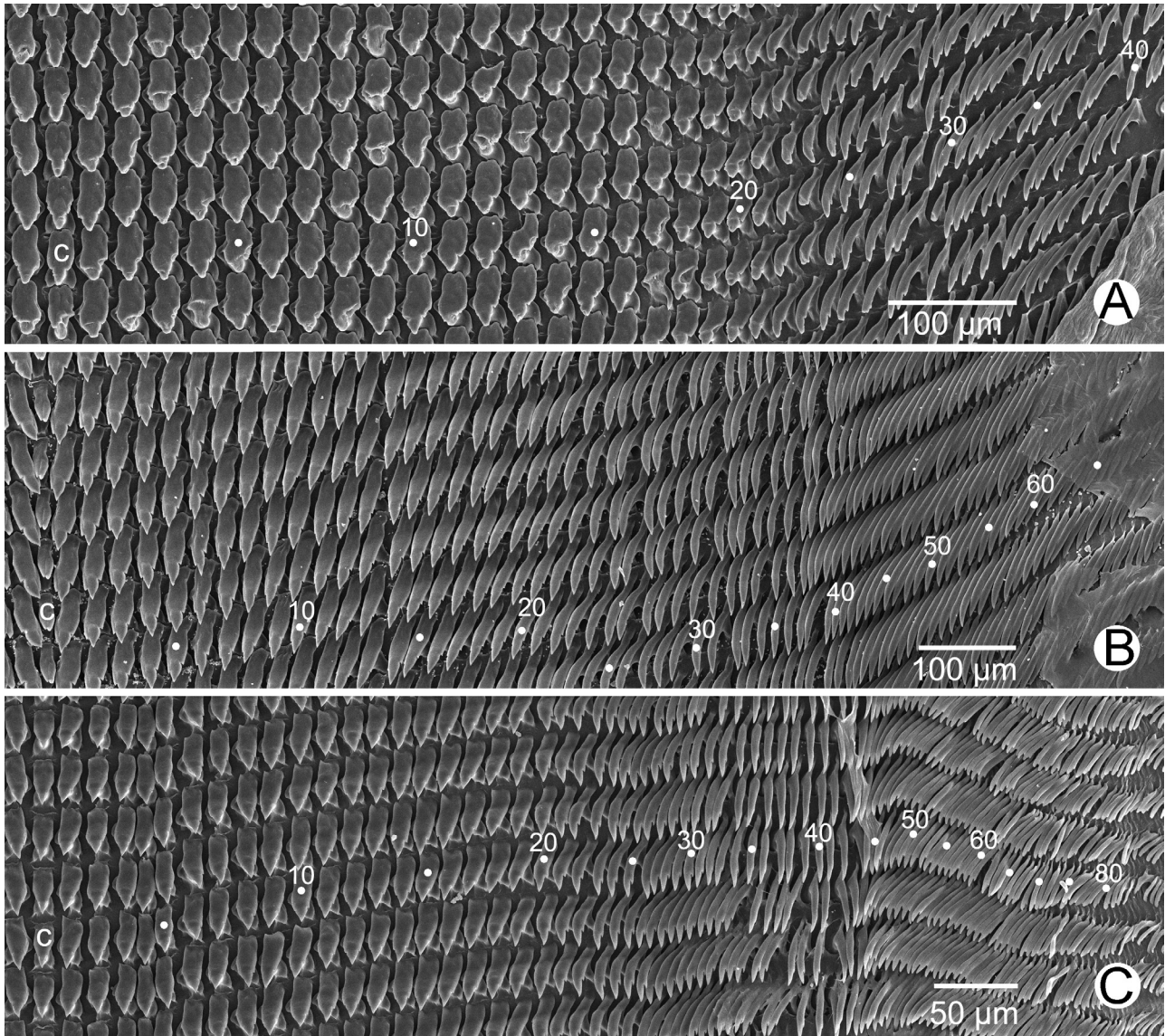
Figure 7. Scanning electron microscope images of radula. A, ***Pseudoquantula lenticularis***, paratype CUMZ 5152. B, *Phuphania crossei*, specimen CUMZ 5147. C, *Pseudoplecta bijuga*, specimen CUMZ 5150. Central tooth is indicated by 'C'. Numbers indicate the tooth order from lateral to marginal end.

meaning 'how little'], in reference to the similar shell to this genus in the family Dyakiidae.

Diagnosis
As the type species.

Description
Shell depressed conic, slightly thin, corneous and moderately translucent. Whorls five to seven slightly convex; suture shallow; embryonic shell finely ribbed. Last whorl angular with strong peripheral keel; upper periphery with strong radial ridges. Aperture sub-ovate; lip simple or thickened inside peristome. Umbilicus perforate.

