

Integrative taxonomic revision of the land snail genus *Sarika* Godwin-Austen, 1907 in Thailand, with descriptions of nine new species (Eupulmonata, Ariophantidae)

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Abstract

Members of the land snail genus *Sarika* Godwin-Austen, 1907 are superficially similar and difficult to differentiate by their shell morphology so that their species limits are still unclear. In order to resolve the taxonomy of this group, a phylogenetic reconstruction of *Sarika* is presented, based on morphological and anatomical characters, as well as on partial sequences of the mitochondrial cytochrome c oxidase subunit I (COI) gene. In total, 23 species of *Sarika* are recognised in Thailand, and nine species are new to science, namely *S. caligina* Pholyotha & Panha, **sp. nov.**, *S. gratesi* Pholyotha & Panha, **sp. nov.**, *S. inferospira* Pholyotha & Panha, **sp. nov.**, *S. lactospira* Pholyotha & Panha, **sp. nov.**, *S. megalogyne* Pholyotha & Panha, **sp. nov.**, *S. melanospira* Pholyotha & Panha, **sp. nov.**, *S. pellosa* Pholyotha & Panha, **sp. nov.**, *S. solei* Pholyotha & Panha, **sp. nov.**, and *S. subheptagyra* Pholyotha & Panha, **sp. nov.** Results from genital examination and COI analyses confirm the monophyly of *Sarika* and its species. The intra- and inter-specific genetic distances of *Sarika* were 0–3.7% and 4.6–12.0%, respectively. Colour images of the living adults, shell, and genitalia along with SEM images of the spermatophore and radula are given. In addition, an identification key and a geographical distribution map of *Sarika* species are provided.

Keywords

Diversity, DNA barcodes, Indochina, limestone, systematics

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Introduction

Thailand contains a high diversity of land snails and high levels of species endemism, which is likely due to its position in the centre of the zoogeographical regions of Indo-Burma and Sundaland, a large extensive range of several limestone and mountainous hills, various kinds of tropical forests, and a high relative humidity (Myers et al. 2000; Gupta 2005; Clements et al. 2006; Naggs et al. 2006; Ridd et al. 2011; Gardner et al. 2015). To date, many groups of land snails in Thailand have been well studied, such as micro-snails (e.g., Tongkerd et al. 2004), the colourful tree snails (e.g., Sutcharit and Panha 2006), carnivorous snails (e.g., Siriboon et al. 2014), and operculate snails (e.g., Nantararat et al. 2014). However, information on the common ground-dwelling land snail genus *Sarika* Godwin-Austen, 1907 is very scanty, so that the taxonomic status of most *Sarika* species is still doubtful and needs to be resolved.

Sarika is a land snail genus in the family Ariophantidae Godwin-Austen, 1883 and is widely distributed in mainland Southeast Asia, especially throughout Thailand (Blanford and Godwin-Austen 1908; Zilch 1959; Solem 1966; Schileyko 2002; Inkhavilay et al. 2019; Pholyotha et al. 2020a, 2020c). Systematic studies of *Sarika* date back from the mid-19th to the early 20th centuries (Pfeiffer 1860; Möllendorff 1894, 1902; Godwin-Austen 1907; Blanford and Godwin-Austen 1908; Tomlin 1929; Laidlaw 1933; Solem 1966). The first genital examination of *Helix resplendens* Philippi, 1846 was done by Godwin-Austen (1898). Nine years later, Godwin-Austen (1907) nominated *Sarika* as a distinct genus from the genus *Macrochlamys* Gray, 1847, and designated *H. resplendens* Philippi, 1846 as the type species of *Sarika*, emphasizing that *Sarika* and *Macrochlamys* have a very similar shell form (depressed shape, closely coiled whorl, polished, thin, and semi-transparent) and general soft anatomy (short to long flagellum, long spermatheca and large dart apparatus). However, the genitalia of *Sarika* possess a straight (or un-coiled) epiphallic caecum, while *Macrochlamys* has a spirally coiled epiphallic caecum (Godwin-Austen 1907; Blanford and Godwin-Austen 1908; Schileyko 2002, 2003; Pholyotha et al. 2018, 2020c; Sajan et al. 2019).

Subsequently, many species have been placed in the genus *Sarika* (Laidlaw 1933; Solem 1966; Panha 1996; Hemmen and Hemmen 2001; Pholyotha et al. 2018, 2020a, 2020c; Inkhavilay et al. 2019). Yet, most previous studies were either species descriptions or checklist, and in Thailand and Malaysia, only a few studies so far have dealt with the genital anatomy (Godwin-Austen 1907; Laidlaw 1933; Solem 1966; Maneevong 2000; Sutcharit and Panha 2008). In Laos, Inkhavilay et al. (2019) published a checklist of the land snails, including several species of *Sarika*. A year later, the genus *Sarika* from Myanmar and Cambodia were taxonomically revised, and two new species from Myanmar and three new species from Cambodia were discovered based on genitalia characters (Pholyotha et al. 2020a, 2020c; Sutcharit et al. 2020). However, knowledge on the genus *Sarika* is still fragmentary because most of the nominal species are described from Thailand. Therefore, we examined the anatomy of specimens collected during intensive field surveys throughout Thailand, and found that the diversity of this genus remains underestimated and its complex relationships are a mystery.

This present study is the first comprehensive taxonomic treatment of the land snail genus *Sarika* based on conchological and anatomical characters and data on the mitochondrial cytochrome c oxidase subunit I (COI) gene. The COI gene has been widely used to resolve the phylogenetic relationships among closely related species in several land snails (Liew et al. 2009; Nantararat et al. 2014; Köhler and Criscione 2015; Hyman and Köhler 2018). Thus, we analysed the COI gene phylogeny of *Sarika* to test the monophyly of each species and to understand the phylogenetic relationships of *Sarika*. This work includes taxonomic updates, illustrations of type specimens (when possible), and descriptions of the living snails, shells, genitalia, radula, and spermatophore. Moreover, nine *Sarika* species are herein described as new to science. An identification key to *Sarika* is provided and the distribution ranges for species are updated.

Materials and methods

Specimen sampling and morphological studies

This work is based on new specimens collected throughout Thailand and voucher specimens deposited in the Chulalongkorn University Museum of Zoology (CUMZ), Bangkok. Living specimens were photographed, euthanised by two-step methods (American Veterinary Medical Association 2020), and then fixed in 95% (v/v) ethanol for morphological and DNA studies. Species identification followed the original descriptions by Godwin-Austen (1907), Blanford and Godwin-Austen (1908) and Pholyotha et al. (2020c), and were then compared to the relevant type specimens. To study anatomy, 3–10 specimens of each species were dissected and examined under a stereomicroscope. Adult shells were used to measure the shell height and shell width, and to count the number of whorls. Shells and genitalia were imaged using a digital camera and a stereomicroscope 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 (SEM; JEOL, JSM-6610 LV).

In the material examined sections, shells refer to empty shells while specimens refer to specimens preserved in ethanol. The Thai terms “Tham” meaning cave, “Wat” meaning temple, and “Phu” and “Khao” for mountain or hill are used throughout for the locality names.

Descriptions of all new species herein are attributed to Pholyotha & Panha.

COI analyses

Details of samples selected for COI analysis are shown in Table 1. DNA was extracted from the foot muscle using the NucleoSpin Tissue Kit (Macherey-Nagel, Germany), following the standard procedure of the manufacturer. A fragment of the mitochondrial cytochrome c oxidase subunit I (COI) gene was amplified from each specimen by PCR using the universal primer pair LCO1491 (5'-GGTCAACAAATCATAAAGATATTGG-3') and HCO2198 (5'-TAAACTTCAGGGTGACCAAAAAATCA-3') (Folmer et al. 1994).

The reaction was performed using standard protocols (Nantararat et al. 2014) with annealing temperatures of 50 °C or 52 °C for 120 s. The amplified PCR products were checked under an UV transilluminator after gel electrophoresis, then commercially sequenced by Bioneer Co., Korea, with the same primers in both directions. Nucleotide sequences were deposited in GenBank under accession numbers: MT894062–MT894119 (see Table 1).

The COI gene sequences were edited and aligned using ClustalW, as implemented in the MEGA7 software (Kumar et al. 2016). Genetic distances between *Sarika* species and related taxa were calculated using Kimura's two-parameter model (K2P) as implemented in MEGA7 (Kumar et al. 2016). The alignments were tested for substitution saturation using DAMBE (Xia 2013). As no saturation was detected in the sequences (Iss < Iss.c with $p < 0.01$), all the codon positions were used in the subsequent analysis. The phylogenetic analyses were conducted using maximum likelihood (ML) and Bayesian inference (BI) and both analyses were performed on-line through the CIPRES Science Gateway (Miller et al. 2010). The ML analyses were performed by using the program RAXML-HPC2 on XSEDE v. 8.2.12 (Stamatakis 2014) with 1000 bootstrap replicates using GTRGAMMA as the model. Prior to the BI analysis, Kakusan4 (Tanabe 2011) identified the best-fit model as follows: the general time reversible model (Tavaré 1986) with gamma distribution for the first and the second COI codon positions, and the HKY model (Hasegawa et al. 1985) for the third COI codon position. The BI analysis was performed by using the program MrBayes on XSEDE v. 3.2.7a (Ronquist et al. 2012) with two simultaneous runs. The analysis was run for 10 million generations (default heating parameter), sampled every 500 generations, starting with a random tree and burn-in set to 50%. Convergence of the two runs was achieved if the average standard deviation of split frequencies were ≤ 0.01 (Ronquist et al. 2012). Bootstrap support values (BS) of $\geq 70\%$ and BI posterior probabilities (PP) of ≥ 0.95 were regarded as significant (Hillis and Bull 1993; Felsenstein 2004; Huelsenbeck and Rannala 2004; Mauro and Agorreta 2010; Hirano et al. 2018).

Anatomical abbreviations

In the descriptions of the genitalia, the term 'proximal' refers to the region closest to the genital opening, while 'distal' refers to the region furthest away from the genital opening. The following abbreviations were used as defined by Godwin-Austen (1907), Blanford and Godwin-Austen (1908), Solem (1966), Sutcharit and Panha (2008), and Pholyotha et al. (2018, 2020b):

ant-ldl	anterior left dorsal lobe;	hf	head filament;
at	atrium;	lsl	left shell lobe;
da	dart apparatus;	p	penis;
e	epiphallus;	pc	penial caecum;
ec	epiphallic caecum;	post-ldl	posterior left dorsal lobe;
fl	flagellum;	pp	penial pilaster;
fo	free oviduct;	prm	penial retractor muscle;
gd	gametolytic duct;	psv	pseudo-verge;
gs	gametolytic sac;	pv	penial verge;

rdl

right dorsal lobe;

rsl

right shell lobe;

ss

sperm sac;

tf

tail filament;

v

vagina;

vd

vas deferens.

Institutional abbreviations

CUMZ

Chulalongkorn University, Museum of Zoology, Bangkok, Thailand

MNHN

Muséum National d'Histoire Naturelle, Paris, France

NHM, NHMUK

The Natural History Museum, London, United Kingdom

NMW

National Museum of Wales, Cardiff, Wales

SMF

Forschungsinstitut und Naturmuseum Senckenberg, Frankfurt am Main, Germany

ZRC

Zoological Reference Collection of the Lee Kong Chian Natural History Museum, National University of Singapore, Singapore

Table 1. Information of all samples used for the phylogenetic study.

Species/ specimen code	CUMZ code	Locality	GenBank accession number
Genus <i>Sarika</i>			
<i>S. resplendens</i>			
C14	7880	Bang Krachao, Phra Pradaeng, Samut Prakan, Thailand	MT894062
C36	7871	Wat Tham Pha Phung, Wang Pong, Phetchabun, Thailand	MT894063
E17	7875	Mountain area near Ang Kep Nam Dan Chumphon, Bo Rai, Trat, Thailand	MT894064
S4–3	7815	Limestone outcrop near Khanom Golden Beach, Khanom, Nakhon Si Thammarat, Thailand	MT894065
S42	7829	Wat Ao Sader, Khanom, Nakhon Si Thammarat, Thailand	MT894066
W9	7886	Wat Tha Khanun, Thong Pha Phum, Kanchanaburi, Thailand	MT894067
W63	7867	Wat Buri Ratchawanaram, Pak Tho, Ratchaburi, Thailand	MT894068
<i>S. dohrniana</i>			
C18	7627	Wat Tham Tham Osot, Muak Lek, Saraburi, Thailand	MT894069
C32	7611	Wat Tham Mongkol Nimit, Mueang, Lopburi, Thailand	MT894070
NE16	7631	Mountain area near Lam Phra Phloeng Dam, Pak Thong Chai, Nakhon Ratchasima, Thailand	MT894071
<i>S. obesior</i>			
W5	7680	Khao Nang Panthurat, Cha-am, Phetchaburi, Thailand	MT894072
W52	7673	Wat Tham Rong, Ban Lat, Phetchaburi, Thailand	MT894073
W54	7676	Khao Lom Muak, Mueang, Prachuap Khiri Khan, Thailand	MT894074
W73	7684	Limestone outcrop in Kui Buri, Kui Buri, Prachuap Khiri Khan, Thailand	MT894075
<i>S. limbata</i>			
S41	7652	Wat Phut Sadi Phupharam, Thung Tako, Chumphon, Thailand	MT894076
S41–2	7652	Wat Phut Sadi Phupharam, Thung Tako, Chumphon, Thailand	MT894077
S55	7653	Wat Tham Khao Lan, Sawi, Chumphon, Thailand	MT894078
S55–2	7653	Wat Tham Khao Lan, Sawi, Chumphon, Thailand	MT894079
<i>S. heptagyna</i>			
W19	7231	Tham Khao Noi Bureau of Monks, Thong Pha Phum, Kanchanaburi, Thailand	MT364980
W25	7232	Tham Dao Wadung, Sai Yok, Kanchanaburi, Thailand	MT364981
W27	7279	Kroeng Krawia, Thong Pha Phum, Kanchanaburi, Thailand	MT894080
<i>S. kawtaoensis</i>			
S3	7762	Limestone outcrop near Khanom Seafood, Khanom, Nakhon Si Thammarat, Thailand	MT894081
S13	7760	Tham Nam Phut, Mueang, Phang-nga, Thailand	MT894082
S28	7759	Wat Suwan Khuha, Mueang, Phang-nga, Thailand	MT894083
S54	7709	Khao Phlu Cave, Pathio, Chumphon, Thailand	MT894084
S118	7738	Kaeo Surakan Cave, Lan Saka, Nakhon Si Thammarat, Thailand	MT894085
<i>S. caligina</i> sp. nov.			
C12	7245	Wat Tham Si Wilai, Chaloeam Phra Kiat, Saraburi, Thailand	MT894086
C12–2	7245	Wat Tham Si Wilai, Chaloeam Phra Kiat, Saraburi, Thailand	MT894087
C12–3	7245	Wat Tham Si Wilai, Chaloeam Phra Kiat, Saraburi, Thailand	MT894088
<i>S. lactospira</i> sp. nov.			
S43	7287	Wat Ao Sader, Khanom, Nakhon Si Thammarat, Thailand	MT894089

Species/ specimen code	CUMZ code	Locality	GenBank accession number
S43–2	7287	Wat Ao Sader, Khanom, Nakhon Si Thammarat, Thailand	MT894090
S44	7291	Khao Krot Bureau of Monks, Khanom, Nakhon Si Thammarat, Thailand	MT894091
S44–2	7291	Khao Krot Bureau of Monks, Khanom, Nakhon Si Thammarat, Thailand	MT894092
<i>S. megalogyne</i> sp. nov.			
S60	7524	Limestone outcrop in Saphli, Pathio, Chumphon, Thailand	MT894093
S143	7909	Limestone outcrop in Saphli, Pathio, Chumphon, Thailand	MT894094
W58	7238	Khao Ma Rong Cave, Bang Saphan, Prachuap Khiri Khan, Thailand	MT364976
<i>S. subheptagyra</i> sp. nov.			
C6	7513	Hup Pa Tar, Lan Sak, Uthai Thani, Thailand	MT894095
C9	7507	Tham Namthip Bureau of Monks, Lan Sak, Uthai Thani, Thailand	MT894096
C34	7511	Hup Pa Tar, Lan Sak, Uthai Thani, Thailand	MT894097
<i>S. hainesi</i>			
C37	7272	Ched Khot Waterfall, Kaeng Khoi, Saraburi, Thailand	MT894098
E2	7237	Pang Sida Waterfall, Watthana Nakhon, Sa Kaeo, Thailand	MT894099
E2–3	7237	Pang Sida Waterfall, Watthana Nakhon, Sa Kaeo, Thailand	MT894100
<i>S. bocourti</i>			
E6	7579	Khao Soi Dao, Soi Dao, Chanthaburi, Thailand	MT894101
E8–2	7596	Trok Nong Waterfall, Khlung, Chanthaburi, Thailand	MT894102
E19	7594	Mountain area near Wat Ban Wang Ka Prae, Pong Nam Ron, Chanthaburi, Thailand	MT894103
S7	7592	Mountain area near Khao Sok Evergreen House, Phanom, Surat Thani, Thailand	MT894104
<i>S. inferospira</i> sp. nov.			
NE6–2	7254	Wat Tham Sai Thong, Nong Kung Si, Kalasin, Thailand	MT894105
NE6–3	7254	Wat Tham Sai Thong, Nong Kung Si, Kalasin, Thailand	MT894106
NE25	7257	Wat Tham Sai Thong, Nong Kung Si, Kalasin, Thailand	MT894107
<i>S. melanospira</i> sp. nov.			
E28	7243	Wat Tham Suwan Phu Pha, Khao Chamao, Rayong, Thailand	MT894108
E28–2	7243	Wat Tham Suwan Phu Pha, Khao Chamao, Rayong, Thailand	MT894109
E28–3	7243	Wat Tham Suwan Phu Pha, Khao Chamao, Rayong, Thailand	MT894110
<i>S. pellosa</i> sp. nov.			
E14	7519	Tham Phet Pho Thong, Khlong Hat, Sa Kaeo, Thailand	MT894111
E40–2	7520	Wat Tham Khao Chakan, Khao Chakan, Sa Kaeo, Thailand	MT894112
E46	7250	Tham Saeng Thian, Khlong Hat, Sa Kaeo, Thailand	MT894113
<i>S. dugasti</i>			
N11	7547	Wat Tham Tong, Chom Thong, Chiang Mai, Thailand	MT894114
N12	7563	Wat Tham Rakhang, Si Samrong, Sukhothai, Thailand	MT894115
W41–2	7574	Chao Por Phawo Shrine, Mae Sot, Tak, Thailand	MT894116
<i>S. solemi</i> sp. nov.			
N18	7298	The limestone karsts with dry forest near Mae La Na Cave, Pang Mapha, Mae Hong Son, Thailand	MT894117
N64	7503	Kew Mae Pan, Chom Thong, Chiang Mai, Thailand	MT894118
N67–2	7911	Mountain area in Chom Thong, Chiang Mai, Thailand	MT894119
Genus <i>Taphrenalla</i>			
<i>T. asamurai</i>			
S18	7153	Wat Tham Wararam, Phanom, Surat Thani, Thailand	MT364934
S34	7153	Wat Tham Wararam, Phanom, Surat Thani, Thailand	MT364936
<i>T. diadema</i>			
S46	7175	Wat Tham Sumano, Srinagarindra, Phatthalung, Thailand	MT364940
S62	7181	Limestone outcrops at Khlong Chaloe, Kong Ra, Phatthalung, Thailand	MT364941
Genus <i>Macrochlamys</i>			
<i>M. aspides</i>			
MY8	7135	Lun Nya Mountain, Hpa an, Kayin, Myanmar	MT364986
<i>M. caverna</i>			
C15	7113	Khao Mon Ing Dharma Practice Place, Ban Mi, Lopburi, Thailand	MT364988
C16	7111	Wat Tham Chang Pueak, Tha Wung, Lopburi, Thailand	MT364987
<i>Macrochlamys</i> sp.			
NE10	7910	Khao Kradong, Mueang, Buriram, Thailand	MT906154
Genus <i>Hemiplecta</i>			
<i>H. distincta</i>			
H54	5267	Tad Pha Suam, Paksong, Champasak, Laos	MT654617
<i>H. humphreysiana</i>			
H7	–	Singapore	MT364994
<i>H. pluto</i>			
H63	–	Laos	MT364995

Results

COI analyses

The partial COI gene sequence data set included 61 specimens of *Sarika* as well as eleven sequences from *Macrochlamys*, *Taphrenalla* Pholyotha & Panha, 2020 and *Hemiplecta* Albers, 1850, which were included as outgroups. The alignment of the COI gene fragments had a length of 655 base pairs. The obtained phylogenetic tree (Fig. 1) recovered 17 species of *Sarika* forming a well-supported clade, including the type species *S. resplendens* and eight new species with high support (BS = 93%, PP = 1). Even though the phylogenetic relationships among taxa were poorly resolved, the members of *Sarika* were always retrieved as a monophyletic clade. A clade of *Sarika* appears as a sister group of *Macrochlamys* + *Taphrenalla*. Together *Sarika* + *Taphrenalla* + *Macrochlamys* formed a well-supported clade (BS = 100%, PP = 1).

The mean genetic distances of the COI gene observed among *Sarika*, *Taphrenalla*, *Macrochlamys*, and *Hemiplecta* ranged from 9.8% (*Taphrenalla* and *Macrochlamys*) to 13.7% (*Sarika* and *Hemiplecta*). Intraspecies divergences within the genus *Sarika* ranged from 0% (*S. bocourti*) to 3.7% (*S. dugasti*), and interspecies divergences ranged from 4.6% (*S. bocourti* and *S. inferospira* sp. nov.) to 12.0% (*S. dugasti* and *S. limbata*), respectively (Table 2).

Systematics

Family Ariophantidae Godwin-Austen, 1883

Genus *Sarika* Godwin-Austen, 1907

Sarika Godwin-Austen, 1907: 179. Blanford and Godwin-Austen 1908: 276. Zilch 1959: 325. Solem 1966: 36. Schileyko 2002: 1288. Sutcharit and Panha 2008: 96. Pholyotha et al. 2020c: 13, 14. Pholyotha et al. 2020a: 5.

Type species. *Helix resplendens* Philippi, 1846, by original designation in Godwin-Austen, 1907: 179.

Diagnostic description. *Shell* thin to moderately solid, semi-translucent, pale milky to brown, depressed discoidal to globosely depressed with 5–8 convex whorls. Shell surface smooth, glossy, with very fine growth lines. Body whorl rounded, angulated to shouldered. Aperture crescentic with simple lip or rarely expanded lip. Umbilicus narrowly opened.

Genitalia with penial retractor muscle attached to tip of epiphallic caecum; penis generally without penial verge, except for *S. consepta* (Benson, 1860) and *S. nana* Pholyotha & Panha, 2020 (see Pholyotha et al. 2020a, 2020c), rarely present pseudo-verge; flagellum short to long; gametolytic duct long; dart apparatus large cylindrical.

Spermatophore long and needle-shaped with three recognizable sections: (i) head filament rather short, (ii) cylindrical sperm sac containing sperm mass, and (iii) tail filament long thick walled tube with small hole in cross section and several spines present.

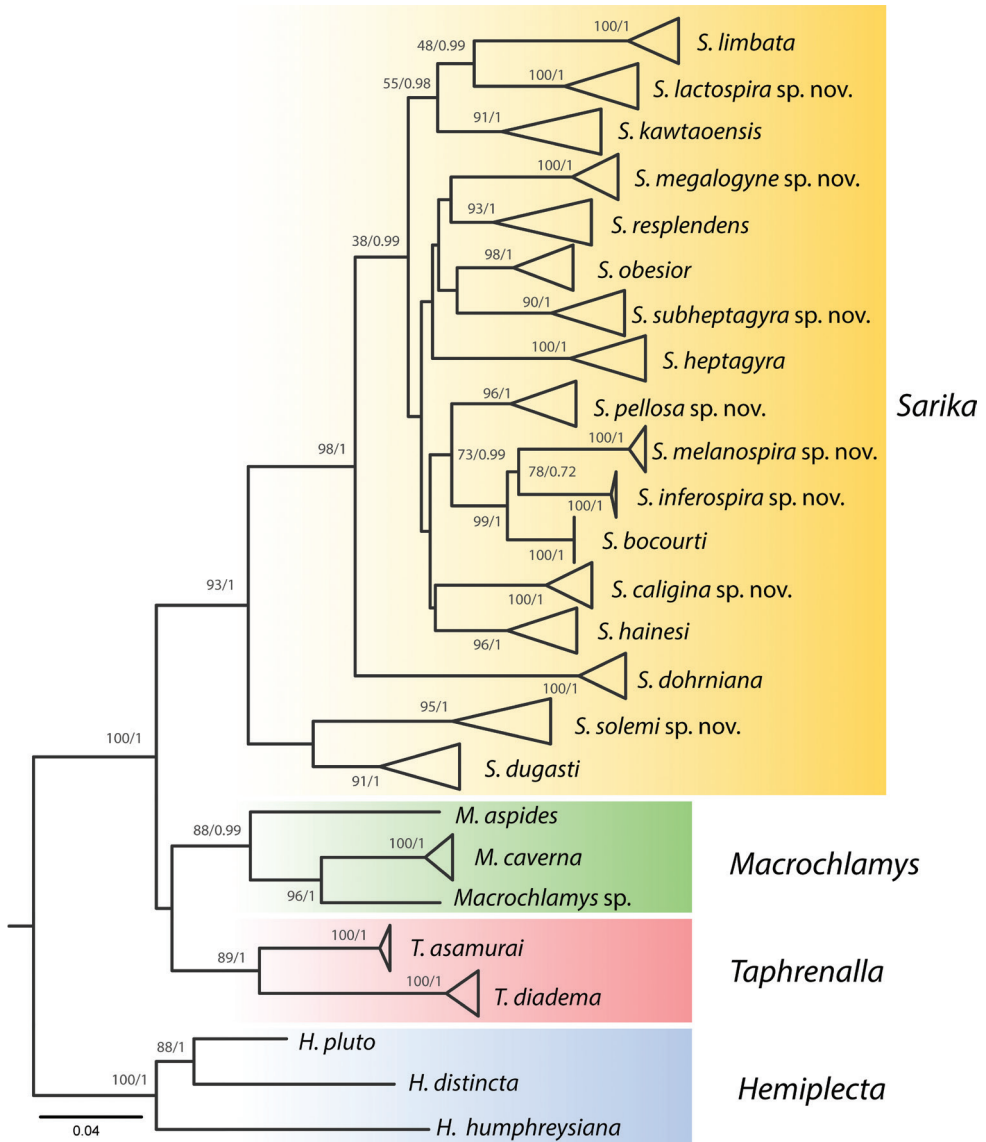


Figure 1. Maximum likelihood tree showing the relationships among species of *Sarika* based on the mitochondrial COI gene sequences. Numbers by the nodes are the ML bootstrap values (left) and Bayesian posterior probabilities (right); shown only for the nodes supported by ML or BI ($\geq 70\%$ and ≥ 0.95). Each clad colour refers to a genus.

Radular teeth with symmetrical tricuspid central tooth, asymmetrical tricuspid lateral teeth, and bicuspid marginal teeth.

Species of *Sarika* with well-developed mantle edge (mantle lobe) with four lobes (one shell lobe and three dorsal lobes) or five lobes (two shell lobes and three dorsal lobes); sole tripartite, lateral foot margin, caudal foss, and caudal horn present.

Table 2. Mean intra-specific and inter-specific genetic divergences among species of *Sarika* from the mitochondrial COI gene sequences estimated by the K2P model. Taxa in **bold** are the new species described herein.

<i>Sarika</i> spp.	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
1 <i>S. resplendens</i>	0.018																
2 <i>S. dohrniana</i>	0.100	0.017															
3 <i>S. obesior</i>	0.059	0.098	0.030														
4 <i>S. limbata</i>	0.085	0.106	0.086	0.012													
5 <i>S. heptagyra</i>	0.077	0.104	0.070	0.094	0.035												
6 <i>S. kawtaoensis</i>	0.069	0.097	0.074	0.072	0.078	0.033											
7 <i>S. caligina</i>	0.075	0.088	0.063	0.086	0.072	0.073	0.011										
8 <i>S. lactospira</i>	0.075	0.101	0.070	0.075	0.093	0.069	0.072	0.023									
9 <i>S. megalogyne</i>	0.064	0.104	0.068	0.078	0.071	0.066	0.074	0.071	0.014								
10 <i>S. subheptagyra</i>	0.065	0.087	0.063	0.090	0.079	0.074	0.082	0.081	0.069	0.024							
11 <i>S. hainesi</i>	0.066	0.091	0.064	0.074	0.074	0.070	0.057	0.073	0.066	0.073	0.024						
12 <i>S. bocourti</i>	0.069	0.104	0.069	0.092	0.079	0.071	0.071	0.081	0.076	0.075	0.070	0					
13 <i>S. inferospira</i>	0.078	0.111	0.074	0.086	0.081	0.083	0.069	0.088	0.079	0.089	0.069	0.046	0.001				
14 <i>S. melanospira</i>	0.080	0.103	0.080	0.097	0.094	0.082	0.081	0.086	0.074	0.082	0.076	0.051	0.053	0.005			
15 <i>S. pellosa</i>	0.064	0.086	0.065	0.086	0.071	0.070	0.060	0.072	0.070	0.071	0.057	0.053	0.065	0.066	0.021		
16 <i>S. dugasti</i>	0.097	0.109	0.103	0.120	0.112	0.111	0.102	0.107	0.104	0.108	0.101	0.107	0.119	0.109	0.101	0.037	
17 <i>S. solemi</i>	0.097	0.110	0.104	0.118	0.110	0.109	0.089	0.110	0.097	0.096	0.102	0.103	0.110	0.105	0.091	0.078	0.029

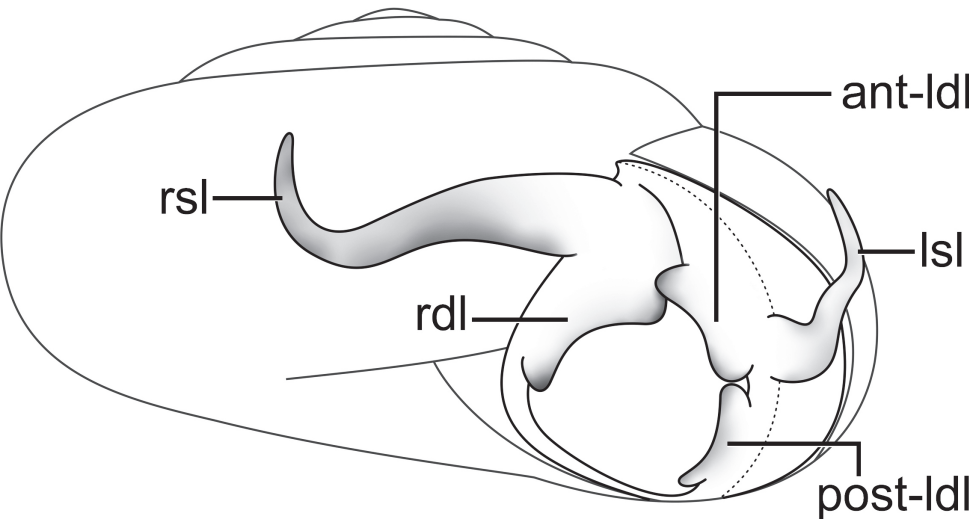


Figure 2. Schematic drawing of the mantle terminology of *Sarika* showing five mantle lobes (two shell lobes and three dorsal lobes).

Remarks. All species of *Sarika* whose genital anatomy is known have a straight (un-coiled) epiphallic caecum and can be divided into three species groups. This informal subdivision is based on the number of mantle lobes, structure of genitalia and spermatophore (when available). It may be helpful as an alternative aid to identification.

Group I: *Sarika resplendens* group. Has five mantle lobes (with left shell lobe; Figs 2, 9A), penis without penial verge and pseudo-verge (Fig. 3D) and spermatophore usually with three spines on the connection between sperm sac and tail filament (Fig. 4B). This group comprises 10 species: *S. resplendens*, *S. dohrniana*, *S. obesior*, *S. limbata*, *S. heptagyra*, *S. kawtaoensis*, *S. caligina* sp. nov., *S. lactospira* sp. nov., *S. megalogyne* sp. nov., and *S. subheptagyra* sp. nov.

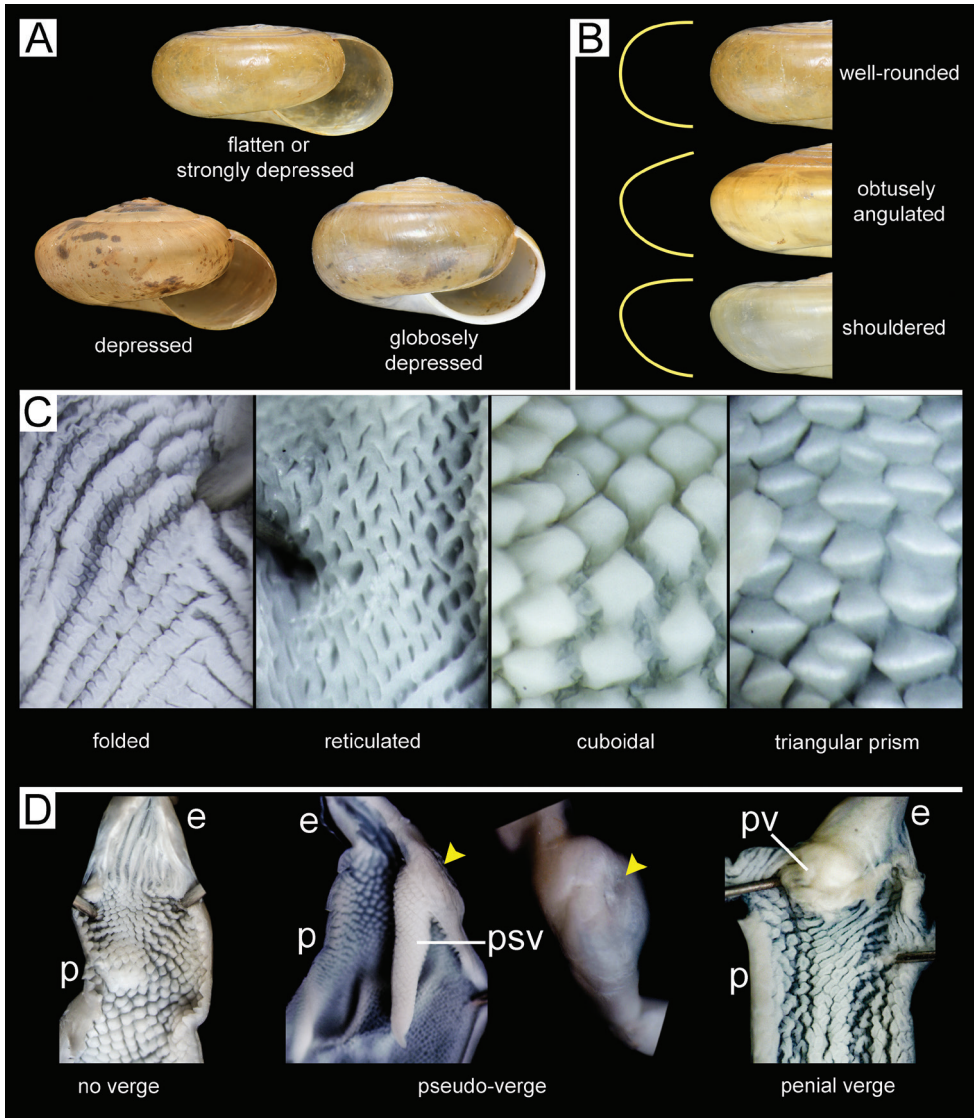


Figure 3. An illustrated synopsis of the shell and penis. **A** shell shape **B** whorl periphery **C** inner sculpture of the penis **D** appendage inside penis (no penial verge, pseudo-verge, and penial verge). Yellow arrowheads indicate the invagination of the penial wall.

Group II: *Sarika hainesi* group. Has four mantle lobes (left shell lobe wanting; Fig. 33A), penis without penial verge and pseudo-verge, and spermatophore usually with two spines on connection between sperm sac and tail filament (Fig. 4B). This group comprises five species: *S. hainesi*, *S. bocourti*, *S. inferospira* sp. nov., *S. melanospira* sp. nov., and *S. pellosa* sp. nov.

Group III: *Sarika dugasti* group. Has five mantle lobes as in group I, penis with pseudo-verge (Fig. 3D), which probably originates from an invagination of the penial

wall to become a large papilla (penial verge like). Unfortunately, no information about the spermatophore. This group comprises two species: *S. dugasti* and *S. solemi* sp. nov.

Key to species of the genus *Sarika* Godwin-Austen, 1907 in Thailand

This identification key is mainly based on the characters of genitalia and spermatophores, and is based on some taxonomic informative characters of shells.

- 1 Apertural lip straight and simple or very slightly thickened in old specimens.....2
- Apertural lip at periphery with invagination of triangular lip (beak-like).....
.....*S. gratesi* sp. nov.
- 2 Penis with pseudo-verge (Fig. 3D)3
- Penis without pseudo-verge and penial verge (Fig. 3D)4
- 3 Shell globosely depressed and well-rounded body whorl *S. dugasti*
- Shell depressed and angular body whorl..... *S. solemi* sp. nov.
- 4 Mantle edge with two shell lobes (left and right shell lobes; Figs 2, 9A)5
- Mantle edge with only right shell lobe (left shell lobe absent; Fig. 33A)..... 14
- 5 Inner wall of penis with reticulated pilasters (Fig. 3C)6
- Inner wall of penis with other types of pilasters (Fig. 3C).....7
- 6 Inner wall of distal part of penis has irregularly oblique folds (Fig. 22B)
..... *S. kawtaoensis*
- Inner wall of distal part of penis has small cuboidal (Fig. 18B)..... *S. limbata*
- 7 Inner wall of penis with triangular prism pilasters (Fig. 3C).....8
- Inner wall of penis with cuboidal pilasters (Fig. 3C)12
- 8 Body whorl slightly rounded to shouldered (Fig. 3B).....9
- Body whorl very rounded (Fig. 3B).....10
- 9 Shell with whitish subsutural band (Figs 10D, 25A, B) and lower spire; flagellum short ca. half of epiphallus (Fig. 26A)*S. lactospira* sp. nov.
- Shell monochrome brownish (without subsutural band) and higher spire; flagellum long ca. same length as penis and epiphallus (Fig. 26C)
.....*S. megalogyne* sp. nov.
- 10 Head filament of spermatophore with obtuse-serrate longitudinal ridges (Fig. 16B) *S. obesior*
- Head filament of spermatophore with smooth longitudinal ridges (Fig. 4A).....11
- 11 Shell with higher spire; shorter vagina and free oviduct (Fig. 22C); spine II and spine III on tail filament of spermatophore start branching near the tip (Fig. 24C).....*S. caligina* sp. nov.
- Shell with lower spire; longer vagina and free oviduct (Fig. 28A); spine II and spine III on tail filament of spermatophore start branching near the base (Fig. 29C).....*S. subheptagyra* sp. nov.
- 12 Tail filament of spermatophore near sperm sac with two spines (Fig. 4B).....
.....*S. dobrniana*
- Tail filament of spermatophore near sperm sac with three spines (Fig. 4B)13

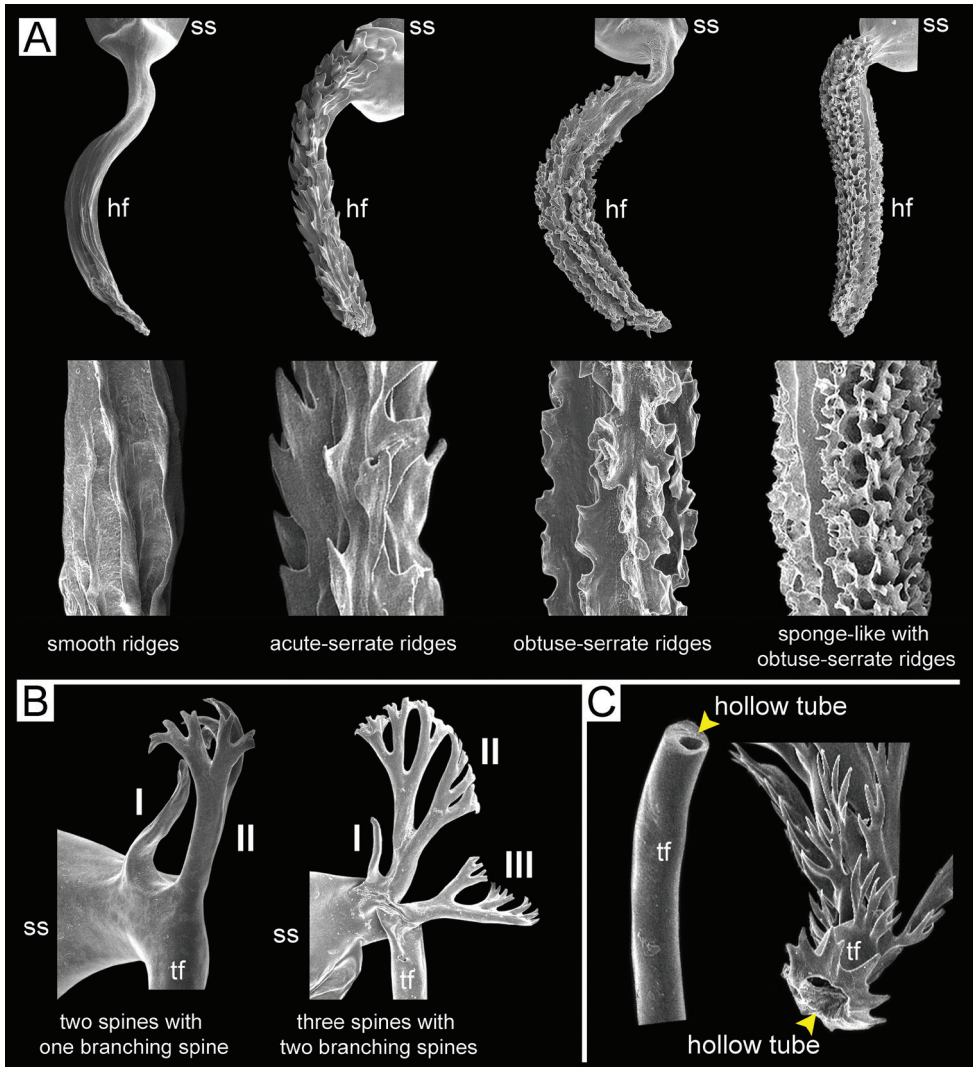


Figure 4. An illustrated synopsis of the spermatophore. **A** sculpture of head filament **B** branching spines on the region near the sperm sac of the tail filament **C** cross section of tail filament with a hollow tube.

- | | | |
|----|--|--------------------------------|
| 13 | Penial retractor muscle very large and thickened (Fig. 12A, C)..... | <i>S. resplendens</i> |
| – | Penial retractor muscle very thin (Fig. 18C)..... | <i>S. heptagyra</i> |
| 14 | Body whorl obtuse angular (Fig. 3B) | 15 |
| – | Body whorl well rounded or shouldered (Fig. 3B)..... | 16 |
| 15 | Head filament of spermatophore with acute-serrate longitudinal ridges (Fig. 37B) | <i>S. bocourti</i> |
| – | Head filament of spermatophore with irregular-serrate longitudinal ridges and numerous porous (Fig. 36B) | <i>S. hainesi</i> |
| 16 | Body whorl strongly shouldered (Fig. 3B)..... | <i>S. inferospira</i> sp. nov. |
| – | Body whorl well rounded or weak shouldered (Fig. 3B)..... | 17 |

- 17 Snail has conspicuous dark spiral band at body whorl below suture (Fig. 33E); flagellum much smaller than epiphallus (Fig. 39C) *S. melanospira* sp. nov.
- Snail monochrome colour (without spiral band at body whorl; Fig. 33F); flagellum slightly smaller than epiphallus (Fig. 41A) *S. pellosa* sp. nov.

Group I: *Sarika resplendens* group: species with left shell lobe and without penial verge and pseudo-verge

***Sarika resplendens* (Philippi, 1846)**

Figs 1, 5, 9A–C, 11A, B, 12, 13, 30A

Helix resplendens Philippi, 1846: 192. Type locality: “Prope Mergui Indiae Orientalis” [Mergui Islands, Myeik District, Tanintharyi Region, Myanmar]. Pfeiffer 1848: 56. Pfeiffer 1849: 227, 228, pl. 110, figs 7–9. Pfeiffer 1868: 100. Hanley and Theobald 1872: 24, pl. 51, fig. 4. Hanley and Theobald 1876: 59, pl. 149, figs 2, 3.

Macrochlamys resplendens: Godwin-Austen 1883: 109, 110, pl. 26, figs 1–3. Godwin-Austen 1898: 49, 50. Collinge 1903: 209. Panha 1996: 34.

