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A new species of the genus *Quantula* Baker, 1941 (Eupulmonata: Dyakiidae) from the southern part of north-eastern Thailand

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Abstract. The land snail genus *Quantula* Baker, 1941 from the southern part of north-eastern Thailand was studied. The results of studies on shell morphology, reproductive anatomy, and molecular phylogeny reveal the distinctions between two species—*Quantula weinkauffiana* (Crosse & Fischer, 1863) and *Quantula doma*, new species. According to shell morphology and genitalia, *Q. weinkauffiana* from Khao Phanom Sawai, Surin Province, has a depressed shell with a whorl descending in front, short gametolytic sac that is connected to the middle part of the amatorial organ, and amatorial organ duct shorter than amatorial organ, whereas *Q. doma*, new species from Khao Sala in Surin, Pha Nam Yoi in Roi Et, and Phu Jor Kor in Mukdahan Provinces has a dome-shaped to depressed conic shell, last whorl not descending in front, and amatorial organ duct longer than amatorial organ. Both species are also phylogenetically separated from each other by mitochondrial DNA phylogeny and COI sequence divergences.

Key words. inner wall of genitalia, phylogenetics, *Quantula striata*, *Quantula weinkauffiana*, *Quantula godwinausteni*

INTRODUCTION

Quantula Baker, 1941 is a genus of pulmonated land snails in the family Dyakiidae, which was originally described as a subgenus of *Dyakia* Godwin-Austen, 1891 using *Nanina striata* Gray, 1834 as the type species. According to checklists of land snails of Thailand published by Panha (1996), Hemmen & Hemmen (2001), and Nabhitabhata (2009), two species of *Quantula* were reported from Thailand—*Quantula striata* (Gray, 1834), from central, eastern, and southern Thailand and *Q. weinkauffiana* (Crosse & Fischer, 1863) from north-eastern Thailand. In the latest checklist of land snails in Thailand by BEDO (2017), three *Quantula* species (including two subspecies) were recorded, comprising *Q. godwinausteni* (Laidlaw, 1931) from Chanthaburi, *Q. striata* (Gray, 1834) from Southern Thailand, *Q. weinkauffiana inflata* from Samui Island, and *Q. weinkauffiana weinkauffiana* from the southern part of north-eastern Thailand.

The members of the family Dyakiidae possess a wide variety of shell and soft body characters (see Figs. 2 & 8 in Jirapatrasilp et al., 2021); therefore, shell morphology alone is not enough for classification. According to Hausdorf (1995), Tumpeesuwan et al., (2007), and Tumpeesuwan & Tumpeesuwan (2014), the presence of a duct from the gametolytic sac (bursa copulatrix or spermatheca) attached to the base of an amatorial organ stimulator is the unique character of this family. However, the genital system anatomy and radula morphology of genus *Quantula* have rarely been studied. According to Worachak et al. (2014) and Hoompuay et al. (2015), the radula morphology and genital system anatomy of *Quantula* are different in many localities in the southern part of north-eastern Thailand. Jirapatrasilp et al. (2021) listed three unnamed *Quantula* species in their phylogenetic tree, two of which are species collected from Thailand, comprising one from eastern Thailand and the southern part of north-eastern Thailand, and another from the northern part of north-eastern Thailand. In this study, we collected and re-examined specimens from the study localities of Worachak et al. (2014) and Hoompuay et al. (2015) in the southern part of north-eastern Thailand and studied their molecular genetic information further. These new pieces of information were combined and analysed with previous information in order to further clarify the taxonomy of the genus *Quantula* in the southern part of north-eastern Thailand.

MATERIAL AND METHODS

Material examined. One hundred and three empty shells and fifty-one living snails of the genus *Quantula* were collected from four localities in the southern part of north-eastern Thailand during 11–14 October 2017. Seventy-four adult shells were assessed for whorl number and the shell height and shell width were measured using digital vernier calipers. The examined specimens were deposited in the land snail collection of the Natural History Museum, Mahasarakham

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Table 1. Species, localities, and GenBank accession numbers for sequences used in this study. Sequences marked * are from Jirapatrasilp et al. (2021).

No.	Specimen No	Species	Localities	28s	COI
1	PKJ	*Quantula doma*, new species	Phu Jor Kor, Mukdahan, Thailand	ON059380	MW649815
2	PNY	*Quantula doma*, new species	Pha Nam Yoi, Roi Et, Thailand	ON059379	MW649813
3	KSH	*Quantula doma*, new species	Khao Sala, Surin, Thailand	OM877375	MW649819
4	KSL	*Quantula doma*, new species	Khao Sala, Surin, Thailand	—	MW649820
5	PSP	*Quantula weinkauffiana* (Crosse & Fischer, 1863)	Khao Panom Sawai, Surin, Thailand	OM877374	MW649818
6	H31	*Asperitas trochus* (Müller, 1774)	Taman Tirtagangga, Bali, Indonesia	MT651601*	MT654630*
7	H9	*Dyakia janus* (Beck, 1837)	Pulau Besar, Johor, Malaysia	MT651593*	MT654622*
8	H57	*Dyakia janus* (Beck, 1837)	Pulau Tioman, Pahang, Malaysia	MT651594*	MT654623*
9	H18	*Quantula weinkauffiana* (Crosse & Fischer, 1863)	Khao Panom Sawai, Surin, Thailand	MT741929*	MT803080*
10	H53	*Quantula weinkauffiana* (Crosse & Fischer, 1863)	Tad Pha Suam, Champasak, Laos	MT741931*	MT803082*
11	CA11	*Quantula weinkauffiana* (Crosse & Fischer, 1863)	Kampong Trach, Kampot, Cambodia	MT741932*	MT803083*
12	CA13	*Quantula weinkauffiana* (Crosse & Fischer, 1863)	Phnom Chhngok Cave, Kampot, Cambodia	MT741933*	MT803084*
13	H30	*Quantula godwinausteni* (Laidlaw, 1931),	Wat Khao Sukim, Chanthaburi, Thailand	MT741925*	MT803077*
14	H23	*Quantula striata* (Grey, 1834)	Singapore Botanic Gardens, Singapore	MT651599*	MT654628*
15	H26	*Quantula striata* (Grey, 1834)	Singapore Botanic Gardens, Singapore	MT741927*	MT803078*
16	H24	*Quantula* sp.1	Wang Tra Krai, Nakhon Nayok, Thailand	MT741934*	MT803086*
17	H50	*Quantula* sp.1	Khao Ang Rue Nai, Chacheongsao, Thailand	MT741935*	MT803087*
18	H60	*Quantula* sp.1	Wat Khao Sala, Surin, Thailand	MT741936*	MT803088*
19	H51	*Quantula* sp.2	Kam Hom Waterfall, Sakon Nakhon, Thailand	—	MT803091*
20	H124	*Quantula* sp.3	Cuc Phuong, Nho Quan, Ninh Binh, Vietnam	—	MT803092*
21	H42	*Phuphania globosa* Tumpeesuwan et al., 2007	Nam Pung Reservoir, Sakon Nakhon, Thailand	MT651595*	MT654624*
22	H12	*Phuphania globosa* Tumpeesuwan et al., 2007	Wat Tam Nam Pok, Khon Kaen, Thailand	MT741921*	MT803073*
23	H67	*Phuphania costata* Tumpeesuwan & Tumpeesuwan, 2014	Pha Phu, Loei, Thailand	MT651596*	MT654625*
24	H125	*Phuphania carinata* Kongim & Panha, 2013	Phu Kiew, Chiayaphum, Thailand	—	MT803070*
25	H61	*Phuphania crossei* (Pfeiffer, 1862)	Sap Chomphu Arboretum, Phetchabun, Thailand	MT741920*	MT803072*
26	H5	*Phuphania crossei* (Pfeiffer, 1862)	Jedkot Waterfall, Saraburi, Thailand	MT651597*	MT654626*