Genitalia with long and slender penis; epiphallus small; vas deferens connected near tip of epiphallus. Gametolytic organ (duct and sac) elongate and located about half of amatorial organ length. Amatorial organ gland composed of two major lobes extending into thick ducts and entering terminal tip of amatorial organ; corneous spike absent. Vagina cylindrical and of similar length to penis.
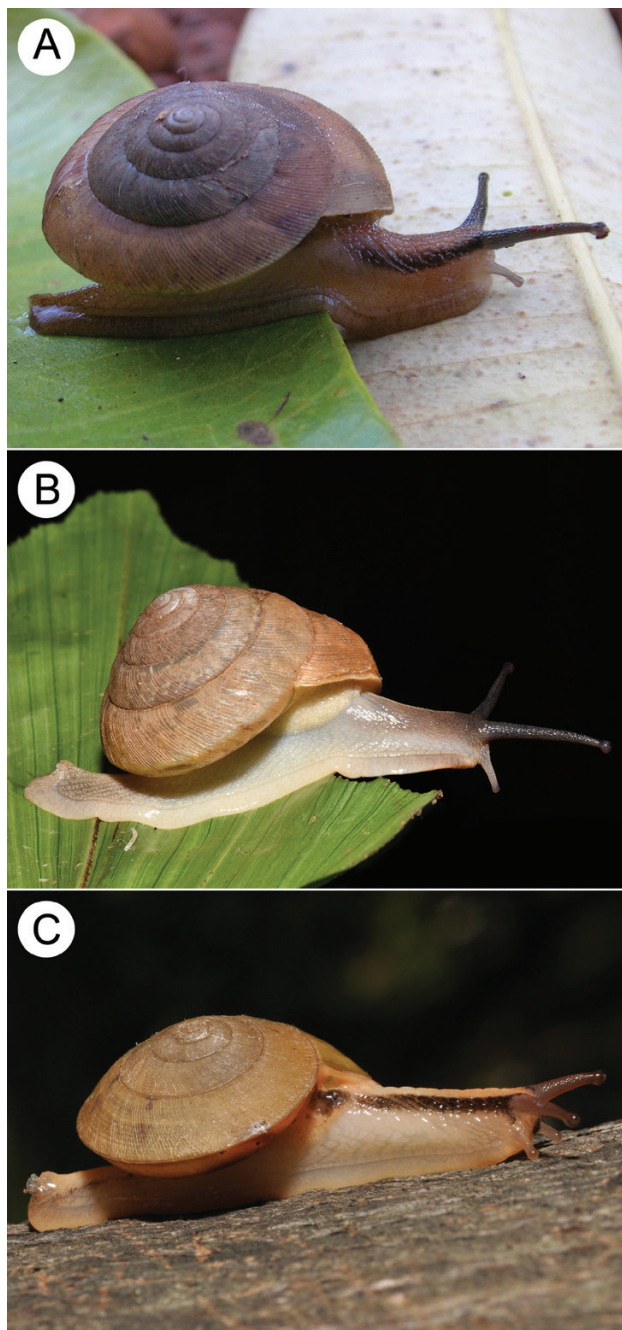
Figure 8. Live specimens of: A, ***Pseudoquantula lenticularis***, paratype CUMZ 5155; B, *Phuphania crossei*, CUMZ 5272; and C, *Pseudoplecta bijuga*, CUMZ 5150.

PSEUDOQUANTULA LENTICULARIS JIRAPATRASILP & PANHA **SP. NOV.**

(FIGS 5A, B, 6A, 7A, 8A)

Z o o b a n k   r e g i s t r a t i o n :   u r n : l s i d : z o o b a n k . org:act:60 646 243-B878-4DF0-BC80-D3BD8646816A

Type specimens

Holotype CUMZ 5153 (Fig. 6A). Paratypes from the type locality: CUMZ 5152 (two specimens in ethanol; Figs 5A, B, 7A), CUMZ 5155 (one specimen in ethanol; Fig. 8A) and NHMUK (one shell).

Type locality

Dry dipterocarp forest with granite rocks at Pang Srida Waterfall, Sra Keo Province, Thailand (14°16′63″N, 101°55′307″E).

Other material examined

CUMZ 5172 (three specimens), Khao Yai, Nakhon Nayok Province, Thailand (13°59′13.6″N, 102°12′18.3″E).

Etymology

The epithet is derived from Latin *lenticula*, a small lens or lentil, referring to the thin and fragile lens-shaped shell.

Diagnosis

Shell depressed conic and thin, with sharp peripheral keel and strong radial ridges on upper shell surface. Amatorial organ gland well developed and consisting of two major lobes with two amatorial gland ducts.

Description

Shell (Fig. 6A): Shell medium (width ≤ 26.9 mm, height ≤ 15.3 mm), dextral, slightly thin, conic to depressed conic, and moderately translucent. Whorls five to seven slightly convex and increasing regularly; suture wide and shallow. Shell colour brownish-yellow to corneous; upper and below periphery without distinct colour. Apex acute; embryonic shell with thin radial ridges and about two whorls. Following whorls with series of thin tubercles arranged on radial ridges; upper periphery with strong radial ridges and weaker below. Last whorl angulated, with strong peripheral keel. Aperture subovate and oblique; lip simple, slightly thickened and whitish inside peristome. Columella little dilated; parietal callus thin and transparent. Umbilicus perforate and deep.

Gentialia (Fig. 5A, B): Atrium short compared with penis (*N* = 5). Penis long, cylindrical tube covered with thin penial sheath. Penial retractor muscle long, thin, and attached to penis. Epiphallus cylindrical tube, about half length of penis and smaller in diameter than penis. Vas deferens relatively smaller diameter, thin tube, and
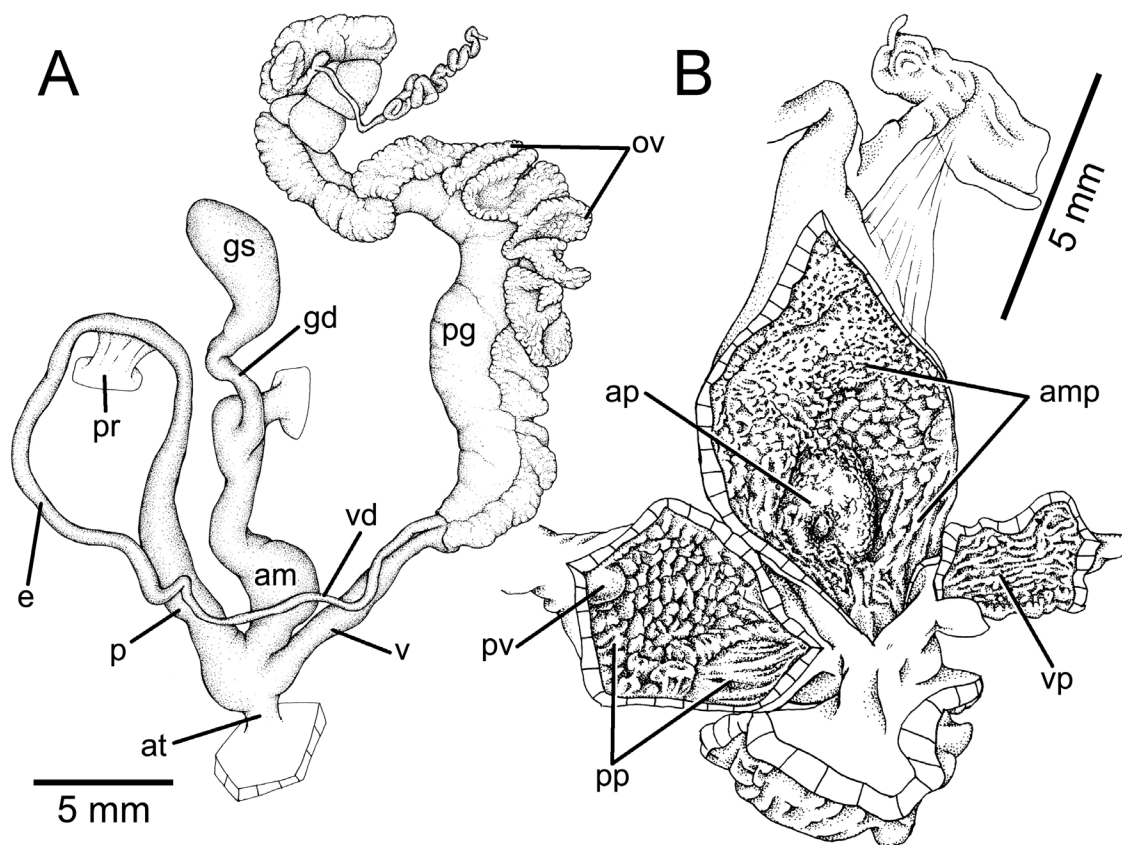
Figure 9. Genitalia of *Pseudoplecta bijuga*, specimen CUMZ 5150: A, whole genitalia; and B, internal wall sculpture of penis, vagina and amatorial organ chamber.