Nanina (*Macrochlamys*) *resplendens*: Tryon 1886: 91, pl. 30, figs 73–76. Fischer and Dautzenberg 1904: 395.

Ariophanta (*Macrochlamys*) *resplendens*: Fischer 1891: 21.

Sarika resplendens: Godwin-Austen 1907: 179–181, pl. 111, figs 3, 3a, pl. 116, figs 2, 2a, 2b. Blanford and Godwin-Austen 1908: 277, 278, Fig. 84. Tomlin 1932: 316. Maassen 2001: 113. Hemmen and Hemmen 2001: 45. Sutcharit and Panha 2008: 96. Schilevko 2011: 34. Abu-Bakar et al. 2014. Inkhavilay et al. 2019: 82, figs 39a, 57a. Pholyotha et al. 2020c: 14, 15, figs 9a, b. Pholyotha et al. 2020a: 5, 6, fig. 2a.

Type material. The type specimens of this species could not be located in the sizable part of Philippi’s collection in Museum für Naturkunde (Berlin), SMF, and NHM (Dance 1986; Coan and Kabat 2017). Coan and Kabat (2017) also stated that other parts of Philippi’s collection were presumably lost during World War II.

Other material examined. **MYANMAR.** Mergui NHMUK ex. Theobald collection: 1898.5.18.157 (13 specimens preserved in ethanol; Fig. 11A). Mergui, Tenasserim: NHMUK 1903.7.1.111 (specimen figured in Godwin-Austen, 1883: pl. 26, Fig. 1). **CAMBODIA.** Cambodia: NHMUK 1903.7.1.112 (specimen figured in Godwin-Austen 1883: pl. 26, Fig. 2). **THAILAND.** Siam: NHMUK 1903.7.1.113 (specimen figured in Godwin-Austen 1883: pl. 26, Fig. 3). **THAILAND-Northeastern.** Area in Khok Ngam, Dan Sai, Loei, 17°21'12.5"N, 101°14'36.0"E: CUMZ 7873. Area in Sila, Mueang, Khon Kaen, 16°27'36.4"N, 102°49'09.4"E: CUMZ 7899. **THAILAND-Eastern.** Bang Krachao, Phra Pradaeng, Samut Prakan, 13°41'16.7"N, 100°33'26.1"E: CUMZ 7880. Phothisat Kuan Im Shrine, Makham, Chanthaburi, 12°43'38.9"N, 102°08'06.8"E: CUMZ 7848. Wat Khao Sam Pong, Makham, Chanthaburi, 12°44'20.3"N, 102°06'57.1"E: CUMZ 7881. Khao Chi Chan, Sattahip, Chon Buri, 12°45'53.2"N, 100°57'24.3"E: CUMZ 7844. Wat Tham Khao Cha Ang On, Bo Thong, Chon Buri, 13°12'32.5"N, 101°39'05.7"E: CUMZ 7862. Mountain area near Ang Kep Nam Dan Chumphon,

Bo Rai, Trat, 12°27'20.2"N, 102°39'59.3"E: CUMZ 7875. Saphan Hin Waterfall, Mueang, Trat, 12°06'07.8"N, 102°42'39.3"E: CUMZ 7887. **THAILAND-Western.** Area near Srinakarin Dam, Si Sawat, Kanchanaburi, 14°23'55.3"N, 99°07'27.3"E: CUMZ 7843. Wat Tham Khao Cha Ang, Dan Makham Tia, Kanchanaburi, 13°48'05.0"N, 99°26'33.9"E: CUMZ 7850. Area in Tha Kha-nun, Thong Pha Phum, Kanchanaburi, 14°44'11.6"N, 98°38'20.7"E: CUMZ 7851. Wat Tha Khanun, Thong Pha Phum, Kanchanaburi, 14°44'30.6"N, 98°38'13.9"E: CUMZ 7864, 7886. Area near Wat Pak Lam Pilok, Thong Pha Phum, Kanchanaburi, 14°37'46.1"N, 98°34'30.3"E: CUMZ 7872. Area near Puprai Tarnnarm Resort, Thong Pha Phum, Kanchanaburi, 14°44'16.3"N, 98°38'37.3"E: CUMZ 7889. Wat Tham Mangkornthong, Mueang, Kanchanaburi, 13°59'10.0"N, 99°30'57.0"E: CUMZ 7852. Area in Ban Pu Toei, Sai Yok, Kanchanaburi, 14°19'36.4"N, 98°58'57.4"E: CUMZ 7863. Lawa Cave, Sai Yok, Kanchanaburi, 14°17'58.7"N, 98°58'54.8"E: CUMZ 7870. Area near Khao Wang Khamen, Sai Yok, Kanchanaburi, 14°22'33.1"N, 98°53'50.1"E: CUMZ 7884. Area near Hellfire Pass, Sai Yok, Kanchanaburi, 14°21'26.2"N, 98°57'02.6"E: CUMZ 7888. Wat Tham Faet, Tha Muang, Kanchanaburi, 13°57'49.3"N, 99°35'01.1"E: CUMZ 7865. Ban Song Karia, Sangkhla Buri, Kanchanaburi, 15°14'46.6"N, 98°25'32.9"E: CUMZ 7235. Wat Tham Sarika, Photharam, Ratchaburi, 13°38'45.8"N, 99°44'11.3"E: CUMZ 7846. Khao Changum, Photharam, Ratchaburi, 13°43'38.2"N, 99°44'34.3"E: CUMZ 7234. Wat Khao Phra, Photharam, Ratchaburi, 13°44'29.8"N, 99°44'44.1"E: CUMZ 7866. Wat Tham Nam, Photharam, Ratchaburi, 13°41'53.7"N, 99°45'24.0"E: CUMZ 7882. Wat Buri Ratchawanaram, Pak Tho, Ratchaburi, 13°22'45.0"N, 99°47'07.5"E: CUMZ 7867. Wat Khao Ban Dai, Nong Ya Plong, Phetchaburi, 13°14'08.5"N, 99°41'19.6"E: CUMZ 7847. Wat Puang Malai, Khao Yoi, Phetchaburi, 13°18'45.4"N, 99°47'01.7"E: CUMZ 7868, 7883. Khao Nok Wua Priest's camp site, Cha-am, Phetchaburi, 12°44'46.9"N, 99°54'12.0"E: CUMZ 7891. Area near Ob Pha resort, Kaeng Krachan, Phetchaburi, 12°53'56.4"N, 99°38'53.8"E: CUMZ 7892. **THAILAND-Central.** Wat Suwankuha (Ariyasatthi Cave), Phatthana Nikhom, Lopburi, 14°47'58.3"N, 100°53'10.0"E: CUMZ 7896. Wat Khao Bang Kraek, Nong Chang, Uthai Thani, 15°18'09.2"N, 99°41'03.7"E: CUMZ 7856. Wat Khao Tham Sua, U Thong, Suphan Buri, 14°22'19.1"N, 99°52'14.4"E: CUMZ 7859. Area near Kamphaengphet Historical Park, Mueang, Kamphaeng Phet, 16°30'27.6"N, 99°31'02.1"E: CUMZ 7860. Wat Thep Sathaporn, Banphot Phisai, Nakhon Sawan, 15°54'48.2"N, 99°53'02.6"E: CUMZ 7855. Limestone outcrop in Umphang, Umphang, Tak, 16°02'42.0"N, 98°48'59.4"E: CUMZ 7898. **THAILAND-Northern.** Tham Luang Pha Wiang, Ban Hong, Lamphun, 18°13'19.1"N, 98°51'28.4"E: CUMZ 7861. Wat Tham Pha Ngam, Mae Phrik, Lampang, 17°28'49.2"N, 99°10'05.3"E: CUMZ 7857. Area near Pingkhong Resort, Chiang Dao, Chiang Mai, 19°28'02.6"N, 98°59'07.7"E: CUMZ 7876. Area near Khun Mai Baan Suan Resort, Mae Ai, Chiang Mai, 20°03'45.8"N, 99°21'33.0"E: CUMZ 7890. Wat Tham Pha Phueng, Chai Prakan, Chiang Mai, 19°44'18.7"N, 99°05'17.2"E: CUMZ 7845. Area in Hang Dong, Chiang Mai, 18°41'17.8"N, 98°54'10.8"E: CUMZ 7895. Si Satchanalai Historical Park, Si Satchanalai, Sukhothai, 17°25'34.8"N, 99°47'20.5"E: CUMZ 7879. Wat Khao Phra Noi, Mueang, Sukhothai, 17°01'07.9"N, 99°40'17.7"E: CUMZ 7894. Limestone outcrop near Golden Pai Resort, Mueang, Mae

Hong Son, 19°21'32.0"N, 97°57'40.4"E: CUMZ 7858. Area in Mae Sariang Highway Division, Mae Sariang Mae Hong Son, 18°12'39.4"N, 97°56'14.1"E: CUMZ 7878. Area in Na Rai Luang, Song Khwae, Nan, 19°19'29.6"N, 100°41'14.1"E: CUMZ 7869. Tham Pha Sing, Song Khwae, Nan, 18°53'01.7"N, 100°45'03.1"E: CUMZ 7877. Wat Amarin Khuha (Wat Khao Tham Muang), Noen Maprang, Phitsanulok, 16°30'03.2"N, 100°41'16.4"E: CUMZ 7853. Tham Tao, Noen Maprang, Phitsanulok, 16°30'31.4"N, 100°39'44.4"E: CUMZ 7874, 7893. Area in Nakhon Thai, Phitsanulok, 17°08'56.0"N, 100°51'44.3"E: CUMZ 7897. Limestone outcrop near Mae Nam Pat, Nam Pat, Uttaradit, 17°44'26.3"N, 100°40'45.4"E: CUMZ 7854. Wat Tham Pha Phung, Wang Pong, Phetchabun, 19°24'09.5"N, 98°55'08.3"E: CUMZ 7871. **THAILAND-Southern.** Wat Tham Sila Tiap, Tha Chana, Surat Thani, 9°30'58.9"N, 99°11'30.1"E: CUMZ 7832. Wat Tham Yai, Tha Chana, Surat Thani, 9°32'20.4"N, 99°11'26.1"E: CUMZ 7841. Wat Nakhawat, Phunphin, Surat Thani, 9°04'33.2"N, 99°09'54.0"E: CUMZ 7834. Wat Tham Wararam, Phanom, Surat Thani, 8°53'03.3"N, 98°40'02.5"E: CUMZ 7822. Limestone outcrop near Khao Sok Nature Resort, Phanom, Surat Thani 8°54'22.6"N, 98°31'45.1"E: CUMZ 7826. Wat Khiri Rat Phatthana, Wiang Sa, Surat Thani 8°31'38.6"N, 99°22'57.4"E: CUMZ 7833. Wat Na San, Na San, Surat Thani, 8°48'30.1"N, 99°22'10.4"E: CUMZ 7825. Area near Khanom Golden Beach, Khanom, Nakhon Si Thammarat, 9°10'58.6"N, 99°52'26.0"E: CUMZ 7815 (Fig. 11B), 7819. Wat Ao Sadet, Khanom, Nakhon Si Thammarat, 9°17'24.0"N, 99°47'18.2"E: CUMZ 7829. Area in Pak Phun, Mueang, Nakhon Si Thammarat, 8°27'44.1"N, 99°58'16.3"E: CUMZ 7840. Lot cave, Nopphitam, Nakhon Si Thammarat, 8°44'11.7"N, 99°38'07.3"E: CUMZ 7824. Wat Tham Thong Panara, Tham Phannara, Nakhon Si Thammarat, 8°25'19.8"N, 99°22'46.4"E: CUMZ 7835. Wat Tham Kanlayanamit, Tham Phannara, Nakhon Si Thammarat, 8°30'48.2"N, 99°22'50.7"E: CUMZ 7836. Hills near Hat Bang Sak, Takua Pa, Phang-nga, 8°46'31.0"N, 98°15'47.0"E: CUMZ 7817, 7818, 7830. Mountain area near Ban Pak Khlong, Kapong, Phang-nga, 8°50'21.2"N, 98°27'41.5"E: CUMZ 7821. Phung Chang Cave, Mueang, Phang-nga, 8°26'33.1"N, 98°30'55.0"E: CUMZ 7827. Mountain area near Khao Lak Resort, Takua Pa, Phang-nga, 8°38'23.8"N, 98°15'12.9"E: CUMZ 7831. Area near Mae Nam Phang-nga, Mueang, Phang-nga, 8°32'43.7"N, 98°28'21.2"E: CUMZ 7837. Tao Thong Waterfall, Thap Put, Phang-nga, 8°29'07.6"N, 98°35'08.5"E: CUMZ 7842. Area near Hat Chao Mai, Sikao, Trang, 7°24'48.9"N, 99°20'45.1"E: CUMZ 7839. Wat Kumphin Banpot, Khuan Kalong, Satun, 6°52'30.8"N, 100°01'02.4: CUMZ 7823. Limestone outcrop near Du Son, Khuan Don, Satun, 6°47'55.5"N, 100°06'43.4"E: CUMZ 7816. Wat Khuha Sawan, Mueang, Phatthalung, 7°37'14.1"N, 100°04'51.8"E: CUMZ 7838. Limestone outcrop in Sakhu, Thalang, Phuket, 8°05'25.1"N, 98°17'54.7"E: CUMZ 7828. Khao Jung Lone Cave, Rattaphum, Songkhla, 7°11'25.8"N, 100°16'59.9"E: CUMZ 7820.

Diagnosis. Shell large, depressed and well-rounded body whorl. Animal with dark grey body and five mantle lobes. Genitalia with straight epiphallic caecum, large penial retractor muscle and small cuboidal penial pilasters. Spermatophore: head filament with irregularly obtuse-serrate longitudinal ridges; tail filament near sperm sac with

three spines and terminal part more than ca. one-third of its length with series of several branching spines.

Description. Shell. Shell comparatively depressed, large size (shell width up to 23.4 mm, shell height up to 11.5 mm), and rather thin. Shell surface smooth and glossy; shell colour pale brown. Whorls $5\frac{1}{2}$ – $6\frac{1}{2}$, increasing regularly; body whorl large and well rounded. Spire slightly to moderately elevated; suture impressed. Aperture crescent-shaped and obliquely opened. Peristome simple. Columellar margin simple and little reflected near umbilicus. Umbilicus narrowly opened (Fig. 11A, B).

Genital organs. Atrium short. Penis cylindrical with thin penial sheath covering proximal penis. Inner sculpture of penis fully covered with cuboidal penial pilasters of variable sizes; proximal area near atrium with very fine longitudinal pilasters then transformed to small pilasters; middle of chamber pilasters much larger than others; distal pilasters reduced to small pilasters. Epiphallus cylindrical, slightly narrower than penis and approximately as long as penis. Epiphallic caecum short, straight, same diameter as proximal epiphallus and located near middle of epiphallus. Penial retractor muscle large, thickened and attached at tip of epiphallic caecum. Flagellum long and slender tube, approximately half of epiphallus length. Vas deferens thin tube connecting distal epiphallus and free oviduct (Fig. 12).

Vagina cylindrical and short approximately one-third of penis length. Dart apparatus large, long cylindrical, and located on atrium at vagina and penis junction. Gametolytic sac bulbous (Fig. 12C with spermatophore); gametolytic duct long and cylindrical. Free oviduct cylindrical, longer than vagina and proximal end encircled with thick tissue (Fig. 12A, C).

Spermatophore long and needle-shaped. Sperm sac enlarged and elongate-oval. Head filament gourd shape with irregularly obtuse-serrate longitudinal ridges. Tail filament very long tube; region near sperm sac with three spines. Spine I located on same base with spine II, simple, short and little curved. Spine II large and long, branching into many spinules near the tip. Spine III shorter than spine II and with complicated branching into small and many spinules. Region furthest away smooth and without spine; terminal part (more than ca. one-third of its length) with series of short to long branching spines that arranged in a row or encircled tail filament tip (Fig. 13).

Radula. Teeth arranged in a wide U-shape with half row formula: 1–(13–14)–70. Central tooth symmetrical tricuspid; mesocone large and triangular shape; ectocones very small. Lateral teeth asymmetrical tricuspid; mesocone pointed cusp, endocone and ectocone very small. Marginal teeth starting at approximately row number 13 or 14 with elongate bicuspid; endocone lanceolate shape; ectocone very small. Outermost teeth very short and smaller than inner teeth (Fig. 30A).

External features. Animal with reticulated skin, dark grey body and dorsally with darker colour than below and foot sole. Caudal foss present; caudal horn raised and rather large. Mantle edge well developed, same colour as body, and with two shell lobes and three dorsal lobes. Shell lobes elongate; right shell lobe larger and longer than left shell lobe. Dorsal lobes large and broad; anterior left dorsal lobe and posterior left dorsal lobe (post-ldl) smaller than right dorsal lobe (Fig. 9A–C).



Figure 5. Geographic distribution of *Sarika resplendens* based on the specimens examined herein.

Distribution. *Sarika resplendens* occurs throughout Thailand (Fig. 5) and mainland Southeast Asia (Schileyko 2011; Inkhavilay et al. 2019). This species can be found throughout the entire year in various humid areas in both natural and highly disturbed habitats. It is very easy to find and is the most common *Sarika* species in human-modified habitats such as plant farms or shaded gardens.

COI analysis. The ML and BI analyses revealed that the individuals of *S. resplendens* ($n = 7$) form a monophyletic group with high support (Fig. 1; BS = 93%, PP = 1). The mean intraspecific genetic distance of *S. resplendens* was 1.8% (Table 2).

Remarks. The type specimen of this species could not be located, only the specimens recognised by Godwin-Austen (1898, 1907) were examined. *Sarika resplendens* was examined in both shell and genitalia by Godwin Austen (1898, 1907), whose specimens were collected from Mergui [topotype] and sent by Theobald. In this study, we examined specimens from Mergui (Theobald collection) deposited in the NHM collections. Genitalia of these historical specimens and the new specimens from Thailand were identical in having a large penial retractor muscle and cuboidal shape of penial pilasters sculpture. In addition, the terminal part of the spermatophore tail filament had a cluster of branching spines. This character was not described or mentioned in Godwin Austen (1898, 1907).

***Sarika dohrniana* (Pfeiffer, 1860)**

Figs 1, 6, 9D, 11C, D, 14A, B, 15, 30B

Helix (*Nanina*) *dohrniana* Pfeiffer, 1860: 136. Type locality: “Siam” [Thailand]. Pfeiffer 1868: 97.

Nanina (*Hemiplecta*) *dohrniana*: Martens 1867: 72.

Nanina (*Xestina*) *dohrniana*: Tryon 1886: 83, pl. 16, figs 23, 24.

Nanina (*Xesta*) *dohrniana*: Fischer and Dautzenberg 1904: 394.

Ariophanta (*Hemiplecta*) *dohrniana*: Fischer 1891: 22.

Sarika dohrniana: Godwin-Austen 1907: 181, 182; Sutcharit and Panha 2008: 96.

Type material. *Syntypes* NHMUK ex. Cuming collection: 20160046 (three shells; Fig. 11C) from Siam [Thailand].

Other material examined. **THAILAND.** Siam: NHMUK 1903.7.1.464 (one shell). **THAILAND-Northeastern.** Dong Phya Fai, Siam: NHMUK 1903.7.1.1702 ex. Flower collection (two shells). Wat Thep Phithak Punnaram, Pak Chong, Nakhon Ratchasima, 14°36'57.3"N, 101°15'34.3"E: CUMZ 7616. Wat Tham Thian Chai Chonprathan, Pak Chong, Nakhon Ratchasima, 14°37'07.5"N, 101°18'15.5"E: CUMZ 7621. Wat Tham Praput, Pak Chong, Nakhon Ratchasima, 14°35'37.6"N, 101°40'16.8"E: CUMZ 7619. Wat Tham Pin Kaeo, Pak Chong, Nakhon Ratchasima, 14°36'26.4"N, 101°37'11.4"E: CUMZ 7622. Wat Tham Sap Muet, Pak Chong, Nakhon Ratchasima, 14°47'14.0"N, 101°25'49.8"E: CUMZ 7624. Wat Tham Santitham, Pak Chong, Nakhon Ratchasima, 14°34'29.7"N, 101°37'36.5"E: CUMZ 7625. Muak Lek Waterfall, Pak Chong, Nakhon Ratchasima, 14°38'36.1"N, 101°12'17.4"E: CUMZ 7632. Mountain area near Lam Phra Phloeng Dam, Pak Thong Chai, Nakhon Ratchasima, 14°32'33.0"N, 101°45'37.0"E: CUMZ 7631. **THAILAND-Central.** Wat Tham Mongkut, Phra Phutthabat, Saraburi, 14°40'40.9"N, 100°50'33.6"E: CUMZ 7620. Tham Rakhang-Tham Kin Non, Phra Phutthabat, Saraburi, 14°42'57.1"N, 100°47'49.3"E: CUMZ 7626. Saeng Tham Cave, Muak Lek, Saraburi: CUMZ 7613. Wat Tham Tham Osot, Muak Lek, Saraburi, 14°42'35.7"N, 101°07'01.5"E: CUMZ 7627. Wat Tham Rattana Buppha, Muak Lek, Saraburi, 14°41'35.3"N, 101°07'50.5"E: CUMZ 7629. Wat Tham Si Wilai, Chaloem Phra Kiat,

Saraburi, 14°42'44.4"N, 100°51'58.5"E: CUMZ 7630, 7633. Wat Tham Phra Phothisat, Kaeng Khoi, Saraburi, 14°34'33.2"N, 101°08'42.6"E: CUMZ 7614, 7618. Wat Tham Khao Kaeo, Kaeng Khoi, Saraburi, 14°36'16.9"N, 101°05'36.6"E: CUMZ 7628. Mountain area in Thap Kwang, Kaeng Khoi, Saraburi, 14°31'32.7"N, 101°01'37.4"E: CUMZ 7635. Wat Tham Mongkol Nimit, Mueang, Lopburi, 14°49'34.1"N, 100°45'28.4"E: CUMZ 7611 (Fig. 11D). Wat Pa Tham Sua, Mueang, Lopburi, 14°48'48.6"N, 100°47'03.9"E: CUMZ 7612. Wat Tham Phrathat, Mueang, Lopburi, 14°48'23.6"N, 100°49'29.7"E: CUMZ 7615. Wat Tham Muang, Mueang, Lopburi, 14°48'07.1"N, 100°46'40.3"E: CUMZ 7617. Wat Tham Phrom Sawat, Phatthana Nikhom, Lopburi, 14°45'32.0"N, 100°56'22.4"E: CUMZ 7623. Wat Pa Tham Ariyasatsi, Phatthana Nikhom, Lopburi, 14°47'58.3"N, 100°53'10.0"E: CUMZ 7636. Mountain area in Chai Badan, Chai Badan, Lopburi, 14°59'21.2"N, 100°52'34.3"E: CUMZ 7634.

Diagnosis. Shell large to very large, depressed to conoid-depressed and rounded to slightly obtusely angulated body whorl. Animal with pale grey body and five mantle lobes. Genitalia with straight epiphallic caecum and small cuboidal penial pilasters. Spermatophore: head filament with irregularly smooth longitudinal ridges; tail filament near sperm sac with two spines and terminal part more than ca. one-eighth of its length with series of several branching spines.

Description. Shell. Shell depressed to conoid-depressed, large to very large size (shell width up to 33.2 mm, shell height up to 18.9 mm) and rather thin to slightly solid. Shell surface smooth, rather coarse above periphery; shell colour yellowish brown to dark brown. Whorls 6–6½, increasing regularly; body whorl large and rounded to slightly obtusely angulated. Spire very much elevated; suture impressed. Aperture crescent-shaped and obliquely opened. Peristome simple. Columellar margin simple and slightly reflected near umbilicus. Umbilicus narrowly opened (Fig. 11C, D).

Genital organs. Atrium short. Penis cylindrical, elongate and with thin penial sheath covering proximal penis. Inner sculpture of penis proximally more than ca. half of penial chamber with very fine longitudinal penial pilasters, and then transformed to small cuboidal pilasters. Epiphallus cylindrical, as long as penis and slightly narrower than penis. Epiphallic caecum short, straight, approximately same diameter as epiphallus, and located near middle of epiphallus. Penial retractor muscle thin and attached at tip of epiphallic caecum. Flagellum slender and long, approximately as long as epiphallus. Vas deferens thin tube connecting distal epiphallus and free oviduct (Fig. 14A, B).

Vagina cylindrical and approximately half of penis length. Dart apparatus enlarged, long cylindrical, and located on atrium at vagina and penis junction. Gametolytic sac bulbous; gametolytic duct long and cylindrical. Free oviduct short, approximately half of vagina length, and proximal end encircled with thick tissue (Fig. 14A).

Spermatophore long and needle-shaped. Sperm sac enlarged and elongate-oval. Head filament gourd shape with irregularly smooth longitudinal ridges. Tail filament very long tube; region near sperm sac with two spines. Spine I simple and little curved. Spine II long and branching into many spinules near the tip. Most of region furthest away smooth and without spine; terminal part (more than ca. one-eighth of its length) with series of short to long branching spines arranged in opposite rows (Fig. 15).

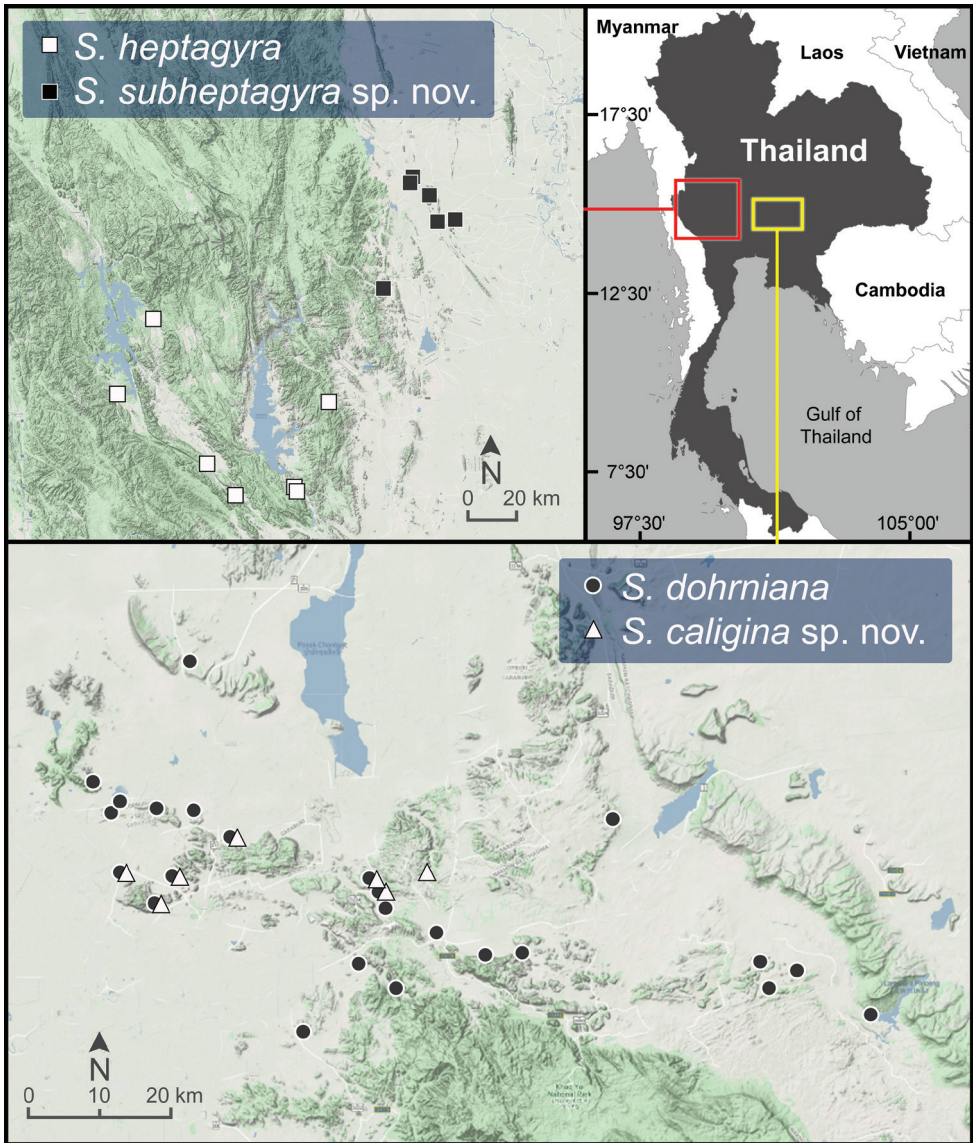


Figure 6. Geographic distribution of *Sarika caligina* sp. nov., *S. dohrniana*, *S. heptagyra*, and *S. subheptagyra* sp. nov. based on the specimens examined herein.

Radula. Teeth with half row formula: 1–(19–20)–80. Central tooth symmetrical tricuspid; lateral teeth asymmetrical tricuspid; marginal teeth elongate bicuspid. Marginal teeth starting at ca. row number 19 or 20 (Fig. 30B).

External features. Animal with reticulated skin and pale grey body, dark creamy mixing with grey foot sole and dark creamy to pale grey caudal horn. Mantle edge well developed and same colour as body (Fig. 9D).

Distribution. *Sarika dohrniana* occurs in the karstic habitats and forested mountains in northeastern and central Thailand (Fig. 6).

COI analysis. The ML and BI analyses of *S. dohrniana* revealed that three individuals formed a monophyletic group with very strong support (Fig. 1; BS = 100%, PP = 1), sister to the rest of most species of *Sarika*, except for *S. solemi* sp. nov. + *S. dugasti*. The mean intraspecific genetic distance of *S. dohrniana* was 1.7% (Table 2).

Remarks. The remarkable characters of *S. dohrniana* are its large size, conoid-depressed shell, the coarser shell surface compared to other *Sarika* species, and the head filament of the spermatophore with its irregularly smooth longitudinal ridges and the two spines on the tail filament near the sperm sac.

Sarika obesior (Martens, 1867)

Figs 1, 8, 9E, 11E, F, 14C, D, 16, 30C

Nanina (*Orobia*) *resplendens* var. *obesior* Martens, 1867: 72, pl. 12, fig. 6. Type locality: “Um Petshaburi nicht selten; auch an der Ostseite des Golfs bei Bang-Pra beobachtet” [Petchaburi Province and Bang Phra, Si Racha District, Chonburi Province, Thailand].

Nanina (*Macrochlamys*) *resplendens obesior*: Tryon 1886: 91, pl. 30, fig. 76.

Sarika obesior: Solem 1966: 36–38, fig. 5b, c; Hemmen and Hemmen 2001: 45; Sutcharit and Panha 2008: 96; Pholyotha et al. 2020c: 18, 19, figs 2f, g, 7e, f, 10a, b, 13d–f.

Type material. The type specimens could not be located and were probably missing from the Museum für Naturkunde (Berlin) collection (T. von Rintelen and C. Zorn, pers. comm., December 2018).

Other material examined. **MYANMAR.** Forest on Kala Island, Myeik District, Tanintharyi Division, 12°25'25.4"N, 98°29'50.6"E: CUMZ 7140, 7141. **THAILAND-Western.** Limestone outcrop in Kaeng Krachan, Kaeng Krachan, Phetchaburi, 12°55'01.0"N, 99°37'48.0"E: CUMZ 7686. Wat Tham Rong, Ban Lat, Phetchaburi, 13°01'31.3"N, 99°55'07.9"E: CUMZ 7673 (Fig. 11F), 7693. Wat Khao Krachiu, Tha Yang, Phetchaburi, 12°57'42.9"N, 99°54'48.8"E: CUMZ 7670. Khao Tamo, Tha Yang, Phetchaburi, 12°47'49.0"N, 99°44'40.0"E: CUMZ 7682. Wat Khiriwong, Khao Yoi, Phetchaburi, 13°20'02.2"N, 99°45'19.9"E: CUMZ 7668. Wat Puang Malai, Khao Yoi, Phetchaburi, 13°18'40.4"N, 99°47'09.2"E: CUMZ 7675 (Fig. 11E). Khao Nang Panthurat, Cha-am, Phetchaburi, 12°50'22.2"N, 99°57'10.0"E: CUMZ 7680, 7681, 7694, 7695. Khao Na Kwang Cave Cha-am, Phetchaburi, 12°51'31.3"N, 99°56'29.3"E: CUMZ 7683, 7690. Wat Tham Jaeng, Cha-am, Phetchaburi, 12°49'39.3"N, 99°56'24.5"E: CUMZ 7667. Khao Ma Rong Cave, Bang Saphan, Prachuap Khiri Khan, 11°12'09.3"N, 99°29'39.8"E: CUMZ 7664, 7669, 7702. Wat Tham Siriwong, Bang Saphan, Prachuap Khiri Khan, 11°23'27.6"N, 99°34'55.3"E: CUMZ 7665, 7697, 7704. Wat Tham Khao Wong, Bang Saphan, Prachuap Khiri Khan, 11°17'28.0"N, 99°29'45.4"E: CUMZ 7666. Ko Thalu, Bang Saphan Noi, Prachuap

Khiri Khan, 11°04'34.4"N, 99°33'37.4"E: CUMZ 7691. Khao Ta Mong Lai, Mueang, Prachuap Khiri Khan, 11°50'00.3"N, 99°49'47.2"E: CUMZ 7674. Khao Lom Muak, Mueang, Prachuap Khiri Khan, 11°47'08.5"N, 99°48'57.9"E: CUMZ 7676. Wat Ao Noi, Mueang, Prachuap Khiri Khan, 11°51'44.0"N, 99°49'20.0"E: CUMZ 7701, 7703. Tham Khao Rak Mai, Thap Sakae, Prachuap Khiri Khan, 11°25'42.1"N, 99°36'18.5"E: CUMZ 7677. Khao Kalok, Sam Roi Yot, Prachuap Khiri Khan, 12°20'13.0"N, 99°59'59.0"E: CUMZ 7678, 7698. Phraya Nakhon Cave, Sam Roi Yot, Prachuap Khiri Khan, 12°11'45.3"N, 100°00'41.8"E: CUMZ 7685. Limestone outcrop near Hat Sam Phraya, Kui Buri, Prachuap Khiri Khan, 12°09'04.0"N, 99°58'58.0"E: CUMZ 7705. Limestone outcrop in Kui Buri, Kui Buri, Prachuap Khiri Khan, 12°08'06.1"N, 99°38'41.2"E: CUMZ 7684, 7692, 7699. Wat Nong Phlap, Hua Hin, Prachuap Khiri Khan, 12°35'29.9"N, 99°43'45.8"E: CUMZ 7233. Pa La-U Waterfall, Hua Hin, Prachuap Khiri Khan, 12°32'17.2"N, 99°27'48.7"E: CUMZ 7700. Lublae Cave, Hua Hin, Prachuap Khiri Khan, 12°36'15.1"N, 99°43'20.9"E: CUMZ 7679. **THAILAND-Southern.** Wat Bonphot Phisai, Lang Suan, Chumphon, 9°56'12.5"N, 99°08'44.2"E: CUMZ 7671. Limestone outcrop in Khlong Sok, Phanom, Surat Thani, 8°50'53.0"N, 98°44'35.3"E: CUMZ 7688. Limestone outcrop near Anurak Community Lodge, Phanom, Surat Thani, 8°53'16.3"N, 98°40'45.2"E: CUMZ 7689. Wat Tham Wararam, Phanom, Surat Thani: CUMZ 7696. Khao Kloi, Don Sak, Surat Thani, 8°52'43.9"N, 98°39'26.5"E: CUMZ 7672.

Diagnosis. Shell medium to large, depressed and well rounded body whorl. Animal with greyish to slightly dark grey body and five mantle lobes. Genitalia with straight epiphallic caecum and triangular prism penial pilasters. Spermatophore: head filament with irregularly obtuse-serrate longitudinal ridges; tail filament near sperm sac with three spines and terminal part more than ca. one-third of its length with series of several branching spines.

Description. The unique shell characters of *S. obesior* are depressed, medium to large size (shell width up to 22.1 mm; shell height up to 11.3 mm), pale brown, well-rounded body whorl, spire elevated, and impressed suture (Fig. 11E, F).

The unique genitalia characters are straight epiphallic caecum; inner wall of penis with very fine longitudinal penial pilasters near atrium, changing to large rhomboid pilasters with acute angle on top (triangular prism shape) (Fig. 14C, D).

Spermatophore long and needle-shaped. Sperm sac (ss) enlarged and elliptical. Head filament gourd shape with irregularly obtuse-serrate longitudinal ridges. Tail filament very long tube; region near sperm sac with three spines. Spine I located near base of spine II, simple and short. Spine II broken. Spine III large with complicated branching into small and many spinules. Region furthest away smooth and without spine; terminal part (more than ca. one-third of its length) with series of short to long branching spines arranged in a row or encircling the tail filament tip (Fig. 16).

Radula with half row formula: 1–(13–14)–60. The morphology of central tooth, lateral, and marginal teeth are similar to that described in Pholyotha et al. (2020c: figs 13d–f). Marginal teeth starting at approximately row number 13 or 14 (Fig. 30C).

Living snail with monochrome greyish to slightly dark grey body. Mantle edge well developed and same colour same body (Fig. 9E).

Distribution. *Sarika obesior* occurs in western and southern Thailand (Fig. 8) and Tanintharyi region in Myanmar (Pholyotha et al. 2020c).

COI analysis. The ML and BI analyses showed that the individuals of *S. obesior* ($n = 4$) formed a monophyletic group with high support (Fig. 1; BS = 98%, PP = 1). The mean intraspecific genetic distance of *S. obesior* was 3.0% (Table 2).

Remarks. This species has recently been re-described and illustrated based on the samples collected from Myeik, Myanmar by Pholyotha et al. (2020c). The topotypic specimens from Petchaburi, Thailand agree well with the previous descriptions. Solem (1966) noted that *S. obesior* differs from *S. hainesi* in having a rounded body whorl and attributed several specimens from northern and eastern Thailand to *S. obesior*. Yet, without the genital anatomy their identification could not be confirmed. Therefore, the specimens from northern and eastern Thailand as reported by Solem (1966) are still doubtful, and to date, the distribution of *S. obesior* is probably restricted to western and southern Thailand and south-eastern Myanmar.

***Sarika limbata* (Möllendorff, 1894)**

Figs 1, 7, 9F, 17A–C, 18A, B, 19, 30D

Macrochlamys limbata Möllendorff, 1894: 148, pl. 16, figs 6, 7. Type locality: “Samui Islands, Gulf of Siam” [Samui Islands, Ko Samui District, Surat Thani Province, Thailand]; Panha 1996: 34; Hemmen and Hemmen 2001: 44.

Nanina (*Macrochlamys*) *limbata*: Fischer and Dautzenberg 1904: 395.

Sarika limbata: Tomlin 1929: 16.

Type material. *Syntypes* SMF 227100 (Fig. 17A) from Insel Samui, Gulf der Siam [Samui Island, Surat Thani, Thailand], SMF 90854/2 (two shells), 90855/4 (four shells), 227101/3 (three shells; Fig. 17B), 227102/1 (one shell).

Other material examined. THAILAND-Southern. Insel Samui, Gulf der Siam [Samui Island, Gulf of Thailand], 9°28'02.9"N, 99°58'43.8"E: SMF 298596/2. Tham Chang Phuek Bureau of Monks, Mueang, Chumphon, 10°26'47.0"N, 99°02'06.0"E: CUMZ 7637, 7647, 7654. Tham Krating Thong Bureau of Monks, Mueang, Chumphon, 10°27'20.6"N, 99°06'20.6"E: CUMZ 7638. Tham Sing, Mueang, Chumphon, 10°25'45.7"N, 99°02'52.7"E: CUMZ 7640. Wat Tham Sanook, Mueang, Chumphon, 10°28'52.3"N, 99°04'31.3"E: CUMZ 7644, 7646. Wat Uthaitam, Mueang, Chumphon, 10°30'24.1"N, 99°07'50.4"E: CUMZ 7658. Pla Cave, Thung Tako, Chumphon, 10°07'58.3"N, 99°08'08.1"E: CUMZ 7639. Wat Phut Sadi Phupharam, Thung Tako, Chumphon, 10°05'37.0"N, 99°04'39.3"E: CUMZ 7652 (Fig. 17C). Tham Pisadan Bureau of Monks, Tha Sae, Chumphon, 10°45'36.7"N, 99°13'45.8"E: CUMZ 7655, 7657. Nang Thong Cave, Pathio, Chumphon, 10°40'14.3"N, 99°17'35.9"E: CUMZ 7641. Wat Tham Khao Plu, Pathio, Chumphon, 10°43'49.6"N, 99°19'19.7"E: CUMZ 7660. Wat Tham Khao Bang Siap, Pathio, Chumphon, 10°40'06.7"N, 99°17'37.9"E: CUMZ 7661. Wat Rat Burana, Lang Suan, Chumphon, 9°56'20.6"N, 99°02'25.7"E: CUMZ 7645. Tham Khao

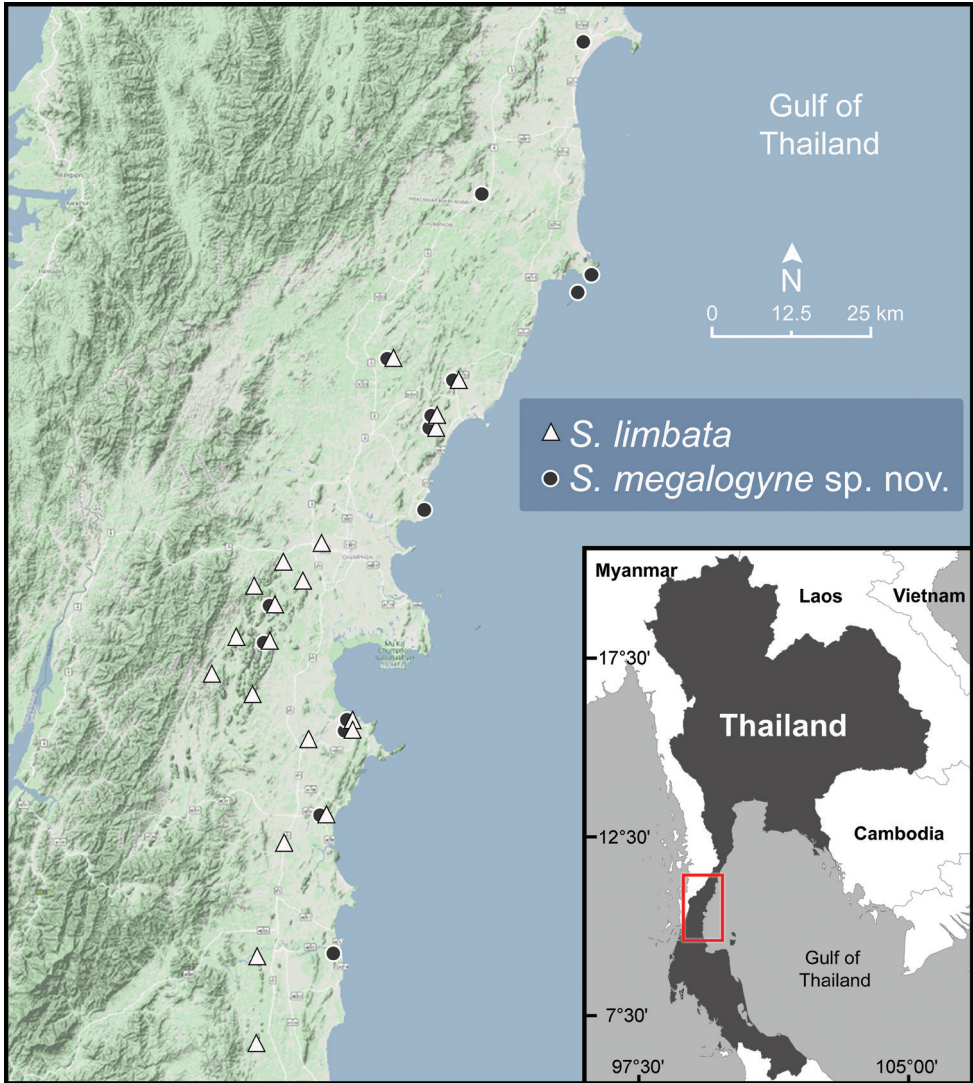


Figure 7. Geographic distribution of *Sarika limbata* and *S. megalogyne* sp. nov. based on the specimens examined herein.

Kriap, Lang Suan, Chumphon, 9°49'03.0"N, 99°02'18.0"E: CUMZ 7649, 7659, 7662, 7663. Tham Khao Lak Bureau of Monks, Sawi, Chumphon, 10°19'39.7"N, 98°58'39.3"E: CUMZ 7642. Tham Nam Lod Thepnimit Bureau of Monks, Sawi, Chumphon, 10°22'36.9"N, 99°00'42.2"E: CUMZ 7643. Cholkhiri Bureau of Monks, Sawi, Chumphon, 10°22'20.1"N, 99°03'29.7"E: CUMZ 7648. Wat Nam Cha, Sawi, Chumphon, 10°17'50.9"N, 99°01'57.4"E: CUMZ 7650. Limestone outcrop in Sawi, Sawi, Chumphon, 10°15'05.0"N, 99°10'25.6"E: CUMZ 7651. Wat Tham Khao Lan, Sawi, Chumphon, 10°15'47.7"N, 99°10'18.1"E: CUMZ 7653. Wat Tham Khwan Mueang, Sawi, Chumphon, 10°14'18.2"N, 99°06'43.3"E: CUMZ 7656.