No.	Specimen No	Species	Localities	28s	COI
27	E14411	*Everettia dominiki* Liew et al., 2009	Mount Trusmadi, Keningau, Sabah, Malaysia	MT741917*	MT803067*
28	H21	*Pseudoquantula lenticularis* Jirapatrasilp & Panha, 2021	Khao Yai, Nakhon Nayok, Thailand	MT741922*	MT803074*
29	H33	*Pseudoquantula lenticularis* Jirapatrasilp & Panha, 2021	Pang Sida Waterfall, Sa Kaeo, Thailand	MT741923*	MT803075*
30	S129	*Cryptozona siamensis* (Pfeiffer, 1856)	Wat Tha Mai Lai, Chumphon, Thailand	MT365718*	MT364992*
31	W4	*Sarika resplendens* (Philippi, 1846)	Khao Cha Ngum, Ratchaburi, Thailand	MT365707*	MT364982*

University, Thailand (NHMSU). Living snails were drowned in water for 24 hours, fixed, and kept in 70% ethanol for genitalia and radula studies.

Molecular phylogenetic methods.

Genetic analysis. DNA was extracted from the foot muscle using a GF-1 Nucleic Acid Extraction Kit (Vivantis Technologies Sdn. Bhd, Malaysia), following the manufacturer's protocol. Partial COI gene sequences were used to estimate the phylogenetic relationships among the collected snails and to evaluate the genetic divergences between the species. Polymerase chain reaction (PCR) of the mitochondrial cytochrome c oxidase subunit 1 (COI) was amplified using primers LCO1490 (5′-GGTCAACAAATCATAAAGATATTGG-3′) and HCO2198 (5′-TAAACTTCAGGGTGACCAAAA AATCA-3′) (Folmer et al., 1994), and sequences from the nuclear rRNA gene 28S rDNA were amplified using primers 28SF4 (5′-AGTACCGTGAGGGAAAGTTG-3′) and 28SR5 (5′-ACGGGACGGGCCGGTGGTGC-3′) (Morgan et al., 2002), with the PCR conditions of an initial denaturation step at 94 ℃ 2 min; 94 °C 30 s, 50 °C 45 s, 72 °C 45 s x 36 cycles; and a final extension step at 72 °C 5 min. The PCR products were purified and sequenced at 1st BASE DNA Sequencing Services (Selangor, Malaysia).

Phylogenetic analysis. Sequences were checked manually for their quality by Bioedit version 7.2.5 (Hall, 1999; 2001). The sequences were aligned by MEGA X (Kumar et al., 2018). All new COI and 28s sequences were deposited in GenBank under numbers MW649813, MW649815, MW649818–MW649820, OM877374–OM877375 and ON059379–ON059380. In addition, all sequences of dyakiid genera proposed by Jirapatrasilp et al. (2021) were included, and sequences of *Cryptozona siamensis* (Pfeiffer, 1856) and *Sarika resplendens* (Philippi, 1846) from GenBank specimens, no. S129 and W4, were used as outgroups (Table 1). The pairwise genetic distances were calculated by the measured distances (p-distances) in MEGA X (Kumar et al. 2018). Phylogenetic trees were obtained using a Bayesian inference (BI) in the program MrBayes version 3.2.6 (Ronquist et al., 2012), neighbourjoining (NJ) analysis by MEGA X (Kumar et al. 2018), and the maximum likelihood (ML) by MEGA X (Kumar et al. 2018) and RAxML version 0.9.0 (Kozlov et al., 2019). The best model and frequency of base were calculated by jModeltest version 2.1.10 (Posada, 2008; Darriba et al., 2012). Phylogenetic trees were arranged and edited using FigTree version 1.4.0 (Rambaut, 2012).

Anatomical analyses.

Radula morphology. The buccal masses were dissected from preserved specimens soaked in 10% NaOH solution. Radula were cleaned and dehydrated with 30%, 50%, 70%, 90%, and 95% ethyl alcohol. Radula were placed on a stub and studied with a scanning electron microscope.

Genital system. The reproductive system was dissected and cleaned with distilled water, and then a picture was taken depicting the reproductive system. Dissected specimens were maintained in 70% ethyl alcohol before being studied under a stereo microscope.

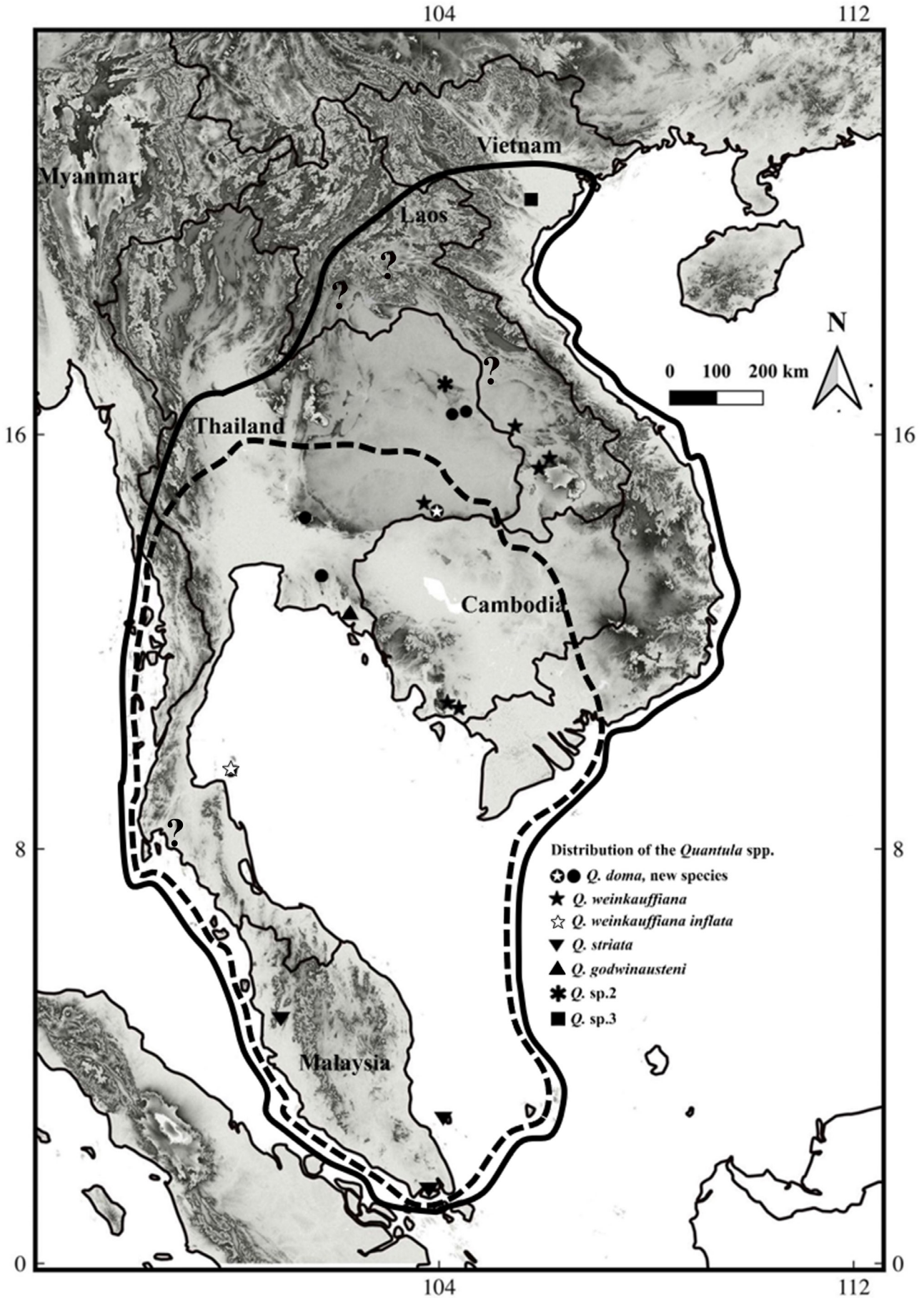

Fig. 1. Distribution range of genus *Quantula* in mainland southeast Asia showing recorded localities of *Quantula* spp.. Dashed line is distribution range proposed by Hausdorf (1995). Localities represented on the distribution map are from this study, Jirapatrasilp et al. (2021), Inkhavilay et al, (2019), Möllendorff (1894), and Thach (2018, 2020). White star in black circle indicates type locality of *Q. doma* new species, Question marks indicate localities without confirmation by anatomical and molecular data.