entering epiphallus apically; flagellum absent. Internal wall of penis with large penial pilasters for nearly entire length of chamber; penial verge absent.

Gametolytic organ (duct and sac) located close to genital opening about half of amatorial organ length. Gametolytic duct cylindrical tube; gametolytic sac slightly swollen and attached to ovary with thin connective tissues. Amatorial organ well developed, enlarged and bulbous and attached to atrium. Amatorial organ glands composed of two major lobes bounded with thin tissue. Each pair of major lobes extends into thick amatorial organ ducts, becoming bound together and entering tip of amatorial organ. Internal wall sculpture of amatorial organ consists of nearly smooth surface of enlarged longitudinal amatorial organ pilasters. Amatorial organ papilla large and conical; corneous spike absent.

Vagina about same length as penis and enlarged cylinder. Oviduct with enlarged lobules; prostate gland bound to oviduct. Internal wall of vagina sculptured with irregular undulated pilasters varying in size from small to large and arranged in longitudinal rows.

Radula (Fig. 7A): Teeth arranged in very wide-angled U-shaped rows, with ~99 (47-(20–22)-1-(20–23)-51) teeth. Central tooth symmetric tricuspid, with triangular-shaped mesocone; ectocones small and dull cusp. Lateral teeth asymmetric tricuspid, triangular in shape and inclined towards central tooth. Endocone nearly wanting; ectocone with dull cusp. Marginal teeth start from tooth 23–25, elongate bicuspid and sword shaped; mesocone large and pointed cusp; ectocone small and pointed cusp. Outermost teeth shorter than inner teeth.

External features (Fig. 8A): Living snail typical dyakiid form; body reticulated and brownish orange. Upper tentacles long and blackish brown; lower tentacles shorter and paler in colour. Dorsal part darker, with dark stripes running from base of tentacles to about one-third of body length. Foot aulacopod and unipartite; foot sole brownish to orange and unspotted.

Distribution

Pang Srida Waterfall, Sra Keo Province and Khao Yai, Nakhon Nayok Province, Thailand.

Remarks

This monotypic genus is only known to occur in the Dong Phayayen-Khao Yai Ranges. It differs from *Quantula* in both shell and genitalia characters as follows. *Pseudoquantula lenticularis* has a thin and fragile lens-shaped shell, with strong peripheral keel and apertural lip thickened and whitish inside aperture in adult specimens. In comparison, both *Q. striata* (the type species of *Quantula*) and *Q. weinkauffiana* have thick and robust dome- to conic-shaped shells, and the last whorl is well rounded to angular. In addition, this new genus and new species has two amatorial organ glands, each of which has its own short and thick ducts, whereas *Quantula* has only one common amatorial organ gland and one thinner and longer duct (Schileyko, 2003: fig. 1776). Furthermore, our molecular phylogeny strongly supported the distinct lineage of this new genus.

GENUS *PHUPHANIA* TUMPEESUWAN, NAGGS & PANHA, 2007

Zoobank registration: urn:lsid:zoobank. org:act:44C02DD2-B4DE-42B3-9AF5-D613B72F5F30

Type species

Phuphania globosa Tumpeesuwan, Naggs & Panha, 2007, by original designation.

Diagnosis

Shell thick or thin; globose to conic shell, with thin radial ridges. Amatorial organ complex well developed; amatorial organ gland fused lobes with two to six clusters of amatorial organ ducts and forming a cap over amatorial organ; amatorial organ papilla with or without corneous spike. Radula with elongate and unicuspid marginal teeth.

Description

Shell conic to ovate conic, thin to thick, with corneous colour. Last whorl well rounded to angular; upper shell surface with prominent radial ridges; below periphery with nearly smooth surface. Aperture sub-ovate; lip simple and slightly thickened in adult snail. Umbilicus perforate.

Genitalia with penis enlarged close to atrium; epiphallus diameter smaller than penis. Gametolytic organ (duct and sac) located on amatorial organ. Amatorial organ well developed; amatorial organ gland fused lobe, with two to six clusters of amatorial organ ducts; corneous spike present or absent.