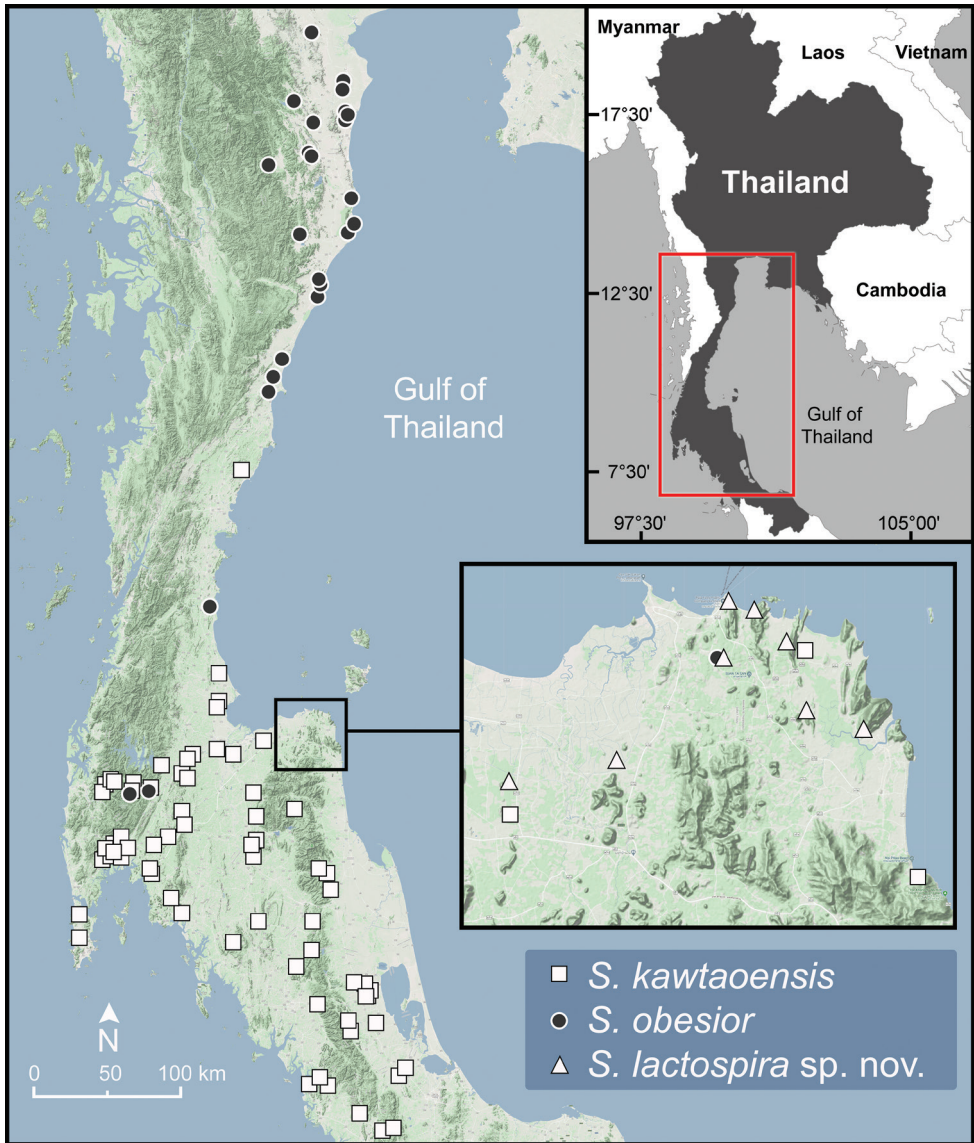


Figure 8. Geographic distribution of *Sarika kawtaoensis*, *S. lactospira* sp. nov., and *S. obesior* based on the specimens examined herein.

Diagnosis. Shell large, depressed and well-rounded body whorl. Animal with pale to dark grey body and five mantle lobes. Genitalia with straight epiphallic caecum and inner penial sculpture with small reticulated pilasters in proximal part and small cuboidal pilasters in distal end. Spermatophore: head filament with irregularly plate-like sculpture; tail filament near sperm sac with three spines and terminal part more than ca. one-third of its length with series of several branching spines.

Description. Shell. Shell depressed, large size (shell width up to 27.0 mm, shell height up to 13.7 mm) and rather thin. Shell surface smooth, shiny; shell colour pale

yellowish brown to pale brown. Whorls 6–6½, increasing regularly; body whorl large and well-rounded. Spire elevated; suture impressed. Aperture crescent-shaped and obliquely opened. Peristome simple. Columellar margin simple and slightly reflected near umbilicus. Umbilicus narrowly opened (Fig. 17A–C).

Genital organs. Atrium short. Penis cylindrical with thin penial sheath covering proximal penis. Inner sculpture of penis proximally more than ca. one-fifth of penial chamber covered with very fine longitudinal penial pilasters, changing to small and thin reticulated pilasters around two-fifth of chamber, and transformed to small cuboidal pilasters at distal end near epiphallus. Epiphallus cylindrical, approximately two times total penis length, and smaller diameter than penis. Epiphallic caecum short, straight, similar diameter as proximal epiphallus, and located near middle of epiphallus. Penial retractor muscle thin and attached at tip of epiphallic caecum. Flagellum very slender, and approximately same length as penis. Vas deferens thin tube connecting distal epiphallus and free oviduct (Fig. 18A, B).

Vagina cylindrical and ca. two-thirds penis length. Dart apparatus large, long, cylindrical, and located on atrium of vagina and penis junction. Gametolytic sac enlarged and bulbous; gametolytic duct long and cylindrical. Free oviduct cylindrical, approximately same length with penis, and proximal end encircled with thick tissue (Fig. 18A).

Spermatophore long and needle-shaped. Sperm sac enlarged and elongate-oval. Head filament gourd shape; region close to sperm sac with irregularly plate-like sculpture then transformed to irregularly acute-serrate longitudinal ridges. Tail filament very long tube; region near sperm sac with three spines. Spine I very reduced to small knob. Spine II was broken but slightly large at base. Spine III (partially broken) with branching into small spines and spinules. Region furthest away smooth and without spine; terminal part (more than ca. one-third of its length) with series of short to long and complicated branching spines, arranged in a row or opposite rows near tail filament tip (Fig. 19).

Radula. Teeth with half row formula: 1–(16–17)–69. Central tooth symmetrical tricuspid; lateral teeth asymmetrical tricuspid; marginal teeth elongate bicuspid. Marginal teeth starting at approximately row number 16 or 17 (Fig. 30D).

External features. Animal with reticulated skin and pale to dark grey body, pale grey foot sole, and dark grey caudal horn. Mantle edge well developed and same colour as body (Fig. 9F).

Distribution. *Sarika limbata* occurs eastwards of the Tenasserim Range to the Phuket Range and is common in Chumphon Province (Fig. 7).

COI analysis. The ML and BI analyses revealed that the samples of *S. limbata* ($n = 4$) formed a monophyletic group with very strong support (Fig. 1; BS = 100%, PP = 1), and sister to *S. lactospira* sp. nov. with only BI support (Fig. 1; PP = 0.99). The mean intraspecific genetic distance of *S. limbata* was 1.2% (Table 2).

Sarika limbata, *S. kawtaoensis*, and *S. lactospira* sp. nov. are phylogenetically closely related, yet only with BI support (Fig. 1). The average interspecific sequence divergences were 7.2% (*S. limbata* and *S. kawtaoensis*), 7.5% (*S. limbata* and *S. lactospira* sp. nov.), and 6.9% (*S. kawtaoensis* and *S. lactospira* sp. nov.) (Table 2).

Remarks. The shell morphology of *S. limbata* is similar to that of *S. kawtaoensis*. The main distinguishing characters of *S. limbata* are the reticulated and cuboidal penial pilasters, and the plate-like and acute-serrate longitudinal ridges on the head filament of the

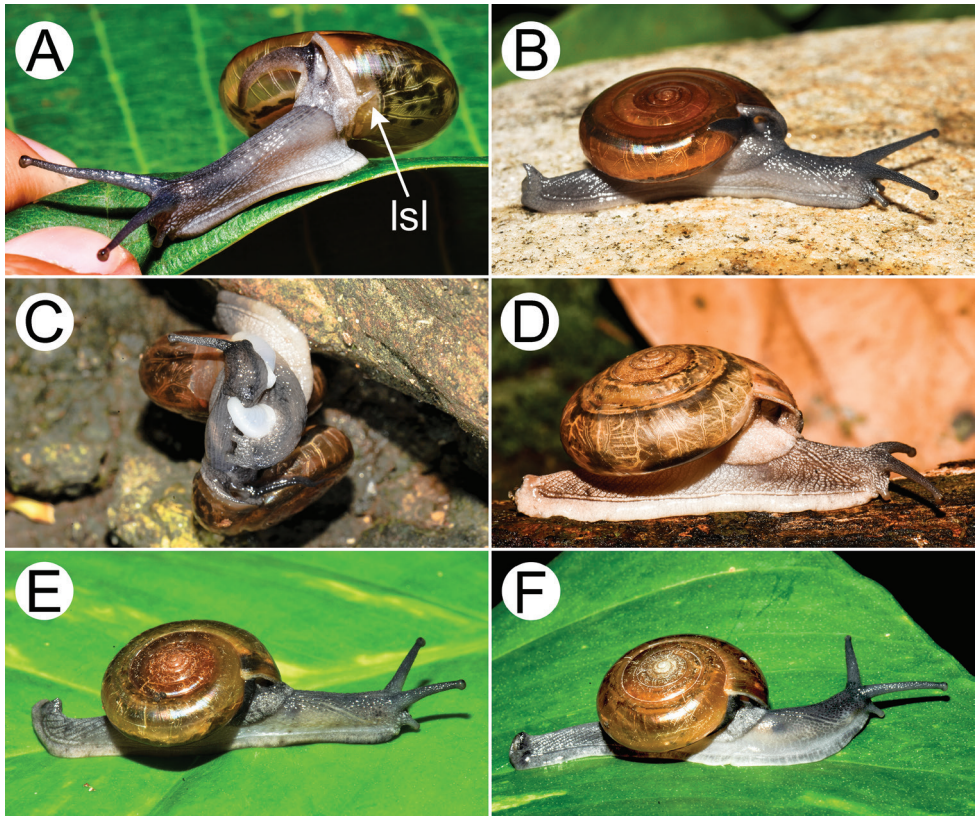


Figure 9. Living snails of group I: *Sarika resplendens* group. **A** *Sarika resplendens* specimen CUMZ 7843 showing left shell lobe lobes (lsl) **B** *S. resplendens* specimen CUMZ 7827 **C** mating pairs of *S. resplendens* CUMZ 7876 **D** *S. dohrniana* specimen CUMZ 7611 **E** *S. obesior* specimen CUMZ 7673 **F** *S. limbata* specimen CUMZ 7652. All not to scale.

spermatophore. In contrast, *S. kawtaoensis* has reticulated and irregular large folded penial pilasters and acute-serrate longitudinal ridges on the head filament of the spermatophore.

***Sarika heptagyra* (Möllendorff, 1902)**

Figs 1, 6, 10A, 17D–F, 18C, D, 20, 30E

Macrochlamys heptagyra Möllendorff, 1902: 155. Type locality: “Kanburi” [Kanchanaburi Province, Thailand].

Nanina (Macrochlamys) heptagyra: Fischer and Dautzenberg 1904: 395.

Type material. *Syntypes* SMF 227096 (Fig. 17D), SMF 227097/3 (three shells; Fig. 17E) from Siam: Kanburi [Kanchanaburi, Thailand].

Other material examined. **THAILAND–Western.** Wat Dao Wadung, Sai Yok, Kanchanaburi, 14°28'23.3"N, 98°50'04.7"E: CUMZ 7232, 7280, 7285. Limestone

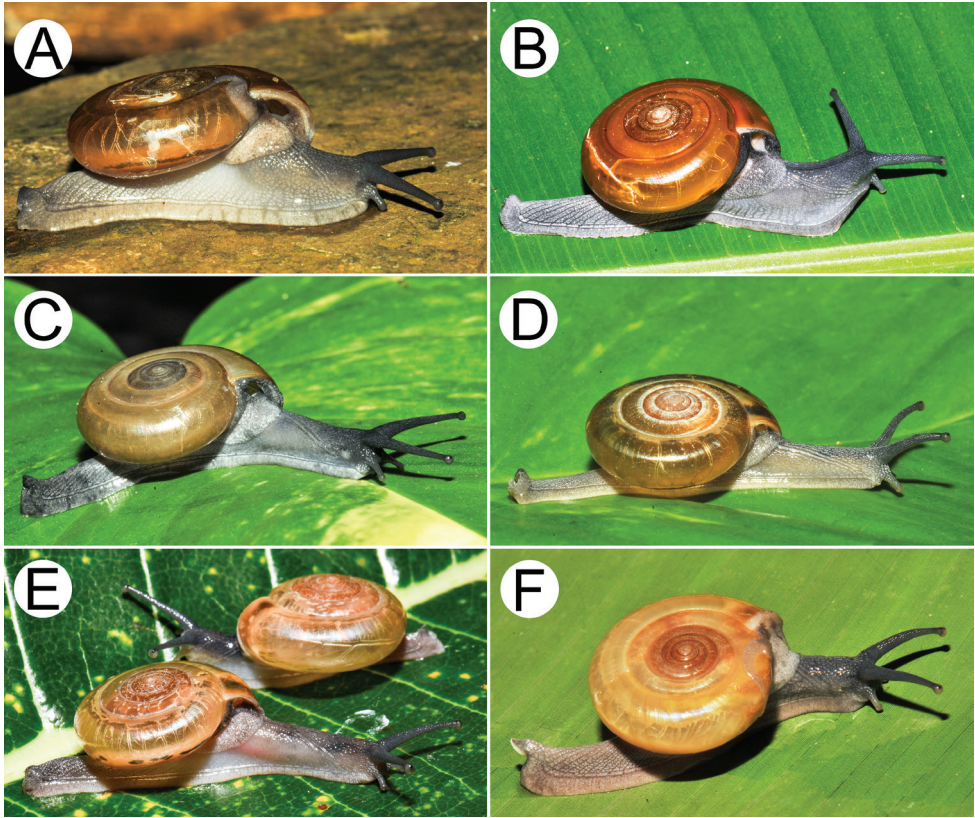


Figure 10. Living snails of group I: *Sarika resplendens* group. **A** *Sarika heptagyra* specimen CUMZ 7279 **B** *S. kawtaoensis* specimen CUMZ 7738 **C** *S. caligina* sp. nov. paratype CUMZ 7245 **D** *S. lactospira* sp. nov. paratype CUMZ 7287 **E** *S. megalogyne* sp. nov. paratype CUMZ 7522 and **F** *S. subheptagyra* sp. nov. paratype CUMZ 7507. All not to scale.

outcrop in Sai Yok, Sai Yok, Kanchanaburi, 14°22'46.0"N, 98°55'50.0"E: CUMZ 7282. Limestone outcrop in Khao Chot, Si Sawat, Kanchanaburi, 14°39'41.7"N, 99°17'09.6"E: CUMZ 7281. Erawan waterfall, Si Sawat, Kanchanaburi, 14°22'07.1"N, 99°08'38.3"E: CUMZ 7283. Limestone outcrop in Tha Kradan, Si Sawat, Kanchanaburi, 14°22'31.8"N, 99°08'38.3"E: CUMZ 7284. Kroeng Krawia, Thong Pha Phum, Kanchanaburi, 14°56'24.7"N, 98°39'47.8"E: CUMZ 7279. Wat Uthum Phon Wanaram (Tham Khao Noi), Thong Pha Phum, Kanchanaburi, 14°41'52.1"N, 98°31'32.7"E: CUMZ 7231 (Fig. 17F).

Diagnosis. Shell large, strongly depressed and well-rounded to slightly shouldered body whorl. Animal with pale grey body and five mantle lobes. Genitalia with straight epiphalllic caecum and cuboidal penial pilasters. Tail filament of spermatophore near sperm sac with three spines and terminal part of tail filament more than ca. one-fourth of its length with series of several branching spines.

Description. Shell. Shell strongly depressed, large size (shell width up to 27.9 mm, shell height up to 13.1 mm) and rather thin. Shell surface smooth and glossy; shell colour

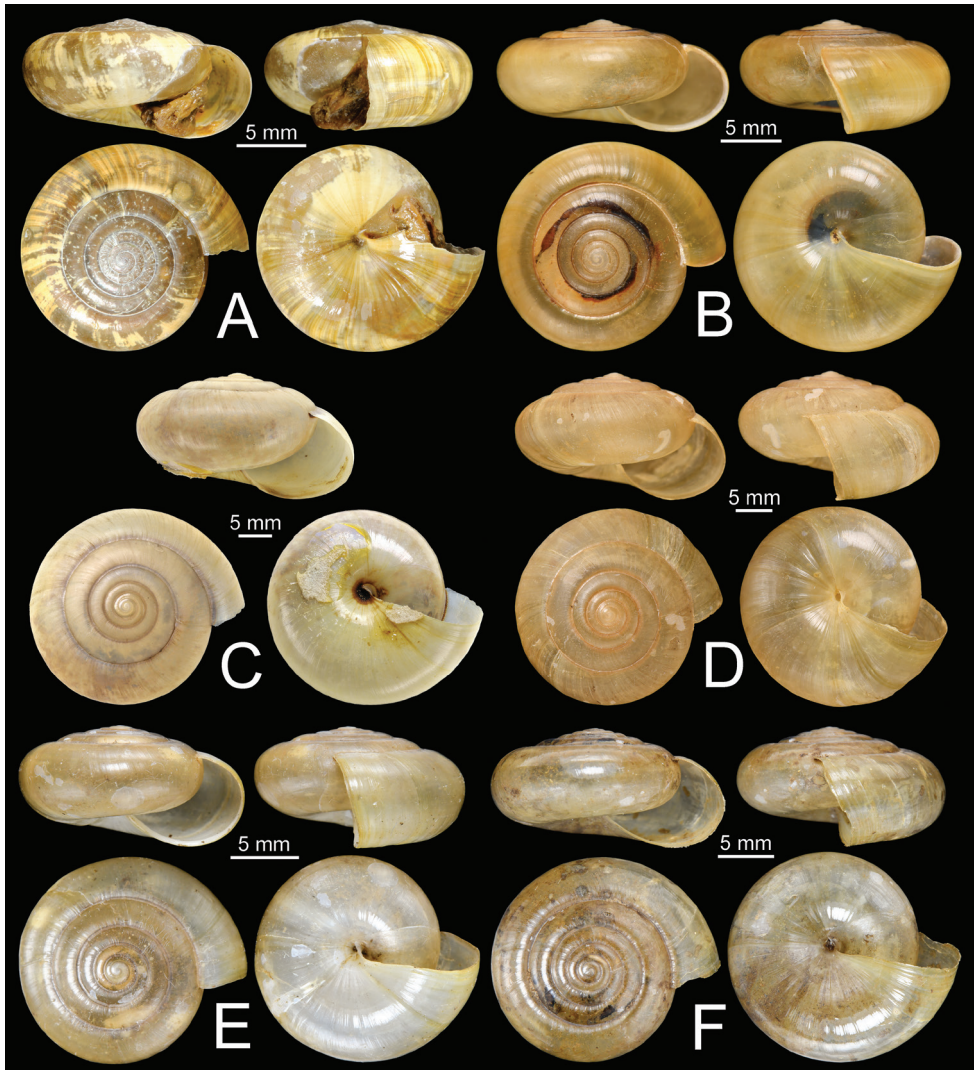


Figure 11. Shells of group I: *Sarika resplendens* group. **A, B** *Sarika resplendens* **A** specimen NHMUK 1898.5.18.157 and **B** specimen CUMZ 7815 **C, D** *S. dobrniana* **C** syntype NHMUK 20160046 and **D** specimen CUMZ 7611. **E, F** *S. obesior* **E** specimen CUMZ 7675 and **F** specimen CUMZ 7673.

pale yellowish brown to very pale brown. Whorls 6–7, increasing regularly; body whorl large, rounded to slightly shouldered. Spire slightly elevated; suture rather impressed. Aperture crescent-shaped and obliquely opened. Peristome simple. Columellar margin simple and slightly reflected near umbilicus. Umbilicus narrowly opened (Fig. 17D–F).

Genital organs. Atrium short. Penis cylindrical with thin penial sheath covering proximal penis. Inner sculpture of penis proximally more than ca. one-third of penial chamber with fine longitudinal penial pilaster to nearly smooth surface, and then modified from small to large cuboidal pilasters arranged in oblique rows. Epiphallus cylindrical,

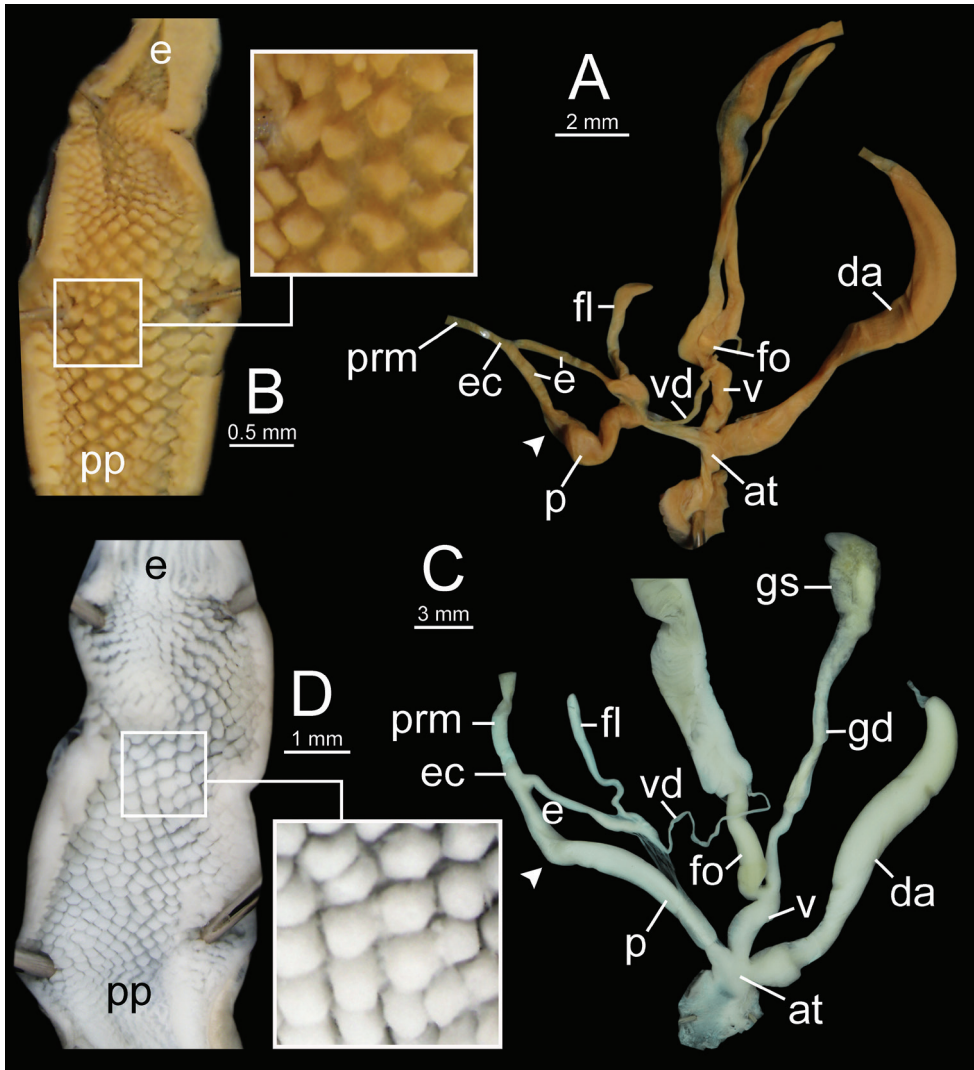


Figure 12. Genitalia of *Sarika resplendens*. **A, B** specimen NHMUK 1898.5.18.157 **A** general view of genital system and **B** internal structure of penis **C, D** specimen CUMZ 7851 **C** general view of the genital system and **D** internal structure of the penis. White arrowhead indicate the end of the penis.

approximately as long as penis but narrower than penis. Epiphallic caecum short, straight, same diameter as epiphallus, located near middle of epiphallus. Penial retractor muscle thin and attached at tip of epiphallic caecum. Flagellum slender, approximately as long as penis. Vas deferens thin tube connecting distal epiphallus and free oviduct (Fig. 18C, D).

Vagina cylindrical, ca. one-third of penis length. Dart apparatus large, long cylindrical, and located on atrium at vagina and penis junction. Gametolytic sac enlarged and bulbous; gametolytic duct long cylindrical. Free oviduct cylindrical, nearly two times of vagina length, and proximal end encircled with thick tissue (Fig. 18C).

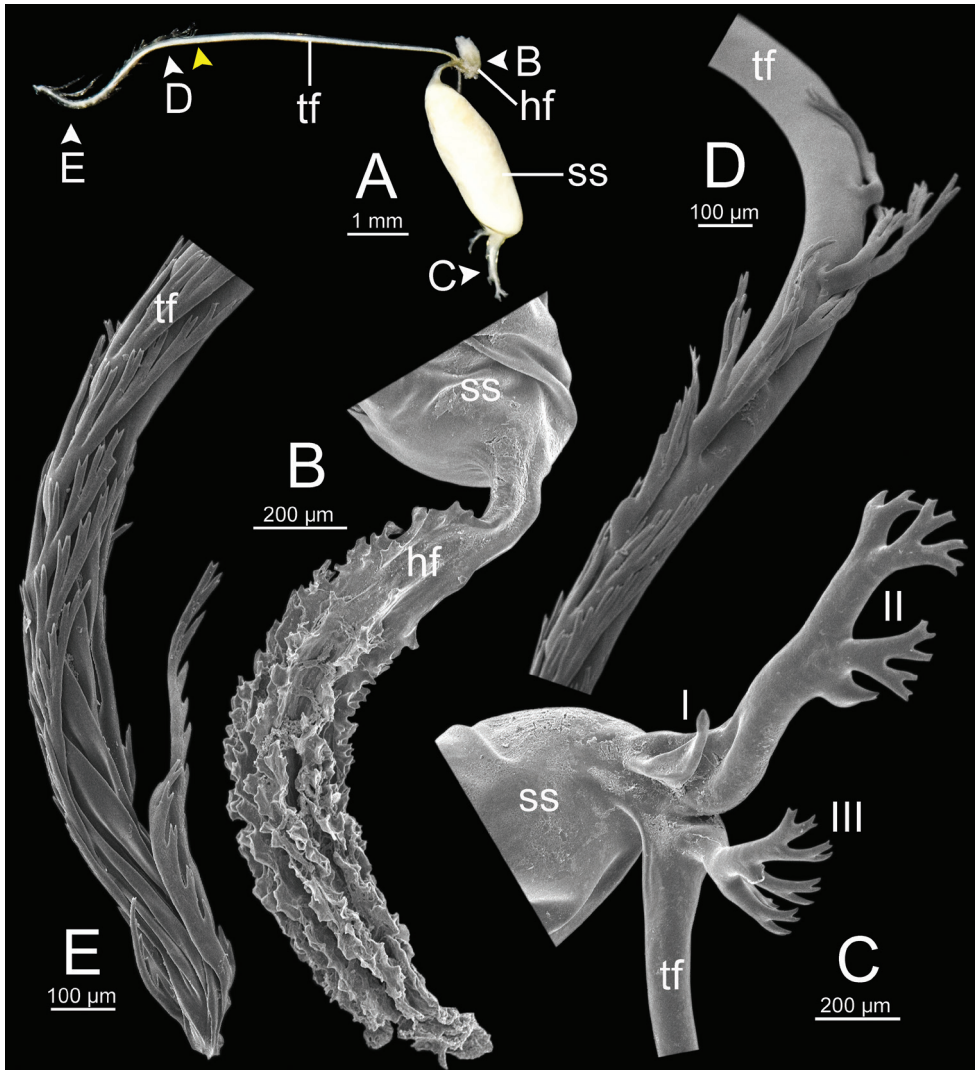


Figure 13. Spermatophore of *Sarika resplendens* specimen CUMZ 7876 **A** general view of the spermatophore **B** head filament with the position a bit twisted **C–E** tail filament showing **C** three spines located close to the sperm sac and **D** region with and without branching spines, and **E** branching spines on the tip region. Yellow arrowhead indicates the end of spines on the tip of the tail filament.

Spermatophore long and needle-shaped. Sperm sac enlarged and elongate-oval. Head filament was missing (incomplete spermatophore). Tail filament very long tube; region near sperm sac with three spines. Spine I simple, curved, and short. Spine II large and long, and branching part was missing. Spine III short and smaller than spine II, and branching part was missing. Region furthest away smooth and without spine; terminal part (more than ca. one-fourth of its length) with a series of short to long branching spines arranged in a row or encircled tail filament tip (Fig. 20).

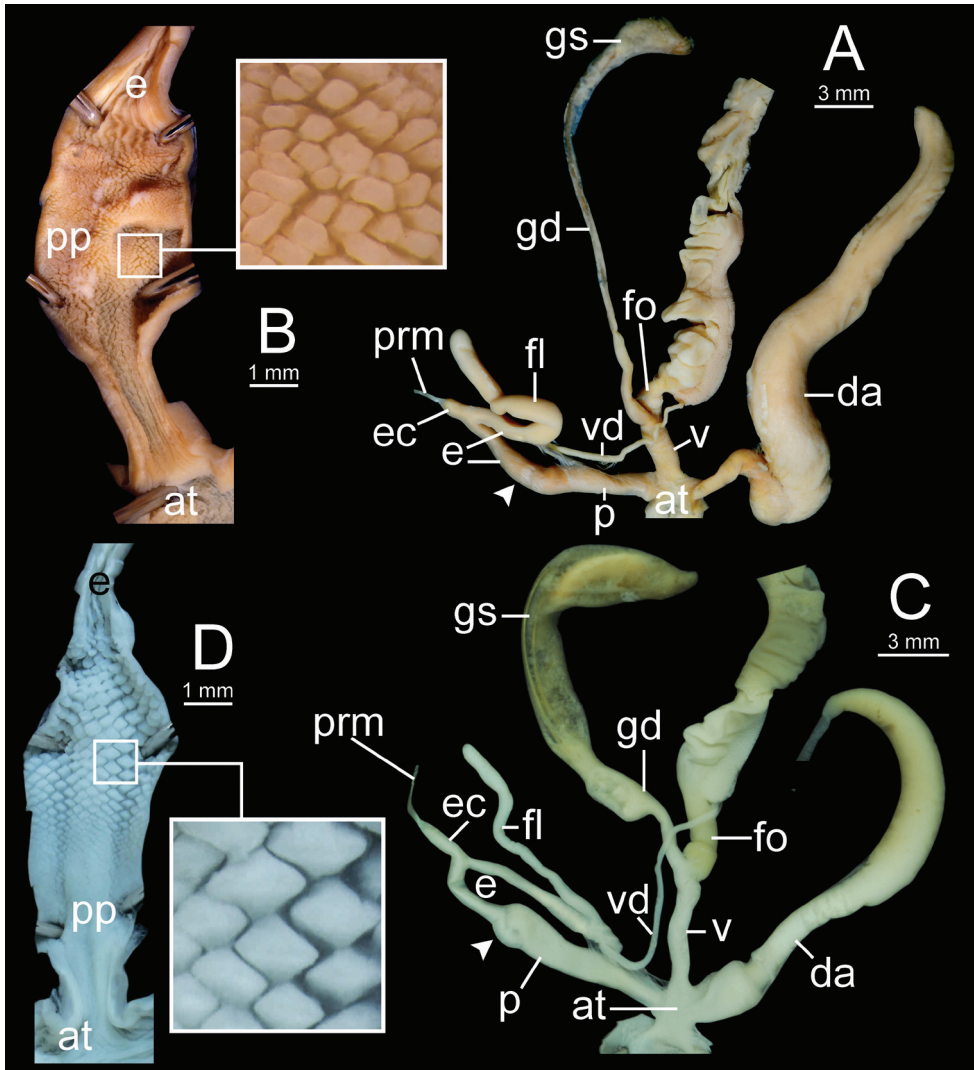


Figure 14. Genitalia. **A, B** *Sarika dohrniana* specimen CUMZ 7633 **A** general view of the genital system and **B** internal structure of the penis **C, D** *Sarika obesior* specimen CUMZ 7673 **C** general view of the genital system and **D** internal structure of penis. White arrowheads indicate the ends of the penes.

Radula. Teeth with half row formula: 1–(11–12)–63. Central tooth symmetrical tricuspid; lateral teeth asymmetrical tricuspid; marginal teeth elongate bicuspid. Marginal teeth starting at approximately row number 11 or 12 (Fig. 30E).

External features. Animal with reticulated skin and pale grey body, dark creamy mixing with grey foot sole and slightly dark grey caudal horn. Mantle edge well developed and same colour as body (Fig. 10A).

Distribution. This species is known from the limestone outcrops in Kanchanaburi Province (Fig. 6).

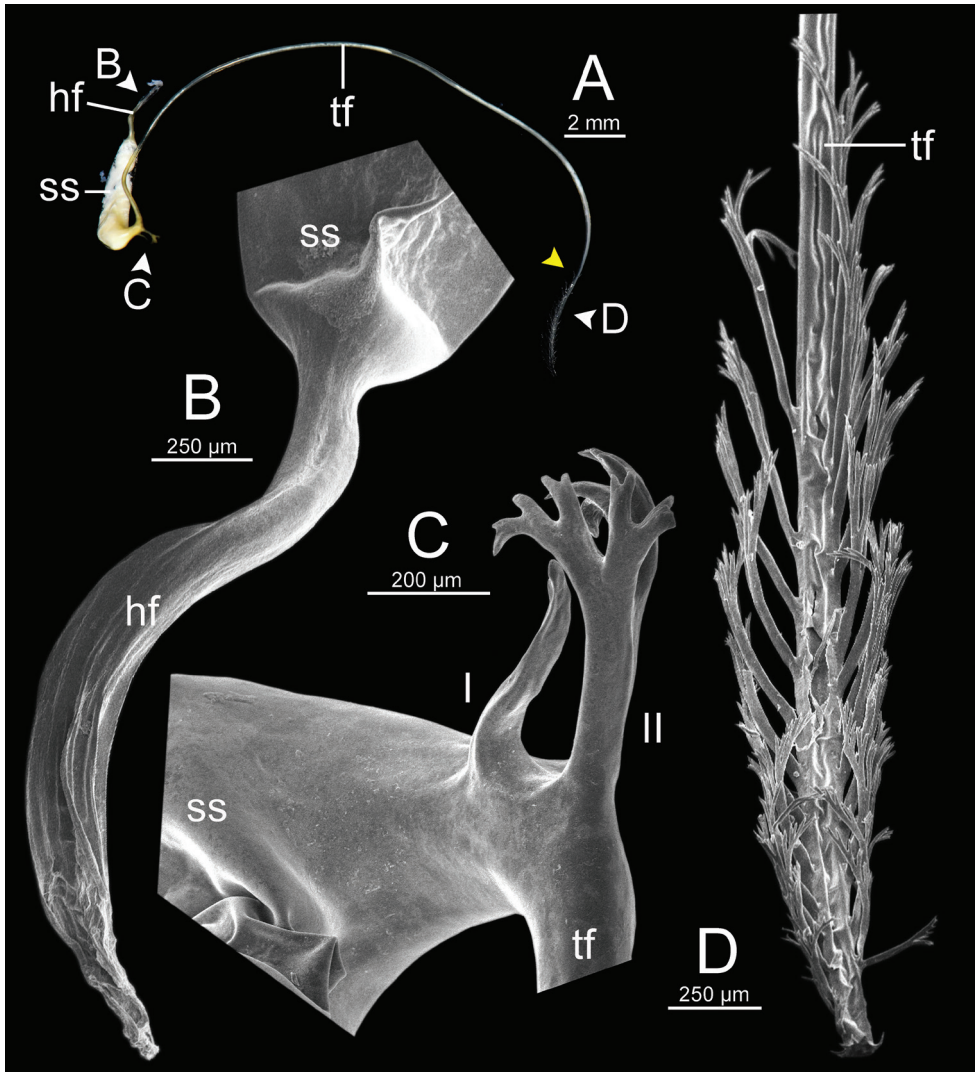


Figure 15. Spermatophore of *Sarika dohrniana* specimen CUMZ 7633 **A** general view of spermatophore **B** head filament **C, D** tail filament showing **C** two spines located close to the sperm sac and **D** tip region of tail filament. Yellow arrowhead indicates the end of the spines from the tip of the tail filament.

COI analysis. The ML and BI analyses showed that the specimens of *S. heptagyra* ($n = 3$) formed a monophyletic group with very strong support (Fig. 1; BS = 100%, PP = 1). The mean intraspecific genetic distance of *S. heptagyra* was 3.5% (Table 2).

Remarks. *Sarika heptagyra* is similar to *S. resplendens*. According to the phylogenetic tree, the relationship between *S. heptagyra* and *S. resplendens* is not clearly resolved (Fig. 1). The average interspecific sequence divergences between them were rather high

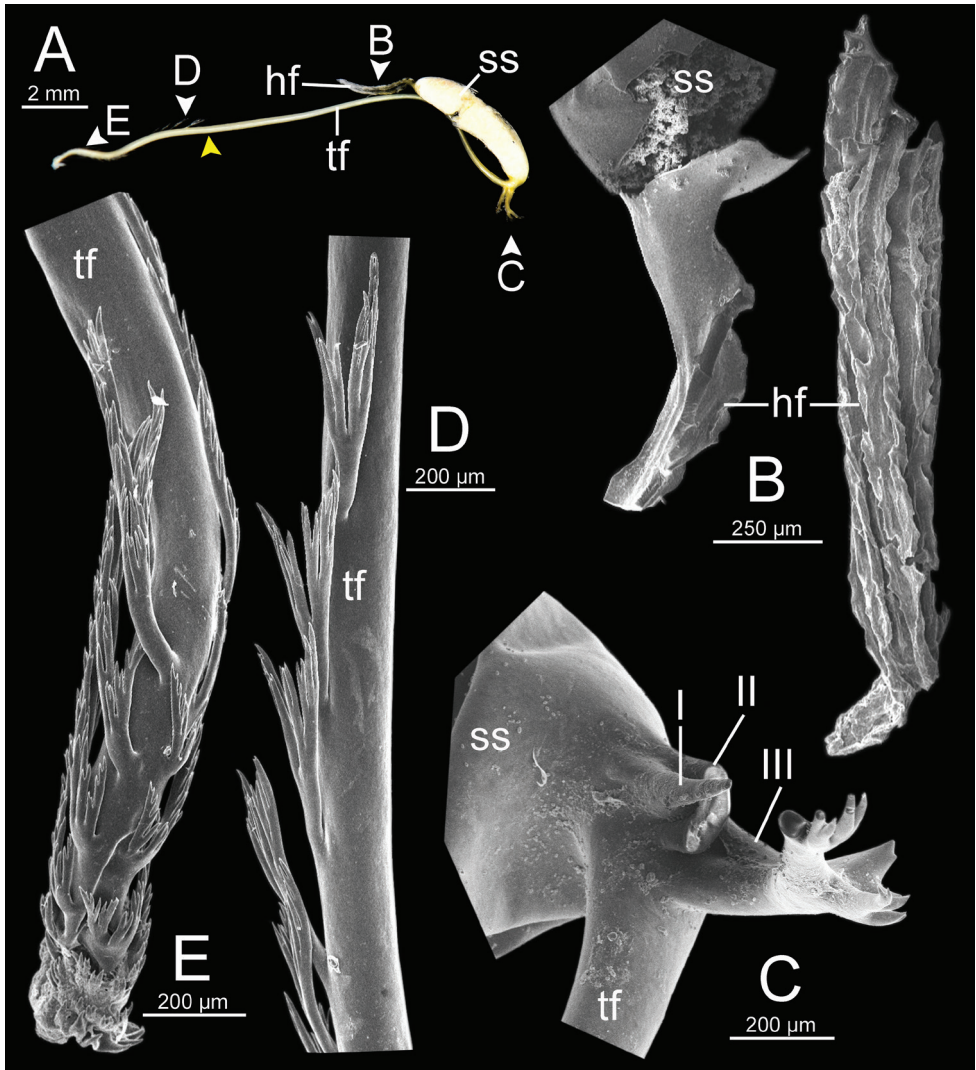


Figure 16. Spermatophore of *Sarika obesior* specimen CUMZ 7678 **A** general view of the spermatophore **B** head filament **C–E** tail filament **C** three spines located close to the sperm sac **D** region with and without branching spines, and **E** branching spines on the tip region. Yellow arrowhead indicates the end of the spines from the tip.

at 7.7% which is in the recognised species range (4.6–12.0%) of interspecies sequence divergence of *Sarika* (see Table 2). Therefore, we have recognised *S. heptagyra* and *S. resplendens* as distinct biological species. The distinguishing character of *S. heptagyra* is its thin and long penial retractor muscle, while *S. resplendens* has very large and thickened penial retractor muscle (Table 2).

Sarika heptagyra seems to be indigenous in limestone habitats in western Thailand.

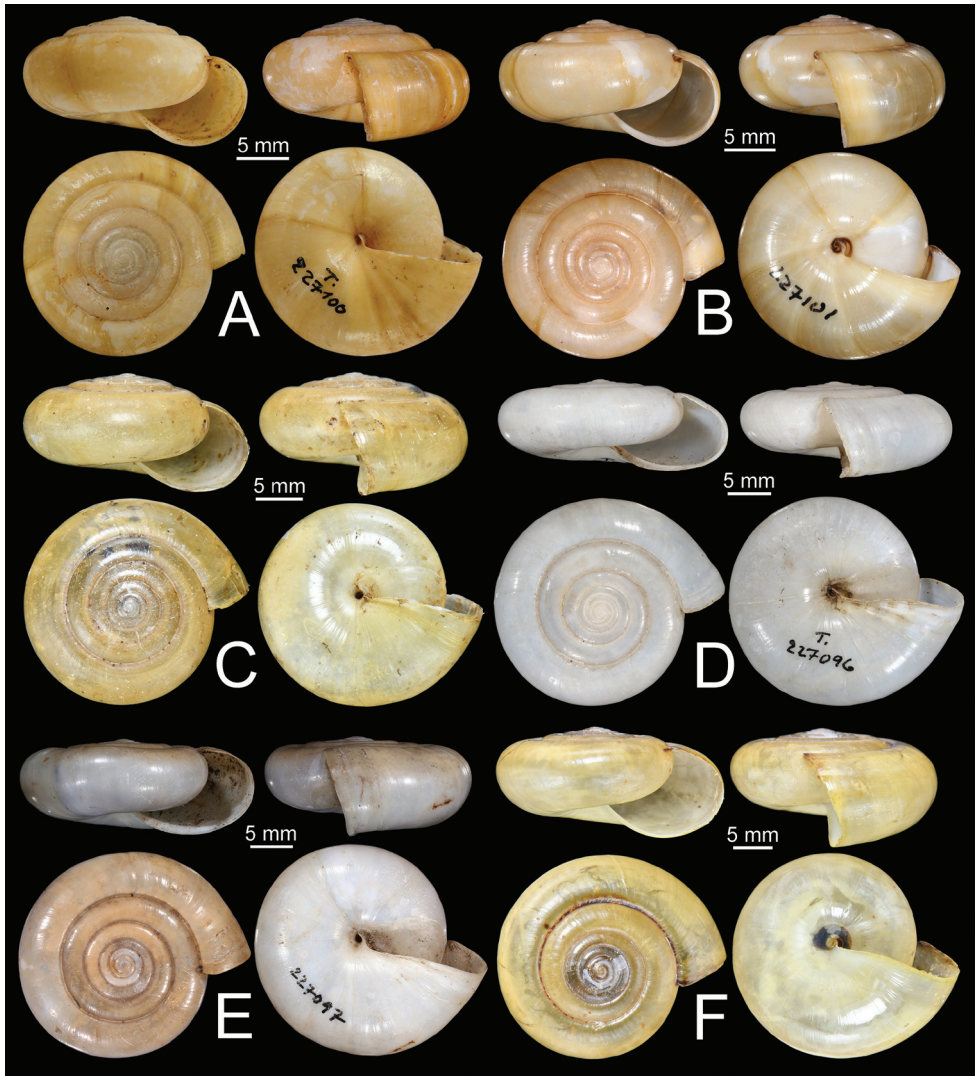


Figure 17. Shells of group I: *Sarika resplendens* group. **A–C** *Sarika limbata* **A** syntype SMF 227100, **B** syntype SMF 227101, and **C** specimen CUMZ 7652 **D–F** *S. heptagyra* **D** syntype SMF 227096 **E** syntype SMF 227097, and **F** specimen CUMZ 7231.