Abbreviations.
ag = albumen gland
am = amatorial organ (= sarcobelum)
amd = amatorial organ duct (= common duct)
amg = amatorial organ gland
amp = amatorial organ pilaster
ap = amatorial organ papilla
at = atrium
C = central tooth
e = epiphallus
fo = free oviduct
gd = gametolytic duct
gs = gametolytic sac
hd = hermaphroditic duct
L = lateral tooth
NHMSU = Natural History Museum, Mahasarakham University, Thailand
p = penis
pp = penial pilaster
pr = penial retractor muscle
ps = papilla spike
v = vagina
vd = vas deferens
vp = vagina pilaster

RESULTS

Molecular phylogenetics. Five COI and four 28S rDNA sequences were obtained from *Quantula* spp. newly collected from the southern part of north-eastern Thailand. Twenty-six COI and 23 28S rDNA sequences of *Quantula* spp., and other dyakiid genera and two outgroup species from Genbank were also used. The alignment of the COI and 28S gene sequence dataset had a length of 1,180 base pairs with nucleotide frequencies of 0.23, 0.20, 0.25, and 0.32 for A, C, G, and T, respectively. The p-distance between all examined species of *Quantula* spp. of Thailand ranged from 0.000 to 0.087 and the p-distance between all examined species of *Quantula* spp. of Southeast Asia ranged from 0.000 to 0.104 (Table 2). The BI analysis was used to reconstruct the phylogenetic tree (Fig. 2), for which the best-fit model for the BI analysis was TIM1+G (-lnL= 7926.3779, gamma shape=0.3820). The *Quantula* spp. are in a monophyletic clade that is well-supported (BI posterior probability 1.00, ML bootstrap 97, NJ bootstrap 90).

According to the present phylogeny, at least two species of *Quantula* from the southern part of north-eastern Thailand are recognised. The depressed-shell *Quantula* from Phanom Sawai, Surin Province was identified as *Quantula weinkauffiana* (Crosse & Fischer, 1863) and it possesses a sharp peripheral keel on the last whorl, parietal side of aperture depressed, gametolytic sac short, connected to middle part of amatorial organ. In addition, *Quantula doma*, new species from Khao Sala, Surin Province has a high-conic shell, gametolytic duct connected at the base of the amatorial organ, and vagina shorter than penis.

SYSTEMATICS

Family Dyakiidae Gude & Woodward, 1921

Subfamily Dyakiinae Gude & Woodward, 1921

Quantula Baker, 1941

Type species. *Nanina striata* Gray, 1834

Quantula weinkauffiana (Crosse & Fischer, 1863)
(Figs. 3A, 4A, 5A–G; Tables 1–3)

Helix weinkauffiana Crosse & Fischer, 1863: 350–351; Crosse & Fischer, 1864: 326, pl. 12, fig. 7.
Hemiplecta weinkauffiana – Morlet, 1889: 124; Dautzenberg & Fischer, 1905: 349; Fischer, 1973: 92; Panha, 1996: 34; Panha & Thanamitramanee, 1997: 2.
Ariophanta (*Hemiplecta*) *weinkauffiana* – Fischer, 1891: 21.
Ariophanta weinkauffiana inflata Möllendorf, 1894: 149.
Nanina (*Xestina*) *weinkauffiana* – Kobelt, 1900: 984–985, pl. 255, figs. 6–8.
Nanina (*Hemiplecta*) *weinkauffiana* var. *minor* Fischer & Dautzenberg, 1904: 394.
Dyakia weinkauffiana – Maneevong, 2000: 46–47, figs. 4–11 (A–B).
Ariophanta (*Cryptozona*) *weinkauffiana* – Schileyko, 2011: 29–30.
Quantula weinkauffiana – Hemmen & Hemmen, 2001: 45; Nabhitabhata, 2009: 249; Jumlong, 2012: 51,72, figs. 4.10, 5.1; Jumlong et al., 2013: 67–68, 71–76, 79, fig. 2D; Worachak, 2014: 40–43, figs. 4.1–4.3; Worachak et al., 2014: 524–529, fig. 2A; Inkhavilay et al., 2019: 71, 119 figs. 32B–D, 55H; Sutcharit et al., 2020b: 21, 23, figs. 9E–F; Jirapatrasilp et al., 2021: 256–257, 261–263, 268–269.
Quantula sp. 2 – Jumlong, 2012: 53, 72, figs. 4.12, 5.1; Worachak, 2014: 45–48, figs. 4.7, 4.8A–E, 4.9A–B
Quantula sp. 5 – Hoompuay, 2016: 40–42, figs. 4.18–4.20
Quantula weinkauffiana inflata – BEDO, 2017: 221.
Quantula weinkauffiana weinkauffiana – BEDO, 2017: 221.

Type locality. Cochinchina (Southern Vietnam).

Material examined. 37 shells and seven living specimens NHMSU-00035; Khao Panom Sawai, Surin Province; 14°46′05.3″N 103°22′17.0″E; 14 October 2017; (Figs. 3A, 4A, 5A–E).

Diagnosis. Shell depressed-conic. Last whorl angular with sharp peripheral keel and descending in front, lip is rather thick and slightly descending (see Inkhavilay et al., 2019: syntype fig. 32B–D; Jirapatrasilp et al., 2021: Fig. 3). Amatorial organ duct shorter than amatorial organ. Gametolytic duct connected to middle part of amatorial organ.

Description. Shell (n= 37) (Fig. 4A): dextral, very depressed conic, brown colour with 5–5¼ whorls, suture shallow, growth line fine. Last whorl angular with strong peripheral keel descending in front. Shell height 10.7–15.6 mm, shell width 20.6–28.1 mm. Apex blunt, peripheral keel very sharp, colour of ventral side of shell is paler than that of dorsal side. Apertural lip simple in light brown, with margin slightly thickened in adult specimens. Umbilicus narrow and deep. Body (n=5) (Fig. 3A): Living snail light orange, with two

Table 2. Pairwise genetic distance values for different species in this study.