Remarks

This genus is widely distributed in central and north-eastern Thailand. Currently, the genus is composed of four nominal species: *Phuphania carinata* Kongim & Panha, 2013, *Phuphania costata* Tumpeesuwan C. & Tumeesuwan S., 2014, *Phuphania crossei* and *Phuphania globosa*, which are distributed along the Phu Phan and Phetchabun Ranges.

PHUPHANIA CROSSEI (PFEIFFER, 1862) **COMB. NOV.**

(FIGS 5C, D, 6B, 7B, 8B)

Zoobank registration: urn:lsid:zoobank. org:act:8701796D-C54F-4A07-B29E-ADCD6351E3B4

Synonymy

Helix crossei Pfeiffer, 1862: 39, pl. 5, figs 2, 3. Type locality: Siam [Thailand].

Helix danae Pfeiffer, 1863 [1862]: 268. Type locality: Laos Mountains, Camboja [Cambodia or Laos]. **New Synonym.**

Nanina (Xestina) crossei – Kobelt, 1900: 983, 984, pl. 255, fig. 5, pl. 256, figs 3, 4.

Nanina (Xestina) danae – Kobelt, 1902: 1076, pl. 273, figs 4–6.

Euplecta danae – Gude, 1903: 6.

Hemiplecta crossei – Gude, 1903: 7.

Nanina (Hemiplecta) crossei – Fischer & Dautzenberg, 1904: 393.

Nanina (Hemiplecta) danae – Fischer & Dautzenberg, 1904: 393.

Hemiplecta (Hemiplecta) crossei – Hemmen & Hemmen, 2001: 43.

Hemiplecta (Hemiplecta) danae – Hemmen & Hemmen, 2001: 44.

Ariophanta (Cryptozona) crossei – Schileyko, 2011: 29.

Ariophanta (Cryptozona) danae – Schileyko, 2011: 29.

Ariophanta crossei – Inkhavilay *et al.*, 2019: 74, fig. 34b.

Ariophanta danae – Inkhavilay *et al.*, 2019: 74, fig. 34c.

Type material examined

Syntype of *Helix crossei* Pfeiffer, 1862, MNHN-IM-2000-1869 (one shell; Inkhavilay *et al.*, 2019: fig. 34b). Syntype of *Helix danae* Pfeiffer, 1863, NHMUK 20092043 (one shell; Inkhavilay *et al.*, 2019: fig. 34c).

Material examined

Sakunotayan Waterfall, Wang Thong District, Phitsanulok Province: CUMZ 5142 (nine shells), 5145 (two specimens in ethanol). Pa Ma Muang Temple, Ban Mung, Nern Maprang District, Phitsanulok Province: CUMZ 5137 (four shells), CUMZ 5141 (eight shells).

Tam Wang Daeng, Nern Maprang District, Phitsanulok Province: CUMZ 5138 (six shells), CUMZ 5140 (one shell), CUMZ 5164 (seven shells). Khao Look Chang, Pakchong District, Nakhon Ratchasrima Province: CUMZ 5139 (two shells), CUMZ 5148 (one specimen in ethanol), CUMZ 5167 (one shell). Tam Yai Nam-nao, Nam-nao District, Phetchabun Province: CUMZ 5144 (one shell). Sap Chomphu Arboretum, Nong Pai District, Phetchabun Province: CUMZ 5146 (one specimen in ethanol), CUMZ 5169 (39 shells). Muak Lek Waterfall, Muak Lek District, Saraburi Province: CUMZ 5143 (one shell). Jed Kot Waterfall, Kaeng Koy District, Saraburi Province: CUMZ 5147 (four specimens in ethanol; Figs 5C, D, 6B, 7B), CUMZ 5168 (seven shells). Wat Tham Phra Phothisat, Kaeng Koy District, Saraburi Province: CUMZ 5272 (four specimens in ethanol; Fig. 8B), CUMZ 5273 (22 shells). Khao Sala, Bau Chet District, Surin Province: CUMZ 5149 (one shell).

Diagnosis
Shell conic, brownish, with last whorl angular and umbilicus narrow. Penis enlarged and cylindrical. Amatorial organ gland fused lobes with three clusters of amatorial organ ducts and forming a cap over amatorial organ; amatorial organ papilla with corneous spike.

Description
Shell (Fig. 6B): Shell medium (width ≤ 35.0 mm, height ≤ 24.5 mm), conic to slightly depressed conic, thickened and dull, dextral and narrow perforate. Whorls six to eight, increasing regularly; suture wide and little depressed. Shell colour brownish to yellowish; below periphery with paler colour than upper periphery. Spire convex; apex acute; embryonic shell small and with fine radial ridges. Shell surface coarse, with nodule lines arranged on fine radial ridges; below periphery with nearly smooth surface around umbilicus. Last whorl angular, with weak peripheral keel. Aperture ovate; parietal callus transparent; lip simple, slightly thickened and little expanded near columellar area. Columella slightly dilated. Umbilicus perforate, narrow and deep.

Genitalia (Fig. 5C, D): Atrium very short compared with penis. Penis enlarged, cylindrical and suddenly tapering to small tube. Epiphallus long, almost same length as penis and approximately similar in diameter to penis. Penial retractor muscle thin and attached between penis and epiphallus. Flagellum absent. Vas deferens smaller in diameter than epiphallus and connected at tip of epiphallus. Internal wall of penis with large and nearly smooth-surfaced longitudinal pilasters for entire length of chamber; penial verge absent.

Gametolytic organ (duct and sac) locates very near the end of amatorial organ. Gametolytic duct cylindrical tube; gametolytic sac gradually swollen to the end. Amatorial organ well developed, enlarged cylinder and attached to atrium. Amatorial organ gland fused lobes, covered amatorial organ ducts and forming a cap over amatorial organ gland. Amatorial organ duct consists of three clusters of ducts; tip of amatorial organ with thin connective tissue. Internal wall sculpture of amatorial organ: region close to atrium consists of smooth surface of longitudinal amatorial organ pilasters; area surrounding papilla consists of corrugated wall. Amatorial organ papilla enlarged, smooth surface and obtuse in shape; tipped with dark spike.