***Sarika kawtaoensis* Tomlin, 1929**

Figs 1, 8, 10B, 21A–D, 22A, B, 23, 31A

Sarika kawtaoensis Tomlin, 1929: 15. Type locality: “Kaw Tao” [Ko Tao, Ko Pha-ngan District, Surat Thani Province, Thailand]. Hemmen and Hemmen 2001: 45.

Type material. *Syntype* NMW 1955.158.01170 (two shells; Fig. 21A) from Kaw Tao [Tao Island, Ko Pangan, Surat Thani].

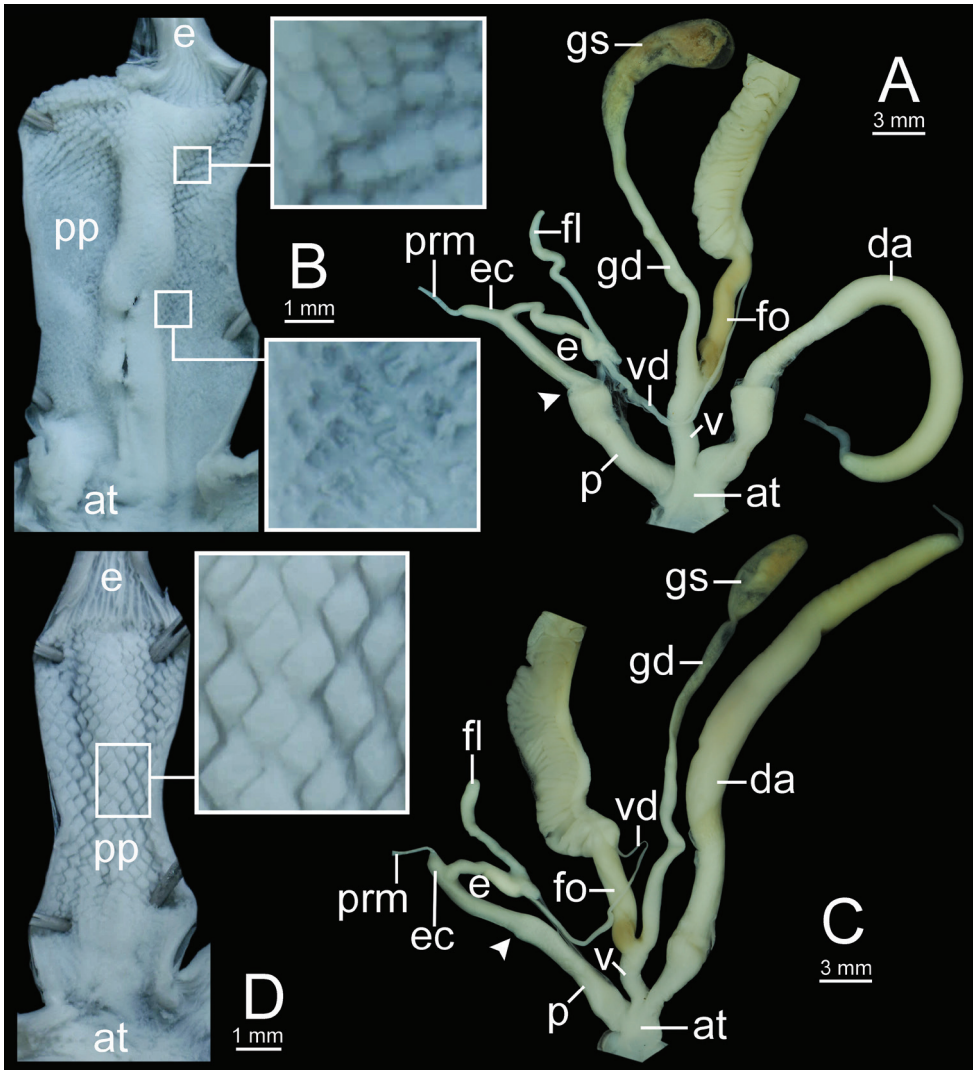


Figure 18. Genitalia. **A, B** *Sarika limbata* specimen CUMZ 7652 **A** general view of the genital system and **B** internal structure of penis **C, D** *S. heptagyra* specimen CUMZ 7279 **C** general view of the genital system and **D** internal structure of penis. White arrowheads indicate the ends of the penes.

Other material examined. THAILAND-Southern. Khao Phlu Cave, Pathio, Chumphon, 10°43'49.1"N, 99°19'13.9"E: CUMZ 7709. Ancient hot springs, Chaiya, Surat Thani, 9°21'51.8"N, 99°11'21.0"E: CUMZ 7706 (Fig. 21B). Wat Tham Sila Tiap, Tha Chana, Surat Thani, 9°30'58.8"N, 99°11'31.8"E: CUMZ 7717, 7750. Wat Wichit Ditatharam, Tha Chana, Surat Thani, 9°33'34.6"N, 99°10'18.3"E: CUMZ 7746. Wat Tham Yai, Tha Chana, Surat Thani, 9°32'21.7"N, 99°11'29.4"E: CUMZ 7752, 7783, 7806. Wat Rattanaram, Tha Chana, Surat Thani, 9°22'42.8"N, 99°11'25.4"E: CUMZ 7777. Tham Wang Badan Bureau of Monks, Khiri Rat Nikhom, Surat Thani,

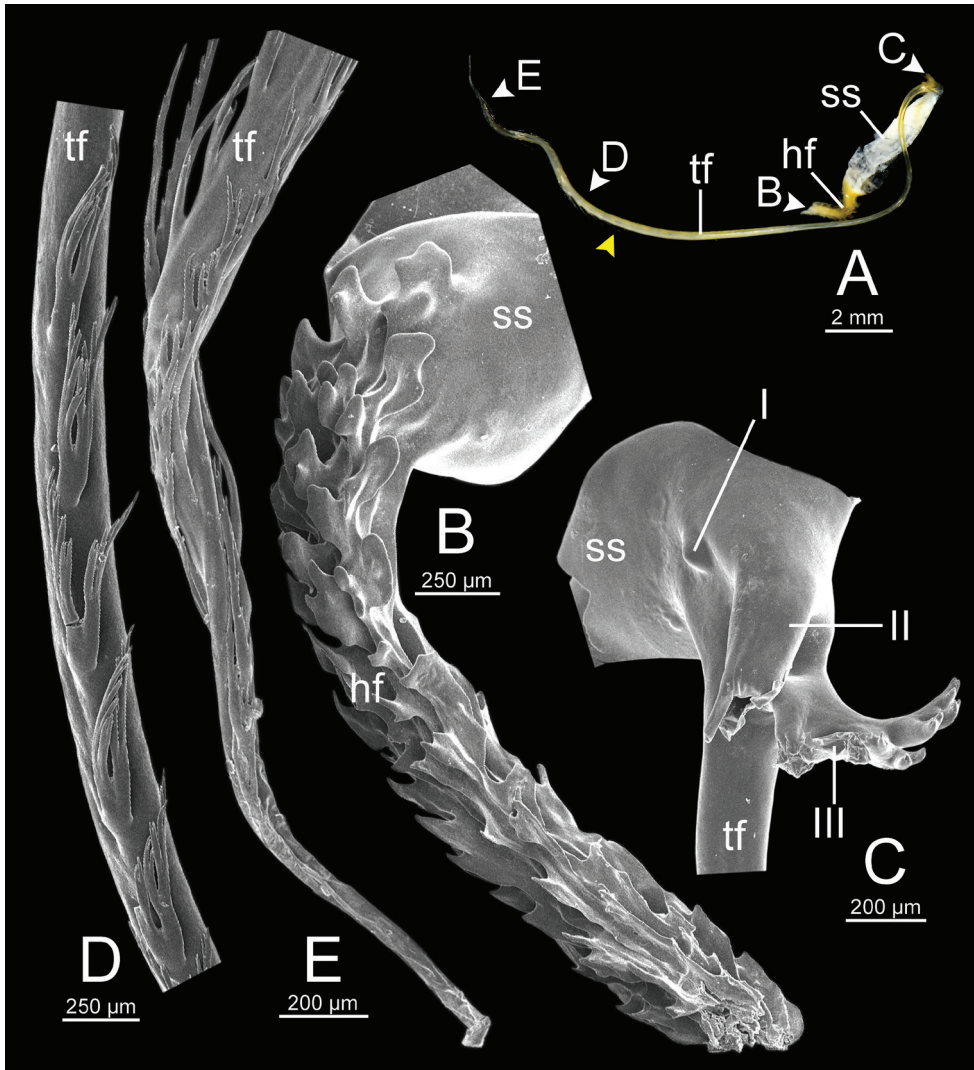


Figure 19. Spermatophore of *Sarika limbata* specimen CUMZ 7652 **A** general view of spermatophore, **B** head filament **C–E** tail filament showing **C** three spines located close to the sperm sac **D** region with and without branching spines, and **E** branching spines on the tip region. Yellow arrowheads indicate the ends of spines from the tip.

8°56'13.0"N, 98°57'24.7"E: CUMZ 7707, 7751. Wat Sathit Khirirom, Khiri Rat Nikhom, Surat Thani, 9°01'48.4"N, 98°59'12.1"E: CUMZ 7236 (Fig. 21D), 7808. Limestone outcrop in Khiri Rat Nikhom, Khiri Rat Nikhom, Surat Thani, 9°00'19.2"N, 98°57'58.8"E: CUMZ 7798. Tham Bo Nam Thip Bureau of Monks, Kanchanadit, Surat Thani, 9°09'55.3"N, 99°35'20.5"E: CUMZ 7712. Wat Tham Khuha, Kanchanadit, Surat Thani, 9°09'17.3"N, 99°28'17.2"E: CUMZ 7802. Wat Khao Phra, Phrasaeng, Surat Thani, 8°37'32.4"N, 98°56'49.8"E: CUMZ 7713. Tham Nam Lod, Phrasaeng,

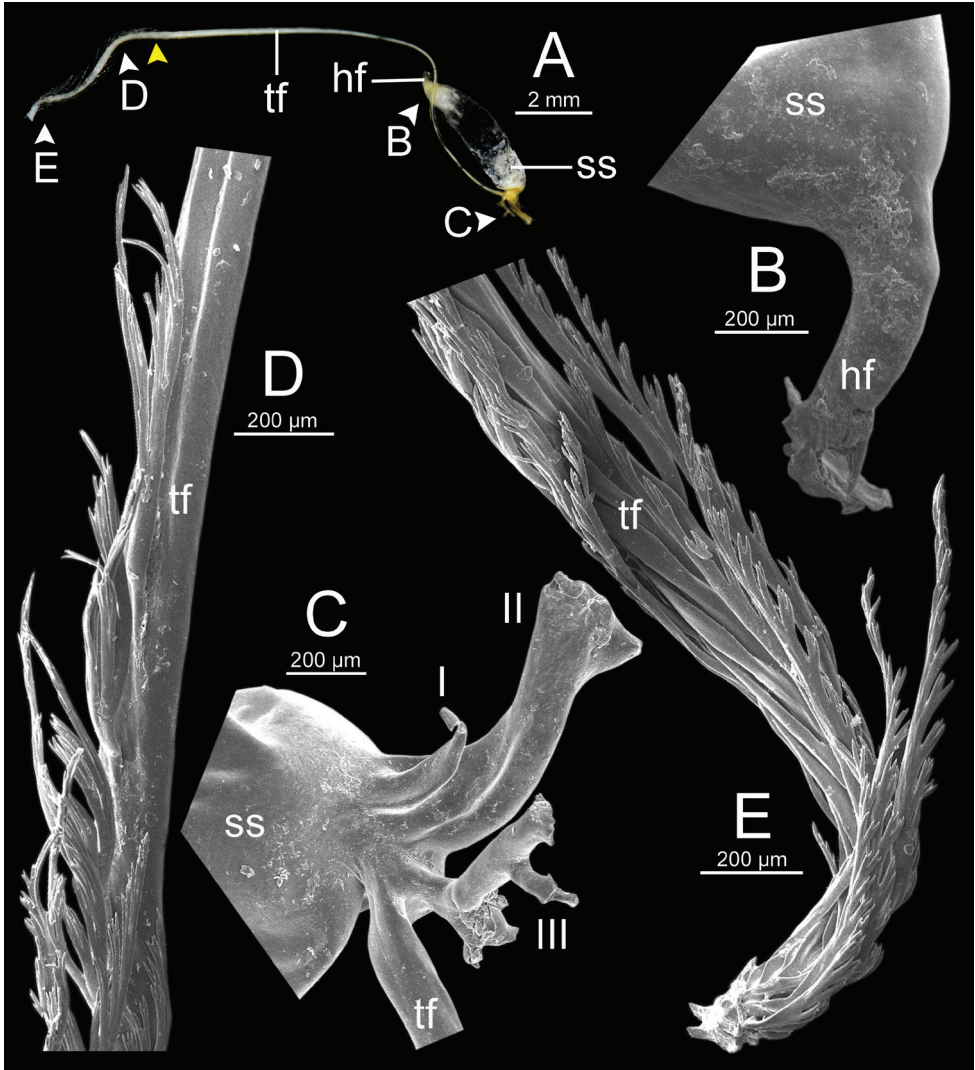


Figure 20. Spermatophore of *Sarika heptagyra* specimen CUMZ 7232 **A** general view of spermatophore, **B** head filament, and **C–E** tail filament showing **C** three spines located close to the sperm sac **D** region with and without branching spines, and **E** branching spines on the tip region. Yellow arrowhead indicates the end of the spines from the tip.

Surat Thani, 8°40'40.4"N, 98°56'39.5"E: CUMZ 7714. Wat Santi Sirom, Phunphin, Surat Thani, 9°03'32.0"N, 99°15'05.4"E: CUMZ 7715. Wat Nakhawat, Phunphin, Surat Thani, 9°04'33.2"N, 99°09'54.0"E: CUMZ 7747. Limestone outcrop in Khlong Sok, Phanom, Surat Thani, 8°53'39.3"N, 98°33'10.7"E: CUMZ 7716, 7757. Limestone outcrop in Khlong Sok, Phanom, Surat Thani, 8°50'51.0"N, 98°44'32.8"E: CUMZ 7755. Wat Tham Wararam, Phanom, Surat Thani, 8°52'56.4"N, 98°39'49.6"E: CUMZ 7739, 7740. Limestone outcrop near Anurak Community Lodge, Phanom,

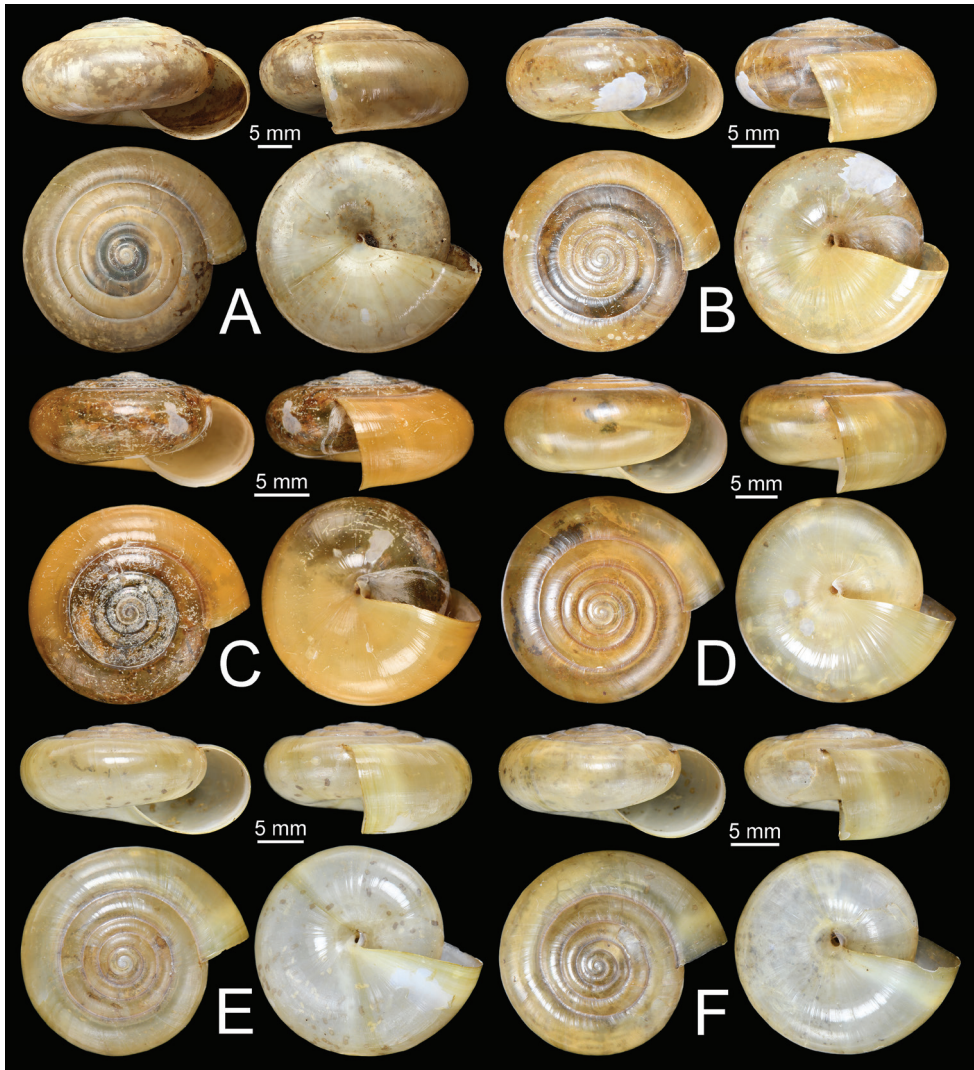


Figure 21. Shells of Group I: *Sarika resplendens* group. **A–D** *Sarika kawtaoensis* **A** syntype NMW 1955.158.01170 **B** specimen CUMZ 7706 **C** specimen CUMZ 7753 and **D** specimen CUMZ 7236 **E, F** *S. caligina* sp. nov. **E** holotype CUMZ 7259, and **F** paratype CUMZ 7245.

Surat Thani, 8°53'20.3"N, 98°40'47.9"E: CUMZ 7741, 7742. Khao Sok, Phanom, Surat Thani, 8°54'55.6"N, 98°31'42.2"E: CUMZ 7743. Mae Yai Waterfall, Phanom, Surat Thani, 8°52'59.9"N, 98°29'58.5"E: CUMZ 7744, 7769. Limestone outcrop near Khao Sok Nature Resort, Phanom, Surat Thani, 8°54'22.6"N, 98°31'45.1"E: CUMZ 7766. Limestone outcrop near Khao Sok Evergreen House, Phanom, Surat Thani, 8°54'38.1"N, 98°31'47.2"E: CUMZ 7767. Limestone outcrop in Saphan Tao, Phanom, Surat Thani, 8°52'27.1"N, 98°38'46.5"E: CUMZ 7800. Limestone outcrop near Ratchaphapha Dam, Ban Ta Khun, Surat Thani, 8°58'20.9"N, 98°48'20.5"E:

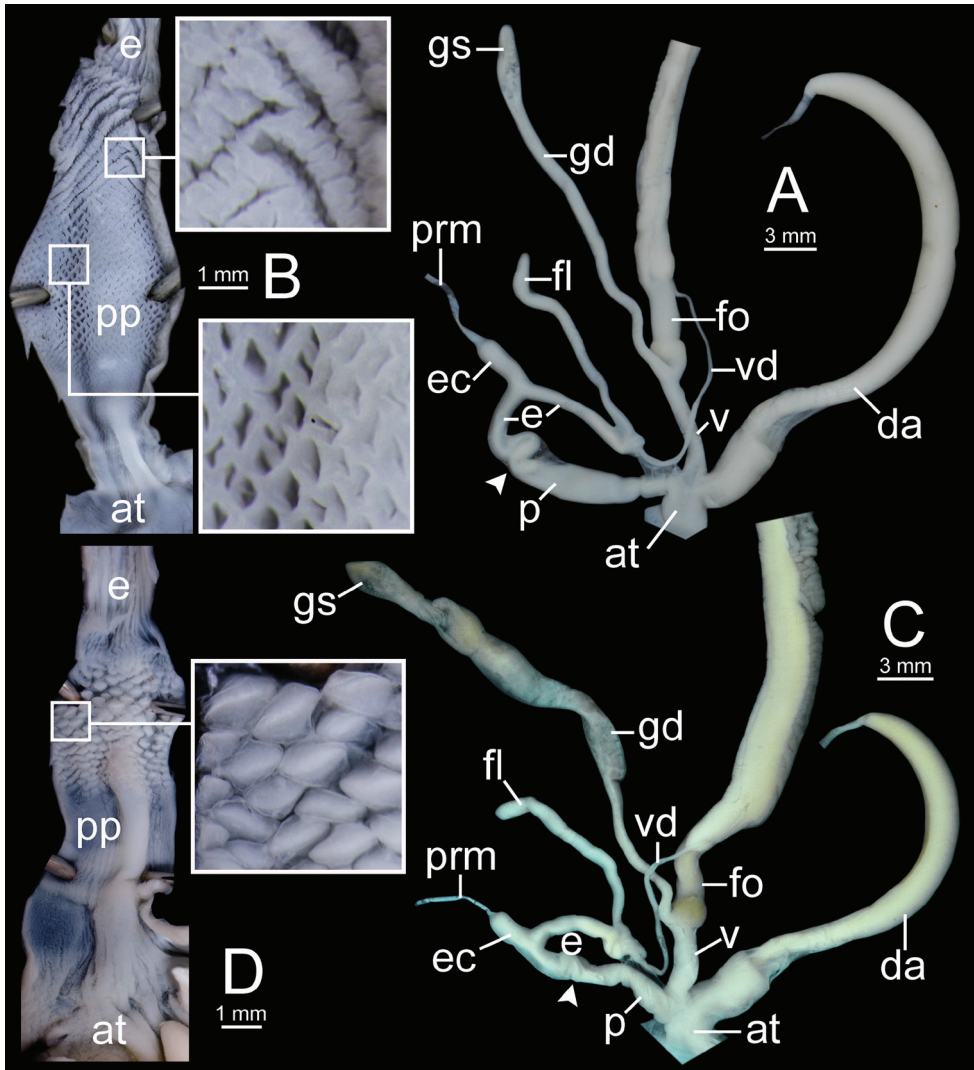


Figure 22. Genitalia. **A, B** *Sarika kawtaoensis* specimen CUMZ 7762 **A** general view of the genital system and **B** internal structure of the penis **C, D** *S. caligina* sp. nov. paratype CUMZ 7245 **C** general view of the genital system and **D** internal structure of the penis. White arrowheads indicate the ends of the penes.

CUMZ 7756, 7809. Limestone outcrop near Khao Wong, Ban Ta Khun, Surat Thani, 8°56'12.4"N, 98°55'48.7"E: CUMZ 7794. Wat Khiri Rat Phatthana, Wiang Sa, Surat Thani, 8°31'38.6"N, 99°22'57.4"E: CUMZ 7745. Wat Na San, Na San, Surat Thani, 8°48'30.1"N, 99°22'10.4"E: CUMZ 7749, 7792, 7807. Tham Khao Khok Maharat Priest's camp site, Na San, Surat Thani, 8°41'34.4"N, 99°22'45.8"E: CUMZ 7778. Limestone outcrop in Thong Nian, Khanom, Nakhon Si Thammarat, 9°17'15.7"N, 99°48'04.8"E: CUMZ 7710. Limestone outcrop near Khanom Seafood, Khanom, Nakhon Si Thammarat, 9°07'27.6"N, 99°52'59.3"E: CUMZ 7754, 7762. Lot cave,

Noppitam, Nakhon Si Thammarat, 8°44'10.0"N, 99°38'06.5"E: CUMZ 7735. Tham Talod, Thung Song, Nakhon Si Thammarat, 8°09'32.0"N, 99°40'41.8"E: CUMZ 7736. Wat Khuha Santayaram (Wat Tham Khao Daeng), Ron Phibun, Nakhon Si Thammarat, 8°14'38.3"N, 99°52'01.0"E: CUMZ 7737, 7799. Kaeo Surakan Cave, Lan Saka, Nakhon Si Thammarat, 8°21'40.4"N, 99°47'07.0"E: CUMZ 7738, 7765. Tham Nam Wang Sri Thammasokrat, Lan Saka, Nakhon Si Thammarat, 8°19'55.0"N, 99°49'59.8"E: CUMZ 7786. Wat Tham Kanlayanamit, Tham Phannara, Nakhon Si Thammarat, 8°30'48.2"N, 99°22'50.7"E: CUMZ 7748. Wat Tham Thong Panara, Tham Phannara, Nakhon Si Thammarat, 8°25'19.8"N, 99°22'46.4"E: CUMZ 7775. Phung Chang Cave, Mueang, Phang-nga, 8°26'33.1"N, 98°30'55.0"E: CUMZ 7719, 7758. Pha Phueng Cave, Mueang, Phang-nga, 8°28'31.8"N, 98°32'20.4"E: CUMZ 7722. Wat Suwan Khuha, Mueang, Phang-nga, 8°25'42.5"N, 98°28'18.1"E: CUMZ 7759, 7812. Tham Nam Phut, Mueang, Phang-nga, 8°27'45.0"N, 98°31'21.6"E: CUMZ 7760, 7784, 7796, 7799. Bang Toci Cave, Mueang, Phang-nga, 8°25'58.6"N, 98°34'01.8"E: CUMZ 7779. Wat Khiriwong, Thap Put, Phang-nga, 8°31'55.6"N, 98°34'37.0"E: CUMZ 7720, 7795, 7804. Tao Thong Waterfall, Thap Put, Phang-nga, 8°29'07.6"N, 98°35'08.5"E: CUMZ 7793. Mountain area near Ban Pak Khlong, Kapong, Phang-nga, 8°50'21.2"N, 98°27'41.5"E: CUMZ 7721. Tham Nalakiring Bureau of Monks, Plai Phraya, Krabi, 8°33'29.5"N, 98°51'44.0"E: CUMZ 7711. Wat Khao Hua Sing, Plai Phraya, Krabi, 8°30'41.4"N, 98°45'39.4"E: CUMZ 7725. Wat Tham Bun Raksa Phupharam, Lam Thap, Krabi, 8°02'13.9"N, 99°23'47.8"E: CUMZ 7773. Limestone outcrop near Than Bok Khorani, Ao Luek, Krabi, 8°23'19.3"N, 98°44'03.5"E: CUMZ 7718, 7723. Sa Yuan Thong Cave, Ao Luek, Krabi, 8°21'47.2"N, 98°44'44.3"E: CUMZ 7789. Limestone outcrop near Emerald Pool, Khlong Thom, Krabi, 7°55'30.3"N, 99°16'05.3"E: CUMZ 7813. Wat Tham Seu, Mueang, Krabi, 8°07'27.1"N, 98°55'26.1"E: CUMZ 7724, 7776, 7791, 7797. Limestone outcrop near Ban Thab Prik School, Mueang, Krabi, 8°10'50.2"N, 98°52'50.4"E: CUMZ 7781. Wat Tham Phraphut, Ratsada, Trang, 7°52'21.5"N, 99°43'40.9"E: CUMZ 7727. Limestone outcrop in Huai Yot, Huai Yot, Trang, 7°44'13.0"N, 99°39'23.0"E: CUMZ 7780. Khao Pu Chao Bureau of Monks, Na Yong, Trang, 7°33'31.2"N, 99°46'40.3"E: CUMZ 7801. Khanti Phon Cave, Thung Wa, Satun, 7°05'07.5"N, 99°47'53.4"E: CUMZ 7726, 7790. Wat Thung Khamin, Thung Wa, Satun, 7°02'57.5"N, 99°50'39.3"E: CUMZ 7728. Khao Thanan, Thung Wa, Satun, 7°03'37.0"N, 99°41'29.3"E: CUMZ 7788. Wat Kumphin Banpot, Khuan Kalong, Satun, 6°52'30.8"N, 100°01'02.4"E: CUMZ 7729. Ton Din Cave, Khuan Don, Satun, 6°43'35.5"N, 100°09'46.5"E: CUMZ 7753 (Fig. 21C), 7770, 7811. Khao Ok Tha Lu, Mueang, Phatthalung, 7°37'30.0"N, 100°05'30.0"E: CUMZ 7730. Wat Khuha Sawan, Mueang, Phatthalung, 7°37'14.1"N, 100°04'51.8"E: CUMZ 7733. Phra Non Cave, Mueang, Phatthalung, 7°40'53.0"N, 100°03'43.6"E: CUMZ 7734. Malai Cave, Mueang, Phatthalung, 7°38'07.9"N, 100°05'05.2"E: CUMZ 7805. Wang Thong Cave, Khuan Khanun, Phatthalung, 7°40'46.2"N, 100°00'49.9"E: CUMZ 7732. Tham Un Ya Ma Nee, Kong Ra, Phatthalung, 7°23'51.3"N, 99°58'36.1"E: CUMZ 7731. Khao Phaya Hong Cave, Kong Ra, Phatthalung, 7°27'48.7"N, 99°57'52.7"E: CUMZ 7814. Wat Tham Khao Chaison,

Khao Chaison, Phatthalung, 7°27'00.7"N, 100°07'52.4"E: CUMZ 7785, 7774, 7787. Kathu Waterfall, Kathu, Phuket, 7°56'04.0"N, 98°19'22.4"E: CUMZ 7761. Limestone outcrop in Sakhu, Thalang, Phuket, 8°05'25.1"N, 98°17'54.7"E: CUMZ 7803. Khao Jung Lone Cave, Rattaphum, Songkhla, 7°11'25.8"N, 100°16'59.9"E: CUMZ 7771. Wat Charoen Phupha, Rattaphum, Songkhla, 7°08'51.1"N, 100°15'36.7"E: CUMZ 7810. Nang Phraya Laed Kaw Bureau of Monks, Sadao, Songkhla, 6°44'29.2"N, 100°15'28.6"E: CUMZ 7772.

Diagnosis. Shell large, depressed to globosely depressed and well-rounded body whorl. Animal with pale to dark grey body with five mantle lobes. Genitalia with a short straight epiphallic caecum. Inner penial sculpture with reticulated pilasters in proximal part and irregular surface folds arranged in oblique row at distal end. Spermatophore with irregularly acute-serrate longitudinal ridges on the head filament, tail filament with three spines, more than ca. half of its length with series of branching spines.

Description. Shell. Shell depressed to globosely depressed, large size (shell width up to 26.6 mm, shell height up to 15.2 mm), and rather thin. Shell surface smooth, polished; shell colour pale warm brown to medium brown. Whorls 6–7, increasing regularly; body whorl large and well rounded. Spire moderately to very much elevated; suture impressed. Aperture crescent-shaped and obliquely opened. Peristome simple. Columellar margin simple and slightly reflected near umbilicus. Umbilicus narrowly opened (Fig. 21A–D).

Genital organs. Atrium short. Penis cylindrical with thin penial sheath covering proximal penis. Inner sculpture of penis divided into three parts; proximally approximately one-third of penial chamber with very finely longitudinal penial pilasters to nearly smooth surface; middle approximately one-third of chamber covered with reticulated pilasters; distally approximately one-third pilaster transformed to irregular surface folds arranged in oblique row. Epiphallus cylindrical, approximately as long as penis and narrower penis. Epiphallic caecum short, straight, diameter slightly larger than epiphallus, and located near middle of epiphallus. Penial retractor muscle thin and attached at tip of epiphallic caecum. Flagellum long slender, approximately as long as epiphallus. Vas deferens thin tube connecting distal epiphallus and free oviduct (Fig. 22A, B).

Vagina cylindrical tube, approximately two-third of penis length. Dart apparatus large, long, cylindrical, and located on atrium at vagina and penis junction. Gametolytic sac bulbous; gametolytic duct long and cylindrical. Free oviduct cylindrical, almost as long as vagina and proximal end encircled with thick tissue (Fig. 22A).

Spermatophore long and needle-shaped. Sperm sac enlarged and elongate-oval. Head filament gourd shape with irregularly acute-serrate longitudinal ridges. Tail filament very long tube; region near sperm sac with three spines. Spine I simple, little curved, and short. Spine II large and long, branching into many spinules near the tip. Spine II almost the same size as spine I, with complicated branching into small spinules. Region furthest away smooth and without spine; terminal part (more than ca. half of its length) with series of long branching spines arranged in a row, and then transformed very long serrate-like spines arranged in opposite rows near the tail filament tip (Fig. 23).

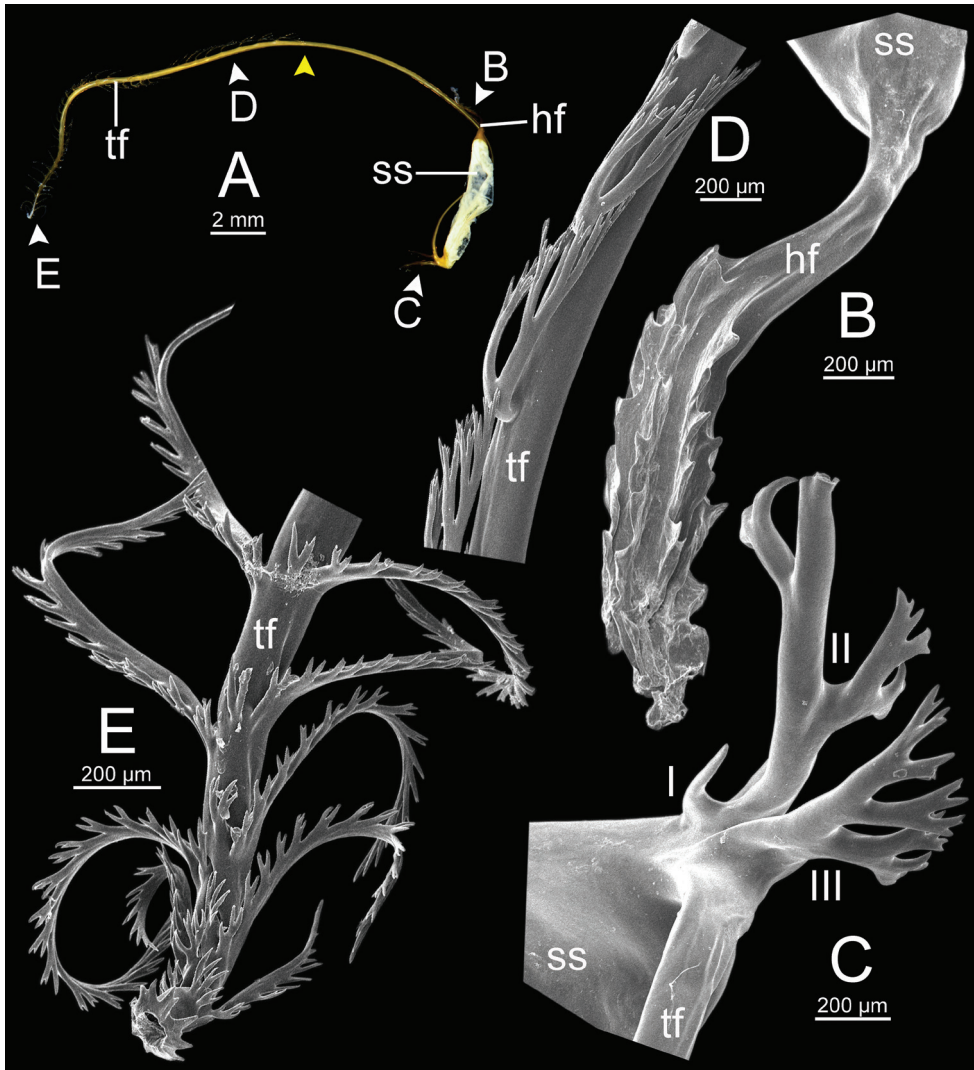


Figure 23. Spermatophore of *Sarika kawtaoensis* specimen CUMZ 7236 **A** general view of spermatophore **B** head filament **C–E** tail filament showing **C** three spines located close to the sperm sac **D** region with and without branching spines and **E** branching spines on the tip region. Yellow arrowhead indicates the end of the spines from the tip.

Radula. Teeth with half row formula: 1–(13–14)–54. Central tooth symmetrical tricuspid; lateral teeth asymmetrical tricuspid; marginal teeth elongate bicuspid. Marginal teeth starting at ca. row number 13 or 14 (Fig. 31A).

External features. Animal with reticulated skin and pale to dark grey body, pale grey foot sole, and dark grey caudal horn. Mantle edge well developed and same colour as body (Fig. 10B).

Distribution. *Sarika kawtaoensis* is widely distributed throughout southern Thailand and occurs in both natural and populated community areas (Fig. 8).

COI analysis. The ML and BI analyses of *S. kawtaoensis* revealed that the five individuals formed a monophyletic group with strong support (Fig. 1; BS = 91%, PP = 1), sister to *S. limbata* + *S. lactospira* sp. nov. yet only with BI support (Fig. 1; PP = 0.98). The mean intraspecific genetic distance of *S. kawtaoensis* was 3.3% (Table 2).

Remarks. *Sarika kawtaoensis* is a variable species in terms of shell shape ranging from nearly flattened (Fig. 21D) to a low-conical spire (Fig. 21A). The reproductive organs in these two shell morphs are identical. In addition, the DNA phylogeny also revealed that these shell variations grouped together with strong support within the clade of *S. kawtaoensis* (Fig. 1).

***Sarika caligina* Pholyotha & Panha, sp. nov.**

<http://zoobank.org/3ADF3132-BB2F-40B6-B050-8469075BBD7B>

Figs 1, 6, 10C, 21E, F, 22C, D, 24, 31B

Type material. *Holotype* CUMZ 7259 (Fig. 21E, width 23.6 mm, height 11.5 mm). *Paratypes* CUMZ 7245 (17 shells and nine specimens preserved in ethanol; Fig. 21F, width 23.4 mm, height 11.9 mm) CUMZ 7246 (five shells and 15 specimens preserved in ethanol), CUMZ 7266 (eight shells), NHMUK 20200281 (two shells), SMF (two shells), ZRC.MOL.017026 (two shells).

Other material examined. **THAILAND-Central.** Wat Tham Mongkut, Phra Phutthabat, Saraburi, 14°40'40.6"N, 100°50'32.3"E: CUMZ 7260. Tham Rakhang-Tham Kin Non, Phra Phutthabat, Saraburi, 14°42'57.2"N, 100°47'50.3"E: CUMZ 7261. Wat Tham Osot, Muak Lek, Saraburi, 14°42'35.8"N, 101°07'02.5"E: CUMZ 7263. Wat Tham Rattana Buppha, Muak Lek, Saraburi, 14°41'35.3"N, 101°07'51.6"E: CUMZ 7264. Muak Lek Waterfall, Muak Lek, Saraburi, 14°43'17.3"N, 101°11'08.6"E: CUMZ 7265. Wat Tham Phrom Sawat, Phatthana Nikhom, Lopburi, 14°45'32.0"N, 100°56'22.4"E: CUMZ 7262.

Type locality. Limestone outcrop with small shrubs at Wat Tham Si Wilai, Chaloe Phra Kiat, Saraburi, Thailand, 14°42'43.9"N, 100°52'01.3"E.

Diagnosis. Shell large, depressed, and pale brown with well-rounded body whorl. Animal with blackish body and five mantle lobes. Genitalia with large, straight epiphallal caecum and triangular prism penial pilasters. Spermatophore: head filament with irregularly smooth longitudinal ridges; tail filament near sperm sac with three spines and terminal part of tail filament more than ca. half of its length with series of several branching spines.

Description. *Shell.* Shell depressed, large size (shell width up to 25.7 mm, shell height up to 12.3 mm), and thin. Surface smooth and polished; shell colour pale brown. Whorls 6–6½, increasing regularly; body whorl large and well rounded. Spire moderately elevated; suture impressed. Aperture crescent-shaped and obliquely opened. Peristome simple. Columellar margin simple and slightly reflected near umbilicus. Umbilicus narrowly opened (Fig. 21E, F).

Genital organs. Atrium short. Penis cylindrical with thin penial sheath covering proximal penis. Inner sculpture of penis proximally more than ca. two-third of penial chamber with very finely longitudinal penial pilasters to nearly smooth surface, and

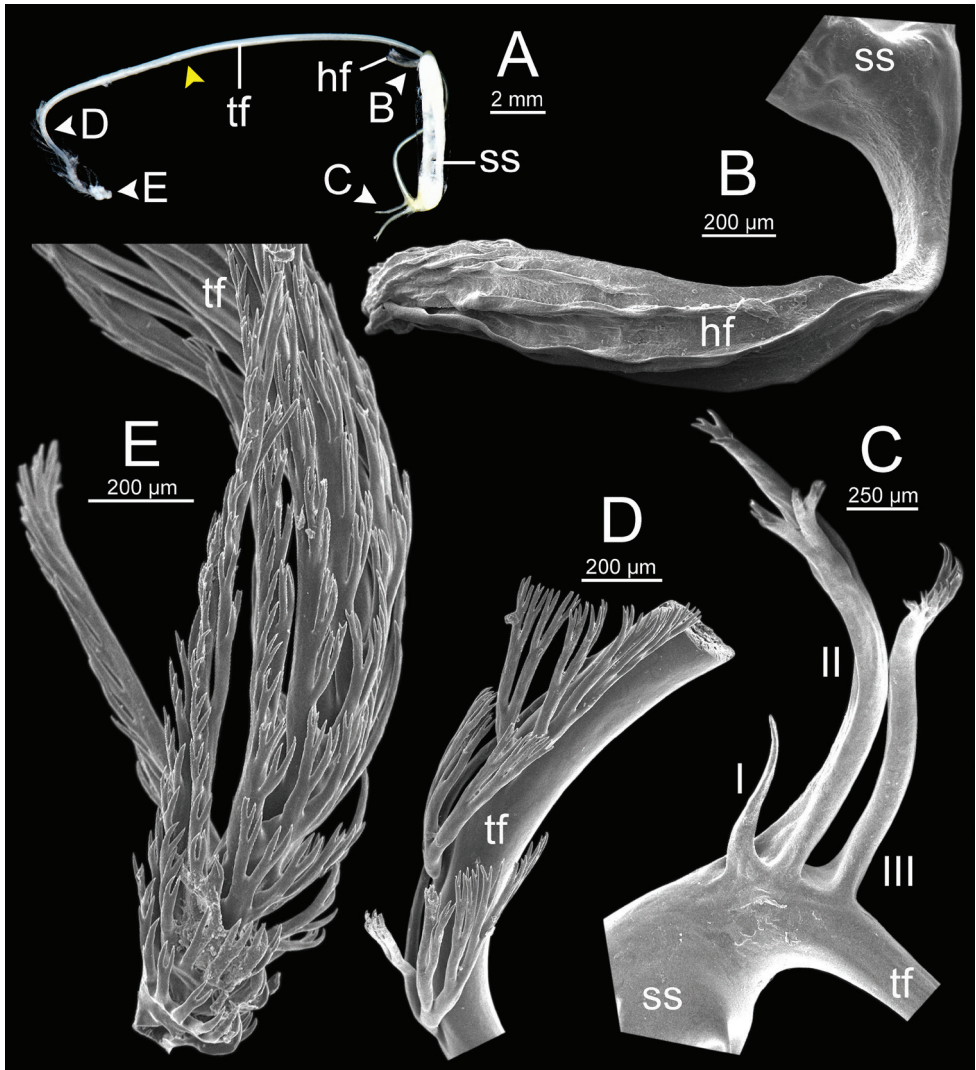


Figure 24. Spermatophore of *Sarika caligina* sp. nov. paratype CUMZ 7245 **A** general view of spermatophore **B** head filament **C–E** tail filament showing **C** three spines located close to the sperm sac **D** region with and without branching spines, and **E** branching spines on the tip region. Yellow arrowhead indicates the end of the spines from the tip.

then gradually modified from small to large rhomboid pilasters with acute angle on top (triangular prism). Epiphallus cylindrical, slightly longer than penis. Epiphallic caecum large, straight and located proximally far from middle of epiphallus. Penial retractor muscle thin and attached at tip of epiphallic caecum. Flagellum long, slender and slightly longer than epiphallus. Vas deferens thin tube connecting distal epiphallus and free oviduct (Fig. 22C, D).

Vagina cylindrical and approximately half of penis length. Dart apparatus large, long cylindrical, and located on atrium at vagina and penis junction. Gametolytic sac enlarged and bulbous; gametolytic duct enlarged and cylindrical (spermatophore inside). Free oviduct cylindrical, slightly shorter than total vagina length and proximal end encircled with thick tissue (Fig. 22C).

Spermatophore long and needle-shaped. Sperm sac enlarged and elongate-oval. Head filament gourd shape with irregularly smooth longitudinal ridges. Tail filament very long tube; region near sperm sac with three spines. Spine I simple, long, and slightly curved. Spine II large and long, branching into short spinules near the tip. Spine III shorter than spine II, branching into small and short spinules at the tip. Region furthest away smooth and without spine; terminal part (more than ca. half of its length) with series of short to long complicated branching spines arranged in a row or encircled the tail filament tip (Fig. 24).