		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28
1	*Quantula doma*, new species (PKJ)																												
2	*Quantula doma*, new species (PNY)	0.008																											
3	*Quantula doma*, new species (KSH)	0.029	0.029																										
4	*Quantula doma*, new species (KSL)	0.029	0.029	0.000																									
5	*Quantula weinkauffiana* (PSP)	0.087	0.084	0.082	0.082																								
6	*Quantula weinkauffiana* (H18)	0.087	0.084	0.082	0.082	0.002																							
7	*Quantula weinkauffiana* (H53)	0.089	0.089	0.084	0.084	0.011	0.009																						
8	*Quantula weinkauffiana* (CA11)	0.087	0.087	0.082	0.082	0.005	0.003	0.006																					
9	*Quantula weinkauffiana* (CA13)	0.084	0.084	0.079	0.079	0.011	0.009	0.009	0.006																				
10	*Quantula striata* (H23)	0.098	0.095	0.090	0.090	0.037	0.035	0.043	0.037	0.037																			
11	*Quantula striata* (H23)	0.098	0.095	0.090	0.090	0.034	0.032	0.040	0.034	0.037	0.003																		
12	*Quantula godwinausteni* (H30)	0.084	0.081	0.084	0.084	0.072	0.070	0.076	0.073	0.073	0.084	0.084																	
13	*Quantula* sp.1 (H60)	0.031	0.031	0.005	0.005	0.082	0.081	0.082	0.081	0.078	0.089	0.089	0.082																

		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28
14	*Quantula* sp.1 (H24)	0.031	0.032	0.037	0.037	0.079	0.078	0.079	0.078	0.078	0.090	0.090	0.072	0.032															
15	*Quantula* sp.1 (H50)	0.027	0.027	0.023	0.023	0.076	0.075	0.076	0.075	0.072	0.084	0.084	0.075	0.021	0.032														
16	*Quantula* sp.2 (H51)	0.072	0.072	0.069	0.069	0.072	0.070	0.076	0.073	0.073	0.090	0.087	0.072	0.067	0.069	0.063													
17	*Quantula* sp.3 (H124)	0.096	0.093	0.092	0.092	0.089	0.087	0.093	0.090	0.089	0.104	0.104	0.076	0.087	0.090	0.084	0.078												
18	*Phuphania globosa* (H42)	0.134	0.131	0.124	0.124	0.110	0.108	0.118	0.111	0.113	0.125	0.122	0.118	0.119	0.119	0.124	0.116	0.122											
19	*Phuphania globosa* (H12)	0.140	0.137	0.131	0.131	0.119	0.118	0.127	0.121	0.119	0.125	0.125	0.121	0.127	0.127	0.131	0.122	0.124	0.032										
20	*Phuphania costata* (H67)	0.130	0.124	0.130	0.130	0.118	0.116	0.121	0.119	0.121	0.133	0.130	0.121	0.128	0.119	0.118	0.130	0.115	0.104	0.115									
21	*Phuphania carinata* (H125)	0.130	0.130	0.133	0.133	0.116	0.115	0.119	0.118	0.119	0.127	0.124	0.125	0.131	0.125	0.115	0.122	0.121	0.108	0.118	0.044								
22	*Phuphania crossei* (H61)	0.139	0.134	0.131	0.131	0.113	0.111	0.116	0.115	0.113	0.125	0.125	0.131	0.127	0.133	0.133	0.115	0.111	0.098	0.105	0.099	0.105							
23	*Phuphania crossei* (H5)	0.139	0.134	0.131	0.131	0.111	0.110	0.115	0.113	0.111	0.124	0.124	0.128	0.127	0.133	0.133	0.115	0.110	0.095	0.102	0.098	0.104	0.005						
24	*Asperitas trochus* (H31)	0.119	0.118	0.119	0.119	0.115	0.113	0.116	0.116	0.119	0.127	0.127	0.115	0.115	0.110	0.115	0.116	0.104	0.122	0.122	0.121	0.113	0.128	0.127					
25	*Dyakia janus* (H9)	0.128	0.128	0.121	0.121	0.118	0.116	0.116	0.115	0.113	0.122	0.122	0.121	0.119	0.124	0.118	0.119	0.104	0.119	0.124	0.118	0.110	0.113	0.113	0.092				
26	*Dyakia janus* (H57)	0.115	0.118	0.113	0.113	0.111	0.110	0.107	0.108	0.107	0.118	0.118	0.111	0.108	0.111	0.107	0.107	0.098	0.119	0.124	0.116	0.115	0.113	0.113	0.087	0.027			
27	*Everettia dominiki* (E14411)	0.144	0.142	0.145	0.145	0.116	0.115	0.122	0.116	0.116	0.121	0.122	0.137	0.144	0.133	0.136	0.127	0.124	0.140	0.148	0.137	0.134	0.142	0.140	0.131	0.128	0.121		
28	*Pseudoquantula lenticularis* (H21)	0.147	0.147	0.139	0.139	0.133	0.131	0.133	0.130	0.130	0.147	0.148	0.151	0.137	0.139	0.134	0.134	0.142	0.134	0.140	0.144	0.137	0.134	0.137	0.131	0.134	0.130	0.145	
29	*Pseudoquantula lenticularis* (H33)	0.150	0.150	0.142	0.142	0.139	0.137	0.139	0.136	0.136	0.147	0.148	0.154	0.140	0.142	0.134	0.137	0.151	0.137	0.144	0.150	0.137	0.136	0.139	0.134	0.137	0.133	0.151	0.012

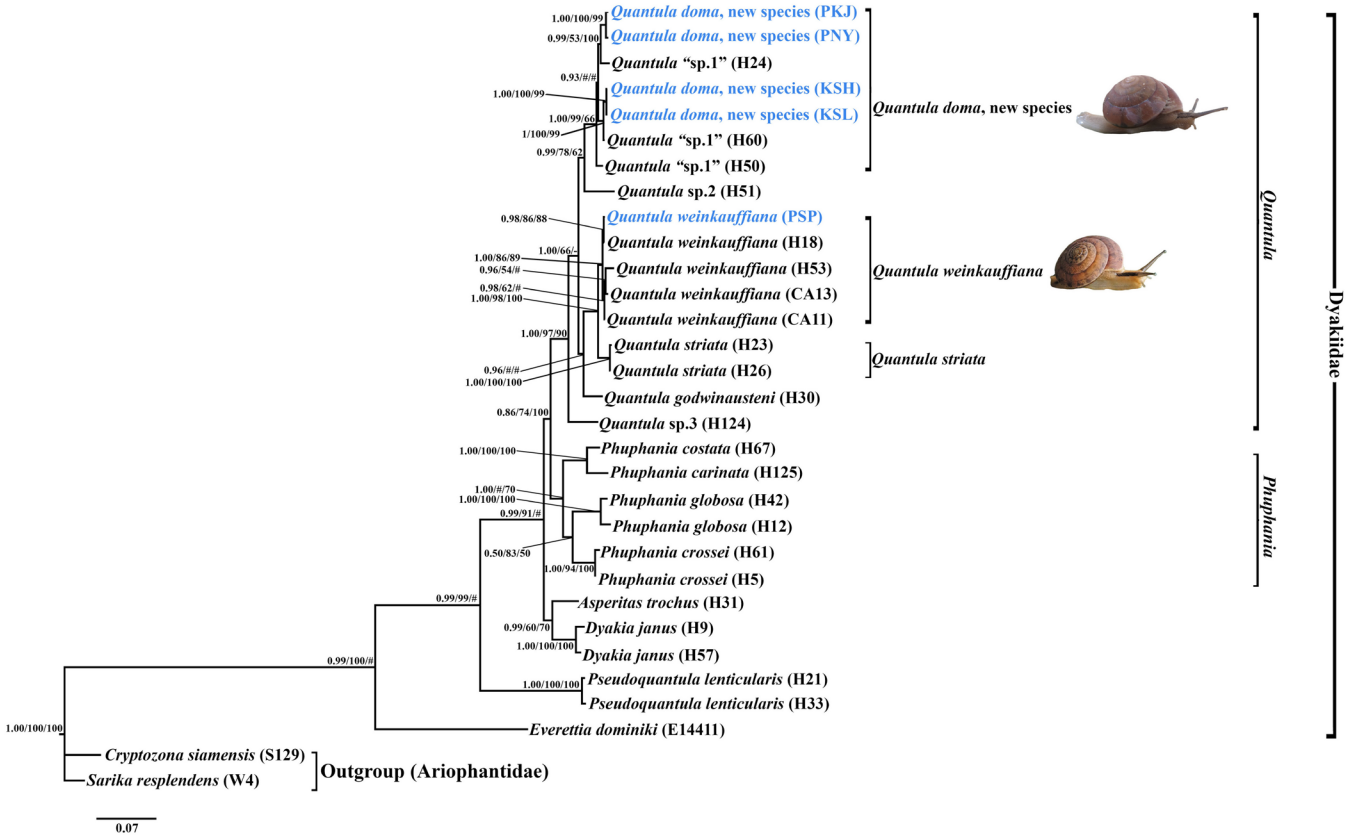

Fig. 2. Bayesian inference (BI) tree of *Quantula* in this study (Blue colour) determined from 28s and COI genes. Numbers at nodes indicate branch support based on posterior probability (BI)/bootstrapping (ML)/bootstrapping (NJ). # Indicates branches that received < 0.50 of posterior probability and received < 50% of bootstrap support. - indicates non-supported branches by bootstrap. Scale bar = 0.1 substitutions/site.

lateral dark brown stripes running from each of upper tentacle backward to pneumostome.