Vagina about same length as penis and cylindrical. Oviduct with enlarged lobules; prostate gland bound to oviduct. Internal wall of vagina: area close to atrium sculptured with irregular, undulated pilasters of similar size and arranged in longitudinal rows then with unpattern irregular surface.

Radula (Fig. 7B): Teeth arranged in very wide-angled U-shaped rows, with ~150 (90-(25–27)-1-(23–26)-60+) teeth. Central tooth relatively small, slightly asymmetric bicuspid, and with pointed cusps. Lateral teeth relatively large, asymmetric tricuspid, elongated in shape and inclined towards central tooth. Mesocone large and pointed cusp; endocone and ectocone very small and pointed cusps. Marginal teeth start from tooth 23–27, elongate, unicuspid and sword shaped; outermost teeth shorter, with apically pointed tip.

External features (Fig. 8B): Living snail typical dyakiid form; body reticulated and yellowish brown. Upper tentacles long and dark grey; lower tentacles shorter and paler in colour. Dorsal part darker, especially near the head. Foot aulacopod and unipartite; foot sole same colour as the body and unspotted.

Remarks
This species has previously been assigned to the family Ariophantidae, for the lack of a prominent keel similar to some ariophantid genera, such as *Ariophanta* Des Moulins, 1829 and *Hemiplecta* Albers, 1850. However, its exact familial or generic assignment could not be resolved owing to the lack of anatomical data. Two nominal species, *Helix crossei* and *H. danae*, were described in consecutive years by L. Pfeiffer, with a rather generic type locality of 'Siam' and 'Lao Mountains, Camboja', respectively. The latter taxon was described based on the Cuming ex. Mouhot collection. Hence, the specimen probably originated from the last journey of H. Mouhot between

Bangkok, Thailand and Luang Phrabang, Laos (see Mouhot, 1864; Inkhavilay *et al*., 2019). We presume that the type specimen of *H. danae* was collected from the same geographical area as *H. crossei*. Specifically, the type localities were possibly in north-eastern Thailand, which is within the current distributional range of recently examined specimens. In addition, the syntypes of both nominal species were identical in all shell characters (Inkhavilay *et al*., 2019). Thus, we consider these names as synonyms.

Phuphania crossei differs from its congeners in having a stronger peripheral keel, more slender gametolytic organ with a longer and more distinct gametolytic duct, and possessing a corneous spike on the amatorial organ papilla, which is absent in other species. The shell and genitalia of this species are more similar to *Phuphania costata* and *Phuphania carinata* than to *Phuphania globosa* in having a peripheral keel and distinct radial ribs, elongate marginal teeth and the lobes of the amatorial organ gland fusing as a thick sac that contains two to four clusters of internal ducts (Kongim & Panha, 2013; Tumpeesuwan & Tumpeesuwan, 2014). However, *Phuphania crossei* has more compact amatorial organ glands and shows a less distinct demarcation between the amatorial organ and its glands. This morphological similarity among *Phuphania carinata*, *Phuphania costata* and *Phuphania crossei* agrees well with the molecular phylogenetic relationship (Fig. 2).

GENUS *PSEUDOPLECTA* LAIDLAW, 1932

Zoobank registration: urn:lsid:zoobank. org:act:51FAB8D6-15A6-4D10-8C66-AC8B4F11FE81

Type species
Rotula bijuga Stoliczka, 1873 by monotypy.

Diagnosis
As the type species.

Remarks
Currently, this genus is composed of only a single species. The genus has a narrow distribution in the central part of Malay Peninsula (southern Thailand to the central part of Peninsular Malaysia).

PSEUDOPLECTA BIJUGA (STOLICZKA, 1873)

(FIGS 6C–F, 7C, 8C, 9)

Zoobank registration: urn:lsid:zoobank. org:act:05AD59EE-788B-4597-BEA9-704F892F2184

Synonymy
Rotula bijuga – Stoliczka, 1873: 14–16, pl. 1, figs 4–7, pl. 2, figs 16–18. Type locality: Penang.
　Macrochlamys pataniensis – Morgan, 1885: 376, pl. 5, fig. 5. Type locality: Naxa dans le district de Rhaman, royaume de Patani.
　Rotularia bijuga – Morgan, 1885: 378.
　Nanina (*Rotula*) *bijuga* – Tryon, 1886: 22, pl. 4, figs 56–59.
　Euplecta bijuga – Möllendorff, 1891: 332. – Collinge, 1903: 208.
　Euplecta pataniensis – Möllendorff, 1891: 333.
　Otesia bijuga convexospira – Möllendorff, 1902: 137. Type locality: Kelantan, Ostküste der Halbinsel Malacca. **New synonym**.
　Pseudoplecta bijuga – Laidlaw, 1932: 91–93, figs 7, 8. – Laidlaw, 1933: 227, 228. – Schileyko, 2003: 1363, 1364, fig. 1779. – Schileyko, 2007: 2112, fig. 1779a. – Foon *et al*., 2017: 65, fig. 25b.
　Pseudoplecta bijuga bijuga – Maassen, 2001: 104.

Type material examined
Possible syntypes of *Rotula bijuga* Stoliczka, 1873, NHMUK 20200203 (two shells; Fig. 6C). Syntype of *Macrochlamys pataniensis* Morgan, 1885, MNHN-IM-2000-34171 (three shells; Fig. 6D).

Material examined
Berenchang Road, Cameron Highlands 4500 ft., NHMUK 1933.3.24.2-3 (two shells; labelled as paratypes of *Pseudoplecta cameroni* n. gen.? n. sp. MSS; Fig. 6E). Gua Matu Madu, Gua Musang, Kelantan, Malaysia: CUMZ 5150 (three specimens in ethanol; Figs 7C, 8C, 9), CUMZ 5151 (one shell; Fig. 6F).