Radula. Teeth with half row formula: 1–(22–23)–66. Central tooth symmetrical tricuspid; lateral teeth asymmetrical tricuspid; marginal teeth elongate bicuspid. Marginal teeth starting at approximately row number 22 or 23 (Fig. 31B).

External features. Animal with reticulated skin and very dark grey body. Foot sole and caudal foss present; caudal horn raised. Five mantle lobes well developed, same colour as body (Fig. 10C).

Etymology. The specific name *caligina* is from the Latin *caliginis* meaning mist, darkness and refers to the blackish colour of body, which characterises this species.

Distribution. *Sarika caligina* sp. nov. occurs in limestone habitats in central Thailand (Fig. 6). However, its habitats are threatened because many small karsts in this area have active quarries for the cement industry.

COI analysis. The ML and BI analyses revealed that the specimens of *S. caligina* sp. nov. ($n = 3$) formed a monophyletic group with very strong support (Fig. 1; BS = 100%, PP = 1). The mean intraspecific genetic distance of *S. caligina* sp. nov. was 1.1% (Table 2).

Remarks. This new species has a shell morphology that resembles *S. resplendens*, *S. heptagyra*, *S. limbata* and *S. kawtaoensis*. The distinguishing characters of this new species are its triangular prism-shaped penial pilasters, while *S. resplendens* and *S. heptagyra* have cuboidal penial pilasters, and *S. limbata* and *S. kawtaoensis* have reticulated penial pilasters. Moreover, *S. caligina* sp. nov. has irregularly smooth ridges on the head filament of the spermatophore, while *S. resplendens* has obtuse-serrate ridges, *S. limbata* has plate-like and acute-serrate ridges, and *S. kawtaoensis* has acute-serrate ridges. Unfortunately, the head filament of *S. heptagyra* was not available for comparison.

Although *S. caligina* sp. nov. and *S. obesior* have a similar penial sculpture, the two species can be distinguished by their spermatophores. *Sarika caligina* sp. nov. has irregularly smooth ridges on the head filament and approximately half of the tail filament contains branching spines, whereas *S. obesior* has obtuse-serrate ridges on the head filament and approximately one-third of the tail filament contains branching spines.

***Sarika lactospira* Pholyotha & Panha, sp. nov.**

<http://zoobank.org/FAD64134-9A20-4C07-8DA2-43A8E8A37EED>

Figs 1, 8, 10D, 25A, B, 26A, B, 31C

Type material. *Holotype* CUMZ 7286 (Fig. 25A, width 21.2 mm, height 10.0 mm). *Paratypes* CUMZ 7287 (28 shells and three specimens preserved in ethanol; Fig. 25B, width 20.5 mm, height 10.2 mm), NHMUK 20200282 (two shells), SMF (two shells), ZRC.MOL.017027 (two shells).

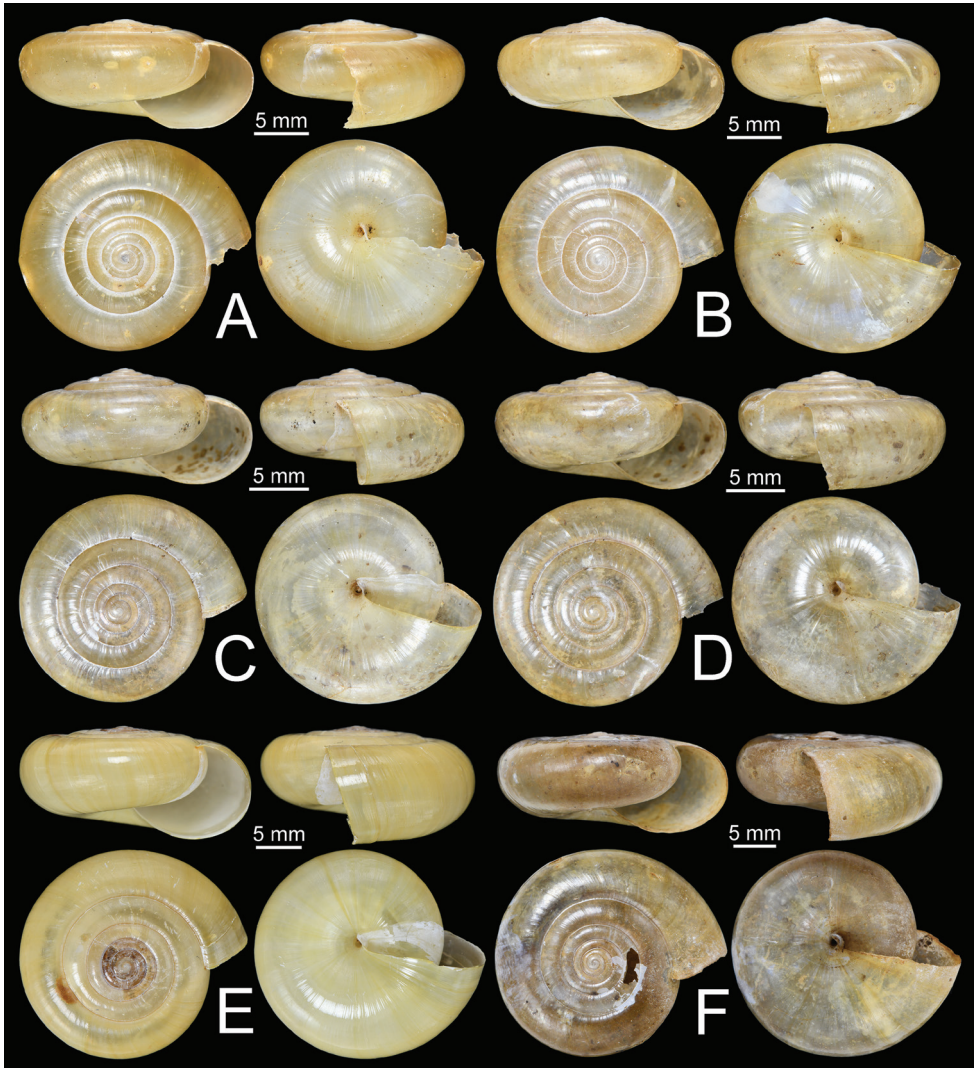


Figure 25. Shells of group I: *Sarika resplendens* group. **A, B** *Sarika lactospira* sp. nov. **A** holotype CUMZ 7286 and **B** paratype CUMZ 7287 **C, D** *S. megalogyne* sp. nov. **C** holotype CUMZ 7521 and **D** paratype CUMZ 7522 **E, F** *S. subheptagyra* sp. nov. **E** holotype CUMZ 7506 and **F** paratype CUMZ 7507.

Other material examined. THAILAND-Southern. Limestone outcrop in Don Sak, Don Sak, Surat Thani, 9°19'21.9"N, 99°44'38.2"E: CUMZ 7288, 7293. Khao Kloi Monastery, Don Sak, Surat Thani, 9°16'47.1"N, 99°44'11.7"E: CUMZ 7290. Limestone outcrop in Nang Kam Beach, Don Sak, Surat Thani, 9°18'54.0"N, 99°45'39.4"E: CUMZ 7294. Khiri Wong Cave, Don Sak, Surat Thani, 9°12'15.9"N, 99°39'45.0"E: CUMZ 7295. Wat Pra Puttabhat Sri Surattthani, Kanchanadit, Surat Thani, 9°11'17.2"N, 99°34'50.6"E: CUMZ 7292. Khao Phanom Wang Bureau of Monks, Kanchanadit, Surat Thani, 9°05'30.9"N, 99°36'19.0"E: CUMZ 7296. Limestone outcrop in Thong Thian, Khanom, Nakhon Si Thammarat, 9°13'27.2"N, 99°50'37.4"E: CUMZ 7289. Khao Krot Bureau of Monks, Khanom, Nakhon Si Thammarat, 9°14'22.5"N, 99°48'04.9"E: CUMZ 7291.

Type locality. Wat Ao Sadet, Khanom, Nakhon Si Thammarat, Thailand, 9°17'20.9"N, 99°47'13.8"E.

Diagnosis. Shell large, depressed, pale yellowish brown with slightly shouldered body whorl and pale milky subsutural band. Animal with grey body and five mantle lobes. Genitalia with a straight epiphallic caecum and triangular prism pilasters on inner penial sculpture.

Description. Shell. Shell depressed, large size (shell width up to 23.6 mm, shell height up to 11.8 mm) and thin. Surface smooth and shiny; shell colour pale yellowish brown. Whorls 6–6½, increasing regularly; body whorl large and slightly shouldered. Spire moderately elevated; suture impressed and with narrow pale milky to whitish subsutural band. Aperture crescent-shaped and obliquely opened. Peristome simple. Columellar margin simple and slightly reflected near umbilicus. Umbilicus narrowly opened (Fig. 25A, B).

Genital organs. Atrium short. Penis cylindrical with thin penial sheath covering proximal penis. Inner sculpture of penis proximally more than ca. half of penial chamber with small longitudinal penial pilasters, and then gradually transformed from small to large rhomboid pilasters with acute angle on top (triangular prism). Epiphallus cylindrical and slightly shorter than twice the penis length. Epiphallic caecum long, straight, similar diameter with epiphallus and located proximally near middle of epiphallus. Penial retractor muscle thin and attached at tip of epiphallic caecum. Flagellum slender, approximately half length of epiphallus. Vas deferens thin tube connecting distal epiphallus and free oviduct (Fig. 26A, B).

Vagina cylindrical and approximately half of penis length. Dart apparatus large, long cylindrical, and located on atrium at vagina and penis junction. Gametolytic sac enlarged and bulbous; gametolytic duct long and enlarged (damaged spermatophore inside). Free oviduct large cylindrical, approximately as long as vagina length, and proximal end encircled with thick tissue (Fig. 26A).

Radula. Teeth with half row formula: 1–(17–18)–64. Central tooth symmetrical tricuspid; lateral teeth asymmetrical tricuspid; marginal teeth elongate bicuspid. Marginal teeth starting at approximately row number 17 or 18 (Fig. 31C).

External features. Animal with reticulated skin and body darker grey above and paler grey near foot sole. Caudal foss and caudal horn present. Five mantle lobes well developed and pale grey colour (Fig. 10D).

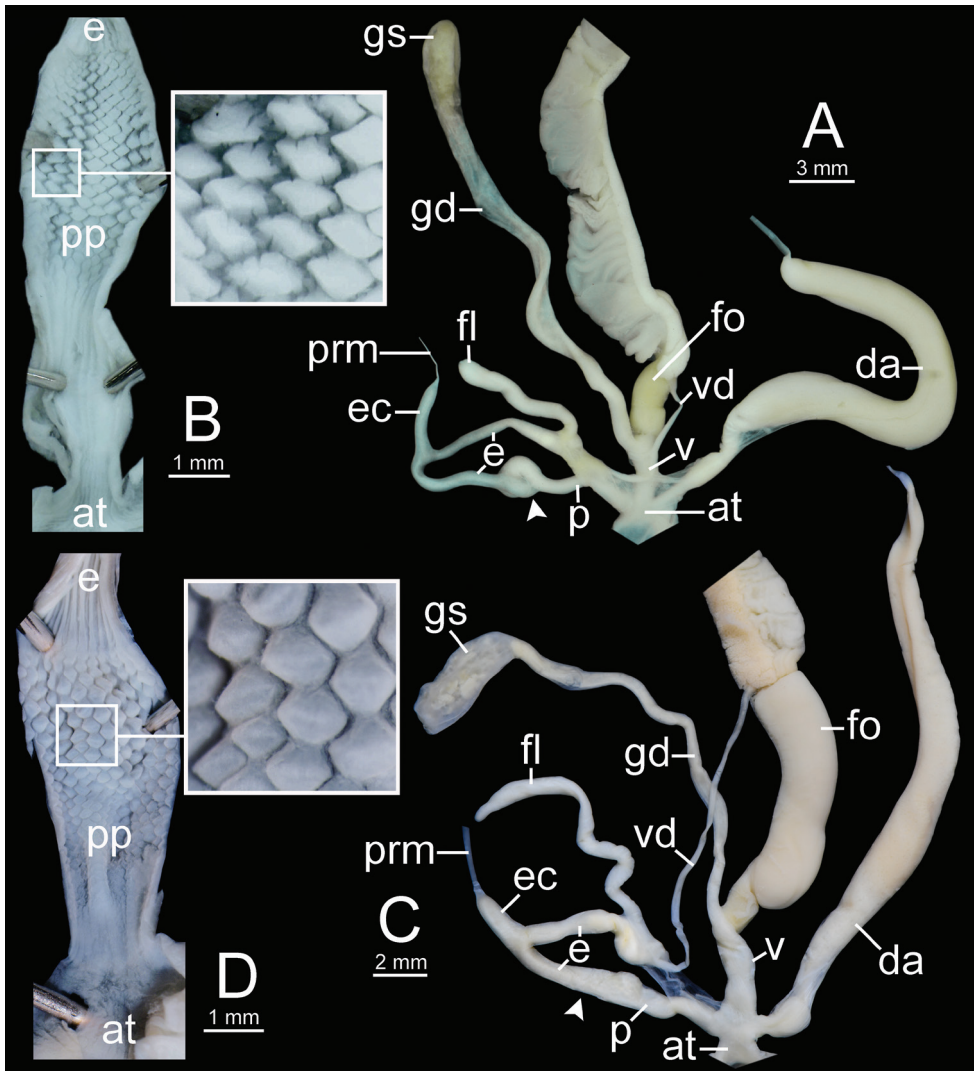


Figure 26. Genitalia. **A, B** *Sarika lactospira* sp. nov. specimen CUMZ 7291 **A** general view of genital system **B** internal structure of penis **C, D** *S. megalogyne* sp. nov. paratype CUMZ 7522 **C** general view of genital system **D** internal structure of penis. White arrowheads indicate the ends of the penes.

Etymology. The specific name *lactospira* is derived from the Latin words *lacteus* meaning milky and *spira* meaning coil. It refers to the pale milky colour below suture.

Distribution. *Sarika lactospira* sp. nov. is restricted to limestone habitats in Surat Thani and Nakhon Si Thammarat provinces (Fig. 8).

COI analysis. The ML and BI analyses revealed that the four individuals of *S. lactospira* sp. nov. formed a monophyletic group with very strong support (Fig. 1; BS = 100%, PP = 1). The mean intraspecific genetic distance of *S. lactospira* sp. nov. was 2.3% (Table 2).

Remarks. *Sarika lactospira* sp. nov. differs from all other species in the *Sarika resplendens* group by having a shouldered body whorl and usually with a narrow whitish subsutural band. In comparison the shell of *S. lactospira* sp. nov. has shouldered body whorl, while, *S. resplendens*, *S. obesior*, *S. limbata*, *S. kawtaoensis*, *S. caligina* sp. nov., and *S. subheptagyra* sp. nov. have a well-rounded body whorl, and *S. dohrniana* has a rounded to slightly obtusely angulated body whorl.

Compared among the shouldered body whorl species, the distinguishing character of *S. lactospira* sp. nov. is the triangular penial pilasters, while *S. heptagyra* has cuboidal penial pilasters.

Although *S. lactospira* sp. nov. and *S. megalogyne* sp. nov. have a similar shell and penial sculpture, the free oviduct and flagellum of *S. lactospira* sp. nov. are much shorter than those of *S. megalogyne* sp. nov. In addition, the COI sequence divergences between both species were rather high (7.1%). Unfortunately, the spermatophore of *S. lactospira* sp. nov. was not available for comparison.

***Sarika megalogyne* Pholyotha & Panha, sp. nov.**

<http://zoobank.org/EB3A8C40-4AFB-4A24-91A0-EFFA2DC4FCF5>

Figs 1, 7, 10E, 25C, D, 26C, D, 27, 31D

Type material. *Holotype* CUMZ 7521 (Fig. 25C, width 19.5 mm, height 9.8 mm).

Paratypes CUMZ 7522 (23 shells and 34 specimens preserved in ethanol; Fig. 25D, width 19.5 mm, height 10.0 mm), CUMZ 7238 (10 specimens preserved in ethanol), CUMZ 7529 (12 shells and 78 specimens preserved in ethanol), CUMZ 7530 (24 shells), CUMZ 7536 (16 specimens preserved in ethanol), CUMZ 7537 (three specimens preserved in ethanol), NHMUK 20200283 (two shells), SMF (two shells), ZRC.MOL.017028 (two shells).

Other material examined. **THAILAND-Western.** Khao Pho Cave, Bang Saphan Noi, Prachuap Khiri Khan, 10°59'25.2"N, 99°21'32.8"E: CUMZ 7540. **THAILAND-Southern.** Pla Cave, Thung Tako, Chumphon, 10°07'58.4"N, 99°08'14.5"E: CUMZ 7523. Tham Sing, Mueang, Chumphon, 10°25'45.9"N, 99°03'11.3"E: CUMZ 7527. Wat Bonphot Phisai, Lang Suan, Chumphon, 9°56'23.8"N, 99°08'51.4"E: CUMZ 7528. Tham Pisadan Bureau of Monks, Tha Sae, Chumphon, 10°45'36.7"N, 99°13'45.8"E: CUMZ 7538. Limestone outcrop in Saphli, Pathio, Chumphon, 10°33'12.0"N, 99°16'34.5"E: CUMZ 7524, 7532. Malagor Cave, Pathio, Chumphon, 10°52'42.9"N, 99°30'30.3"E: CUMZ 7525. Nang Thong Cave, Pathio, Chumphon, 10°40'14.3"N, 99°17'35.9"E: CUMZ 7526. Wat Tham Khao Plu, Pathio, Chumphon, 10°43'49.6"N, 99°19'19.7"E: CUMZ 7539. Wat Tham Khao Bang Siap, Pathio, Chumphon, 10°40'06.7"N, 99°17'37.9"E: CUMZ 7534. Ko Wiang, Pathio, Chumphon, 10°50'43.3"N, 99°28'46.5"E: CUMZ 7909. Cholkhiri Bureau of Monks, Sawi, Chumphon, 10°22'23.9"N, 99°03'38.1"E: CUMZ 7531. Limestone outcrop in Sawi, Sawi, Chumphon, 10°15'16.9"N, 99°10'01.2"E: CUMZ 7533. Wat Tham Khao Lan, Sawi, Chumphon, 10°15'47.0"N, 99°10'28.1"E: CUMZ 7535.

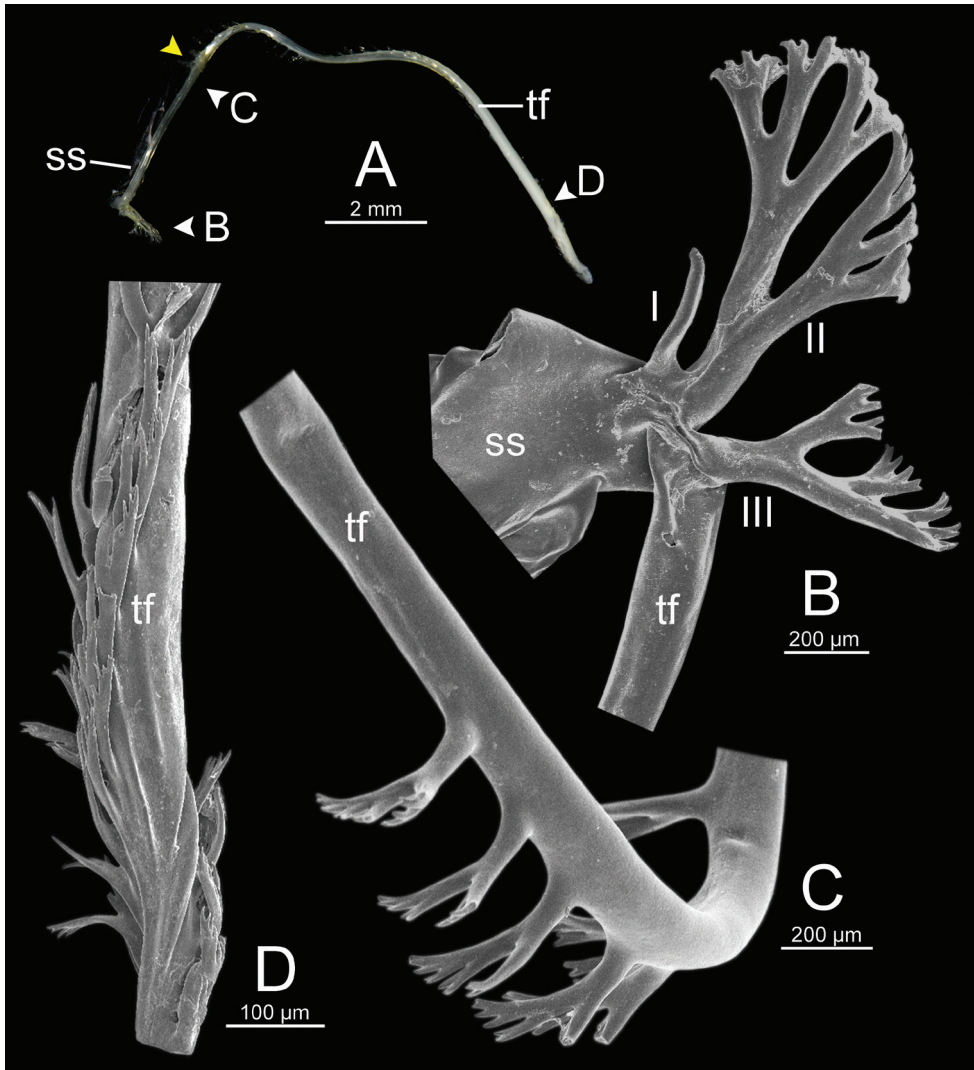


Figure 27. Spermatophore of *Sarika megalogyne* sp. nov. paratype CUMZ 7522 **A** general view of the spermatophore and **B–D** tail filament showing **B** three spines located close to the sperm sac **C** region with and without branching spines, and **D** branching spines on the tip region. Yellow arrowheads indicate the end of the spines from the tip.

Type locality. Limestone outcrop at Khao Ma Rong Cave, Bang Saphan, Prachuap Khiri Khan, Thailand, 11°12'09.2"N, 99°29'48.7"E.

Diagnosis. Shell medium to large, depressed and very pale brown with well-rounded to slightly shouldered body whorl. Animal with grey body and five mantle lobes. Genitalia with a straight epiphallic caecum, very large free oviduct and triangular prism-shaped pilasters on inner penial sculpture. Spermatophore: tail filament near sperm sac with three spines and terminal part more than ca. three-quarters of its length with series of several branching spines.

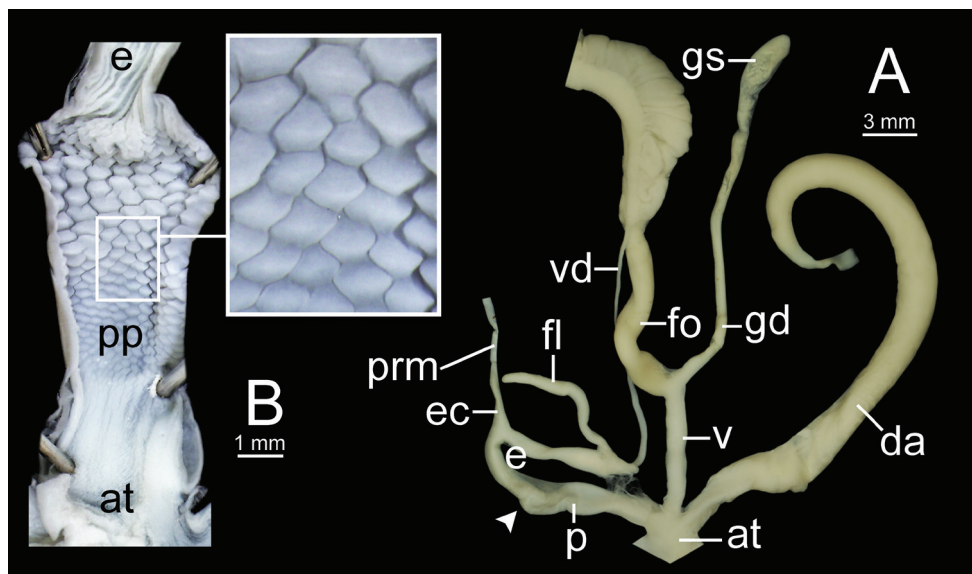


Figure 28. Genitalia. **A, B** *Sarika subheptagyra* sp. nov. paratype CUMZ 7507 **A** general view of the genital system and **B** internal structure of the penis. White arrowhead indicate the end of the penis.

Description. Shell. Shell depressed, medium to large size (shell width up to 21.2 mm, shell height up to 11.3 mm), and thin. Surface smooth and glossy; shell colour very pale brown. Whorls 6–6½, increasing regularly; body whorl slightly well rounded to slightly shouldered. Spire moderately to very much elevated; suture impressed. Aperture crescent-shaped and obliquely opened. Peristome simple. Columellar margin simple and slightly reflected near umbilicus. Umbilicus narrowly opened (Fig. 25C, D).

Genital organs. Atrium short. Penis cylindrical with thin penial sheath covering proximal penis. Inner sculpture of penis proximally more than ca. one-third of penial chamber with very finely longitudinal penial pilasters to nearly smooth surface, and then gradually modified from small to large rhomboid pilasters with acute angle on top (triangular prism). Epiphallus cylindrical, slightly longer than penis length. Epiphallic caecum large, straight, diameter slightly larger than epiphallus, and located proximally near middle of epiphallus. Penial retractor muscle thin and attached at tip of epiphallic caecum. Flagellum long slender and slightly longer than epiphallus. Vas deferens thin tube connecting distal epiphallus and free oviduct (Fig. 26C, D).

Vagina cylindrical, enlarged and slightly shorter than penis. Dart apparatus large, long cylindrical, and located on atrium at vagina and penis junction. Gametolytic sac enlarged and bulbous; gametolytic duct long and cylindrical. Free oviduct enlarged cylindrical, extremely long, approximately three times of vagina length (Fig. 26C).

Spermatophore long and needle-shaped. Sperm sac and head filament were missing. Tail filament long tube; region near sperm sac with three spines. Spine I simple and short. Spine II large, long, and with complicated branching spines into spinules near the tip. Spine III smaller than spine II and with complicated branching spines into spinules. Region furthest away smooth and without spine; terminal part (approximately

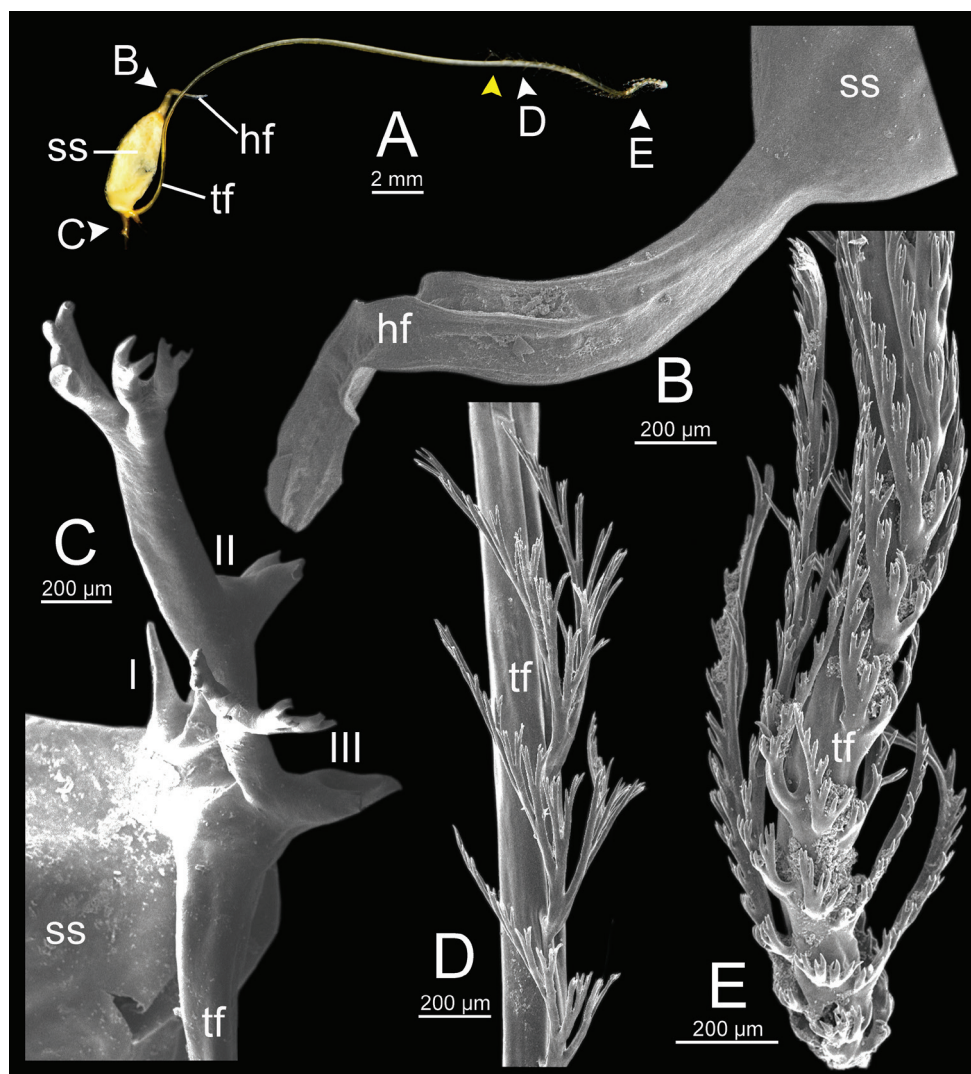


Figure 29. Spermatophore of *Sarika subheptagyra* sp. nov. paratype CUMZ 7507 **A** general view of spermatophore **B** head filament, and **C–E** tail filament showing **C** three spines located close to the sperm sac **D** region with and without branching spines, and **E** branching spines on the tip region. Yellow arrowhead indicates the ends of the spines from the tip.

three-quarters of its length) with series of long complicated branching spines into spinules arranged in a row, and then transformed to very long serrate-like spines arranged in opposite rows near the tail filament tip (Fig. 27).

Radula. Teeth with half row formula: 1–(13–14)–55. Central tooth symmetrical tricuspid; lateral teeth asymmetrical tricuspid; marginal teeth elongate bicuspid. Marginal teeth starting at approximately row number 13 or 14 (Fig. 31D).

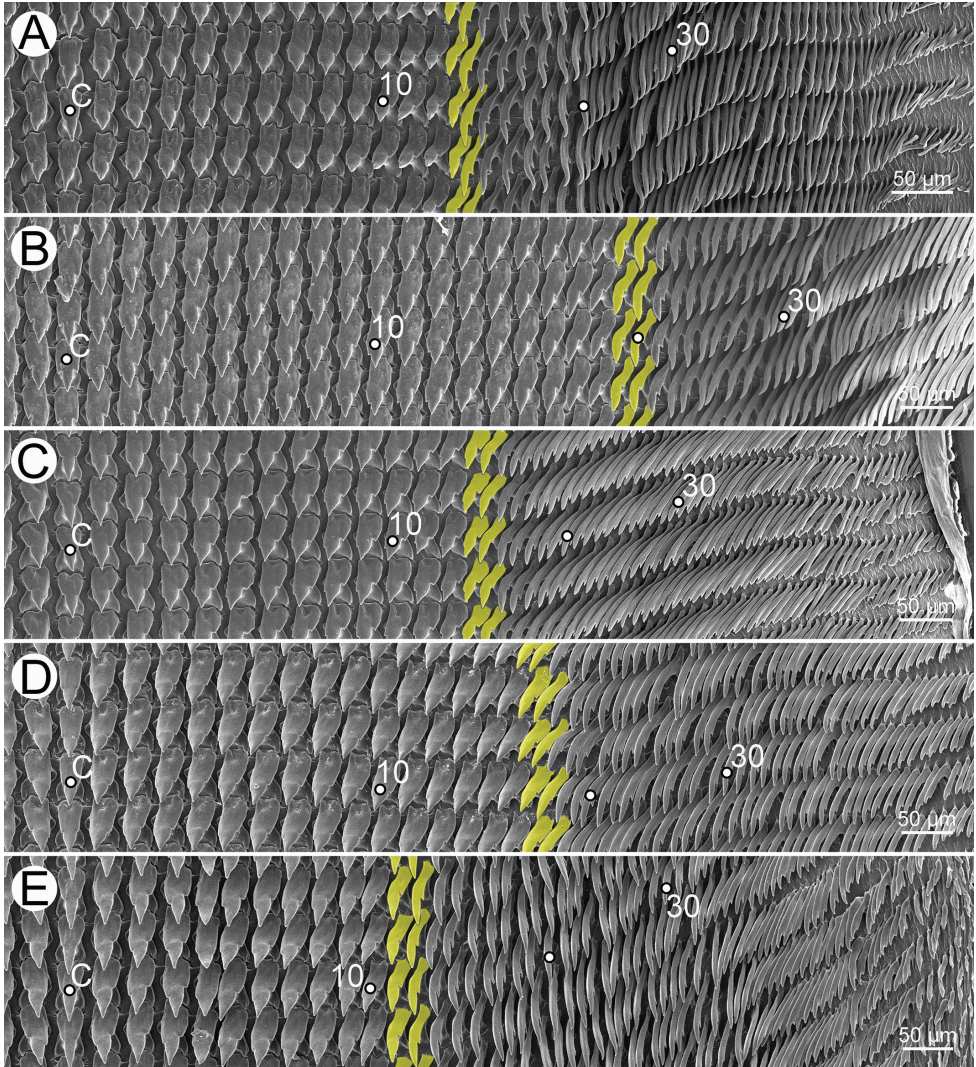


Figure 30. Representative SEM images of the radula. **A** *Sarika resplendens* specimen CUMZ 7851 **B** *S. dohrniana* specimen CUMZ 7633 **C** *S. obesior* specimen CUMZ 7673 **D** *S. limbata* specimen CUMZ 7652 **E** *S. heptagyra* specimen CUMZ 7279. Central tooth indicated by 'C'; yellow colour indicates lateral teeth in the transition to marginal teeth.

External features. Animal with reticulated skin and body darker grey above and paler grey near foot sole. Caudal foss and caudal horn present. Five mantle lobes well developed and pale grey in colour (Fig. 10E).

Etymology. The specific name *megalogyne* is derived from the Greek word *megale* meaning large and the Greek *gyne* meaning female. It refers to the female part of genital organs with a very large free oviduct, which characterises this species.

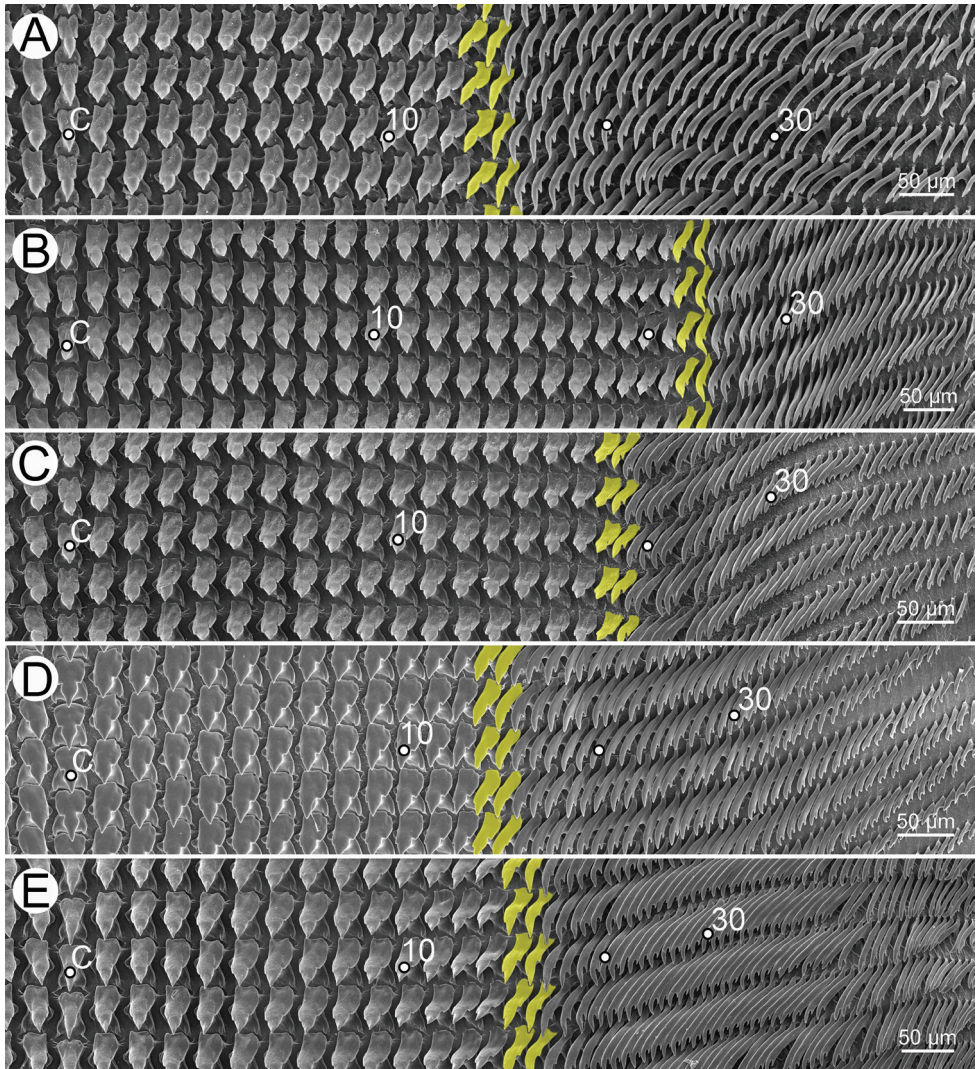


Figure 3 I. Representative SEM images of the radula. **A** *Sarika kawtaoensis* specimen CUMZ **B** *S. caligina* sp. nov. paratype CUMZ 7245 **C** *S. lactospira* sp. nov. specimen CUMZ 7291 **D** *S. megalogyne* sp. nov. specimen CUMZ 7531, and **E** *S. subheptagyra* sp. nov. paratype CUMZ 7507. Central tooth indicated by 'C'; yellow colour indicates lateral teeth in the transition to marginal teeth.

Distribution. *Sarika megalogyne* sp. nov. is common in Prachuap Khiri Khan and Chumphon provinces (Fig. 7). This species is often found under leaves of small trees and shrubs on limestones.

COI analysis. The ML and BI analyses of *S. megalogyne* sp. nov. revealed that all samples ($n = 3$) formed a clade with very strong support (Fig. 1; BS = 100%, PP = 1). The mean intraspecific genetic distance of *S. megalogyne* sp. nov. was 1.4% (Table 2).

Remarks. *Sarika megalogyne* sp. nov. and *S. caligina* sp. nov. have similar genitalia and penial sculpture. However, *S. megalogyne* sp. nov. has a much longer free oviduct

and flagellum than *S. caligina* sp. nov. In addition, the spermatophore of *S. megalogyne* sp. nov. with more than ca. three-quarters of the tail filament contains branching spines, whereas the spermatophore of *S. caligina* sp. nov. with more than ca. only half of the tail filament contains branching spines. Furthermore, the genetic distance between these two species is high (7.4%).

***Sarika subheptagyra* Pholyotha & Panha, sp. nov.**

<http://zoobank.org/9D3F1C60-3FDC-4950-AE84-AAE1B12863CE>

Figs 1, 6, 10F, 25E, F, 28, 29, 31E

Type material. *Holotype* CUMZ 7506 (Fig. 25E, width 25.5 mm, height 12.5 mm).

Paratypes CUMZ 7507 (four shells and six specimens preserved in ethanol; Fig. 25F, width 26.4 mm, height 12.0 mm), CUMZ 7514 (11 specimens preserved in ethanol), NHMUK 20200284 (two shells).

Other material examined. **THAILAND-Central.** Tham Khao Wong, Ban Rai, Uthai Thani, 15°01'53.4"N, 99°27'21.1"E: CUMZ 7508. Khao Chong Lom, Ban Rai, Uthai Thani, 15°16'51.6"N, 99°43'08.4"E: CUMZ 7509. Wat Khao Chueak Charoen Tham, Ban Rai, Uthai Thani, 15°16'17.2"N, 99°41'43.6"E: CUMZ 7515. Hup Pa Tat, Lan Sak, Uthai Thani, 15°22'33.8"N, 99°37'49.5"E: CUMZ 7510, 7511, 7512, 7513. Wat Thep Muang Thong, Lan Sak, Uthai Thani, 15°24'59.5"N, 99°35'36.6"E: CUMZ 7516.

Type locality. Tham Namthip Bureau of Monks, Lan Sak, Uthai Thani, Thailand, 15°25'57.5"N, 99°35'19.6"E.

Diagnosis. Shell large, strongly depressed and pale yellowish brown to pale brown with very rounded body whorl. Animal with grey body and five mantle lobes. Genitalia with a straight epiphallic caecum and triangular prism pilasters on inner penial sculpture. Spermatophore: head filament with irregularly smooth longitudinal ridges; tail filament near sperm sac with three spines and terminal part of tail filament more than more than ca. one-fourth of its length with series of branching spines.

Description. *Shell.* Shell strongly depressed, large size (shell width up to 26.4 mm, shell height up to 12.4 mm), and thin. Surface smooth and glossy; shell colour pale yellowish brown to pale brown. Whorls 6–6½, increasing regularly; body whorl large and well rounded. Spire slightly elevated; suture impressed. Aperture crescent-shaped and opening obliquely. Peristome simple. Columellar margin simple and slightly reflected near umbilicus. Umbilicus narrowly opened (Fig. 25E, F).

Genital organs. Atrium short. Penis cylindrical with thin penial sheath covering proximal penis. Inner sculpture of penis proximally more than ca. one-third of penial chamber with very finely longitudinal penial pilasters to nearly smooth surface, and then gradually transformed from small to large rhomboid with acute angle on top (triangular prism). Epiphallus cylindrical, long and approximately one and half times as long as penis. Epiphallic caecum short, straight, and located proximally near middle of epiphallus, penial retractor muscle thin and attached at tip of epiphallic caecum. Flagellum long and slender, approximately as long as penis. Vas deferens thin tube connecting distal epiphallus and free oviduct (Fig. 28).

Vagina cylindrical and approximately as long as penis. Dart apparatus large, long cylindrical, located on atrium at vagina and penis junction. Gametolytic sac enlarged and bulbous; gametolytic duct long, cylindrical. Free oviduct cylindrical, longer than vagina and proximal end encircled with thick tissue (Fig. 28A).

Spermatophore long and needle-shaped. Sperm sac enlarged and elongate-oval. Head filament gourd shape with irregularly smooth longitudinal ridges. Tail filament very long tube; region near sperm sac with three spines. Spine I simple and rather short. Spine II large and long and branching into very small spinules. Spine III relatively smaller than spine II and branching into very small spinules. Region furthest away smooth and without spine; terminal part (more than ca. one-fourth of its length) with series of long branching spines into spinules arranged in a row, and then transformed to very long serrate-like spines arranged in opposite rows near the tail filament tip (Fig. 29).

Radula. Teeth with half row formula: 1–(14–15)–68. Central tooth symmetrical tricuspid; lateral teeth asymmetrical tricuspid; marginal teeth elongate bicuspid. Marginal teeth starting at approximately row number 14 or 15 (Fig. 31E).

External features. Animal with reticulated skin and pale to dark grey body. Foot sole and caudal foss present; caudal horn raised. Five mantle lobes well developed and same colour as body (Fig. 10F).

Etymology. The specific name *subheptagyra* is derived from the Latin word *sub* meaning under, from, somewhat, and less than, and the word *heptagyra* referring to shell similar to *S. heptagyra*.

Distribution. This species occurs only in Uthai Thani Province and is restricted to limestone habitats (Fig. 6).

COI analysis. The ML and BI analyses indicated that the samples of *S. subheptagyra* sp. nov. (n = 3) formed a monophyletic group with good support (Fig. 1; BS = 90%, PP = 1). The mean intraspecific genetic distance of *S. subheptagyra* sp. nov. was 2.4% (Table 2).

Remarks. *Sarika subheptagyra* sp. nov. differs from *S. heptagyra* in having longer vagina and free oviduct, and triangular prism-shaped penial pilasters, while *S. heptagyra* have cuboidal penial pilasters. Moreover, the COI sequence divergences between them is high (7.9%).

Compared with *S. resplendens*, *S. subheptagyra* sp. nov. has a longer vagina and free oviduct, thin penial retractor muscle, and triangular prism-shaped penial pilasters. *Sarika resplendens* has a shorter vagina and free oviduct, a very large and thickened penial retractor muscle, and cuboidal-shaped penial pilasters. Additionally, the genetic distance between both species is fairly high (6.5%).