Genitalia (n=5) (Fig. 5A–E): Penis short, cylindrical. Epiphallus shorter and slender than penis. Inner wall of penis with three very short and thin longitudinal pilasters near atrium, with other regions smooth (Fig. 5D). Vas deferens short. Penial retractor muscle absent. Gametolytic sac short with gametolytic duct connecting to middle part of amatorial organ. Amatorial organ cylindrical, gradually larger at distal portion. Inner part of this portion, without longitudinal pilaster, but, with short amatorial organ papilla, which is robust, cylindrical and not exceeding half of distance between distal end of amatorial organ and junction of gametolytic duct. Orange papilla spike present (Fig. 5B, C). Inner wall of distal part with transverse lamella or nearly smooth surface, whereas, in proximal part before junction of gametolytic duct with two longitudinal pilasters (Fig. 5C). Amatorial organ duct shorter than amatorial organ. Vagina longer than penis. Surface of inner wall of vagina undulated, proximally with thin transverse lamellae (Fig. 5E).

Radula (n=5) (Fig. 5F–G): There are approximately 78 rows of teeth, each of which comprises 73–173 teeth, formula (19–62) + (17–24) + 1 + (17–24) + (19–62). Central tooth tricuspid, lanceolate, smaller than lateral teeth. Lateral teeth tricuspid, oblique lanceolate. Marginal teeth unicuspid, sword shaped.

Remarks. Images published in Inkhavilay et al. (2019) included the syntype, MNHN-IM-2000-27780 (Fig. 32B), specimens from Savannakhet (Figs. 32C, 55H), and specimens from Champasak (Fig. 32D). The type specimen possesses a sharp peripheral keel and thickened peristome. These characters resemble specimens from Phanom Sawai and in Schileyko (2003: Fig. 1776A), which illustrated the drawing of a shell identified as "*Quantula striata*". According to the shell morphology and distribution, the shell from Southern Vietnam illustrated in Schileyko (2003) should be identified as *Quantula weinkauffiana*. However, "*Ariophanta weinkauffiana inflata*" and "*Nanina (Hemiplecta) weinkauffiana minor*", which were described from localities outside north-eastern Thailand, need clarification of their taxonomic status via further study. From the result of molecular phylogeny of Dyakiidae by Jirapatrasilp et al. (2021), *Quantula weinkauffiana* individuals from Khao Panom Sawai, Surin (Thailand), Champasak (Laos), and Kampot (Cambodia) were in the same clade with high support (BI= 100%). Considering the result from this study, the intraspecific genetic distances among the *Quantula weinkauffiana* populations of Laos, Cambodia, and Phanom Sawai were low, as they ranged from 0.2–1.1%, while within the Panom Sawai population, it was 0.2% (Table 2), and the *Quantula weinkauffiana* clade obtained strong support (Fig. 2) (BI posterior probability of 1.00 and 86% for ML, and 89% for NJ bootstrap replicate).

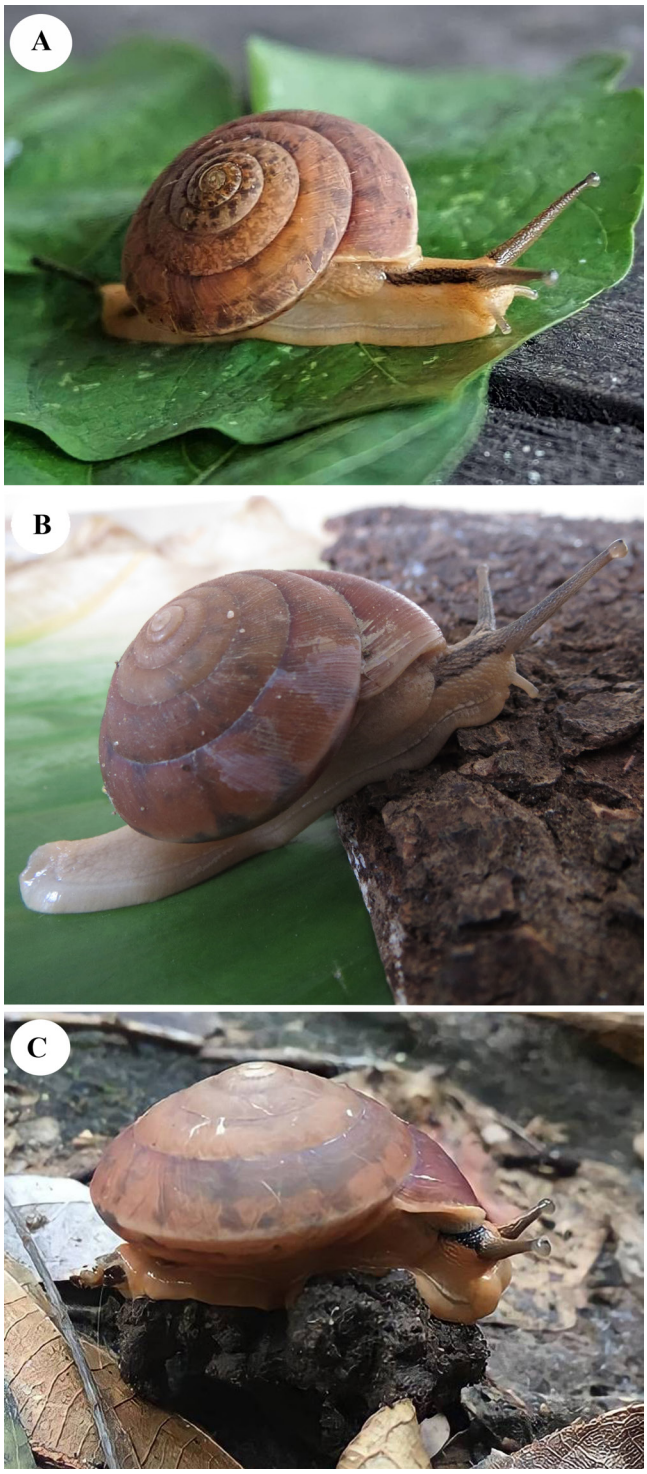

Fig. 3. Living snails of *Quantula* spp. in the southern part of north-eastern Thailand. A, *Q. weinkauffiana* (NHMSU-00035) from Phanom Sawai, Surin; B–C, *Q. doma*, new species: B, NHMSU-00049 from Khao Sala, Surin; C, NHMSU-00051 from Phu Jor Kor, Mukdahan.

Distribution. Southern Vietnam, Cambodia, Southern Laos, and North-eastern Thailand (Crosse & Fischer, 1863; Schileyko, 2011; Inkhavilay et al., 2019; Sutcharit et al., 2020b). In Thailand, this species is currently recorded from Khao Panom Sawai, Surin Province (Jirapatrasilp et al., 2021 and this study).