Diagnosis
Shell small, slightly thin, depressed to ovate conic, with fine radial ridges. Penis long, with penial verge inside. Gametolytic organ located close to terminal part of amatorial organ; amatorial organ gland and duct absent; amatorial organ papilla without corneous spike.

Description
Shell (Fig. 6C–F): Shell small (width ≤ 17.8 mm, height ≤ 11.3 mm), dextral, slightly thin, strongly depressed to ovate conic and moderately translucent. Whorls six to eight, little convex and increasing regularly; suture wide and shallow. Shell colour corneous; upper and below periphery with indistinct colour. Apex acute; embryonic shell with nearly smooth surface and ~1½

whorls. Following whorls with series of thin nodules arranged on fine radial ridges; upper periphery with strong radial ridges and weaker below. Last whorl angulated, with strong peripheral keel. Aperture sub-ovate and oblique; lip simple and slightly thickened. Columella little dilated; parietal callus transparent. Umbilicus perforate and deep.

Genitalia (Fig. 9): Atrium short. Penis close to atrium enlarged, cylindrical and gradually tapering to small tube. Epiphallus long, almost the same length as penis and approximately similar diameter to penis. Penial retractor muscle with thick band, very short compared with penis, and attached between penis and epiphallus. Flagellum absent. Vas deferens relatively smaller diameter than epiphallus and connected at tip of epiphallus. Internal wall of penis with large and corrugated penial pilasters surrounding penial verge and nearly smooth surface close to atrium; penial verge small and low conical shape.

Gametolytic organ (duct and sac) close to terminal part of amatorial organ. Gametolytic duct cylindrical tube; gametolytic sac enlarged at the end. Amatorial organ well-developed cylinder and attached to atrium; region close to atrium swollen, round (with amatorial organ papilla inside); region close to gametolytic sac enlarged cylinder, with thick retractor muscle. Amatorial organ gland and duct absent. Internal wall sculpture of amatorial organ: close to atrium consists of irregular and smooth-surfaced amatorial organ pilasters, gradually modified to corrugated and nearly smooth wall. Amatorial organ papilla obtuse in shape, with corrugated surface; corneous spike absent.

Vagina about two-thirds the length of penis and cylindrical. Oviduct with enlarged lobules; prostate gland bound to oviduct. Internal wall of vagina mostly sculptured with irregular, undulated pilasters of similar size and arranged in longitudinal rows.

Radula (Fig. 7C): Teeth arranged in wide-angled U-shaped rows, with ~190 (93-(22–20)-1-(21–23)-98). Central tooth symmetric tricuspid with triangular-shaped mesocone; ectocones small and dull cusp. Lateral teeth asymmetric tricuspid, triangular in shape and inclined towards central tooth; endocone and ectocone nearly wanting. Marginal teeth start from tooth 20–23, elongate, obliquely bicuspid and sword shaped; endocone large and pointed cusp; ectocone small and pointed cusp. Outermost teeth shorter than inner teeth and ectocone small.

External features (Fig. 8C): Living snail typical dyakiid form; body reticulated and pale orange. Tentacles long and brown. Dorsal part darker, with black stripes running from base of tentacles to pneumostome. Foot aulacopod and unipartite; foot sole brownish to orange and unspotted.

Remarks

This species was originally described from Penang [Island, Malaysia], with detailed description and illustration by Stoliczka (1873). Later, de Morgan (1885) described *Macrochlamys pataniensis* from 'Naxa dans le district de Rhaman, royaume de Patani' [Raman District, Pattani Province, Thailand] as a distinct species, without any detail on internal anatomy. These two nominal species have been treated as distinct ever since, and their generic placements were hypothetical. Later, Laidlaw (1932) could not affiliate Stoliczka's species to any existing genus and therefore introduced the genus *Pseudoplecta*, and Laidlaw (1933) treated *M. pataniensis* as a junior synonym to this species. Here, we synonymize *M. pataniensis* with *Pseudoplecta bijuga* because this species shows a large variation in spire height [see Stoliczka (1873): pl. 1, figs 4–7], and *M. pataniensis* is considered to be within the range of this variation. In addition, the shell-based description of *Otesia bijuga convexospira* by von Möllendorff (1902) is also contained within the variation, and the type locality was within the distributional range of this species. Hence, we treat this nominal taxon as a synonym of *Pseudoplecta bijuga*.

DISCUSSION

PHYLOGENETIC RELATIONSHIPS WITHIN THE DYAKIIDAE

This study is the first molecular phylogenetic investigation of the Dyakiidae since the morphologically based phylogeny published 25 years ago (Hausdorf, 1995). The present phylogeny confirms that all genera (except *Elaphroconcha* and *Sasakina*, which were not included in this study) are members of the family Dyakiidae. This validates the three synapomorphies of this family *sensu* Laidlaw (1931): (1) an amatorial organ furnished with accessory glands attached to its upper pole by one or more coiled tubules; (2) a gametolytic sac attached to the amatorial organ; and (3) an absence of shell lobes (except for *Pseudoplecta*; see the last paragraph of this section).

Given that *Dyakia* was retrieved as polyphyletic in this study, the sinistral keeled shell as one of the diagnostic characters of this genus requires further investigation (Laidlaw, 1963; Schileyko, 2003). However, there are differences in the number of amatorial organ gland lobes between the Bornean and the Malay Peninsular clades. For instance, *Dyakia hugonis* (Pfeiffer, 1863) of the Bornean clade possesses

five major lobes, whereas *Dyakia janus* (Beck, 1837) of the Peninsular clade possesses three major lobes (Godwin-Austen, 1891; Sutcharit *et al.*, 2012).

Rhinocochlis is retrieved as the sister clade to the Bornean *Dyakia*, which was supported by the presence of the sinistral keeled shell. However, *Rhinocochlis* is distinct from *Dyakia* in having only two amatorial organ glands and the distinct lens-shaped semitransparent shell (Schileyko, 2003). Interestingly, the dextral *Asperitas trochus* (Müller, 1774) was included in the *Dyakia* + *Rhinocochlis* clade, although its relationships with Peninsular *Dyakia* and Bornean *Dyakia* + *Rhinocochlis* could not be resolved. Hence, to understand the evolution of the amatorial organ glands in Dyakiidae and improve the taxonomic classification of *Asperitas*, *Dyakia* and *Rhinocochlis*, more species of each of the genera, covering the entire distributional ranges, need to be included in a future study.