Sarika subheptagyra sp. nov. differs from *S. caligina* sp. nov. in having a lower spire, longer vagina, and free oviduct, and spine II and spine III on spermatophore start branching near the base, while *S. caligina* sp. nov. has a higher spire, shorter vagina and free oviduct, and spine II and spine III on spermatophore start branching near the tip. In addition, the genetic distance between these two new species is high (8.2%).

Group II: *Sarika hainesi* group: species without left shell lobe and without penial verge or pseudo-verge

***Sarika hainesi* (Pfeiffer, 1856)**

Figs 1, 32, 33B, 34A–C, 35A, B, 36, 43A

Helix hainesi Pfeiffer, 1856a: 32. Type locality: “Siam” [Thailand]; Pfeiffer 1856b: 75, 76, pl. 21, figs 1–3.

Nanina (Orobia) hainesi: Martens 1867: 73; Pfeiffer 1868: 122.

Nanina (Macrochlamys) hainesi: Tryon 1886: 96, pl. 32, figs 36–38; Fischer and Dautzenberg 1904: 395.

Ariophanta (Macrochlamys) hainesi: Fischer 1891: 20.

Macrochlamys hainesi: Saurin 1953: 113.

Sarika hainesii [sic]: Hemmen and Hemmen 2001: 45.

Sarika hainesi: Inkhavilay et al. 2019: 82, fig. 38f.

Type material. *Syntype* NHMUK ex. Cuming collection: 20200290 (three shells; Fig. 34A) from Siam [Thailand].

Other material examined. **THAILAND-Northeastern.** Wat Tham Khao Wong, Pak Chong, Nakhon Ratchasima, 14°35'15.5"N, 101°20'33.5"E: CUMZ 7273. Wat Tham Thep Nimit, Pak Chong, Nakhon Ratchasima, 14°34'18.7"N, 101°33'38.5"E: CUMZ 7268. Wat Tham Thian Chai Chonprathan, Pak Chong, Nakhon Ratchasima, 14°36'58.5"N, 101°18'35.3"E: CUMZ 7270. Wat Thep Phithak Punnaram, Pak Chong, Nakhon Ratchasima, 14°36'58.5"N, 101°15'55.9"E: CUMZ 7271. Lam Phra Phloeng area, Pak Thong Chai, Nakhon Ratchasima, 14°35'44.0"N, 101°50'07.4"E: CUMZ 7274. Wat Tham Praput, Pak Chong, Nakhon Ratchasima, 14°35'37.5"N, 101°40'17.8"E: CUMZ 7269. **THAILAND-Eastern.** Pang Sida Waterfall, Watthana Nakhon, Sa Kaeo, 13°59'36.4"N, 102°12'21.2"E: CUMZ 7237 (Fig. 34B, C), 7267. **THAILAND-Central.** Ched Khot Waterfall, Kaeng Khoi, Saraburi, 14°28'22.3"N, 101°10'01.7"E: CUMZ 7272.

Diagnosis. Shell large, depressed, obtusely angulated body whorl. Animal with pale grey body and four mantle lobes. Genitalia with a large and straight epiphallic caecum, and a triangular prism shape of penial pilasters. Spermatophore with irregularly obtuse-serrate longitudinal ridges with numerous pores on the head filament, tail filament with two spines and more than ca. half of its length with series of long branching spines.

Description. *Shell.* Shell depressed, large size (shell width up to 28.1 mm, shell height up to 14.9 mm) and rather thin. Shell surface smooth and polished; shell colour pale yellowish brown to pale brown. Whorls 6–7, size increasing regularly; body whorl large and obtusely angled. Spire moderately elevated; suture impressed. Aperture crescent-shaped and obliquely opened. Peristome simple. Columellar margin simple and slightly reflected near umbilicus. Umbilicus narrowly opened (Fig. 34A–C).

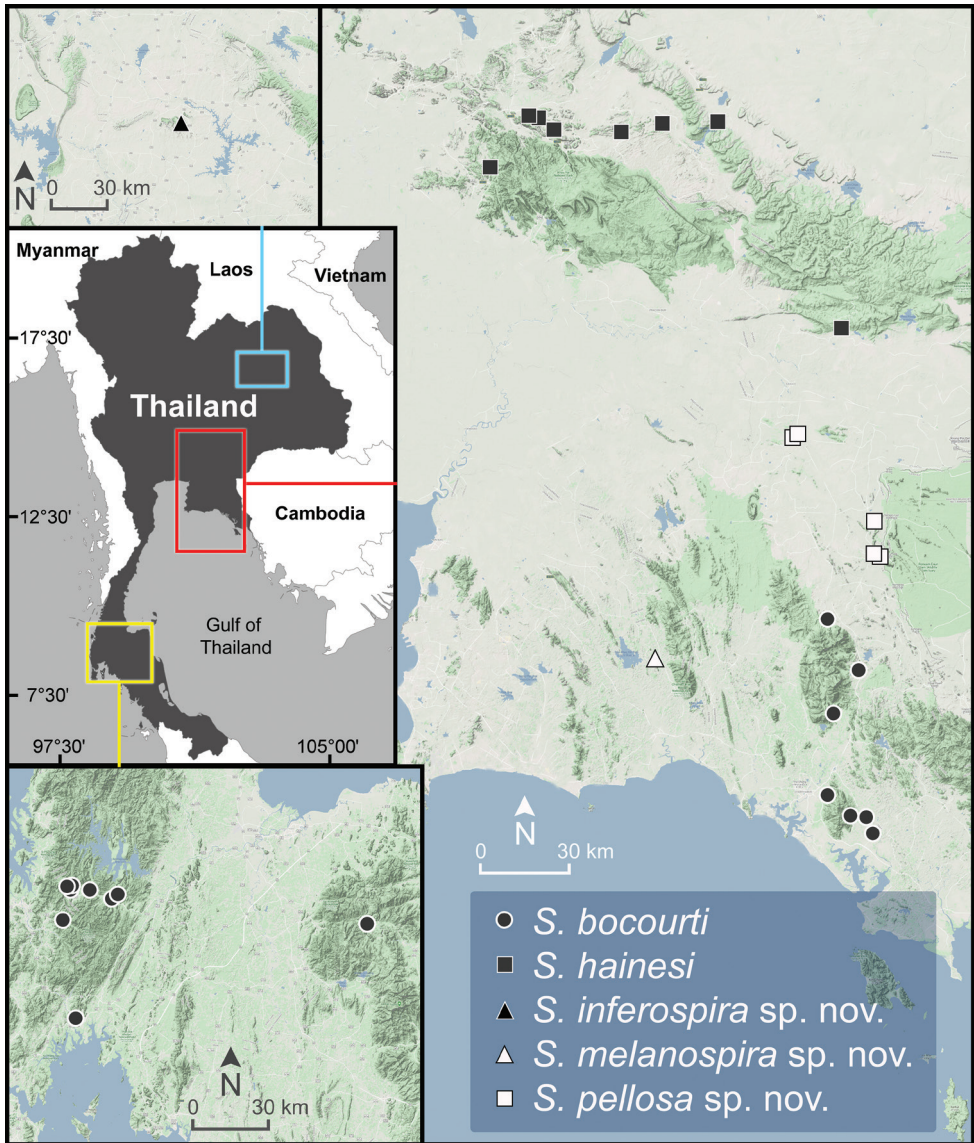


Figure 32. Geographic distribution of *Sarika bocourti*, *S. hainesi*, *S. inferospira* sp. nov., *S. melanospira* sp. nov. and *S. pellosa* sp. nov. based on examined specimens herein.

Genital organs. Atrium short. Penis cylindrical with thin penial sheath covering proximal penis. Inner sculpture of penis proximally more than ca. half of penial chamber with very finely longitudinal penial pilasters to nearly smooth surface, and then gradually transformed from small to large rhomboid pilasters with acute angle on top (triangular prism). Epiphallus cylindrical, approximately one and half times total penis length, and narrower than penis. Epiphallic caecum short, straight, same diameter as proximal epiphallus, and located near middle of epiphallus. Penial retractor muscle thin

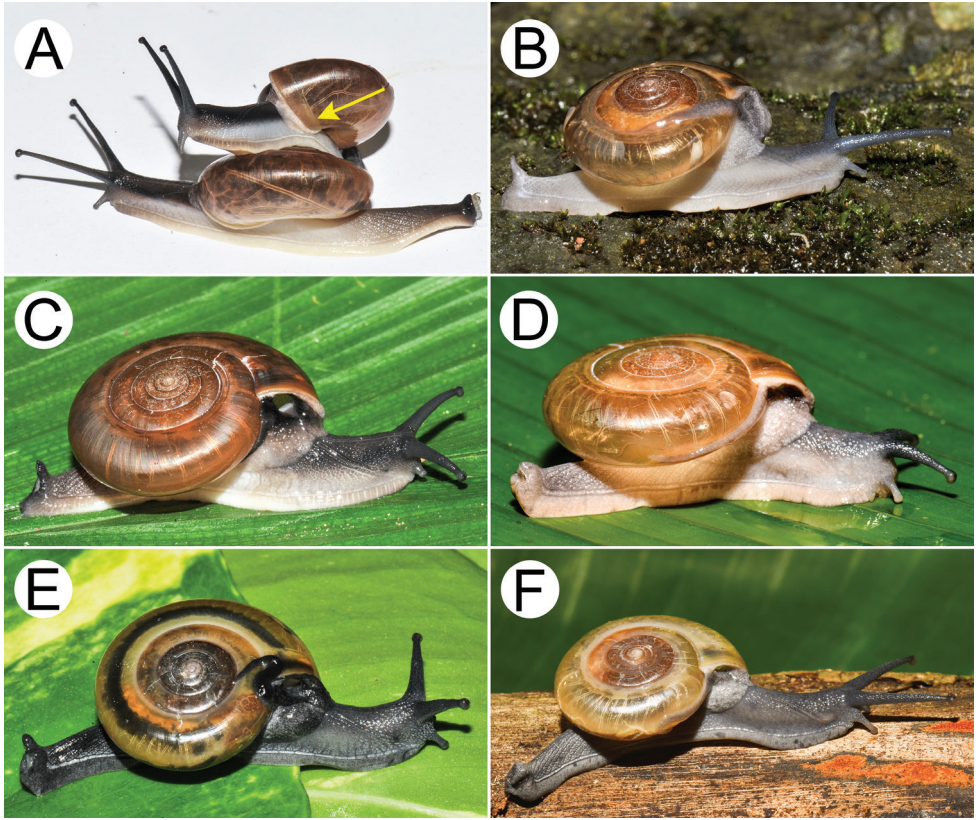


Figure 33. Living snails of group II: *Sarika hainesi* group. **A** *Sarika bocourti* specimen CUMZ 7591 showing no left shell lobe (yellow arrow) **B** *S. hainesi* specimen CUMZ 7237 **C** *S. bocourti* specimen CUMZ 7591 **D** *S. inferospira* sp. nov. specimen CUMZ 7257 **E** *S. melanospira* sp. nov. paratype CUMZ 7243, and **F** *S. pellosa* sp. nov. paratype CUMZ 7517. Not to scale.

and attached at tip of epiphallic caecum. Flagellum long slender and almost as long as penis. Vas deferens thin tube connecting distal epiphallus and free oviduct (Fig. 35A, B).

Vagina cylindrical and slightly shorter than penis. Dart apparatus enlarged, long cylindrical and located on atrium at vagina and penis junction. Gametolytic sac enlarged and bulbous (with spermatophore inside); gametolytic duct long and cylindrical. Free oviduct cylindrical, approximately as long as vagina, and proximal end encircled with thick tissue (Fig. 35A).

Spermatophore long and needle-shaped. Sperm sac enlarged and elongate-oval. Head filament gourd shape and irregularly obtuse-serrate longitudinal ridges with numerous pores (sponge-like). Tail filament very long tube; region near sperm sac with two spines. Spine I located on same base with spine II, short and simple. Spine II large, long and very complicated branching into many spinules. Region furthest away smooth and without spine; terminal part (more than ca. half of its length) with series of long branching spines arranged in an arrow or encircled tail filament tip (Fig. 36).

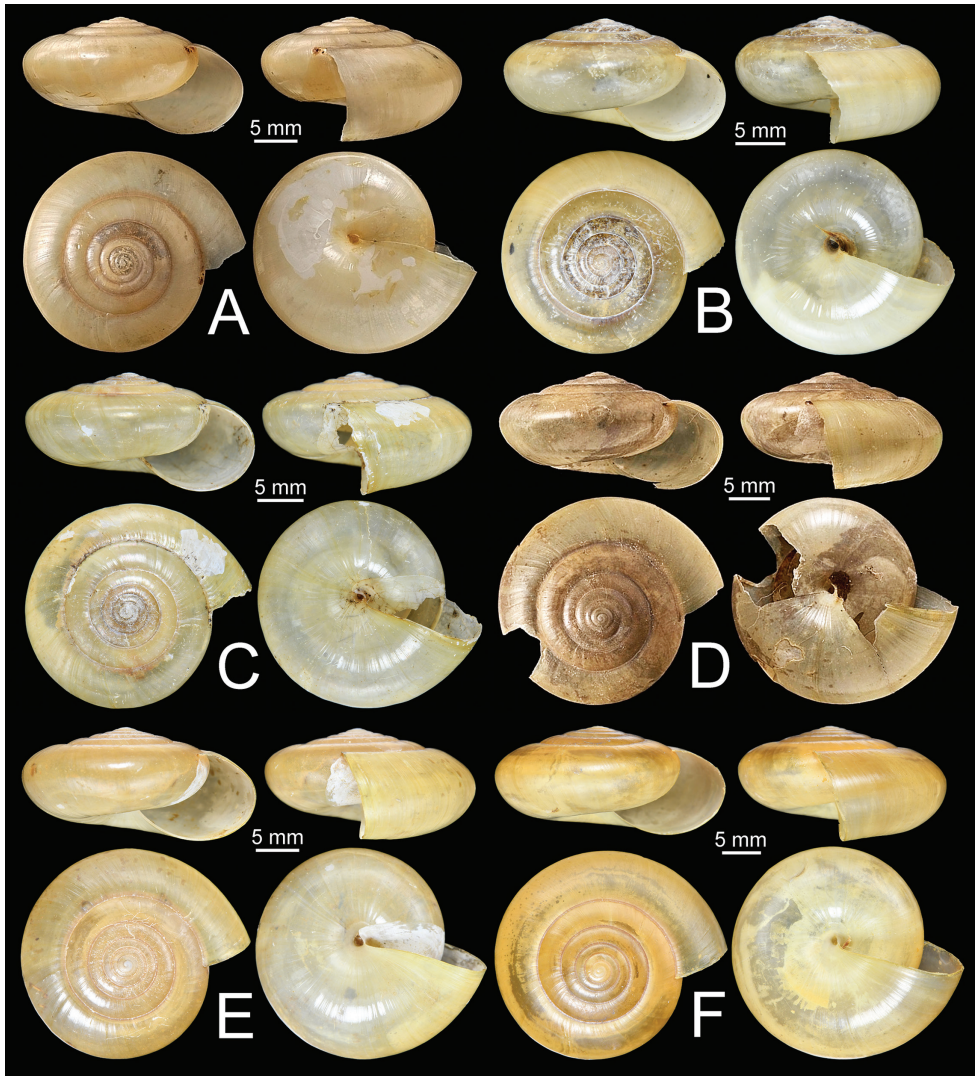


Figure 34. Shells of Group II: *Sarika hainesi* group. **A–C** *Sarika hainesi* **A** syntype NHMUK 20200290 and **B, C** specimen CUMZ 7237 **D–F** *S. bocourti* **D** syntype NHMUK 1893.2.4.1076–1077 **E** specimen CUMZ 7590, and **F** specimen CUMZ 7592.

Radula. Teeth with half row formula: 1–(10–11)–61. Central tooth symmetrically tricuspid; lateral teeth asymmetrically tricuspid; marginal teeth elongated and bicuspid. Marginal teeth starting at approximately row number 10 or 11 (Fig. 43A).

External features. Animal with reticulated skin and pale grey body. Mantle edge well developed, pale grey, with one shell lobe, and three dorsal lobes. Dorsal lobes large and broad; anterior and posterior left dorsal lobes smaller than right dorsal lobe. Right shell lobe large and long and left shell lobe absent (Fig. 33B).

Distribution. This species is known only from the Dong Phaya Yen and Sankamphaeng Ranges in Saraburi and Nakhon Ratchasima provinces (Fig. 32).

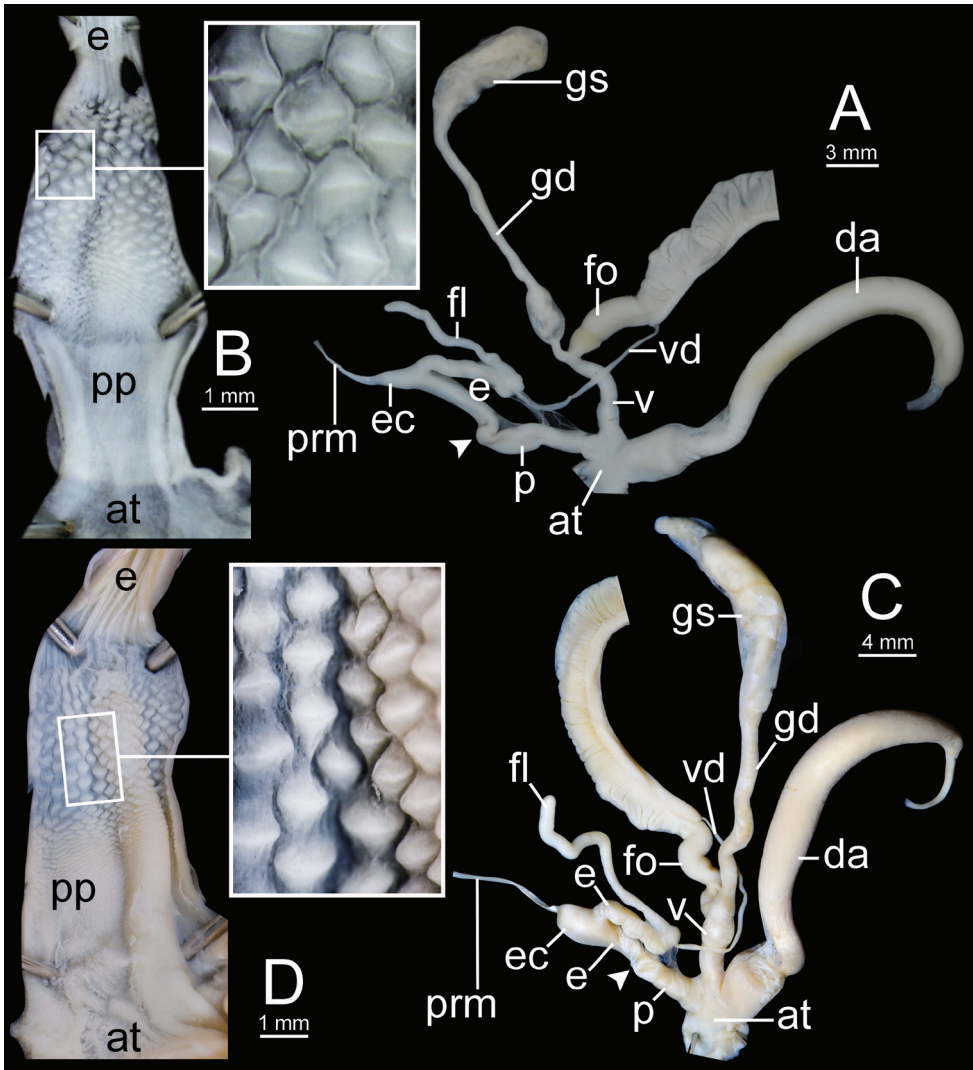


Figure 35. Genitalia. **A, B** *Sarika hainesi* specimen CUMZ 7237 **A** general view of the genital system and **B** internal structure of the penis. **C, D** *Sarika bocourti* specimen CUMZ 7591 **C** general view of the genital system and **D** internal structure of the penis. White arrowheads indicate the ends of the penes.

COI analysis. The ML and BI analyses revealed that the individuals of *S. hainesi* ($n = 3$) formed a monophyletic group with high support (Fig. 1; BS = 96%, PP = 1). The mean intraspecific genetic distance of *S. hainesi* was 2.4% (Table 2).

Remarks. The type locality of *S. hainesi* was recorded simply as “Siam”. Later, Pfeiffer (1856b: 76) stated that the described specimens were received from W.A. Haines. Although Haines had never visited Thailand, he described four land snail species from Thailand based on materials sent by the American physician S.R. House (Haines 1858: 157–158). We presumed that the Cumming ex. Haines specimen (syn-type) was also received from S.R. House who lived in Bangkok from 1847–1876

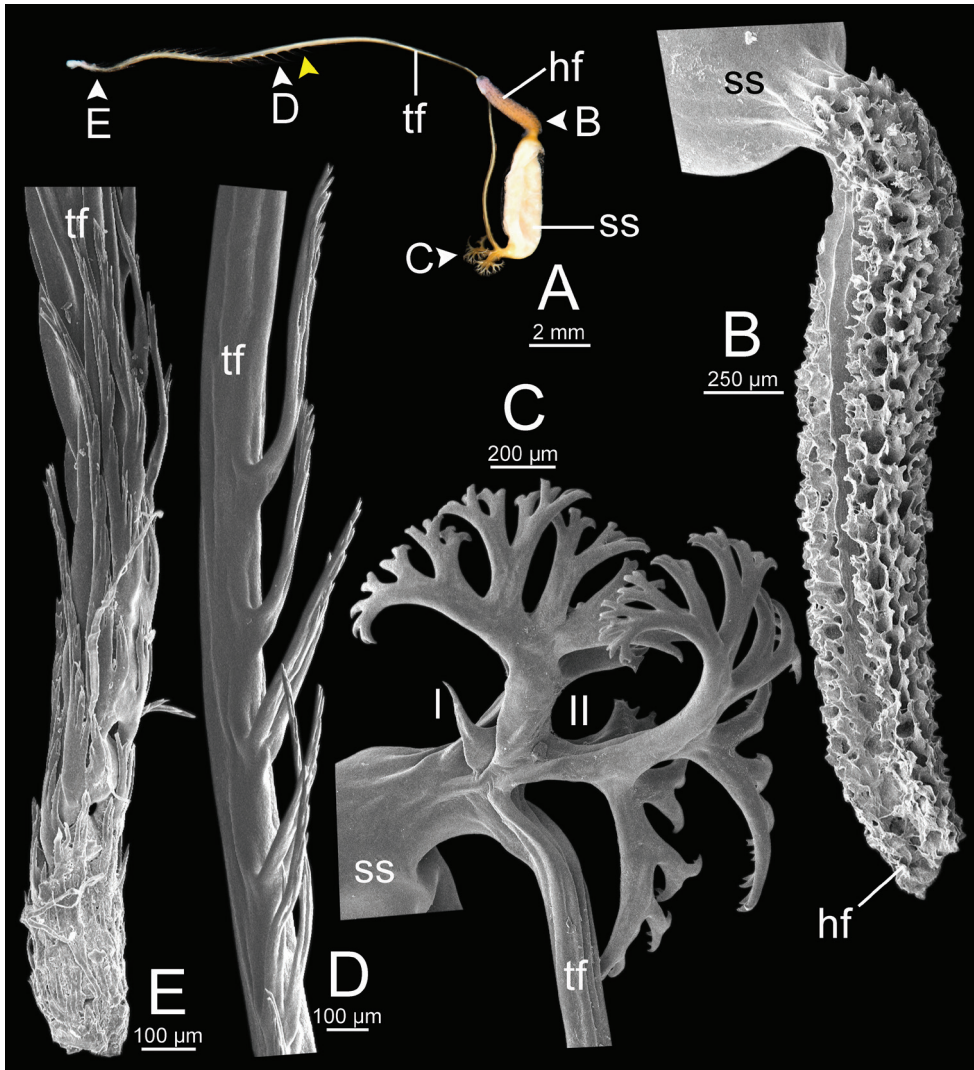


Figure 36. Spermatophore of *Sarika hainesi* specimen CUMZ 7237 **A** general view of the spermatophore **B** head filament, and **C–E** tail filament showing **C** two spines located close to the sperm sac **D** region with and without branching spines, and **E** branching spines on the tip region. Yellow arrowhead indicates the end of the spines from the tip.

(Feltus 1924). Therefore, the type locality of *S. hainesi* from central Thailand is the most likely. In addition, the specimen from central Thailand (*S. hainesi* s. s.) matched the syntypes in almost all the shell characters; however, the genitalia obviously differ from *S. aff. hainesii* sensu Solem (1966) from northern Thailand (Chiang Mai Province). We consider the northern Thailand populations as misidentified and propose them here as an undescribed species, *S. solemi* sp. nov. Moreover, the COI sequence divergences between *S. hainesi* and *S. solemi* sp. nov. are very high (10.2%).

Sarika hainesi was first reported from Thailand (Pfeiffer 1856a) and then from Laos (Saurin 1953; Inkhavilay et al. 2019). However, the specimens from Laos are shells only, and so the distribution of *S. hainesi* s. s. in Laos still needs to be confirmed.

***Sarika bocourti* (Morelet, 1875)**

Figs 1, 32, 33A, C, 34D–F, 35C, D, 37, 43B

Helix bocourti Morelet, 1875: 249. Type locality: “Lespece provient de Battambang, dans le Cambodge” [Battambang Province, Cambodia]; Breure et al. 2018: 222, 223, figs 135, 136.

Nanina (*Macrochlamys*) aff. *bocourti* [sic]: Tryon 1886: 89, pl. 29, figs 43–45.

Ariophanta (*Xesta*) *bocourti*: Fischer 1891: 20.

Nanina (*Xesta*) *bocourti*: Fischer and Dautzenberg 1904: 394.

Sarika bocourti: Pholyotha et al. 2020a: 7, 8, fig. 2b; Sutcharit et al. 2020: 27.

Type material. *Syntype* NHMUK 1893.2.4.1076–1077 (two shells; Fig. 34D) from Battambang [Battambang Province, Cambodia].

Other material examined. CAMBODIA. Samov Mountain, Phnom Sampov, Banan, Battambang, 13°01'33.6"N, 103°06'03.6"E: CUMZ 7900. THAILAND-Eastern. Wat Trok Nong Lang, Khlung, Chanthaburi, 12°32'16.3"N, 102°16'33.8"E: CUMZ 7578. Trok Nong Waterfall, Khlung, Chanthaburi, 12°32'39.4"N, 102°14'13.5"E: CUMZ 7580, 7582, 7583, 7585, 7590 (Fig. 34E), 7591, 7596, 7608. Khao Kao Priest's camp site, Khlung, Chanthaburi, 12°29'26.8"N, 102°18'49.6"E: CUMZ 7598. Khlong Narai Waterfall, Mueang, Chanthaburi, 12°34'53.4"N, 102°10'34.2"E: CUMZ 7597, 7601, 7610. Wat Khao Banchob, Makham, Chanthaburi, 12°51'09.1"N, 102°12'12.7"E: CUMZ 7581. Khao Soi Dao, Soi Dao, Chanthaburi, 13°06'31.0"N, 102°12'01.5"E: CUMZ 7579, 7584, 7586, 7609. Mountain area near Khao Soi Dao, Soi Dao, Chanthaburi, 13°07'49.3"N, 102°10'57.2"E: CUMZ 7600. Mountain area near Wat Ban Wang Ka Prae, Pong Nam Ron, Chanthaburi, 12°58'10.9"N, 102°16'20.6"E: CUMZ 7594. THAILAND-Southern. Mountain area near Khao Sok Nature Resort, Phanom, Surat Thani, 8°54'22.6"N, 98°31'45.1"E: CUMZ 7587. Mountain area near Khao Sok Evergreen House, Phanom, Surat Thani, 8°54'38.1"N, 98°31'47.2"E: CUMZ 7592 (Fig. 34F), 7606. Mountain area near Anurak Community Lodge, Phanom, Surat Thani, 8°53'16.2"N, 98°40'52.9"E: CUMZ 7593, 7603. Wat Tham Wararam, Phanom, Surat Thani, 8°53'03.3"N, 98°40'02.5"E: CUMZ 7604. Wat Tham Phanthurat, Phanom, Surat Thani, 8°54'36.9"N, 98°31'28.3"E: CUMZ 7595. Mountain area near Ban Ya Plong, Phanom, Surat Thani, 8°54'33.0"N, 98°34'51.6"E: CUMZ 7605. Lot cave, Nopphitam, Nakhon Si Thammarat, 8°44'10.0"N, 99°38'06.5"E: CUMZ 7602. Limestone outcrop in Tham Nam Phut, Mueang, Phang-nga, 8°27'49.7"N, 98°32'37.0"E: CUMZ 7607. Mountain area near Ban Pak Khlong, Kapong, Phang-nga, 8°47'54.8"N, 98°30'40.6"E: CUMZ 7588.

Diagnosis. Shell large, depressed, obtusely angulated body whorl and higher shell spire. Animal with pale to dark grey body and four mantle lobes. Genitalia with a large and straight epiphallic caecum, and triangular prism shaped penial pilasters. Spermatophore with irregularly acute-serrate longitudinal ridges on the head filament, tail filament with two spines and more than ca. two-thirds of its length with series of short branching spines.

Description. Shell. Shell depressed, large to very large size (shell width up to 33.1 mm, shell height up to 16.1 mm) and rather thin. Shell surface smooth and polished; shell colour pale yellowish brown to brown. Whorls 6–7, increasing regularly; body whorl large and obtusely angulated. Spire moderately to very much elevated; suture impressed. Aperture crescent-shaped and obliquely opened. Peristome simple. Columellar margin simple and slightly reflected near umbilicus. Umbilicus narrowly opened (Fig. 34D–F).

Genital organs. Atrium short. Penis cylindrical with thin penial sheath covering proximal penis. Inner sculpture of penis proximally more than ca. half of penial chamber with very finely longitudinal penial pilasters to nearly smooth surface, and then gradually transformed from small to large rhomboid pilasters with acute angle on top (triangular prism). Epiphallus cylindrical, slightly longer than penis, and approximately same diameter as penis. Epiphallic caecum short, straight, approximately similar diameter with penis, and located near middle of epiphallus. Penial retractor muscle thin and attached at tip of epiphallic caecum. Flagellum long slender and slightly longer than epiphallus. Vas deferens thin tube connecting distal epiphallus and free oviduct (Fig. 35C, D).

Vagina cylindrical and approximately as long as penis. Dart apparatus enlarged, long cylindrical, and located on atrium at vagina and penis junction. Gametolytic sac enlarged and bulbous (with spermatophore inside); gametolytic duct cylindrical. Free oviduct cylindrical, nearly two times of vagina length, and proximal end encircled with thick tissue (Fig. 35C).

Spermatophore long and needle-shaped. Sperm sac enlarged and elongate-oval. Head filament gourd shape with irregularly acute-serrate longitudinal ridges. Tail filament very long tube; region near sperm sac with two spines. Spine I simple and rather short. Spine II very large at base and divided in two spines and then each one branching into many spinules near the tip. Region furthest away smooth without spine; terminal part (more than ca. two-thirds of its length) with series of short branching spines arranged in a row and transformed to long serrate-like spines arranged in opposite rows near the tail filament tip (Fig. 37).

Radula. Teeth with half row formula: 1–(12–13)–61. Central tooth symmetrical tricuspid with large mesocone and very small to nearly absent ectocone; lateral teeth asymmetrical tricuspid with large mesocone and very small to nearly absent endocone and ectocone; marginal teeth elongate bicuspid. Marginal teeth starting at approximately row number 12 or 13 (Fig. 43B).

External features. Animal with reticulated skin, pale to dark grey body and darker than foot sole, and dark grey caudal horn. Mantle edge well developed and pale grey colour. Shell lobes and dorsal lobes shape and structure like *S. hainesi* (Fig. 33A, C).

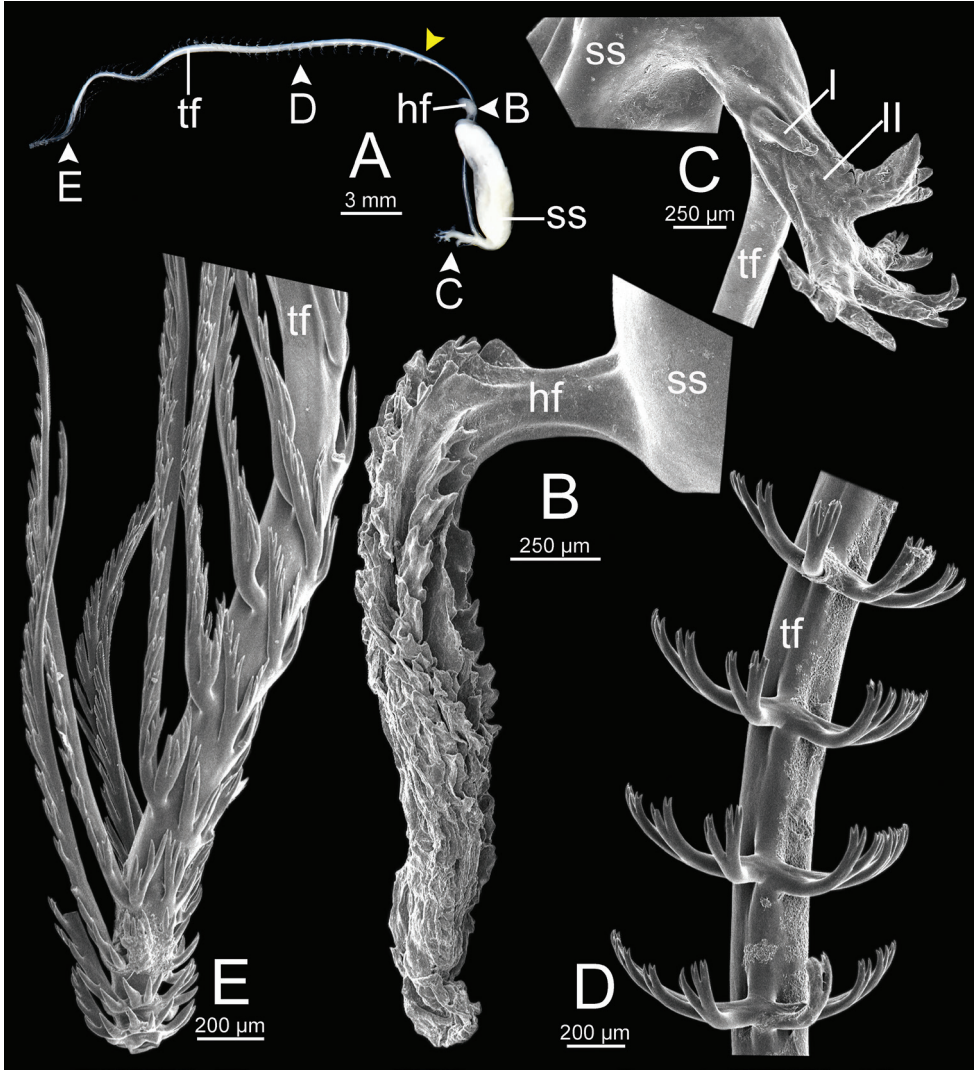


Figure 37. Spermatophore of *Sarika bocourti* specimen CUMZ 7591 **A** general view of the spermatophore **B** head filament, and **C–E** tail filament showing **C** two spines located close to the sperm sac **D** branching spines on middle region **E** branching spines on the tip region. Yellow arrowhead indicates the end of the spines from the tip.

Distribution. This species is known from several localities in Chanthaburi Province, eastern Thailand and Surat Thani, Nakhon Si Thammarat and Phang-nga provinces, southern Thailand (Fig. 32), and Battambang Province, Cambodia (Morelet 1875; Pholyotha et al. 2020a). *Sarika bocourti* is common in both human-influenced habitats, such as plantations or gardens, and natural habitats.

COI analysis. The ML and BI analyses showed that the four specimens of *S. bocourti* represent a single haplotype, sister group to *S. inferospira* sp. nov. + *S. melanospira* sp. nov. with strong support (Fig. 1; BS = 99%, PP = 1).

Remarks. Specimens from Chanthaburi Province, eastern Thailand were identical with the syntype of *S. bocourti* that was described from Battambang Province, Cambodia. Both the shell morphology and genital anatomy of the disjunct populations from southern Thailand agree well with the populations from eastern Thailand. From the COI gene phylogeny, all specimens from southern Thailand are retrieved as monophyletic with *S. bocourti* from eastern Thailand and with no variation in the COI sequences (Table 2). The eastern and southern populations of *S. bocourti* are possibly shaping up by sea level fluctuation in the last glacial periods recorded in tree-dwelling snails and centipedes (Prasankok et al. 2007; Siriwtut et al. 2015). Further investigation by adding more samples and genetic markers would help elucidate the phylogeographical history of this species.

Although shell morphology of *S. bocourti* and *S. hainesi* is quite similar, the genitalia and spermatophore are clearly distinct. *Sarika bocourti* has larger epiphallic caecum, and a spermatophore with a head filament with acute-serrate ridges, and the tail filament has fewer branching spines. *Sarika hainesi* has a smaller epiphallic caecum, and a spermatophore with a head filament with a sponge-like appearance and the tail filament has more branching spines. In addition, the genetic distance between these two species is rather high (7.0%).

***Sarika inferospira* Pholyotha & Panha, sp. nov.**

<http://zoobank.org/CE4EE71E-7FCE-4696-BDEE-A145178CBAE3>

Figs 1, 32, 33D, 38A, B, 39A, B, 40, 43C

Type material. *Holotype* CUMZ 7254 (Fig. 38A, width 25.3 mm, height 11.5 mm). *Paratypes* CUMZ 7255 (two shells and 13 specimens preserved in ethanol; Fig. 38B, width 24.8 mm, height 11.0 mm) CUMZ 7256 (four shells), 7257 (four specimens preserved in ethanol), NHMUK 20200285 (two shells).

Type locality. Wat Tham Sai Thong, Nong Kung Si, Kalasin, Thailand, 16°50'11.3"N, 103°14'18.7"E.

Diagnosis. Shell large, strongly depressed, very pale yellowish brown with shouldered body whorl. Animal with grey colour and four mantle lobes. Genitalia with a large straight epiphallic caecum, and triangular prism pilasters on inner penial sculpture. Spermatophore: tail filament near sperm sac with two spines and a series of several branching spines occurring continually to the middle region; middle region becoming smooth, spineless and then terminal part approximately half of its length with a series of branching spines.

Description. *Shell.* Shell strongly depressed, large size (shell width up to 29.3 mm, shell height up to 13.9 mm) and thin. Surface smooth and polished; shell colour very pale yellowish brown. Whorls 6–6½, increasing regularly; body whorl large and shouldered. Spire slightly elevated; suture impressed. Aperture crescent-shaped and obliquely opened. Peristome simple. Columellar margin simple and slightly reflected near umbilicus. Umbilicus narrowly opened (Fig. 38A, B).

Genital organs. Atrium short. Penis cylindrical with thin penial sheath covering proximal penis. Inner sculpture of penis proximally more than ca. half of penial chamber with very finely longitudinal penial pilasters to nearly smooth surface, and

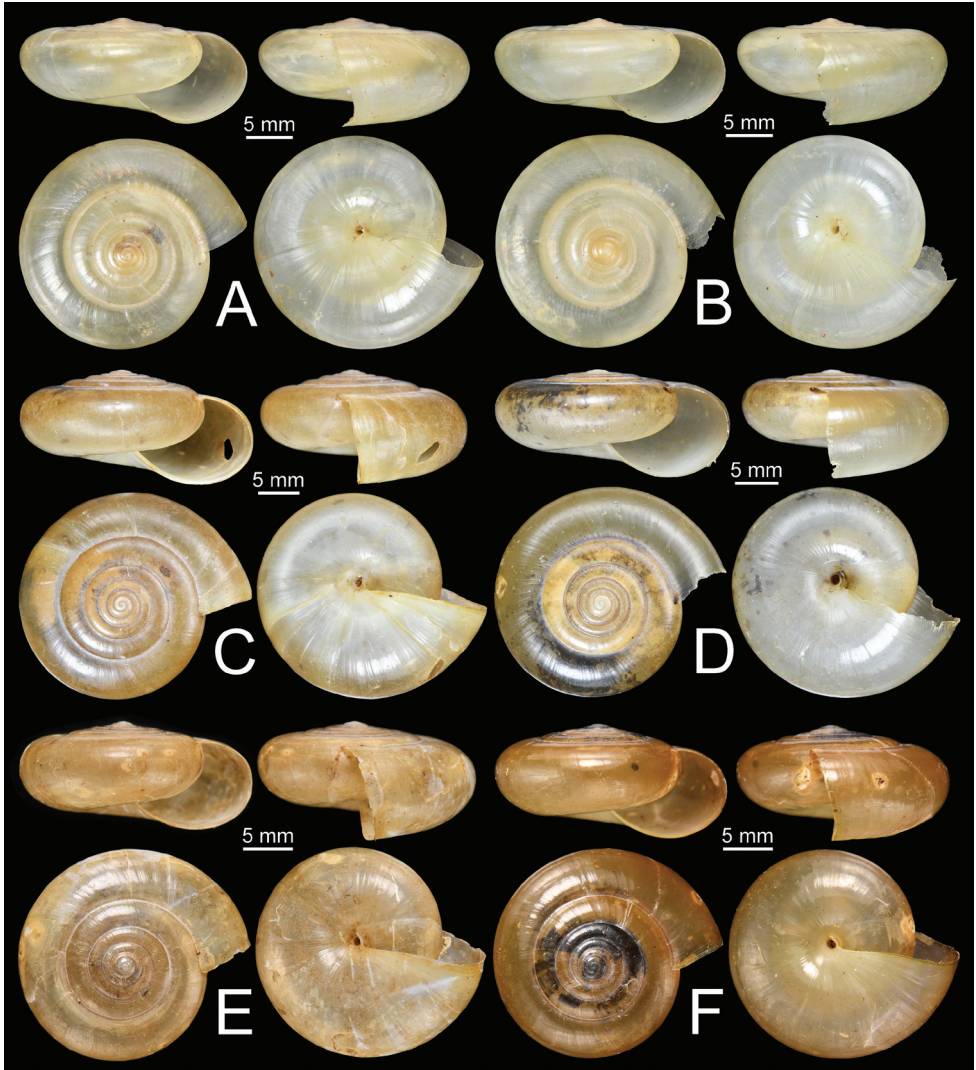


Figure 38. Shells of Group II: *Sarika hainesi* group. **A, B** *Sarika inferospira* sp. nov. **A** holotype CUMZ 7254 and **B** paratype CUMZ 7255 **C, D** *S. melanospira* sp. nov. **C** holotype CUMZ 7258 and **D** paratype CUMZ 7243 **E, F** *S. pellosa* sp. nov. **E** holotype CUMZ 7249 and **F** paratype CUMZ 7517.

then gradually transformed from small to large rhomboid pilasters with acute angle on top (triangular prism). Epiphallus cylindrical and approximately the as long as penis. Epiphallic caecum short, straight, diameter larger than epiphallus, and located near middle of epiphallus. Penial retractor muscle thin and attached at tip of epiphallic caecum. Flagellum long, slender and nearly one and half times of epiphallus length. Vas deferens thin tube connecting distal epiphallus and free oviduct (Fig. 39A, B).

Vagina cylindrical, short, and approximately two-third of penis length. Dart apparatus large, long cylindrical and located on atrium at vagina and penis junction.