Fig. 4. Shell morphology of *Quantula* spp. in the southern part of north-eastern Thailand. A, *Q. weinkauffiana*, specimen NHMSU-00035 from Phanom Sawai, Surin; B–C, *Q. doma*, new species: B, holotype NHMSU-00048 from Khao Sala, Surin; C, NHMSU-00050 from Phu Jor Kor, Mukdahan.

***Quantula doma*, new species**
(Figs. 3B–C, 4B–C, 6A–J; Tables 1–3)

Quantula sp. – Jumlong et al., 2013: 71–72, 74–76, 78–79, fig. 3.
Quantula weinkauffiana – Worachak, 2014: 40–42, figs. 4.1A–B, 4.2 A–C, 4.3 B–C.
Quantula sp. 1 – Worachak, 2014: 43–45, figs. 4.4A, 4.5A–E, 4.6A–B.
Quantula sp. 1 – Jirapatrasilp et al., 2021: 193 (1), 262–263.
Quantula striata – Hoompuay, 2016: 22–25, figs. 4.1–4.3.
Quantula sp. 6 – Hoompuay, 2016: 43–45, figs. 4.21–4.24.

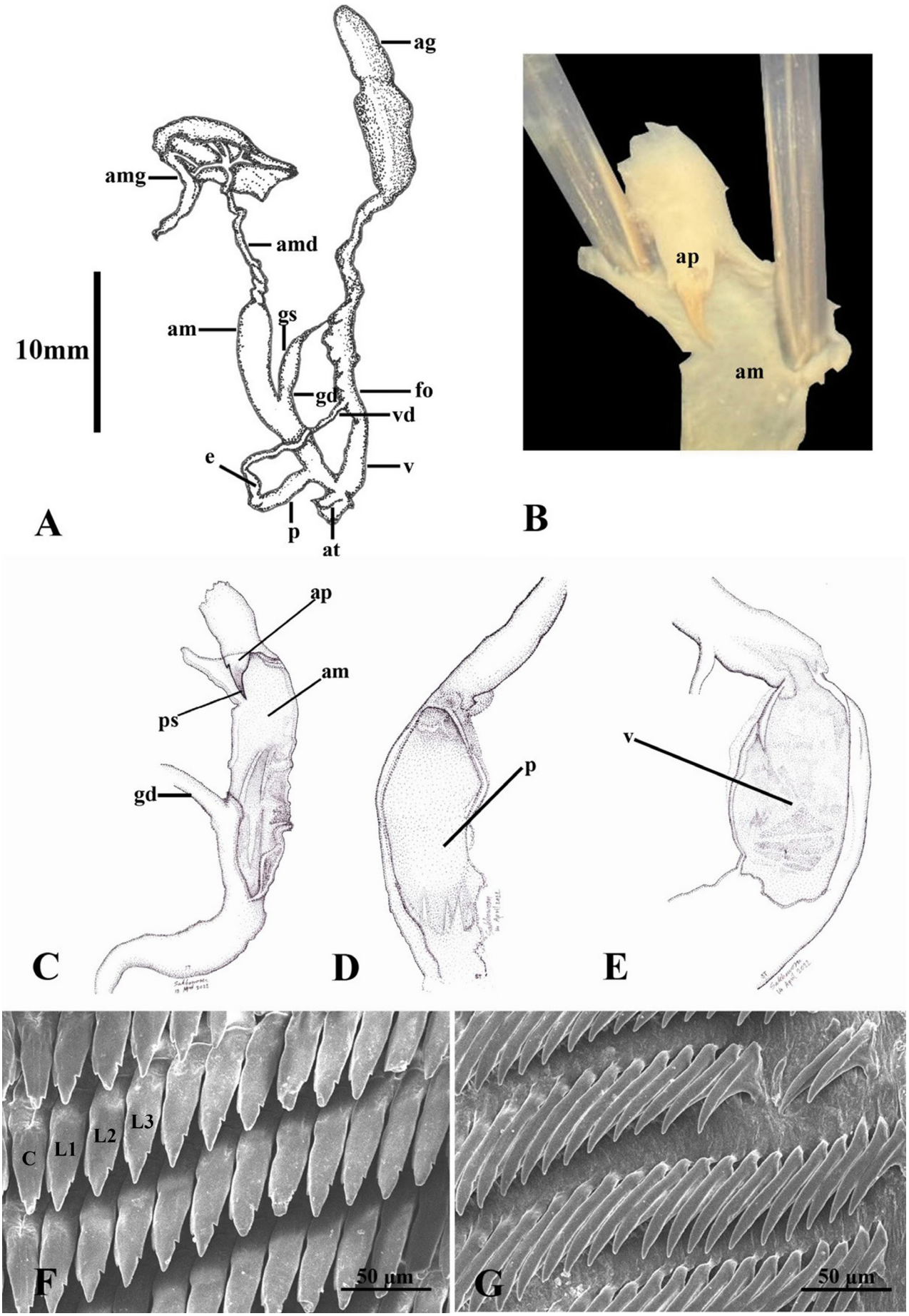

Fig. 5. *Quantula weinkauffiana* genital system and radula morphology, specimen NHMSU-00035. A, genital system (adapted after Hoompuay, 2016); B–E, inner structure of genital system; B and C, amatorial organ (am); D, penis (p); E, vagina (v); F, right side of central teeth (C) and lateral teeth (L); G, right side of marginal teeth (F & G, adapted from Hoompuay, 2016).