Previously, *Phuphania* was postulated to be related closely to *Bertia*, *Everettia* and *Kalamantania* based on the absence of a common amatorial organ duct and the occurrence of more than four amatorial organ gland lobes (Tumpeesuwan *et al.*, 2007). However, our molecular phylogenetic analysis revealed a sister-group relationship between *Phuphania* and *Quantula* despite the clear difference in the amatorial organ between the two genera. *Phuphania* possesses two to six clusters of numerous amatorial organ ducts that end with clusters of fused lobes of amatorial organ glands, forming an ovate cap covering an amatorial organ. In contrast, *Quantula* possesses only a long common amatorial organ duct that branches and ends with more than ten lobes of amatorial organ glands. Moreover, the shapes of the gametolytic sac and duct differ between these two genera, and *Quantula* also shows an absence of the gametolytic retractor muscle (Schileyko, 2003; Tumpeesuwan *et al.*, 2007; Kongim & Panha, 2013; Tumpeesuwan & Tumpeesuwan, 2014). Thus, similarity in genital characters is not always shown among closely related land snail taxa, and the evolution of those characters has been attributed to the effect of ecological factors (Köhler & Criscione, 2015).

Although *Pseudoplecta* lacks an amatorial organ gland, which is one of the diagnostic characters of the Dyakiidae, the genus had already been affiliated to this family by Baker (1941). Later, Thiele (1934) proposed the subfamily Pseudoplectinae to accommodate only this genus. Bouchet *et al.* (2017) synonymized this subfamily with Dyakiidae because *Pseudoplecta* did not form a sister group to the remaining Dyakiidae in the phylogeny proposed by Hausdorf (1995). However, this synonymization was disregarded by Schileyko (2003). Our phylogenetic analysis supports the synonymization of the Pseudoplectinae and the inclusion of *Pseudoplecta* in this family based on the

morphology, showing that *Pseudoplecta* possesses two out of three synapomorphies, namely the absence of shell lobes and the opening of the gametolytic sac at the terminal part of the amatorial organ (Laidlaw, 1931; Fig. 9A). Nevertheless, *Pseudoplecta* was not recovered as the sister to the other dyakiid genera but was revealed as the sister clade to *Everettia* in the Bayesian phylogenetic and the most parsimonious cladistic analysis. Hence, in contrast to previous suggestion (Baker, 1941), *Pseudoplecta* should not be recognized as ancestral. This also suggests the secondary loss of amatorial organ glands in *Pseudoplecta*. The complete or partial loss of the stimulatory organ is widespread in Stylommatophora (Barker, 2001; Koene & Schulenburg, 2005; Hirano *et al.*, 2014). Nonetheless, the exact relationship between *Pseudoplecta* and *Everettia* requires further scrutiny.

MORPHOLOGICAL CONVERGENCE AND CRYPTIC DIVERSITY

Several studies have revealed that shell characters often contain weak phylogenetic signals, and convergence in genital characters has been more frequently identified as more land snail groups have been examined (Hyman & Ponder, 2010; Criscione & Köhler, 2013; Hirano *et al.*, 2014; Köhler & Criscione, 2015). Other studies on Camaenidae have suggested that shell shape and morphology of the genitalia might be characterized by the retention of plesiomorphic character states (Köhler & Criscione, 2015), whereas radular morphology in general reflects ecological adaptations to different diets (Hausdorf, 1998; Barker & Efford, 2004; Margry, 2013). Likewise, our cladistic analysis revealed that the characters related to shell shape, radula and genitalia used in this study are often homoplastic at the generic level of Dyakiidae, depicting that the combination of several characters is needed to distinguish each genus (Table 1). Regarding the species level, morphological cryptic diversity of both shell shape and genitalia was identified to be high in Bornean *Everettia*, whereas the interspecific differences are mainly based on shell sculptures, body coloration and mantle markings (Liew *et al.*, 2009). In addition, *Quantula* has been found to be more diverse and widespread than previously thought (Hemmen & Hemmen, 2001; Schileyko, 2003; Inkhavilay *et al.*, 2019; Sutcharit *et al.*, 2020). This study also displays both cases of similar shell shape among different clades and different shell shapes within the same clade (Fig. 3). Comprehensive study of finer morphological characters is thus needed to discover the diagnostic characters of each *Quantula* clade.

Several hypotheses of the transformation series within the Dyakiidae were made based on the number

of ducts and the complexity in gland structure of the amatorial organ. Hausdorf (1995) proposed that *Quantula* possesses the plesiomorphic state of an amatorial organ joining to its lobes by a long common duct, whereas *Kalamantania* and *Everettia* possess the synapomorphic state of amatorial organ lobes without a common duct. Furthermore, by extending Hausdorf's transformation series, Tumpeesuwan *et al.* (2007) hypothesized that the genitalia of *Bertia* are more derived than those of *Everettia* and that *Phuphania* possesses the most derived state in the Dyakiidae. However, our molecular phylogenetic analyses indicated that the amatorial organ lobes without a common duct is a plesiomorphic state. In contrast, the common amatorial organ duct found in *Dyakia* and *Quantula* is an apomorphic state but retrieved as homoplastic. Thus, we could formulate the hypothesis of evolution of the amatorial organ from possessing multiple ducts to a common duct, the condition of which evolved multiple times in dyakiid lineages.