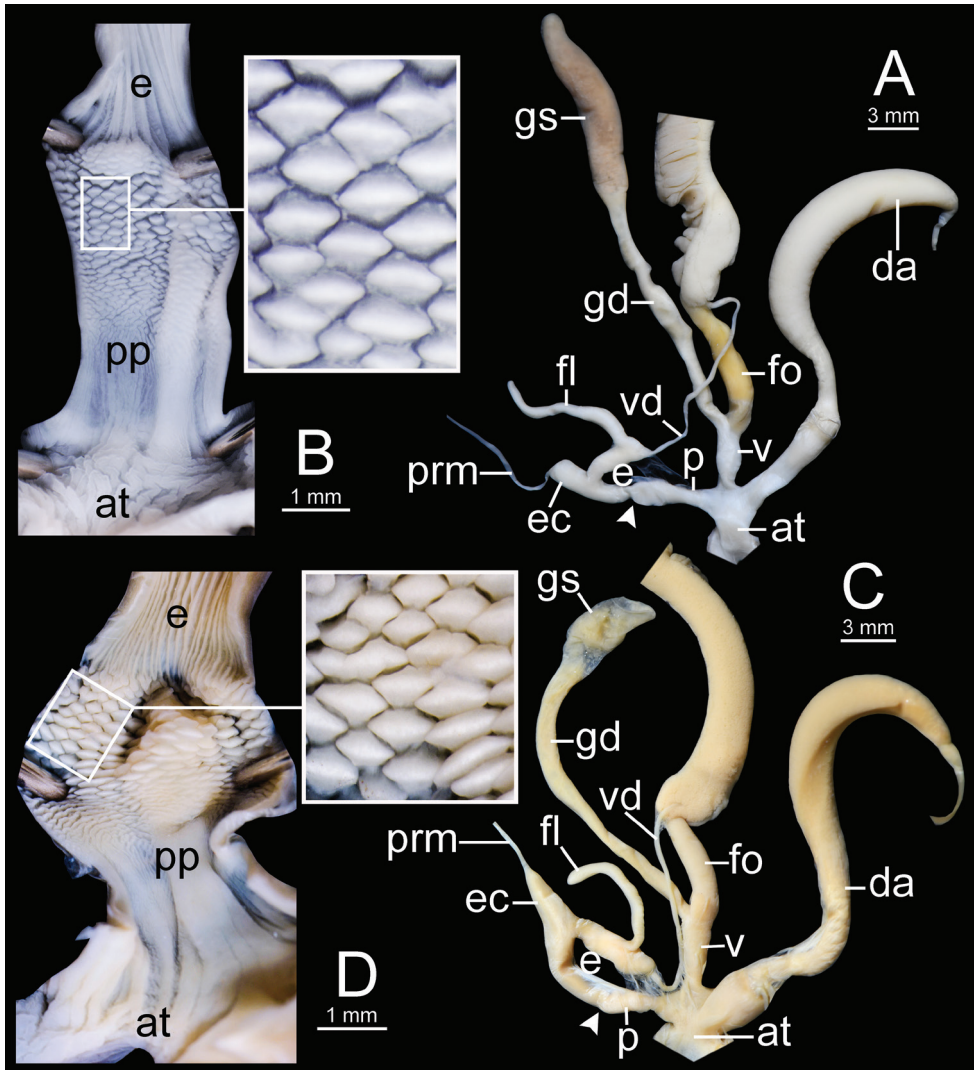


Figure 39. Genitalia. **A, B** *Sarika inferospira* sp. nov. specimen CUMZ 7257 **A** general view of the genital system and **B** internal structure of the penis **C, D** *S. melanospira* sp. nov. paratype CUMZ 7243 **C** general view of the genital system and **D** internal structure of the penis. White arrowheads indicate the ends of the penes.

Gametolytic sac enlarged and bulbous; gametolytic duct long cylindrical. Free oviduct cylindrical, approximately two and half times of vagina length (Fig. 39A).

Spermatophore long and needle-shaped. Sperm sac enlarged and elongate-oval. Head filament was missing (incomplete spermatophore). Tail filament very long tube and region near sperm sac with two spines. Spine I simple and long. Spine II slightly longer and larger than spine I and branching into many small spinules. Continuously on tail filament with short branching spines arranged in a row, modified to longer branching spines arranged in several rows around middle region, and then become smooth and without spine (Fig. 40A at yellow line). Terminal part of tail filament

(more than ca. one-fourth of its length) with series of long branching spines arranged in opposite rows and tail filament tip with no spine (Fig. 40).

Radula. Teeth with half row formula: 1–(13–14)–59. Central tooth symmetrical tricuspid; lateral teeth asymmetrical tricuspid; marginal teeth elongate bicuspid. Teeth shape is similar to that of *S. resplendens*. Marginal teeth starting at approximately row number 13 or 14 (Fig. 43C).

External features. Animal with reticulated skin and body colour with dark grey above and creamy-grey below. Creamy-grey foot sole and dark creamy-grey caudal horn. Four mantle lobes well developed and pale grey colour. Left shell lobe absent (Fig. 33D).

Etymology. The specific epithet *inferospira* is derived from the Latin word *infer* meaning low and the Latin word *spira* meaning coil. It refers to the strongly depressed shell with low spire.

Distribution. *Sarika inferospira* sp. nov. is only known from sandstone habitats with dry dipterocarp forest at the type locality (Fig. 32).

COI analysis. The ML and BI analyses revealed that the individuals of *S. inferospira* sp. nov. ($n = 3$) formed a monophyletic group with very strong support (Fig. 1; BS = 100%, PP = 1), sister group to *S. melanospira* sp. nov. with only ML support (Fig. 1; BS = 78%). The mean intraspecific genetic distance of *S. inferospira* sp. nov. was 0.1% (Table 2).

Remarks. *Sarika inferospira* sp. nov. is distinguished from *S. hainesi* and *S. bocourti* by having a strongly depressed shape, shouldered body whorl, and spermatophore smooth or without spine on the middle part of tail filament. *Sarika hainesi* and *S. bocourti* have a depressed shell with a higher spire and obtusely angulated body whorl. In addition, the tail filament of spermatophore contains a series of short branching spines more than ca. half of its length in *S. hainesi* and more than ca. two-thirds of its length in *S. bocourti*.

***Sarika melanospira* Pholyotha & Panha, sp. nov.**

<http://zoobank.org/EB33505F-3BA4-440C-BBC4-2B4CE631F7AA>

Figs 1, 32, 33E, 38C, D, 39C, D, 43D

Type material. *Holotype* CUMZ 7258 (Fig. 38C, width 28.3 mm, height 13.3 mm).

Paratypes CUMZ 7243 (ten shells and 44 preserved specimens in ethanol; Fig. 38D, width 26.5 mm, height 11.7 mm) CUMZ 7244 (four shells and two preserved specimens in ethanol), NHMUK 20200286 (two shells), SMF (two shells), ZRC. MOL.017029 (two shells).

Type locality. Wat Tham Suwan Phu Pha, Khao Chamao, Rayong, Thailand, 12°59'24.1"N, 101°39'28.8"E.

Diagnosis. Shell large, dextral, depressed and pale brown with rounded to weak shouldered body whorl. Animal with blackish body, four mantle lobes and mantle covered by spiral black band below the suture at the body whorl. Genitalia with a large straight epiphallic caecum and triangular prism pilasters on inner penial sculpture.

Description. *Shell.* Shell depressed, large size (shell width up to 29.3 mm, shell height up to 13.3 mm) and thin. Surface smooth and polished; shell colour pale brown.

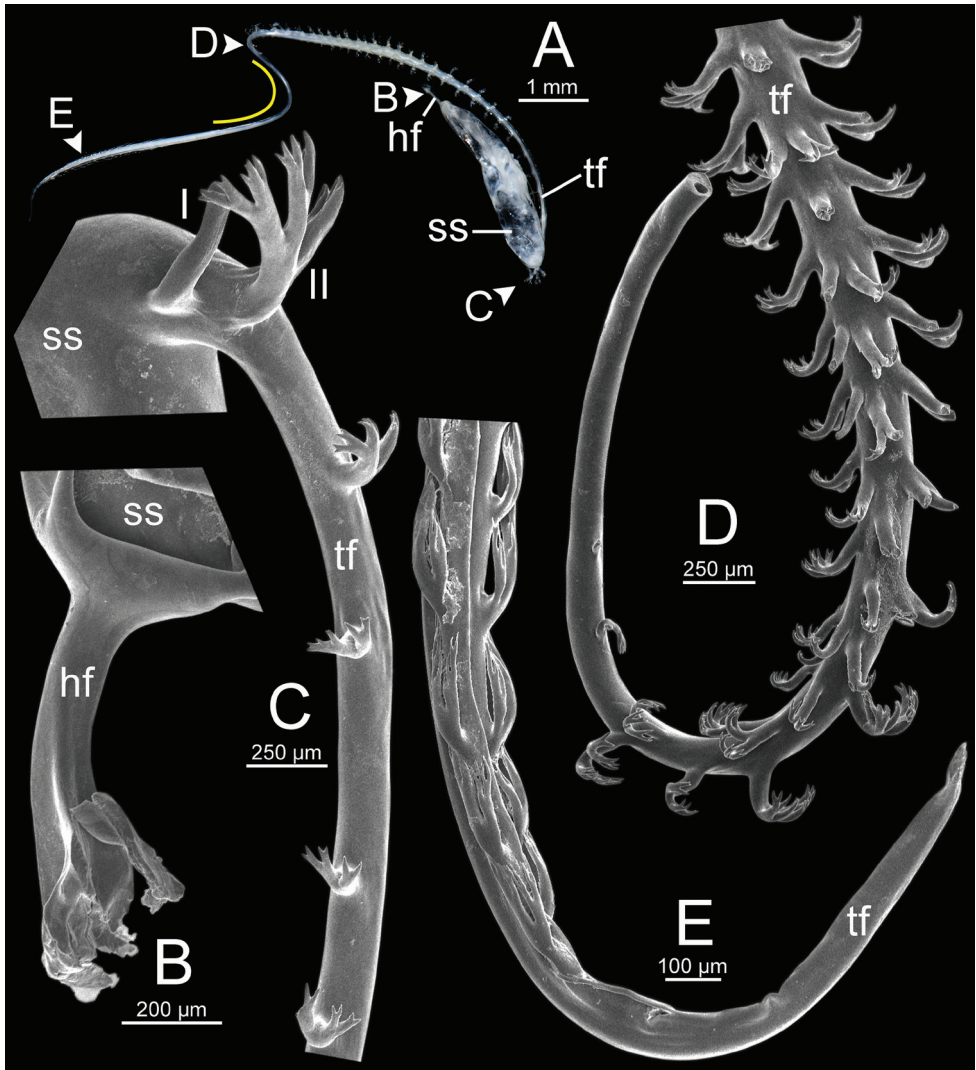


Figure 40. Spermatophore of *Sarika inferospira* sp. nov. specimen CUMZ 7257 **A** general view of spermatophore **B** head filament and **C–E** tail filament showing **C** two spines located close to the sperm sac **D** region with and without branching spines, and **E** branching spines on the tip region. Yellow line indicates the region with no spine.

Whorls 6–6½, increasing regularly; body whorl large, rounded to weak shouldered. Spire slightly to moderately elevated; suture impressed. Aperture crescent-shaped and obliquely opened. Peristome simple. Columellar margin simple and slightly reflected near umbilicus. Umbilicus narrowly opened (Fig. 38C, D).

Genital organs. Atrium short. Penis cylindrical with thin penial sheath covering proximal penis. Inner sculpture of penis proximally more than ca. half of penial chamber with very finely longitudinal penial pilasters to nearly smooth surface, and

then gradually transformed from small to large rhomboid pilasters with acute angle on top (triangular prism). Epiphallus cylindrical and nearly two times penis length. Epiphallic caecum short, straight, slightly larger than epiphallus and located near middle of epiphallus. Penial retractor muscle thin and attached at tip of epiphallic caecum. Flagellum slender, narrower than epiphallus and approximately as long as penis. Vas deferens thin tube connecting distal epiphallus and free oviduct (Fig. 39C, D).

Vagina long cylindrical and approximately as long as penis. Dart apparatus large, long cylindrical, and located on atrium at vagina and penis junction. Gametolytic sac enlarged and bulbous; gametolytic duct long cylindrical. Free oviduct cylindrical, nearly as long as vagina (Fig. 39C).

Radula. Teeth with half row formula: 1–(17–18)–59. Central tooth symmetrical tricuspid; lateral teeth asymmetrical tricuspid; marginal teeth elongate bicuspid. Teeth shape is similar to that of *S. resplendens*. Marginal teeth starting at approximately row number 17 or 18 (Fig. 43D).

External features. Animal with reticulated skin and blackish body. Mantle with conspicuous blackish spiral band at the body whorl below the suture. Creamy-grey foot sole and blackish caudal horn. Four mantle lobes well developed and blackish. Left shell lobe absent (Fig. 33E).

Etymology. The specific epithet *melanospira* is derived from the Greek word *melanos* meaning black or dark, and the Latin word *spira* meaning coil. It refers to the mantle being covered by a spiral black band at the body whorl.

Distribution. *Sarika melanospira* sp. nov. is only known from the limestone habitats at the type locality (Fig. 32).

COI analysis. The ML and BI analyses showed that the individuals of *S. melanospira* sp. nov. ($n = 3$) formed a monophyletic group with very strong support (Fig. 1; BS = 100%, PP = 1). The mean intraspecific genetic distance of *S. melanospira* sp. nov. was 0.5% (Table 2).

Remarks. Among the *Sarika hainesi* group, this new species differs from *S. hainesi*, *S. bocourti*, and *S. inferospira* sp. nov. in having a rounded to very weak shouldered body whorl. *Sarika hainesi* and *S. bocourti* have an obtusely angulated body whorl and *S. inferospira* sp. nov. has a shouldered body whorl.

***Sarika pellosa* Pholyotha & Panha, sp. nov.**

<http://zoobank.org/BDA78F68-B700-42D9-8710-30E461EEC205>

Figs 1, 32, 33F, 38E, F, 41, 42, 43E

Type material. *Holotype* CUMZ 7249 (Fig. 38E, width 23.6 mm, height 11.0 mm).

Paratypes CUMZ 7517 (two shell and four specimens preserved in ethanol; Fig. 38F, width 23.6 mm, height 11.5 mm) CUMZ 7519 (three specimens preserved in ethanol), NHMUK 20200287 (two shells).

Other material examined. **THAILAND-Eastern.** Tham Saeng Thian, Khlong Hat, Sa Kao, 13°18'57.2"N, 102°19'57.2"E: CUMZ 7250. Tham Nam Khao Siva, Khlong

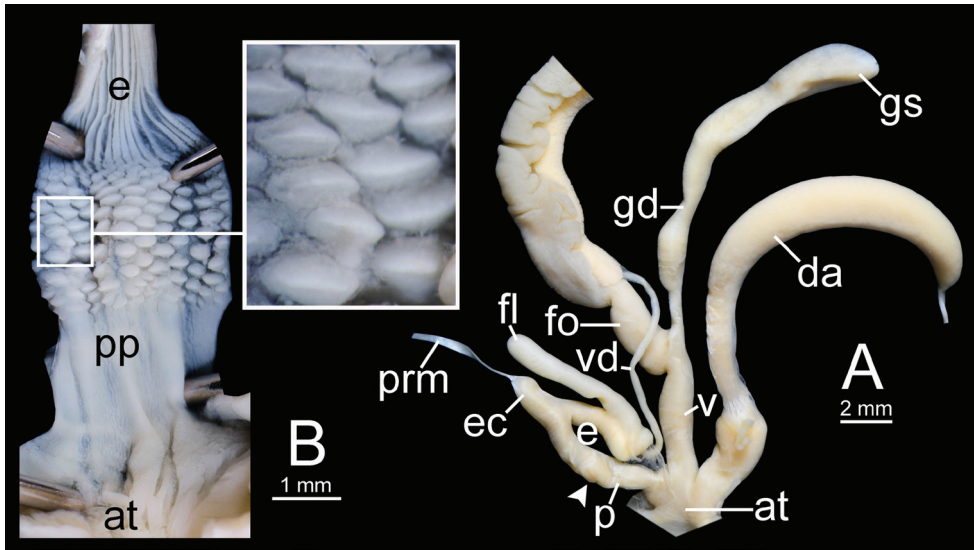


Figure 41. Genitalia. **A, B** *Sarika pellosa* sp. nov. paratype CUMZ 7517 **A** general view of the genital system and **B** internal structure of the penis. White arrowhead indicates the end of the penis.

Hat, Sa Kaew, 13°19'15.1"N, 102°19'40.1"E: CUMZ 7251. Limestone outcrop in Khao Chakan, Khao Chakan, Sa Kaew, 13°39'49.4"N, 102°05'39.7"E: CUMZ 7518. Wat Tham Khao Chakan, Khao Chakan, Sa Kaew, 13°39'38.0"N, 102°05'02.8"E: CUMZ 7520.

Type locality. Tham Phet Pho Thong, Khlong Hat, Sa Kaew, Thailand, 13°25'02.5"N, 102°19'25.6"E.

Diagnosis. Shell large, depressed to strongly depressed, pale brown to dark brown with rounded to weak shouldered body whorl. Animal with blackish body and four mantle lobes. Genitalia with a large straight epiphallal caecum and triangular prism pilasters on inner penial sculpture. Spermatophore: tail filament near sperm sac with three spines and terminal part more than ca. one-third of its length with series of branching spines.

Description. Shell. Shell depressed to strongly depressed, large size (shell width up to 24.7 mm, shell height up to 12.0 mm), and thin. Surface smooth and shiny; shell colour very pale brown to dark brown. Whorls 6–6½, increasing regularly; body whorl large and rounded to weak shouldered. Spire moderately elevated; suture impressed. Aperture crescent-shaped and obliquely opened. Peristome simple. Columellar margin simple and slightly reflected near umbilicus. Umbilicus narrowly opened (Fig. 38E, F).

Genital organs. Atrium short. Penis cylindrical with thin penial sheath covering proximal penis. Inner sculpture of penis proximally more than ca. half of penial chamber with very finely longitudinal penial pilasters to nearly smooth surface, and then gradually transformed from small to large rhomboid pilasters with acute angle on top (triangular prism). Epiphallus enlarged cylindrical and approximately two times penis length. Epiphallal caecum large, straight, similar to epiphallus diameter and located near middle of epiphallus. Penial retractor muscle thin and attached at tip of epiphallal caecum. Flagellum long and enlarged approximately as long as epiphallus. Vas deferens thin tube connecting distal epiphallus and free oviduct (Fig. 41).

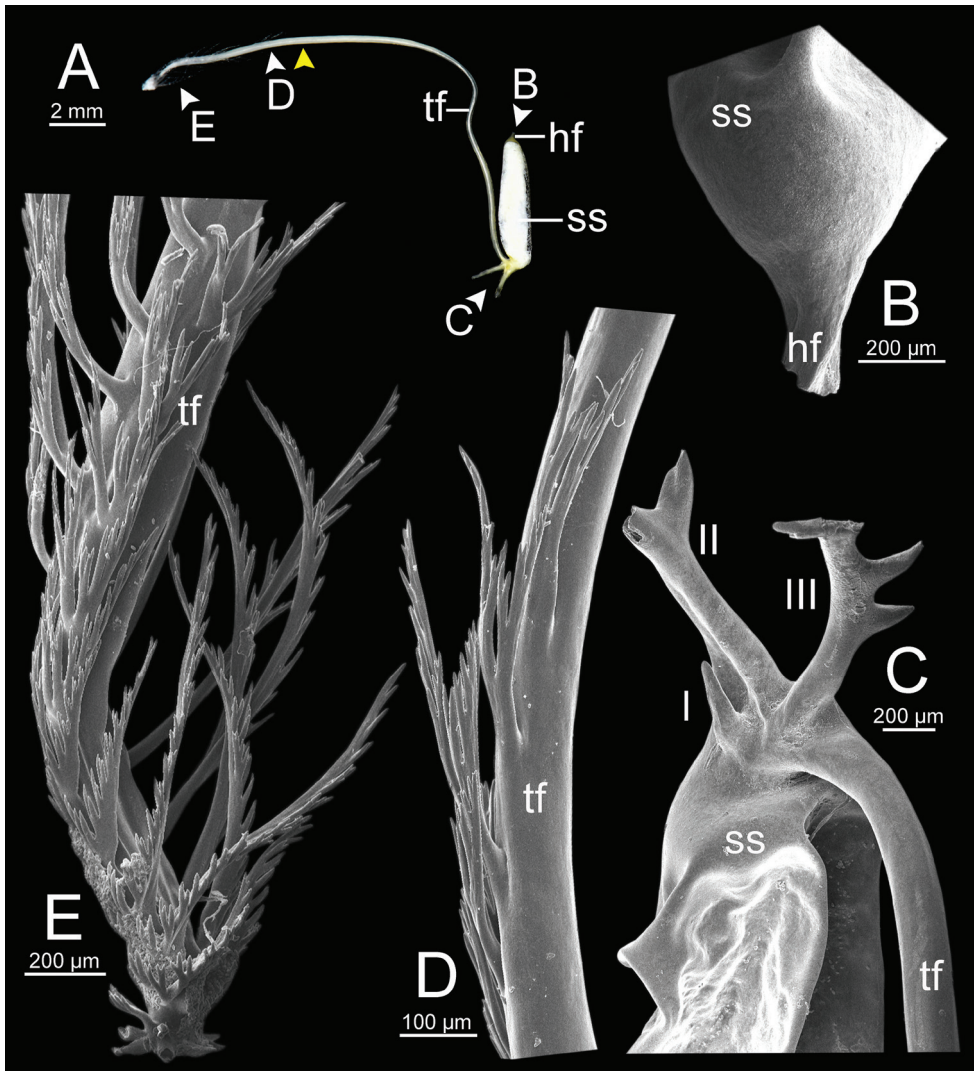


Figure 42. Spermatophore of *Sarika pellosa* sp. nov. paratype CUMZ 7517 **A** general view of the spermatophore **B** head filament, and **C–E** tail filament showing **C** three spines located close to the sperm sac, **D** region with and without branching spines, and **E** branching spines on the tip region. Yellow arrowhead indicates the end of the spines from the tip.

Vagina long cylindrical and approximately twice as long as penis. Dart apparatus large, long cylindrical, and located on atrium at vagina and penis junction. Gametolytic sac enlarged and bulbous; gametolytic duct enlarged cylindrical (spermatophore inside). Free oviduct cylindrical, slightly shorter than vagina (Fig. 41A).

Spermatophore long and needle-shaped. Sperm sac enlarged and elongate-oval. Head filament was missing (incomplete spermatophore). Tail filament very long tube; region near sperm sac with three spines. Spine I simple and rather short. Spine II large and long, and most of branching spines probably missing. Spine III smaller than spine

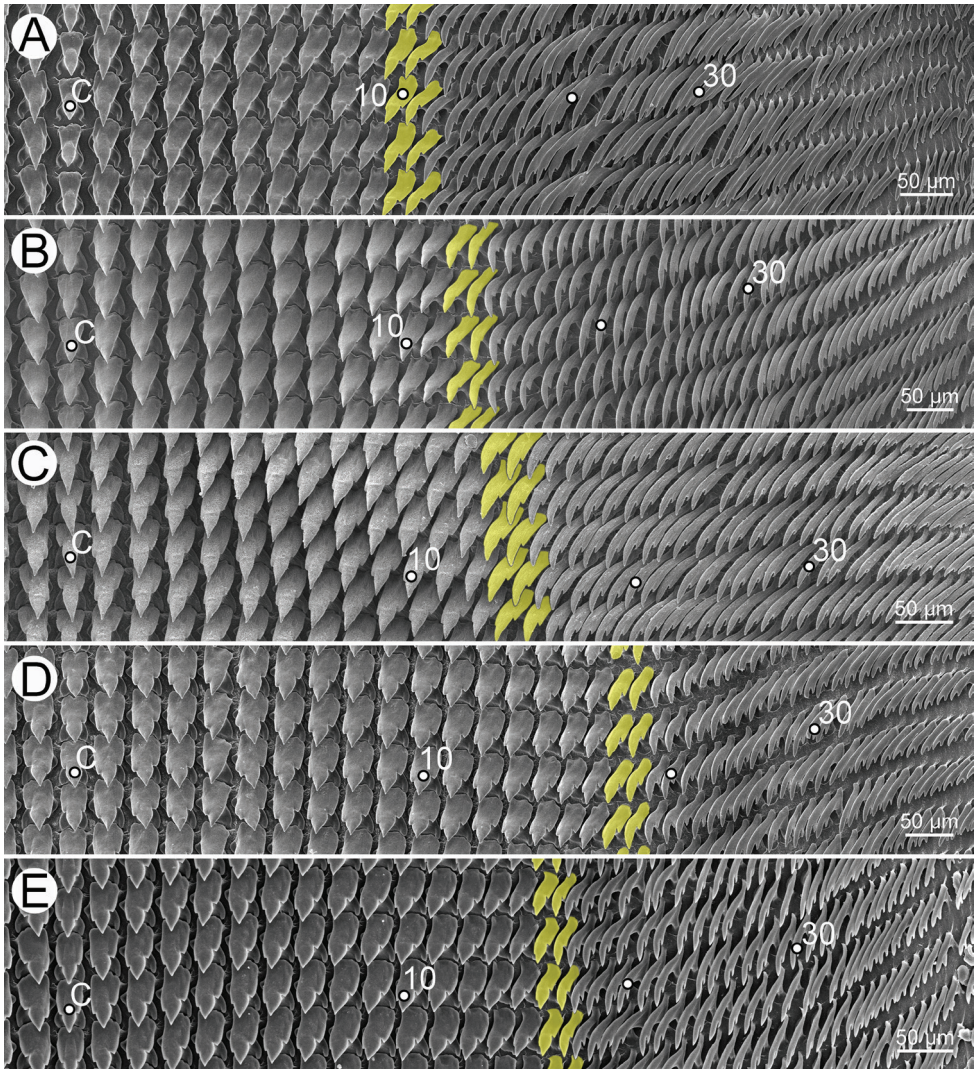


Figure 43. Representative SEM images of the radula. **A** *Sarika hainesi* specimen CUMZ 7237 **B** *S. bocourti* specimen CUMZ 7597 **C** *S. inferospira* sp. nov. paratype CUMZ 7255 **D** *S. melanospira* sp. nov. paratype CUMZ 7243, and **E** *S. pellosa* sp. nov. specimen CUMZ 7251. Central tooth indicated by 'C'; Yellow colour indicates lateral teeth with the transition to marginal teeth.

II, branching into small spines and spinules. Region furthest away smooth and without spine; terminal part (more than ca. one-third of its length) with series of long branching spines arranged in a row or encircled the tail filament tip (Fig. 42).

Radula. Teeth with half row formula: 1–(15–16)–50. Central tooth symmetrical tricuspid; lateral teeth asymmetrical tricuspid; marginal teeth elongate bicuspid. Marginal teeth starting at approximately row number 15 or 16 (Fig. 43E).

External features. Animal with reticulated skin and blackish body. Foot sole and caudal foss present; caudal horn raised. Four mantle lobes well developed and same colour as body. Left shell lobe absent (Fig. 33F).

Etymology. The specific name *pellosa* is from the Greek word *pellos* meaning dusky and refers to the blackish body that characterises this species.

Distribution. This species is only known from several limestone karsts in Sa Kao Province (Fig. 32).

COI analysis. The ML and BI analyses of *S. pellosa* sp. nov. (n = 3) revealed that all specimens formed a well-supported clade (Fig. 1; BS = 96%, PP = 1), sister group to *S. inferospira* sp. nov. + *S. melanospira* sp. nov. + *S. bocourti* with moderate support (Fig. 1; BS = 73%, PP = 0.99). The mean intraspecific genetic distance of *S. pellosa* sp. nov. was 2.1% (Table 2).

Remarks. The shell of *S. pellosa* sp. nov. differs from other species in *Sarika hainesi* group by having a rounded to very weak shouldered body whorl. In contrast, the shells of *S. hainesi* and *S. bocourti* have obtusely angulated body whorls and *S. inferospira* sp. nov. has a shouldered body whorl.

The shell of this new species is generally similar to *S. melanospira* sp. nov. The distinguishing characters of *S. pellosa* sp. nov. are a broader body whorl, larger size of flagellum, vagina and free oviduct, and animal without a dark spiral band, while *S. melanospira* sp. nov. has a broad body whorl, smaller size of flagellum, vagina and free oviduct, and animal with a dark spiral band below the suture at the body whorl. In addition, the average interspecific sequence divergences between *S. pellosa* sp. nov. and *S. melanospira* sp. nov. are fairly high (6.6%). Therefore, we treat them as two separate species.

Group III: *Sarika dugasti* group: species with left shell lobe and penial pseudo-verge.

Sarika dugasti (Morlet, 1891)

Figs 1, 44, 45A, 46A, B, 47A, B, 48A

Macrochlamys dugasti Morlet, 1891a: 25, 26. Type locality: “forêts des bords du Ménam-Pinh, Laos occidental” [forest edges of Ping River, Thailand]; Fischer-Piette 1950: 159; Panha 1996: 34; Hemmen and Hemmen 2001: 44.

Ariophanta (Macrochlamys) dugasti: Morlet 1891b: 231, 239, 240, pl. 5, figs 1, 1a; Fischer 1891: 20.

Nanina (Macrochlamys) dugasti: Fischer and Dautzenberg 1904: 395.

Sarika dugasti: Tomlin 1929: 16. Maneevong 2000: 31, fig. 4–3; Sutcharit and Panha 2008: 96; Schileyko 2011: 34. Inkhavilay et al. 2019: 149, fig. 59f; Pholyotha et al. 2020c: 19, Fig. 9f.

Type material. **Syntype** MNHN-IM-2000-27884 (one shell; Fig. 46A) from Forêts des bords du Ménam-Pinh, Laos occidental [forest edges of Ping River, Thailand]. Possible syntype NHMUK 1893.12.8.31 (one shell).

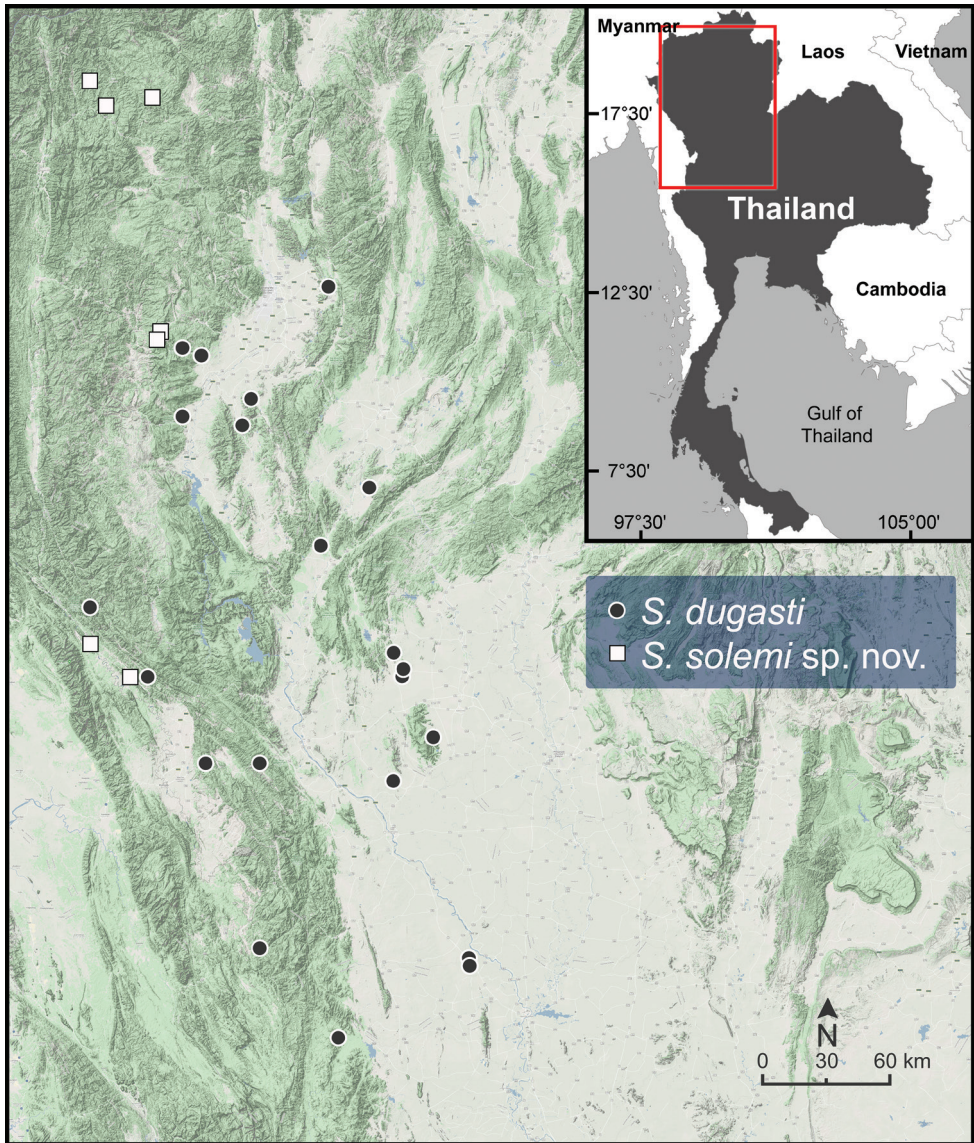


Figure 44. Geographic distribution of *Sarika dugasti* and *S. solemi* sp. nov. based on the specimens examined herein.

Other material examined. **MYANMAR.** Phaboo, Salwin Valley, Burma: NHMUK 1891.3.17.559 60 (two shells). Moulmein: NHMUK 1887.06.1.1 (two shells). **THAILAND.** Siam: NHMUK 1903.7.1.100, NHMUK 1901.1.06.38 (specimen figured in Blanford and Godwin-Austen 1908: Fig. 48), SMF 90841/2 (two shells). **THAILAND-Western.** Wat Tham Inthanin, Mae Sot, Tak, 16°46'01.4"N, 98°40'21.5"E: CUMZ 7567. Limestone outcrop in Mae Sot, Mae Sot, Tak, 16°45'40.8"N, 98°43'08.1"E: CUMZ 7568, 7569. Chao Por Phawo Shrine, Mae Sot, Tak, 16°46'16.9"N, 98°41'09.1"E: CUMZ 7571, 7572, 7573, 7574. Limestone outcrop in Tha Song

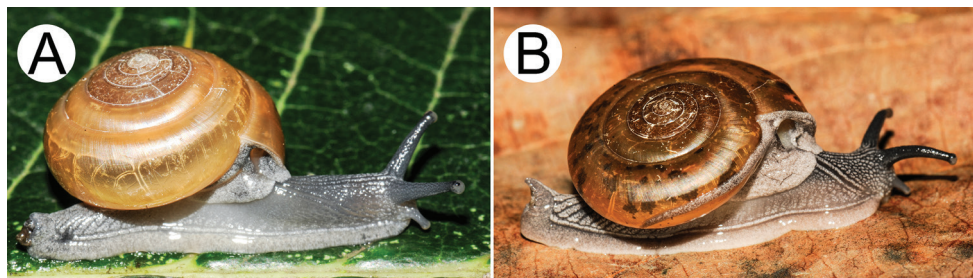


Figure 45. Living snails of Group III: *Sarika dugasti* group. **A** *Sarika dugasti* specimen CUMZ 7563 and **B** *S. solemi* sp. nov. paratype CUMZ 7298. Not to scale.

Yang, Tha Song Yang, Tak, 17°27'11.8"N, 98°10'39.2"E: CUMZ 7570. Ban Nam Ok Hu, Tha Song Yang, Tak, 17°07'54.4"N, 98°23'41.5"E: CUMZ 7575. Limestone outcrop in Umphang, Umphang Tak, 16°00'53.4"N, 98°56'47.7"E: CUMZ 7576. **THAILAND-Central.** Pitsunaloke, Siam: NHMUK 1903.2.4.82–84 (four shells). Limestone area near Huai Kha Khaeng, Lan Sak, Uthai Thani, 15°36'31.1"N, 99°19'15.0"E: CUMZ 7543. Limestone outcrop in Phran Kratai, Phran Kratai, Kamphaeng Phet, 16°40'40.1"N, 99°32'27.1"E: CUMZ 7541. Wat Khao Huai Lung, Banphot Phisai, Nakhon Sawan, 15°55'30.2"N, 99°52'28.9"E: CUMZ 7564. Wat Thep Sathaporn, Banphot Phisai, Nakhon Sawan, 15°54'48.7"N, 99°53'04.0"E: CUMZ 7565, 7566. Tham Yok, Ban Dan Lan Hoi, Sukhothai, 17°08'15.9"N, 99°33'00.5"E: CUMZ 7542 (Fig. 46B). Limestone outcrop in Na Choeng Khiri, Khiri Mat, Sukhothai, 16°52'38.7"N, 99°41'35.1"E: CUMZ 7557. Tham Lom-Tham Wang, Si Samrong, Sukhothai, 17°13'30.3"N, 99°31'53.0"E: CUMZ 7558, 7559, 7560. Wat Tham Rakhang, Si Samrong, Sukhothai, 17°09'54.2"N, 99°33'36.2"E: CUMZ 7561, 7562, 7563. **THAILAND-Northern.** Lampun, Siam: SMF 298588/2 (two shells). Lampoon, Siam: NHMUK MacAndrew Coll. Acc. No. 1563 (three shells), NHMUK Kennard Coll. Acc. No. 1824 (one shell), NHMUK ex. 392 (five shells). Tham Luang Pha Wiang, Ban Hong, Lamphun, 18°13'18.7"N, 98°51'27.7"E: CUMZ 7551, 7552, 7553, 7554, 7577. Erawan Cave, Pa Sang, Lamphun, 18°19'38.4"N, 98°52'17.9"E: CUMZ 7555, 7556. Wat Tham Pha Ngam, Mae Phrik, Lampang, 17°28'49.6"N, 99°10'05.3"E: CUMZ 7549. Wat Tham Suk Kasem Sawan, Thoen, Lampang, 17°42'40.0"N, 99°12'25.2"E: CUMZ 7550. Wachirathan Waterfall, Chom Thong, Chiang Mai, 18°32'31.2"N, 98°35'53.7"E: CUMZ 7544. Borichinda Cave, Chom Thong, Chiang Mai, 18°30'02.8"N, 98°40'20.4"E: CUMZ 7545, 7546. Wat Tham Tong, Chom Thong, Chiang Mai, 18°15'19.8"N, 98°34'48.0"E: CUMZ 7547. Wat Tham Muang On, Mae On, Chiang Mai, 18°47'46.3"N, 99°14'05.5"E: CUMZ 7548.

Diagnosis. Shell medium, globosely depressed, pale to dark brown with well-rounded body whorl. Animal with greyish body and five mantle lobes. Genitalia with a long straight epiphallic caecum and long pseudo-verge. Inner penial sculpture with small cuboidal pilasters in proximal part, then reticulated pilasters in the middle, and larger cuboidal pilasters in distal end.

Description. Shell. Shell globosely depressed, medium size (shell width up to 17.2 mm, shell height up to 10.5 mm), and rather thin. Shell surface smooth and shining;

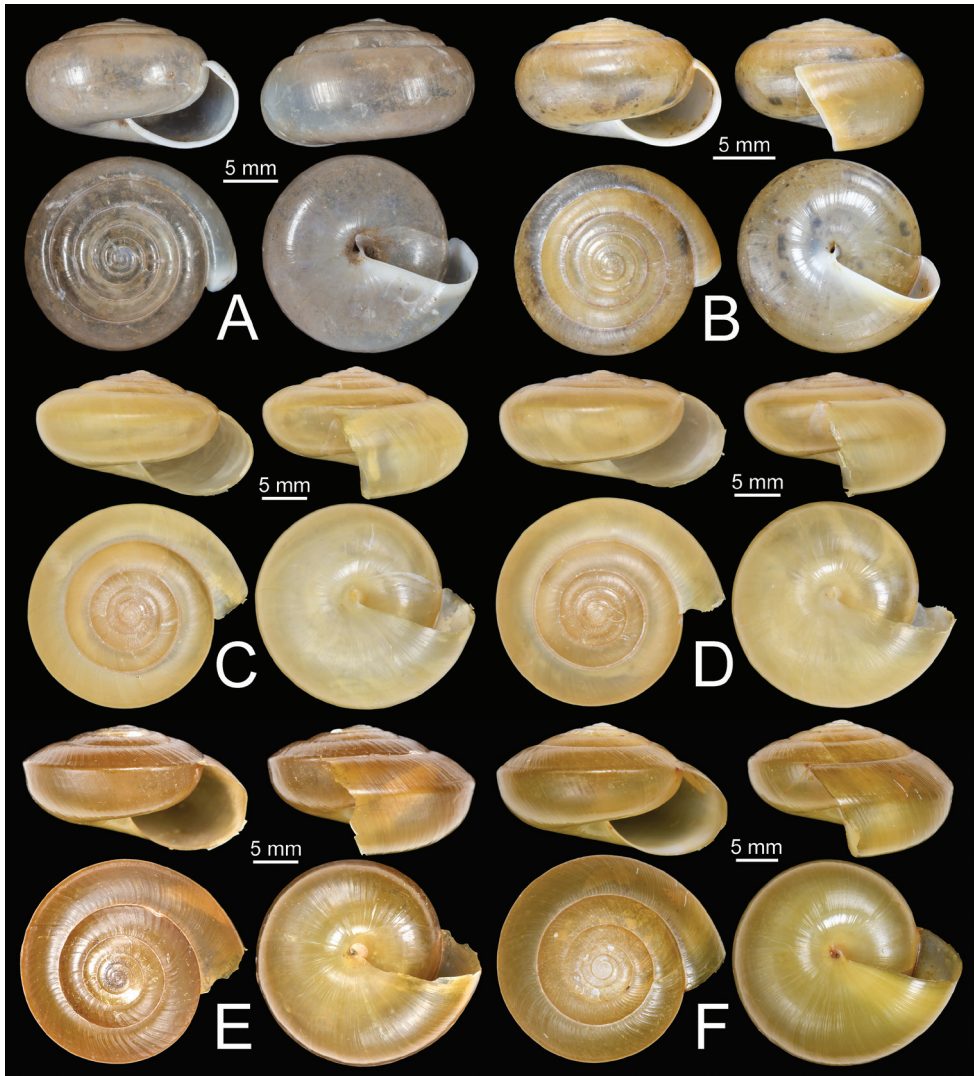


Figure 46. Shells of Group III: *Sarika dugasti* group. **A, B** *Sarika dugasti* **A** syntype MNHN-IM-2000-27884 and **B** specimen CUMZ 7542, **C–F** *S. solemi* sp. nov. **C** holotype CUMZ 7297 **D** paratype CUMZ 7298, and **E, F** specimen CUMZ 7503.

shell colour very pale to dark brown. Whorls $6\frac{1}{2}$ – $7\frac{1}{2}$, increasing regularly; body whorl large and well rounded. Spire much elevated; suture impressed. Aperture crescent-shaped and obliquely opened. Peristome simple and slightly thickened. Columellar margin simple and slightly reflected near umbilicus. Umbilicus narrowly opened (Fig. 46A, B).

Genital organs. Atrium short. Penis long cylindrical with thin penial sheath covering penis. Proximal penis rather slender; distal penis enlarged with pseudo-verge inside. Inner sculpture of penis proximally with very finely longitudinal penial pilasters to nearly smooth surface, then transformed to small cuboidal and reticulated pilaster in middle and modified to larger cuboidal pilasters at distal end. Pseudo-verge elon-

gate conic and approximately one-third of penis length. Epiphallus cylindrical, and narrower than distal penis. Epiphallic caecum very long, straight, and same diameter as epiphallus. Penial retractor muscle thin and attached at tip of epiphallic caecum. Flagellum long, slender, and approximately as long as penis. Vas deferens thin tube connecting distal epiphallus and free oviduct (Fig. 47A, B).

Vagina short and approximately one-third of penis length. Dart apparatus large, long cylindrical, and located on atrium at vagina and penis junction. Gametolytic organ (sac and duct) small and long cylindrical tube. Free oviduct cylindrical, approximately as long as vagina, and proximal end encircled with thick tissue (Fig. 47A).

Radula. Teeth with half row formula: 1–(11–12)–47. Central tooth symmetrical tricuspid; lateral teeth asymmetrical tricuspid; marginal teeth elongate bicuspid. Marginal teeth starting at approximately row number 11 or 12 (Fig. 48A).

External features. Animal with reticulated skin, greyish body, slightly pale colour on foot sole and darker colour on caudal horn. Mantle edge well developed with three dorsal lobes and two shell lobes, and similar colour to body (Fig. 45A).

Distribution. *Sarika dugasti* occurs in central, north and western Thailand along the Tenasserim Ranges (Fig. 44) and the Salween Valley, east of the Dawna Ranges in Myanmar (Blanford and Godwin-Austen 1908; Pholyotha et al. 2020c). However, the literature records from Laos, Nepal and Vietnam (Schileyko 2011; Inkahvilay et al. 2019) are still uncertain.

COI analysis. The ML and BI analyses revealed that the individuals of *S. dugasti* ($n = 3$) formed a monophyletic group with good support (Fig. 1; BS = 91%, PP = 1). The mean intraspecific genetic distance of *S. dugasti* was 3.7% (Table 2).

Remarks. *Sarika dugasti* can be distinguished from all other known *Sarika* species by having a dome-shaped shell with narrow aperture and genitalia with a very long epiphallic caecum and long pseudo-verge. Other *Sarika* species tend to have a flattened to depressed shell with a wide aperture and genitalia without penial verge. Although we surveyed during the wet season, only immature snails were collected, and so the radula and genitalia of sub-adult specimens are illustrated here.

Sarika solemi Pholyotha & Panha, sp. nov.

<http://zoobank.org/FC15ADFA-11D7-413F-8AED-21FE6C7C2B27>

Figs 1, 44, 45B, 46C–F, 47C, D, 48B

Sarika aff. *hainesii* [sic]: Solem 1966: 38, 39, fig 5a (non Pfeiffer 1856a: 32); Sutcharit and Panha 2008: 96.

Type material. *Holotype* CUMZ 7297 (Fig. 46C, width 24.4 mm, height 13.5 mm).

Paratypes CUMZ 7298 (15 shells and 26 specimens preserved in ethanol; Fig. 46D, width 24.8 mm, height 12.7 mm), NHMUK 20200288 (two shells), SMF (two shells), ZRC.MOL.017030 (two shells).