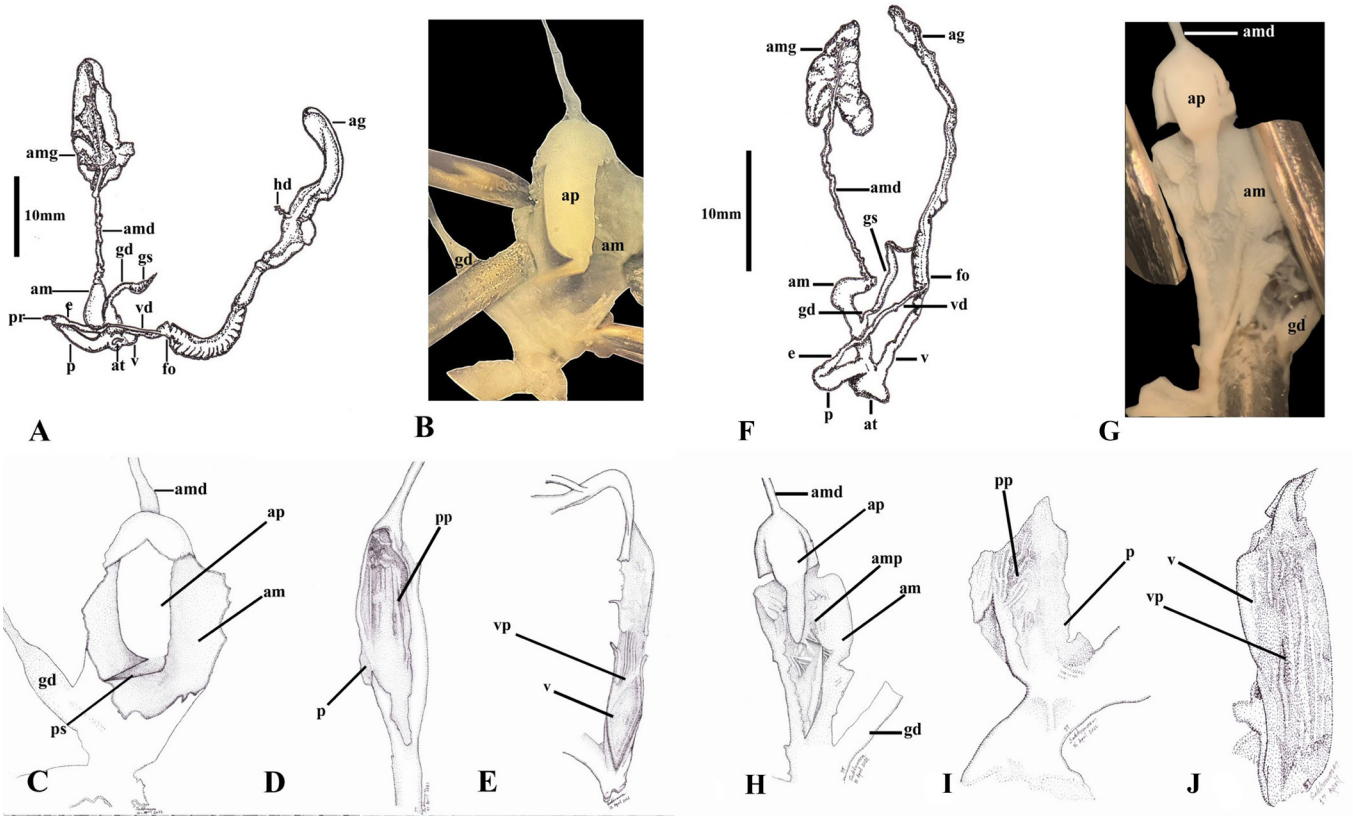

Fig. 6. *Quantula doma*, new species; A–E, genital system of paratype NHMSU-00049 from Khao Sala, Surin Province. A, genital system (adapted after Hoompuay, 2016); B–E, inner structure of genital system; B and C, amatorial organ (am); D, penis (p); E, vagina (v); F–J, genital system of NHMSU-00051 from Phu Jor Kor, Mukdahan Province. F, genital system (adapted after Hoompuay, 2016); G–J, inner structure of genital system; G and H, amatorial organ (am); I, penis (p); J, vagina (v).

Material examined. Holotype: NHMSU-00048 (Fig. 4B) from Khao Sala, Buachet District, Surin Province; 14°25′50.5″N 103°56′15.6″E; 14 October 2017; SH = 18.69 mm, SW = 28.61 mm. Paratypes: 47 shells (25 adults & 22 juveniles), 28 living specimens; same data as holotype; NHMSU-00049. One shell (NHMSU-00050) from Phu Jor Kor, Nong Soong District, Mukdahan Province; (16°22′22.1″N, 104°22′32.2″E), 11 October 2017 (Fig. 4C); Two adult and three juvenile shells, and nine living specimens (NHMSU-00051) same locality as NHMSU-00050; One adult and one juvenile shells and two living specimens (NHMSU-00052); Pha Nam Yoi, Nong Phok District, Roi Et Province, Thailand; 16°19′22.3″N 104°19′33.4″E; 11 October 2017; seven adult and three juvenile shells, and five living specimens (NHMSU-00053), same data with NHMSU-00052.

Diagnosis. Last whorl angular with peripheral keel, not descending in front. Amatorial organ duct longer than amatorial organ.

Etymology. The specific epithet is derived from the Latin word ‘domus’ meaning roof, referring to the fact that its shell shape is similar to a hemispherical roof.

Description. Shell (n=48, 26 adult & 22 juveniles from Khao Sala (Fig. 4B) and n=20, 11 adults & 9 juveniles from Phu Jor Kor and Pha Nam Yoi (Fig. 4C)): Dextral, dome-shaped to depressed-conic lenticular, with 6–6¼ whorls, suture shallow, growth line prominent. Last whorl angular with peripheral keel, but less sharp than *Q. wienkauffiana*. Shell height 14.8–21.9 mm, shell width 25.1–35.3 mm. Apex blunt, shell light brown, ventral side paler than dorsal side. Apertural lip simple and thick, and slightly expanded at columellar side in adult specimens. Umbilicus narrow and deep.

Body (n=28 from Khao Sala (Fig. 3B) and n = 11 from Phu Jor Kor and Pha Nam Yoi (Fig. 3C)): Living snail orange brown, with two lateral light brown or dark stripes running from base of each upper tentacle backward to pneumostome.

Genitalia (n=13, comprising three specimens from Khao Sala (one specimen from Hoompuay, 2016) (Fig. 6A–E), three specimens from Phu Jor Kor, and seven specimens from Pha Nam Yoi (five specimens from Hoompuay, 2016) (Fig. 6F–J): Penis short, cylindrical, inner wall with robust longitudinal penial pilaster alternating with 1–2 thin longitudinal pilasters (Fig. 6D), whereas specimens from Phu Jor Kor sculptured with irregular undulate penial pilasters arranged in inclined and longitudinal rows (Fig. 7D). Epiphallus shorter than penis. Vas deferens longer than penis. Gametolytic duct connecting to basal part of amatorial organ, basally bulbous, distally with short and small duct. Tapering gametolytic sac long, robust (Fig. 6A). Amatorial organ elliptical, with inner wall smooth. Papilla of amatorial organ strong, long, reaching junction of gametolytic duct. Corneous spike present (Fig. 6B–C). Amatorial organ duct longer than amatorial