REVERSAL OF SHELL COILING

Multiple origins of the left–right coiling reversal in terrestrial snails seem to be the norm rather than the exception (Schilthuizen & Davison, 2005; Gittenberger *et al.*, 2012). In the Dyakiidae, at least two reversal events can be identified: the first leads to *Bertia cambojiensis* (Reeve, 1860) and the second to the ancestor of the *Dyakia* + *Asperitas* + *Rhinocochlis* and an additional reversal from the sinistral ancestor to dextral *Asperitas*. Shell coiling reversal has also been reported to occur multiple times at the species and population levels in other families, e.g. Camaenidae: *Amphidromus* Albers, 1850 (Sutcharit *et al.*, 2007; Nakadera *et al.*, 2010) and *Satsuma* Adams, 1868 (Hoso *et al.*, 2010); Clausiliidae: *Albinaria* Vest, 1867 (Kornilios *et al.*, 2015); and Orculidae: *Schileykula* Gittenberger, 1983 (Harl *et al.*, 2020). The most prominent hypothesis explaining this phenomenon is sexual isolation or single gene speciation (Hoso *et al.*, 2010; but see Ueshima & Asami, 2003; Yamamichi & Sasaki, 2013; Koch *et al.*, 2017; Richards *et al.*, 2017), which gives rise to new species or even new genera multiple times.

Past studies have reported that some dyakiid species exhibited both types of shell coiling within the same population; for example, in *Elaphroconcha javacensis* (Férrusac, 1821) reported by Dharma (1991) from East Java, and *Dyakia mackensiana* (Souleyet, 1841) reported by von Martens (1867) from Borneo, Sumatra and Singapore. It would be interesting to determine whether reversals in shell coiling at the

genus, species and population levels have the same molecular basis.

One of the selective advantages of reversal in shell coiling is an adaptation against predation by the snail-eating snake family Pareidae (Hoso *et al.*, 2010), which is widespread in Southeast Asia (Uetz *et al.*, 2019) and overlaps with the distribution of the sinistral dyakiid genera. Earlier experiments revealed that sinistral snails are more likely to survive snake predation (Hoso *et al.*, 2010; Danaisawadi *et al.*, 2016). Furthermore, the small population size caused by restricted distribution and fragmented populations, such as in *Bertia* (Hun *et al.*, 2019), might accelerate the fixation of the non-adaptive shell coiling allele. This is similar to the taxa endemic to oceanic islands that exhibit a high number of sinistral genera in the absence of snail-eating snakes (Hoso, 2012).

HISTORICAL BIOGEOGRAPHY OF THE DYAKIIDAE

Hausdorf (1995) proposed that mainland Southeast Asia and the Malay Peninsula represent the ancestral ranges of Dyakiidae based on a cladogram yielding *Quantula* as the first diverging lineage. Another sister lineage then diverged into one clade comprising *Elaphroconcha*, *Pseudoplecta* and *Sasakina*, mainly occupying Sumatra, Java, Bali to Flores, with another clade comprising *Asperitas*, *Dyakia*, *Everettia* and *Kalamantania*, mainly occupying Borneo and Sulawesi. In contrast, our analysis yielded mainland Southeast Asia (the Annamite Range and Khorat Plateau) as the ancestral range of Dyakiidae, after the addition of *Bertia* and *Pseudoquantula*, whereas *Quantula* was not retrieved as the first diverging lineage (Fig. 4). In addition, this scenario suggests that several lineages dispersed and diversified in Borneo and there was at least one dispersal event to Bali (as in *Asperitas*). North-to-south dispersal in Southeast Asia has also been reported in other animal taxa (e.g. Gorog *et al.*, 2004; Wood *et al.*, 2012; Gorin *et al.*, 2020).

The proposed ancestral range of *Asperitas* + *Dyakia* + *Kalamantania* + *Everettia* in Borneo as suggested by Hausdorf (1995) agrees with our analysis. However, in this study, Borneo was also the ancestral range of *Rhinocochlis* and *Pseudoplecta*, whereas Hausdorf (1995) indicated the ancestral range of *Pseudoplecta* to be in Sumatra and the Lesser Sunda Islands. The position of the Bornean taxa at the terminal part of the tree is in accord with the later accretion of Borneo to Sundaland (Metcalfe, 2017), in which the dispersal from the Khorat Plateau into Borneo might occur. Some lineages of *Dyakia* and *Pseudoplecta* might have dispersed back to Peninsular Malaysia, which is a scenario of back colonization

similar to the case of mite harvestman (Clouse & Giribet, 2010).

The future inclusion of more *Asperitas*, *Dyakia*, *Elaphroconcha*, *Pseudoplecta* and *Sasakina* species from the Greater and Lesser Sunda Islands in the phylogenetic framework would extend our understanding in the biogeographical scenario within Sundaland, and the inclusion of *Craterodiscus* and *Staffordia* might elucidate the origin of the Dyakiidae within the limacoid clade. Although fossils of the dyakiid snails have not yet been reported, time calibration of the phylogeny using other lines of evidence, e.g. geographical events (Liew *et al*., 2020), is crucial to discuss diversification events through time and space in this region.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

Figure S1. The 50-majority rule consensus tree retrieved from the maximum parsimony analysis of morphological data.

Figure S2. The full results of ancestral area reconstructions applying: A, DEC+J model in BIOGEOBEARS; and B, DEC module. The most likely state of each node is displayed in each pie chart.

Table S1. List of gene fragments, names and sequences of the forward (F) and reverse (R) primers, annealing temperatures and references.

Table S2. Results of model tests in BIOGEOBEARS implemented in the RASP program.

Table S3. List of some characters of the genitalia and their abbreviations that were named and used in a different manner in other studies compared with the present study.

Table S4. General DNA sequence features of dyakiid snails in this study for each of the three gene fragments.

Table S5. Percentage of uncorrected pairwise intergeneric distances for the partial *COI* (above the diagonal) and 16S rRNA (below the diagonal) gene fragments among the dyakiid genera. Intrageneric distances for *COI*/16S are shown on the diagonal.

Table S6. Percentage of uncorrected pairwise intergeneric distances for the partial 28S gene fragments among the dyakiid genera. Intrageneric distances for 28S are shown on the diagonal.

Table S7. Results of tree length and fit measures of the maximum parsimony analysis of morphological data.