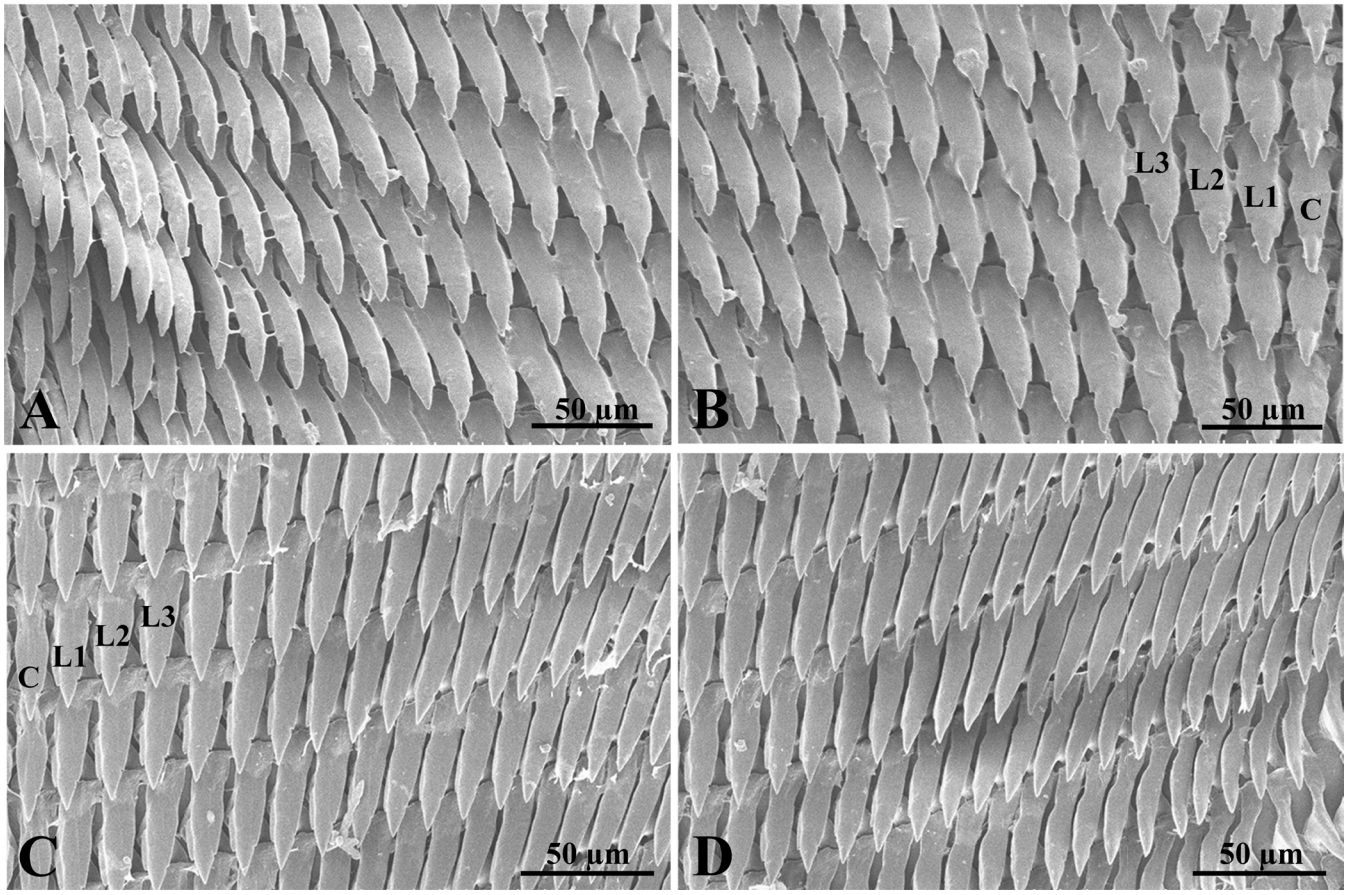

Fig. 7. Radula morphology of *Quantula doma*, new species. A–B, paratype NHMSU-00049 from Khao Sala, Surin Province; A, left side of marginal teeth; B, left side of central teeth and lateral teeth. C–D, NHMSU-00051 from Phu Jor Kor, Mukdahan Province; C, right side of central teeth and lateral teeth. D, right side of marginal teeth.

organ. Vagina and free oviduct shorter than penis. Inner wall of vagina smooth, with 3–4 thin longitudinal pilasters on median part (Fig. 6E). Specimens from Phu Jor Kor has gametolytic duct connecting to middle part of amatorial organ. Gametolytic sac cylindrical, long. Amatorial organ long, cylindrical, with inner wall sculptured with irregular undulated short pilasters. Papilla of amatorial organ robust, cylindrical, distally finger-shaped, without terminal corneous spike. Vagina longer than penis, internally with four to five longitudinal pilasters. Amatorial organ duct nearly as long as, or slightly longer than amatorial organ.

Radula (n=13, comprising three specimens from Khao Sala (one specimen from Hoompuay, 2016) (Fig. 7A–B) three specimens from Phu Jor Kor, and seven specimens from Pha Nam Yoi (five specimens from Hoompuay, 2016) (Fig. 7C–D): with 83–90 rows of teeth. Each row with 83–123 teeth, formula: (24–42) + (17–19) + 1 + (17–19) + (24–42) in specimens from Khao Sala, and approximately 70–82 rows of teeth, each of which comprises 91–123 teeth. Fomula: (31–43) + (14–18) + 1 + (14–18) + (31–43) in specimens from Phu Jor Kor and Pha Nam Yoi. Central and lateral teeth lanceolate, tricuspid. Marginal teeth bicuspid and gradually changing to unicuspid and sword shaped.

Distribution. *Quantula doma*, new species, is found in sandstone mountains of the southern part of north-eastern Thailand, in the Surin, Roi Et, and Mukdahan Provinces.

Remarks. According to the genetic distance and phylogenetic analysis, *Quantula* "sp. 1" from Khao Sala in Jirapatrasilp et al. (2021) (specimen no. H60, COI and 28s accession numbers MT803088 and MT741936) is clustered with the *Q. doma*, new species (specimen no. KSH and KSL). Genetic distances within the Khao Sala population are around 0.5% (Table 2), and all specimens have rather strong support (Fig. 2) (BI posterior probability of 1.00 and 100% for ML, and 99% for NJ bootstrap replicate), based on which we conclude that specimen H60, KSH and KSL represent the same species as *Q. doma*, new species. Although conchologically this new species looks similar to *Q. simonei* Thach & Huber 2018 from Laos (see Thach, 2018: plate 49, figs. 580, 581 top), in *Q. doma*, new species, the last whorl is angulate with weak peripheral keel and has an open umbilicus, whereas in *Q. simonei*, the last whorl is well-inflated without peripheral keel, and the umbilicus is mostly covered by the columella portion of the apertural lip.

DISCUSSION

In Thailand, mid-sized, depressed-conic dextral land shells with a sharp peripheral keel on the last whorl have traditionally been identified as "*Hemiplecta weinkauffiana*" or *Quantula weinkauffiana* (Panha, 1996; Panha & Thanamitramanee, 1997; Hemmen & Hemmen, 2001; Nabhitabhata, 2009). Recently, the reproductive anatomy of *Quantula* specimens

has been studied from many localities in the southern part of north-eastern Thailand, and the results reveal that there are differences in many populations (Worachak et al., 2014; Hoompuay et al., 2015). Molecular phylogeny has been applied for confirmation of the classification of dyakiid snails, in which genital organs are more likely to reflect their systematic position (Sutcharit et al., 2020a; Jirapatrasilp et al., 2021; Pholyotha et al., 2021).

In this study, we employed COI and 28S rDNA sequences of *Quantula* spp. and some other genera from Jirapatrasilp et al. (2021) in our phylogenetic analysis. The genetic distance and phylogenetic tree (Table 2 and Fig. 2) confirmed the classification using the shell morphology and reproductive anatomy, which suggest that specimens of *Quantula* from the southern part of north-eastern Thailand consist of at least two species, i.e., *Q. doma*, new species, and *Q. weinkauffiana*. Both species have high variability in shell form but we can separate each species by genital characters and phylogenetic methods. However, the northern population of *Q. doma*, new species differ from the southern population due to the absence of a papilla spike in the amatorial organ (Fig. 6G–H), and sculptures on the inner wall of the amatorial organ, penis, and vagina (Fig. 6H–J). The genetic distances between two localities of the northern population are around 0.8%, and according to the phylogenetic results, specimens from both localities are in the same clade with strong support (Fig. 2).

The sequence of *Quantula* "sp. 1" (H24) as proposed by Jirapatrasilp et al. (2021) from Wang Tra Krai (Table 2) had p-distances between both localities of the northern population of *Q. doma*, new species as 3.1% and 3.2%, respectively, and also formed a sister group to the northern population of *Q. doma*, new species, with rather strong support (Fig. 2). Based on these analyses, we could conclude that *Quantula* "sp. 1" (H24) is *Q. doma*, new species, but the genital information of this population needs to be provided by further study. *Quantula* "sp. 1" (H60) from Khao Sala, Surin Province in Jirapatrasilp et al. (2021), is also now confirmed to be *Quantula doma*, new species, as the p-distances between both specimens from the same locality in the study were 0.5% and also it also formed a sister group to *Q. doma*, new species with strong support (Fig. 2). The southern population of *Q. doma*, new species from Khao Sala possesses unique characters, i.e. vagina shorter than penis, amatorial organ cylindrical and short, gametolytic duct connecting to basal amatorial organ, and papilla of amatorial organ with spike reaching to the junction of gametolytic duct.

Other *Quantula* "sp. 1" populations are still in question. *Quantula* "sp. 1" (H50) from Khao Ang Rue Nai, Chacheongsao Province in Jirapatrasilp et al. (2021) are separated from the tree with 1.00 for BI posterior probability, and 99% and 66% bootstrap support for ML and NJ, but genetic distance suggests it is close to both populations of *Q. doma*, new species (p-distances 2.3% for southern population and p-distances 2.7% for northern population). Both *Quantula* sp. 2 and *Quantula* sp. 3 have large genetic distances when compared to other *Quantula* spp and appear to be distinct species (Fig. 2). This agrees with Jirapatrasilp et al. (2021) and further morphological and taxonomic studies are needed.

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