Other material examined. **THAILAND–Western.** Ban Nam Ok Hu, Tha Song Yang, Tak, 17°08'01.2"N, 98°22'01.8"E: CUMZ 7504. Mae Usu Cave, Tha Song Yang, Tak,

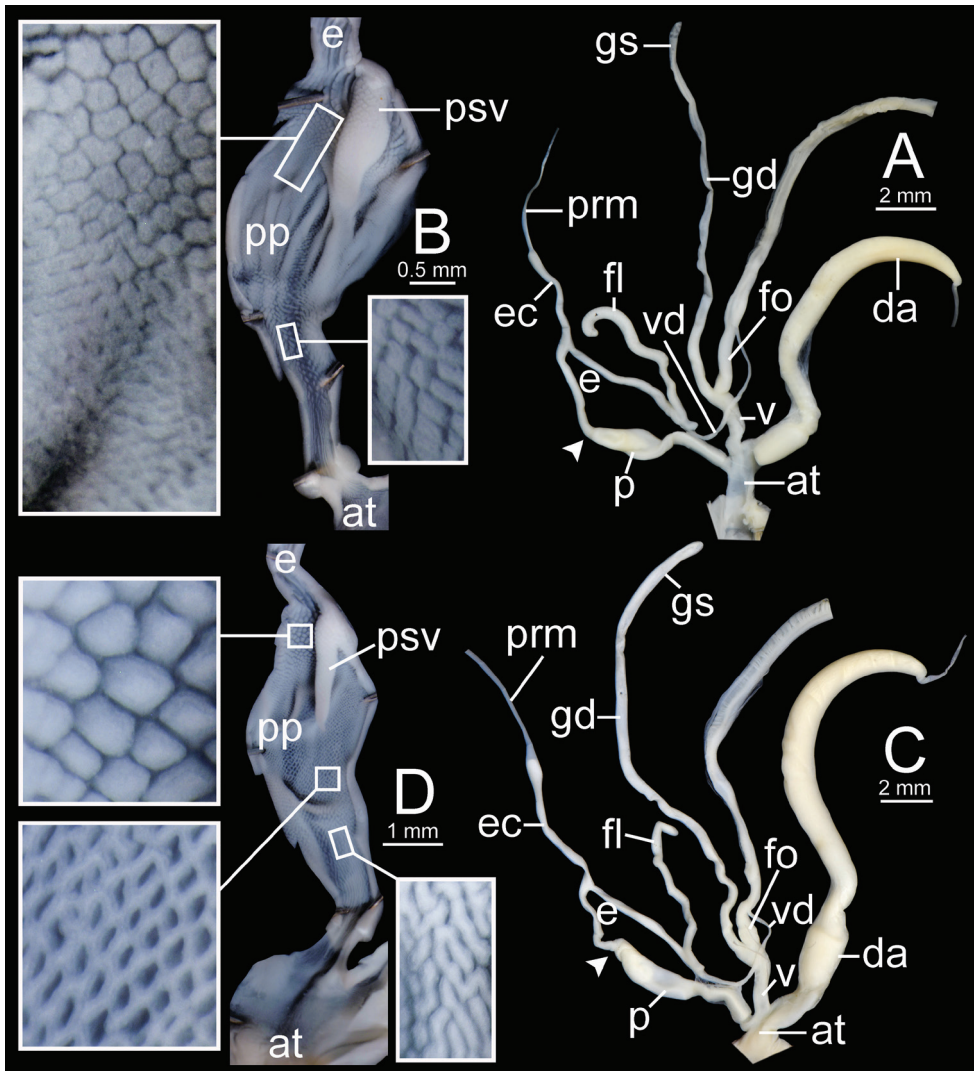


Figure 47. Genitalia. **A, B** *Sarika dugasti* specimen CUMZ 7542 **A** general view of the genital system and **B** internal structure of the penis **C, D** *S. solemi* sp. nov. paratype CUMZ 7298 **C** general view of the genital system and **D** internal structure of the penis. White arrowheads indicate the ends of the penes.

17°18'14.7"N, 98°09'20.8"E: CUMZ 7505. **THAILAND-Northern.** Mountain area in Mae Na Toeng, Pai, Mae Hong Son, 19°34'40.5"N, 98°25'55.9"E: CUMZ 7300. Wat Pang Kham, Pang Mapha, Mae Hong Son, 19°41'03.3"N, 98°12'30.5"E: CUMZ 7501. Huai Nam Dang, Mae Taeng, Chiang Mai, 19°18'48.9"N, 98°36'19.2"E: CUMZ 7299. Kew Mae Pan, Chom Thong, Chiang Mai, 18°33'21.1"N, 98°28'56.0"E: CUMZ 7503 (Fig. 46E, F). Doi Inthanon, Chom Thong, Chiang Mai, 18°35'16.9"N, 98°29'13.4"E: CUMZ 7502. Mountain area in Chom Thong, Chiang Mai, 18°32'05.2"N, 98°31'02.8"E: CUMZ 7911.

Type locality. The limestone karsts with dry forest near Mae La Na Cave, Pang Mapha, Mae Hong Son, Thailand, 19°34'25.5"N, 98°13'01.8"E.

Diagnosis. Shell large, depressed and yellowish brown to brown with obtusely angulated to angulated body whorl. Animal with creamy-grey body and five mantle lobes. Genitalia with a long straight epiphallic caecum and long pseudo-verge. Inner penial sculpture with irregularly short folded pilasters in proximal part, then reticulated pilasters in the middle, and cuboidal pilasters in distal end.

Description. Shell. Shell depressed, large size (shell width up to 26.5 mm, shell height up to 15.0 mm) and rather thin. Surface rather smooth and polished; shell colour yellowish brown to brown. Whorls 6–6½, increasing regularly; body whorl large and obtusely angulated to angulated. Spire moderately to very much elevated; suture impressed. Aperture crescent-shaped and obliquely opened. Peristome simple. Columellar margin simple and slightly reflected near umbilicus. Umbilicus narrowly opened (Fig. 46C–F).

Genital organs. Atrium short. Penis cylindrical with thin penial sheath covering proximal penis. Proximal penis rather slender; distal penis enlarged with pseudo-verge inside. Inner sculpture of penis proximally with very finely longitudinal penial pilasters to nearly smooth surface, then changed to irregularly short folded pilasters, modified to reticulated pilasters in middle, and modified to cuboidal pilasters at distal end. Pseudo-verge long conic, approximately one-third of total penis length. Epiphallus long cylindrical and narrower than distal penis. Epiphallic caecum very long, straight, and almost same diameter as epiphallus. Penial retractor muscle thin and attached at tip of epiphallic caecum. Flagellum long slender, and approximately as long as penis. Vas deferens thin tube connecting distal epiphallus, and free oviduct (Fig. 47C, D).

Vagina cylindrical and approximately one-fourth of penis length. Dart apparatus large, long cylindrical, and located on atrium at vagina and penis junction. Gametolytic organ (sac and duct) small and long duct. Free oviduct cylindrical and proximal end encircled with thick tissue (Fig. 47C).

Radula. Teeth with half row formula: 1–(12–13)–54. Central tooth symmetrical tricuspid; lateral teeth asymmetrical tricuspid; marginal teeth elongate bicuspid. Marginal teeth starting at approximately row number 12 or 13 (Fig. 48B).

External features. Animal with reticulated skin and dark creamy mixing with grey to dark grey body, very pale grey foot sole and pale grey caudal horn. Five mantle lobes well developed and same colour as body (Fig. 45B).

Etymology. The specific name *solemi* is named in honor of Dr. Alan Solem, who first discovered and described the genitalia of this species but under the name *Sarika* aff. *hainesii*.

Distribution. *Sarika solemi* sp. nov. seems to be restricted to western and northern Thailand along the Tenasserim Ranges (Fig. 44). This species occurs in forested mountains and is highly abundant in limestone habitats.

COI analysis. The ML and BI analyses showed that the individuals of *S. solemi* sp. nov. (n = 3) formed a monophyletic group with high support (Fig. 1; BS = 95%, PP = 1). The mean intraspecific genetic distance of *S. solemi* sp. nov. was 2.9% (Table 2).

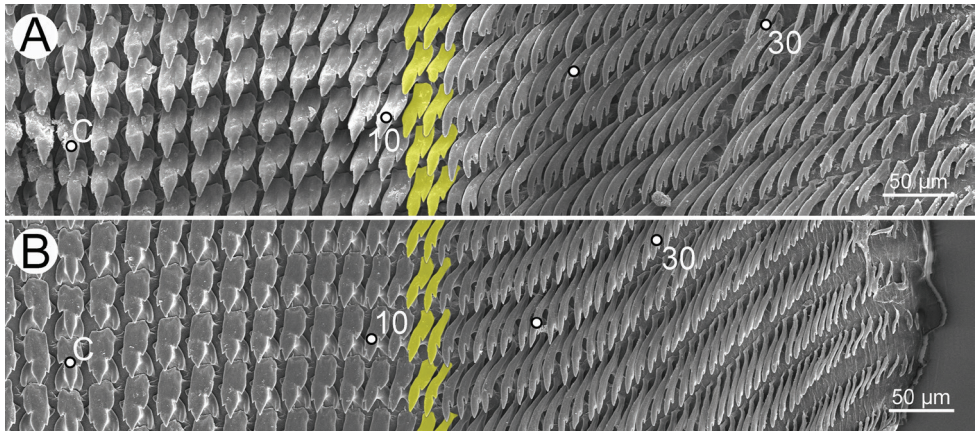


Figure 48. Representative SEM images of the radula. **A** *Sarika dugasti* specimen CUMZ 7574 and **B** *S. solemi* sp. nov. paratype CUMZ 7298. Central tooth indicated by 'C'; Yellow colour indicates lateral teeth with the transition to marginal teeth.

Remarks. Solem (1966) examined and described the genitalia of specimens from northern Thailand and referred them to as “*Sarika* aff. *hainesii*”. In this study, we collected and examined several new specimens from northern Thailand and found that the genitalia were identical with those described and illustrated in Solem (1966: 38, 39, fig 5a). We here recognised these populations as new species. *Sarika solemi* sp. nov. has similar shell morphology to *S. hainesi* s.s., but the distinguishing characters are the number of mantle lobes and genitalia. This new species has five mantle lobes and genitalia with very long epiphallic caecum and long pseudo-verge, while *S. hainesi* s. s. has four mantle lobes, and genitalia with shorter epiphallic caecum and without pseudo-verge.

Sarika solemi sp. nov. is a variable species in terms of body whorl with obtusely angulated periphery (Fig. 46C, D) to obvious angulated periphery (Fig. 46E, F). All shell morphs are identical in genital characters and form a well-supported clade in COI analysis.

Species of doubtful status or uncertain record for Thailand

The following six species have never been examined for their genitalia and no living specimens could be collected in this study. However, we assign them to the genus *Sarika* following current literature and based on their shell characters. They have a relatively large shell diameter (greater than 20 mm), and a smooth and polished shell surface. *Macrochlamys* from Thailand (Pholyotha et al. 2018) tend to have a much smaller shell diameter (less than 20 mm) than the genus *Sarika* (see Table 5). However, living specimens are still necessary for examination of the reproductive organs to ascertain their generic placement.

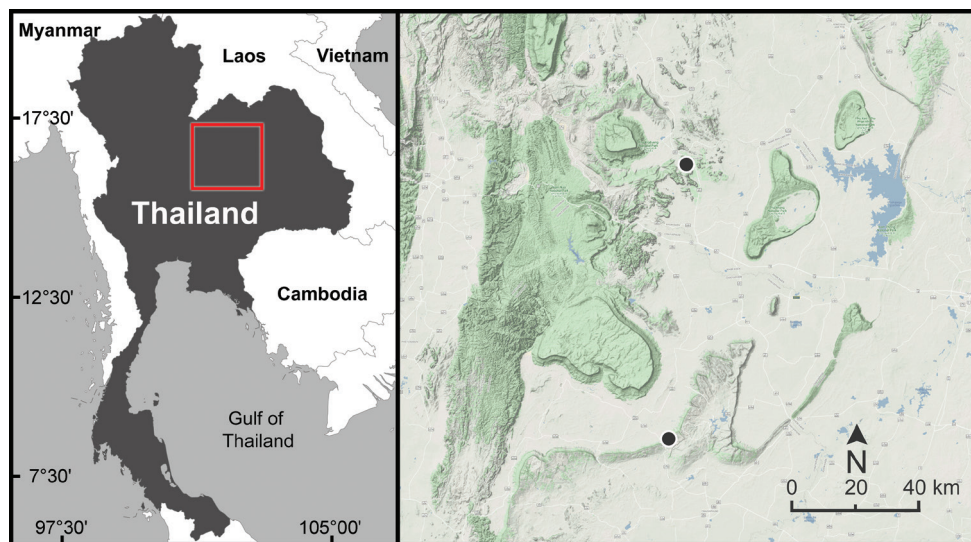


Figure 49. Geographic distribution of *Sarika gratesi* sp. nov. based on the specimens examined herein.

***Sarika gratesi* Pholyotha & Panha, sp. nov.**

<http://zoobank.org/B61773AB-0762-4B4D-A097-162ED9C43720>

Figs 49, 50A, B

Type material. *Holotype* CUMZ 7275 (Fig. 50A, width 16.5 mm, height 8.8 mm). *Paratypes* CUMZ 7276 (10 shells; Fig. 50B, width 16.0 mm, height 8.3 mm), 7912 (30 shells), NHMUK 20200289 (two shells), SMF (two shells), ZRC.MOL.017031 (two shells).

Other material examined. **THAILAND-Northeastern.** Dry dipterocarp forest at Phu Lan Kha, Nong Bua Daeng, Chaiyaphum, 16°00'00.9"N, 101°52'33.4"E: CUMZ 7277.

Type locality. The limestone outcrop with dry deciduous forest at Tham Phraya Nakarat (Cave), Chum Phae, Khon Kaen, Thailand, 16°48'30.3"N, 101°57'13.7"E.

Diagnosis. Shell medium-sized, depressed to strongly depressed, and pale brown. Aperture irregular with peristome rather simple above then expanded middle with curved inside aperture and thickened below periphery.

Description. *Shell.* Shell depressed to strongly depressed or nearly flattened, medium-sized (shell width up to 17.4 mm, shell height up to 8.8 mm), rather thin, and slightly opaque. Shell surface smooth, polished and with thin growth lines; shell colour pale brown. Whorls 6–7, increasing regularly; body whorl large and well rounded. Spire little to moderately elevated; suture impressed. Aperture crescent-shaped and open obliquely; peristome irregular. Apertural lip at upper periphery simple; at periphery with invagination of triangular lip (beak-like); at below periphery rather thickened inside aperture and little expanded. Columellar margin straight, slightly thickened and expanded near umbilicus. Umbilicus narrowly opened (Fig. 50A, B).

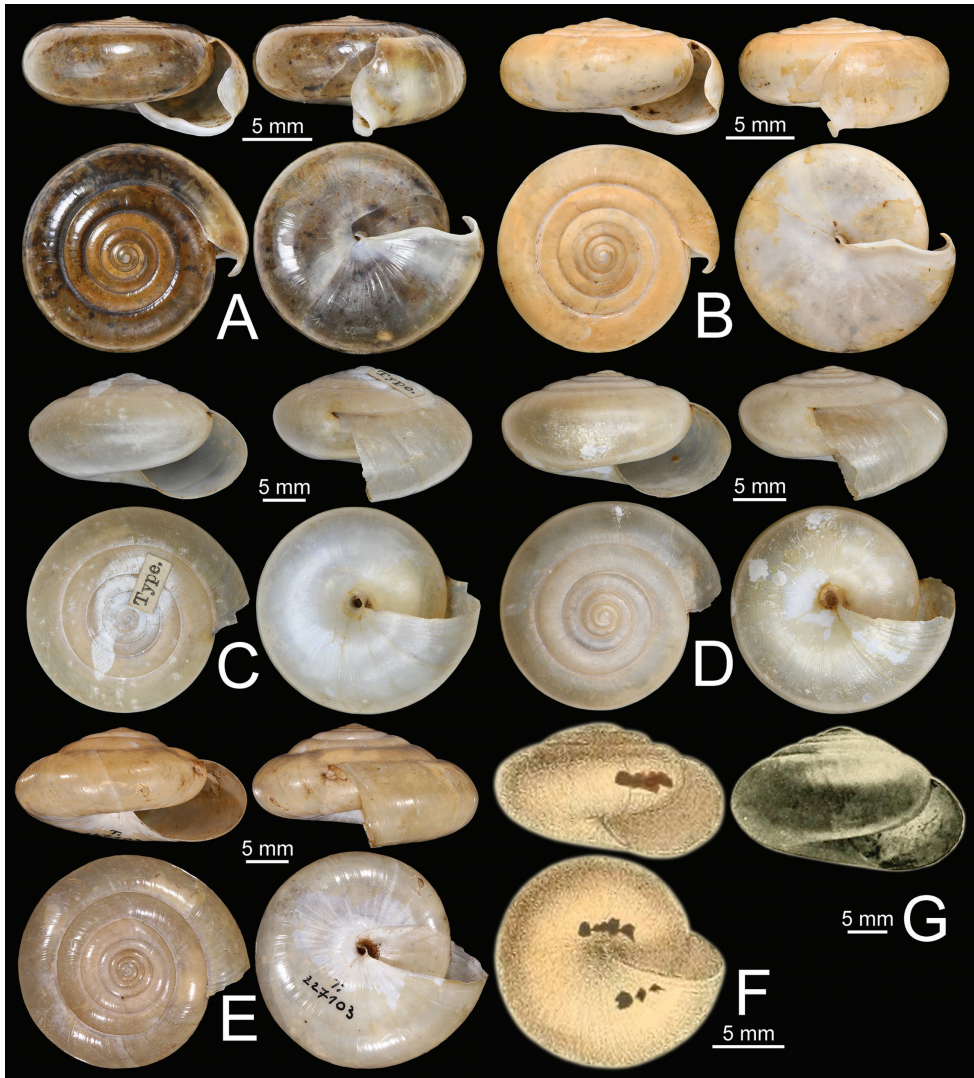


Figure 50. Shells of *Sarika* spp. **A, B** *Sarika gratesi* sp. nov. **A** holotype CUMZ 7275 and **B** paratype CUMZ 7276 **C, D** *S. pumicata* syntype NHMUK 1893.2.4.980–981 **E** *S. octogyra* holotype SMF 227103/1 **F** *S. benoitii* modified from Crosse and Fischer (1863) **G** *S. rex* modified from Preston (1909).

Etymology. The specific name *gratesi* is named in honour to Admiral Chorchat Gra-tes of the Royal Thai Navy, who made possible many fieldtrips especially the remote islands areas in Thailand.

Distribution. *Sarika gratesi* sp. nov. is currently known from the restricted area of the dry deciduous and dry dipterocarp forests in Khon Kaen and Chaiyaphum provinces (Fig. 49).

Remarks. This new species is easy to distinguish from all known *Sarika* as well as *Macrochlamys* species by its unique beak-like lip, while all other species in these two

genera have simple to little thickened lips. Only, *Macrochlamys aspides* (Benson, 1863) from Myanmar tends to have a slightly thickened and expanded lip at below periphery, but *Sarika gratesi* sp. nov. has a projecting and curved triangular shape lip at the periphery. *Sarika gratesi* sp. nov. is identical to *Sarika* because its shells are matched with *Sarika* more than the Siam *Macrochlamys* (Pholyotha et al. 2018).

***Sarika subcornea* (Pfeiffer, 1861)**

Helix subcornea Pfeiffer, 1861: 20. Type locality: “Siam” [Thailand]; Pfeiffer 1868: 102, 103.

Nanina (Orobia) subcornea: Martens 1867: 73.

Nanina (Macrochlamys) subcornea: Tryon 1886: 92; Fischer and Dautzenberg 1904: 395.

Ariophanta (Macrochlamys) subcornea: Fischer 1891: 21.

Nanina subcornea: Fischer and Dautzenberg 1904: 395; Hemmen and Hemmen 2001: 45.

Sarika subcornea: Maassen 2001: 114.

Type material. The type specimen could not be located in the NHM collections.

Diagnosis. Shell depressed, medium size (shell width up to 13.6 mm, shell height up to 6.0 mm) and thin. Shell surface smooth and shining; shell colour whitish horny. Whorls 7½, increasing regularly; body whorl well rounded. Spire elevated; suture impressed. Aperture crescent-shaped and obliquely opened. Peristome simple and slightly thickened. Columellar margin simple. Umbilicus narrowly opened.

Remarks. The original description is not illustrated, type specimen could not be traced, and no new specimens have been reported so far. Hanley and Theobald (1876: 59, pl. 149, Figs 2, 3) illustrated this species based on a specimen from “Phie Than” [Payathonzu, Myanmar]. But, Blanford and Godwin-Austen (1908) stated that this specimen was instead a juvenile shell of *S. resplendens*. Recently, Maassen (2001) also reported *S. subcornea* as a new record from Kedah, Malaysia, but unfortunately without illustration. Therefore, the taxonomic status of this species is still unclear, and we retained this species within the genus *Sarika* as per Maassen (2001). Godwin-Austen (1883) noted that *S. subcornea* is distinguished from other species by the relatively more numerous and more closely wound whorls.

***Sarika benoiti* (Crosse & Fischer, 1863)**

Fig. 50F

Zonites benoiti Crosse & Fischer, 1863: 346, pl. 14, fig. 4. Type locality: “in loco Fuyen-Moth dicto, Cochinchine” [Phu Yen Province, Vietnam].

Helix benoiti: Pfeiffer 1868: 99; Morelet 1875: 248.

Nanina (Macrochlamys) benoiti: Tryon 1886: 90, pl. 30, fig. 57, 58.

Ariophanta (Macrochlamys?) benoiti: Fischer 1891: 20.

Macrochlamys benoiti: Ancey 1898: 128, pl. 9, Fig. b; Saurin 1953: 113; Schileyko 2011: 30, 31.

Sarika benoiti: Inkhavilay et al. 2019: 81, Fig. 38c; Pholyotha et al. 2020a: 7.

Type material. No type material could be located in the MNHN collections. The illustration from the original description is reproduced here (Fig. 50F).

Diagnosis. Shell depressed, medium size (shell width up to 16.0 mm, shell height up to 9.0 mm), and thin. Shell surface smooth and shining; shell colour brownish. Whorls 6, increasing regularly; body whorl well rounded. Spire elevated; suture impressed. Aperture crescent-shaped and obliquely opened. Peristome simple. Columellar margin simple. Umbilicus narrowly opened (Fig. 50F).

Remarks. This species was described based on a specimen from south-central Vietnam (Crosse and Fischer 1863). Up to now, *Sarika benoiti* has been recorded throughout the Indochina countries (Ancey 1898, Fischer and Dautzenberg 1904, Saurin 1953, Schileyko 2011, Inkhavilay et al. 2019). However, these records remain equivocal and tentative because of unavailable distinguished genital data. In Thailand, *Sarika benoiti* was recorded from eastern Thailand based on specimens from the Pavie collection (Fischer and Dautzenberg 1904).

In this study, the specimens from the eastern part of Thailand agreed well with the syntype of *S. bocourti* (Fig. 34A) where its type locality is in Battambang, Cambodia. Based on shell morphology, *S. benoiti* (Fig. 50F) differs slightly from *S. bocourti* in having a smaller sized and well-rounded body whorl, whereas *S. bocourti* has a larger sized shell (shell width up to 33 mm) and obtusely angulated body whorl.

Sarika pumicata (Morelet, 1875)

Fig. 50C, D

Helix pumicata Morelet, 1875: 248, pl. 12, Fig. 2. Type locality: “Ajuthia, Siam” [Phra Nakhon Si Ayutthaya Province, Thailand]; Breure et al. 2018: 399, Figs 901, 902.

Nanina (Macrochlamys) pumicata: Tryon 1886: 89, pl. 29, Figs 40–42; Fischer and Dautzenberg 1904: 395.

Ariophanta (Xesta) pumicata: Fischer 1891: 20.

Sarika pumicata: Godwin-Austen 1907: 181, pl. 116, Fig. 1; Sutcharit and Panha 2008: 96.

Macrochlamys pumicata: Panha 1996: 34; Hemmen and Hemmen 2001: 44.

Type material. *Syntype* NHMUK 1893.2.4.980–981 (two shells; Fig. 50C, D) from Siam [Thailand].

Other material examined. Siam: NHMUK 1901.1.6.246 (one broken shell, specimen dissected by Godwin-Austen 1907) ex. Daly collection.

Diagnosis. Shell depressed to conoid-depressed, large size (shell width up to 26.0 mm, shell height up to 16.0 mm) and rather thin. Shell surface smooth, slightly shining above and more shining below; shell colour brownish. Whorls 7, increasing regularly; body whorl large and obtusely angulated. Spire high-conical; suture impressed.

Aperture crescent-shaped and obliquely opened. Peristome simple. Columellar margin simple. Umbilicus narrowly opened (Fig. 50C, D).

Remarks. Godwin-Austen (1907: 181, pl. 116, Fig. 1) examined the rehydrated specimens from Thailand and placed this species in the genus *Sarika*. We have examined the specimen dissected (only shell remained) by Godwin-Austen (NHMUK 1901.1.6.246) and noticed that the shell morphology slightly differs from the syntypes. The dissected specimen has a rounded body whorl and lower spire, whereas the syntypes have obtusely angulated body whorl and higher spire. Unfortunately, we could not find any specimens identical to the syntypes during this survey. Additional specimens with precise collection locality and anatomical studies are necessary to confirm the taxonomic position of this species.

Sarika ochtogyra (Möllendorff, 1902)

Fig. 50E

Macrochlamys ochtogyra Möllendorff, 1902: 154, 155. Type locality: “Bangkok”; Hemmen and Hemmen 2001: 44.

Type material. *Syntype* SMF 227103/1 (one shell; Fig. 50E) from Siam: Bangkok.

Diagnosis. Shell depressed, large to very large size (shell width up to 31.8 mm, shell height up to 16.0 mm) and thin. Shell surface rather smooth surface with obvious growth lines; shell colour yellowish brown. Whorls 8, increasing regularly; body whorl large and obtusely angulated. Spire high-conical; suture impressed. Aperture crescent-shaped and obliquely opened. Peristome simple. Columellar margin simple. Umbilicus narrowly opened (Fig. 50E).

Remarks. Compared to the species with shell width greater than 30 mm, *S. ochtogyra* can be distinguished from *S. rex* by having eight whorls and obtusely angulated periphery, while *S. rex* has seven whorls and rounded periphery.

Sarika ochtogyra is currently known only from the type locality in Thailand. Originally, it was described based on a collection made by the butterfly collector, H. Frühstorfer (Lamas 2005). The type locality “Siam: Bangkok” is probably not the location where the type specimen was collected. After surveys throughout Thailand, we could find neither *Sarika* nor *Macrochlamys* with large shell sizes that match well with the type specimen.

Sarika rex (Preston, 1909)

Fig. 50G

Macrochlamys rex Preston, 1909: 202, pl. 8, fig. 2. Type locality: “Nan-ko, Siam” [Thailand]; Adam, 1971: 58.

Type material. The unique name bearing type could not be located. The photograph of the type specimen from the original description is reproduced herein (Fig. 50G).

Diagnosis. Shell conoid-depressed, large to very large size (shell width up to 30.0 mm, shell height up to 16.0 mm) and thin. Shell surface rather smooth with fine growth lines, polished below but not polished above; shell colour pale yellowish brown. Whorls $6\frac{1}{2}$, increasing regularly; body whorl large and rounded. Spire very high-conical; suture impressed. Aperture crescent-shaped and obliquely opened. Peristome simple. Columellar margin simple. Umbilicus narrowly opened (Fig. 50G).

Remarks. We assigned this species to the genus *Sarika* due to its very large shell size, and none of any *Macrochlamys* species could reach that diameter (Table 5). Preston (1909) noted that *S. rex* is a large-sized species and is generally similar to *S. pumicata*, but *S. rex* tended to have more tumid and higher spire than *S. pumicata*, as well as a rounded body whorl, whereas *S. pumicata* has an obtusely angulated periphery.

Sarika rex is known only from the type locality in Thailand; however, the precise type locality could not be determined. To date, no living specimen that matches this species has been found, and the generic assignment is still provisional. New specimens with precise collection locality and genital anatomy are necessary to verify the taxonomic position of this species.

Conclusions

This study updates the state of knowledge of malacofaunal diversity in Thailand and the results increase the number of *Sarika* species recognised in the country to 23, nine of which are new species. Our analyses of morphology and molecular phylogeny resolve and support all *Sarika* species anatomically examined herein (see Fig. 1; Tables 2–5).

Sarika resplendens is regarded as one of the most common and widespread snail species in Thailand and this species is believed to have been accidentally introduced by human activities. However, most of the *Sarika* species have narrow distributional ranges restricted to individual habitats such as sandstone, granite, limestone or forested mountainous areas, and they show allopatric and sympatric distribution patterns, possibly resulting from limited dispersal abilities and the complex geography of the areas. The low dispersal capacities and a narrow ecological niche of land snails may reduce genetic exchange between populations (Shimizu and Ueshima 2000). A conspicuous feature of Thailand is the many extensive ranges of limestone karsts and outcrops scattered throughout the country (Gupta 2005; Naggs et al. 2006; Ridd et al. 2011). Limestone karsts in the humid tropics contain a high diversity of microhabitats that are conducive for land snail speciation and endemism (Clements et al. 2006; Foon et al. 2017).

The subdivision of *Sarika* into three groups (*resplendens*, *hainesi*, and *dugasti*) has been not yet resolved. Therefore, future studies combined with other genetic markers for molecular phylogenetic analyses will be necessary to clarify these subdivisions and may reveal a hypothesis of the evolution and biogeography of this genus.

Table 3. Shell measurements of *Sarika* species in Thailand. The superscript indicates spermatophore morphology reference: ¹ this study, ² Pfeiffer (1861), ³ Crosse and Fischer (1863), ⁴ Morelet (1875), ⁵ Möllendorff (1902), and ⁶ Preston (1909).

<i>Sarika</i> species (no. specimens)	Shell width (mm), mean \pm SD	Shell height (mm), mean \pm SD	Number of whorls
1 <i>S. resplendens</i> ¹ (n = 10)	21.0–23.4, 22.1 \pm 1.0	9.9–11.5, 10.6 \pm 0.5	5½–6½
2 <i>S. dohrniana</i> ¹ (n = 10)	27.1–33.2, 30.0 \pm 2.1	15.2–18.9, 17.1 \pm 1.2	6–6½
3 <i>S. obesior</i> ¹ (n = 10)	19.7–22.1, 20.8 \pm 0.8	10.1–11.3, 10.7 \pm 0.4	5½–6½
4 <i>S. limbata</i> ¹ (n = 11)	23.6–27.0, 25.0 \pm 1.1	11.1–13.7, 12.2 \pm 0.8	6–6½
5 <i>S. heptagyna</i> ¹ (n = 3)	21.9–27.9, 25.8 \pm 3.4	10.6–13.1, 12.0 \pm 1.3	6–7
6 <i>S. kawtaoensis</i> ¹ (n = 11)	22.4–26.6, 24 \pm 1.5	12.1–15.2, 13.3 \pm 0.9	6–7
7 <i>S. caligina</i> sp. nov. ¹ (n = 10)	22.7–25.7, 24.6 \pm 0.8	10.2–12.3, 11.6 \pm 0.6	6–6½
8 <i>S. lactospira</i> sp. nov. ¹ (n = 10)	21.1–23.6, 22.5 \pm 0.9	10.1–11.8, 10.9 \pm 0.6	6–6½
9 <i>S. megalogyne</i> sp. nov. ¹ (n = 10)	17.8–21.2, 19.2 \pm 1.0	9.3–11.3, 10.0 \pm 0.6	6–6½
10 <i>S. subheptagyna</i> sp. nov. ¹ (n = 10)	23.7–26.4, 25 \pm 0.9	10.6–12.4, 11.6 \pm 0.5	6–6½
11 <i>S. hainesi</i> ¹ (n = 10)	21.6–28.1, 24.0 \pm 2.2	10.8–14.9, 11.9 \pm 1.3	6–7
12 <i>S. bocourti</i> ¹ (n = 10)	29.7–33.1, 30.2 \pm 1.3	13.8–16.1, 15.1 \pm 0.8	6–7
13 <i>S. inferospira</i> sp. nov. ¹ (n = 4)	24.8–29.3, 26.8 \pm 2.1	11.0–13.9, 12.4 \pm 1.4	6–6½
14 <i>S. melanospira</i> sp. nov. ¹ (n = 12)	24.3–29.3, 26.0 \pm 1.5	11.6–13.3, 12.1 \pm 0.5	6–6½
15 <i>S. pellosa</i> sp. nov. ¹ (n = 8)	20.8–24.7, 23.4 \pm 1.2	9.3–12.0, 10.7 \pm 0.8	6–6½
16 <i>S. dugasti</i> ¹ (n = 10)	14.6–17.2, 15.8 \pm 0.7	9.1–10.5, 9.7 \pm 0.4	6½–7½
17 <i>S. solemi</i> sp. nov. ¹ (n = 12)	21.0–26.5, 23.2 \pm 1.6	11.5–15.0, 12.5 \pm 1.0	6–6½
18 <i>S. gratesi</i> sp. nov. ¹ (n = 8)	14.8–17.4, 16.2 \pm 0.8	7.6–8.8, 7.9 \pm 0.4	6–7
19 <i>S. subcornea</i> ²	12.5–13.6	6.0	7½
20 <i>S. benoitii</i> ³	14.0–16.0	9.0	6
21 <i>S. pumicata</i> ⁴	23.0–26.0	16.0	7
22 <i>S. ochrogyna</i> ⁵	31.8	16.0	8
23 <i>S. rex</i> ⁶	30.0	16.0	6½

Table 4. Shell morphology, mantle lobes, genitalia and spermatophore of *Sarika* species in Thailand. The visualisation of each character is linked to illustrations in Figures 2–4. Taxa in **bold** are the new species described herein. The superscript indicates spermatophore morphologies: ¹ Shape of ridges on head filament (hf) of spermatophore. ² Number of spines on tail filament close to sperm sac. ³ Length of terminal part of tail filament that contained spines / total length of tail filament.

Species	Shell shape	Body whorl	Left shell lobe	Inner penial sculpture	Penial verge	Ridges on head filament ¹	No. of spines ²	Tail filament ³
<i>S. resplendens</i>	depressed	well-rounded	present	cuboidal	absent	obtuse-serrate	3	1/3
<i>S. dohrniana</i>	depressed to conoid-depressed	rounded to slightly obtusely angulated	present	cuboidal	absent	smooth	2	1/8
<i>S. obesior</i>	depressed	well-rounded	present	triangular prism	absent	obtuse-serrate	3	1/3
<i>S. limbata</i>	depressed	well-rounded	present	reticulated / cuboidal	absent	plate-like with acute-serrate	3	1/3
<i>S. heptagyra</i>	strongly depressed	well-rounded to slightly shouldered	present	cuboidal	absent	n.a.	3	1/4
<i>S. kawtaensis</i>	depressed to globosely depressed	well-rounded	present	reticulated / folded	absent	acute-serrate	3	1/2
<i>S. caligina</i>	depressed	well-rounded	present	triangular prism	absent	smooth	3	1/2
<i>S. lactospira</i>	depressed	slightly shouldered	present	triangular prism	absent	n.a.	n.a.	n.a.
<i>S. megalogyne</i>	depressed	well-rounded to slightly shouldered	present	triangular prism	absent	n.a.	3	3/4
<i>S. subheptagyra</i>	strongly depressed	well-rounded	present	triangular prism	absent	smooth	3	1/4
<i>S. hainesi</i>	depressed	obtusely angulated	absent	triangular prism	absent	sponge-like with obtuse-serrate	2	1/2
<i>S. bocourti</i>	depressed	obtusely angulated	absent	triangular prism	absent	acute-serrate	2	2/3
<i>S. inferospira</i>	strongly depressed	shouldered	absent	triangular prism	absent	n.a.	2	*
<i>S. melanospira</i>	depressed	rounded to weak shouldered	absent	triangular prism	absent	n.a.	n.a.	n.a.
<i>S. pellosa</i>	strongly depressed to depressed	rounded to weak shouldered	absent	triangular prism	absent	n.a.	3	1/3
<i>S. dugasti</i>	globosely depressed	well-rounded	present	smaller cuboidal / reticulated / larger cuboidal	pseudo-verge	n.a.	n.a.	n.a.
<i>S. solemi</i>	depressed	obtusely angulated to angulated	present	irregularly short folded / reticulated / cuboidal	pseudo-verge	n.a.	n.a.	n.a.
<i>S. gratesi</i>	strongly depressed to depressed	well-rounded	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.
<i>S. subcornea</i>	depressed	well-rounded	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.
<i>S. benoitii</i>	depressed	well-rounded	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.
<i>S. pumicata</i>	depressed to conoid-depressed	obtusely angulated	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.
<i>S. ochtogyra</i>	depressed	obtusely angulated	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.
<i>S. rex</i>	Conoid-depressed	rounded	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.

* *Sarika inferospira* sp. nov. has a tail filament with a series of branching spines along its length, except near the middle part which is spineless.

Table 5. Taxa attributed to *Macrochlamys* and *Sarika* from mainland Southeast Asia, as classified by their maximum shell width and maximum whorl numbers. Data are taken from the original descriptions and additional references. Taxa in **bold** are anatomically examined and have confirmed generic placements. The superscript indicates references: ¹ Godwin-Austen (1907) and Blanford and Godwin-Austen (1908), ² Laidlaw (1933), ³ Solem (1966), ⁴ Maneevong (2000), ⁵ Sutcharit and Panha (2008), ⁶ Pholyotha et al. (2018), ⁷ Pholyotha et al. (2020a), ⁸ Pholyotha et al. (2020c), ⁹ this study.

	Maximum number of whorls			
	whorl < 5	5 ≤ whorl < 6	6 ≤ whorl < 7	whorl ≥ 7
Small size (shell width ≤ 10 mm)	<i>M. kumabensis</i> <i>M. patens</i> <i>M. pauxillula</i> <i>M. perpaula</i>	<i>M. bartoni</i> <i>M. brachystia</i> ⁸ <i>M. brunnea</i> <i>M. callojuncta</i> <i>M. cauisa</i> <i>M. curvilabris</i> <i>M. hatchongi</i> <i>M. noxia</i> <i>M. petasus</i> ⁸ <i>M. poongee</i> <i>M. rejectella</i> <i>M. salwinensis</i> <i>M. spreta</i> <i>M. subpetasus</i>	<i>M. euspira</i> <i>M. jousoufi</i>	<i>M. ramburianus</i>
Medium size (10 < shell width < 20)	—	<i>M. aurantia</i> ⁶ <i>M. chaos</i> <i>M. coleus</i> ⁶ <i>M. declivis</i> <i>M. hypoleuca</i> <i>M. malaccana</i> <i>M. psyche</i> <i>M. tanymentula</i> ⁶ <i>M. zero</i> <i>S. nana</i> ⁷ <i>S. planata</i> ²	<i>M. aspides</i> ⁸ <i>M. caverna</i> ⁶ <i>M. excepta</i> <i>M. lemma</i> ⁶ <i>M. nebulosa</i> <i>M. stenogyra</i> <i>M. stephoides</i> <i>S. benoiti</i>	<i>M. notha</i> <i>S. concavata</i> ⁸ <i>S. consepta</i> ⁸ <i>S. dugasti</i> ^{4,9} <i>S. gratesi</i> sp. nov. <i>S. subcornea</i>
Large size (20 ≤ shell width < 30)	—	<i>M. douvillei</i> <i>M. glyptorhapha</i> <i>M. tenuigranosa</i>	<i>M. kelantanensis</i> ^{6,8} <i>S. birmana</i> <i>S. caligina</i> sp. nov. ⁹ <i>S. inferospira</i> sp. nov. ⁹ <i>S. khmeriana</i> ⁷ <i>S. lactoconcha</i> ⁷ <i>S. lactospira</i> sp. nov. ⁹ <i>S. limbata</i> ⁹ <i>S. lopa</i> ⁸ <i>S. megalogyne</i> sp. nov. ⁹ <i>S. melanospira</i> sp. nov. ² <i>S. obesior</i> ^{8,9} <i>S. pellosa</i> sp. nov. ⁹ <i>S. resplendens</i> ^{1,9} <i>S. solemi</i> sp. nov. ^{3,9} <i>S. subheptagyra</i> sp. nov. ⁹	<i>M. despecta</i> <i>S. hainesi</i> ⁹ <i>S. heptagyra</i> ⁹ <i>S. kawtaoensis</i> ⁹ <i>S. pumicata</i>
Very large size (shell width ≥ 30 mm)	—	—	<i>S. dohrniana</i> ⁹ <i>S. rex</i>	<i>S. bocourti</i> ⁹ <i>S. octogyra</i>

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Redescription of *Pseudophera heveli* Kramer (Hemiptera, Cicadellidae) with the first description of the female

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Abstract

Pseudophera heveli Kramer is redescribed from Monteverde, Costa Rica. The female is described for the first time. Fifteen images of the species are provided, including genitalia.

Keywords

Auchenorrhyncha, Neotropical, new species, Proconiini, sharpshooter

Introduction

Sharpshooters are members of the cosmopolitan Cicadellinae, the third largest leafhopper subfamily, with over 2,500 valid species among 357 genera. Sixty-three of these genera, and 468 species, belong to the New World tribe Proconiini (Young 1968; Marucci et al. 2002; Godoy 2005; Rakitov and Godoy 2005; McKamey 2007), which includes the genus *Pseudophera* Melichar.

Species of the genus *Pseudophera* are among the largest leafhoppers, ranging in length from 16 to 20.5 mm. Young (1968) revised the genus and listed six valid species, including one new species and a new synonym. He reported the distribution of the genus as Mexico (one species), Central America (four species), and one species each in Colombia, Ecuador, and Suriname. Subsequently, Kramer (1976) described *P. heveli* from Costa Rica, Nielson and Godoy (1995) described *P. chelicerata* and

P. jimenezi from Costa Rica, and Emmrich (1999) described *P. paraensis* from Brazil and *P. zelayaensis* from Nicaragua, bringing the total number of species to eleven. As Young (1968) noted, *Pseudophera* is “distinguished by its large size and by its earlike, thick, rounded lobe on the epimeron of the metathorax” (Figs 2, 5). McKamey (2007) listed all species in the genus and Wilson et al. (2009) provided habitus images of 10 of them (not *P. zelayaensis*), including a female of *P. heveli* in the California Academy of Sciences, San Francisco, California, also from Monteverde, Puntarenas Province, Costa Rica. The new specimens, all from the type locality, represent both genders but were collected three years apart.

Materials and methods

In providing distribution data, quotation marks separate labels and a vertical line separates lines on a label. All examined specimens are deposited in the United States National Museum of Natural History, Smithsonian Institution, Washington, DC (USNM).

Terminology for general morphology was based on Young (1968) and Dietrich (2005), while leg chaetotaxy follows Rakitov (1998).

A Leica MZ12 stereomicroscope was used to examine structures. The body length was measured using a digital micrometer. A manual 5 mm micrometer was used to determine ratios between other, shorter distances.

The abdomen was detached, macerated in a warmed 10% KOH solution for 24 hours at room temperature, bathed in water, then acetic acid to stop the reaction. After dissection, structures were stored in a glass microvial containing glycerin and pinned beneath the specimen.

Images were taken with a Canon 5Dsr camera with an adjustable 65mm lens. Photos were taken using Capture One Pro version 10.1.2, 64 Bit, Build 10.1.2.23 imaging software, aided by CamLift version 2.9.7.1. The specimen was lit using two adjustable Dynalite MH2050 RoadMax flash heads, each attached to a Manfrotto 244 arm. The light was diffused using a simple, lampshade-style cone of translucent paper between the specimen and light sources. After individual “slices” were photographed, they were compiled into a single, composite image using Zerene Stacker – USDA SI-SEL Lab Bk imaging system, version 1.04, Build T201706041920. Stacked images were enhanced and edited in Adobe Photoshop CSS Extended version 12.0. The scale bar (in Fig. 1) was generated through Photoshop directly from the metadata of the photo.

Results

Pseudophera heveli Kramer, 1976

Figs 1–13

Diagnosis. Pronotum with dorsal processes, short and directed dorsally.



Figures 1–5. *Pseudophera beveli*. Male (1–3) and female (4,5) 1–3 habitus in dorsal, lateral, and anterior views, respectively 4 detail of undissected female sternum, ventral view 5 habitus, lateral view. Scale bar: 8 mm (1).

Description. Measurements (mm). Total length (from anterior of head to tip of forewings in repose) female 18.6, male 18.4; crown length female 2.9, male 2.8; transocular distance female 4.3, male 4.2; interocular distance female and male 3.0; distance

between compound eye and mesal line female and male 1.5; distance between ocellus and mesal line female 0.7, male 0.6; pronotum maximum width female 4.0, male 3.9; pronotum maximum length female and male 3.2; forewing length female 12.1, male 11.8; length of metathoracic femur female 3.0, male 2.6; length of metathoracic tibia female 5.3, male 5.7.

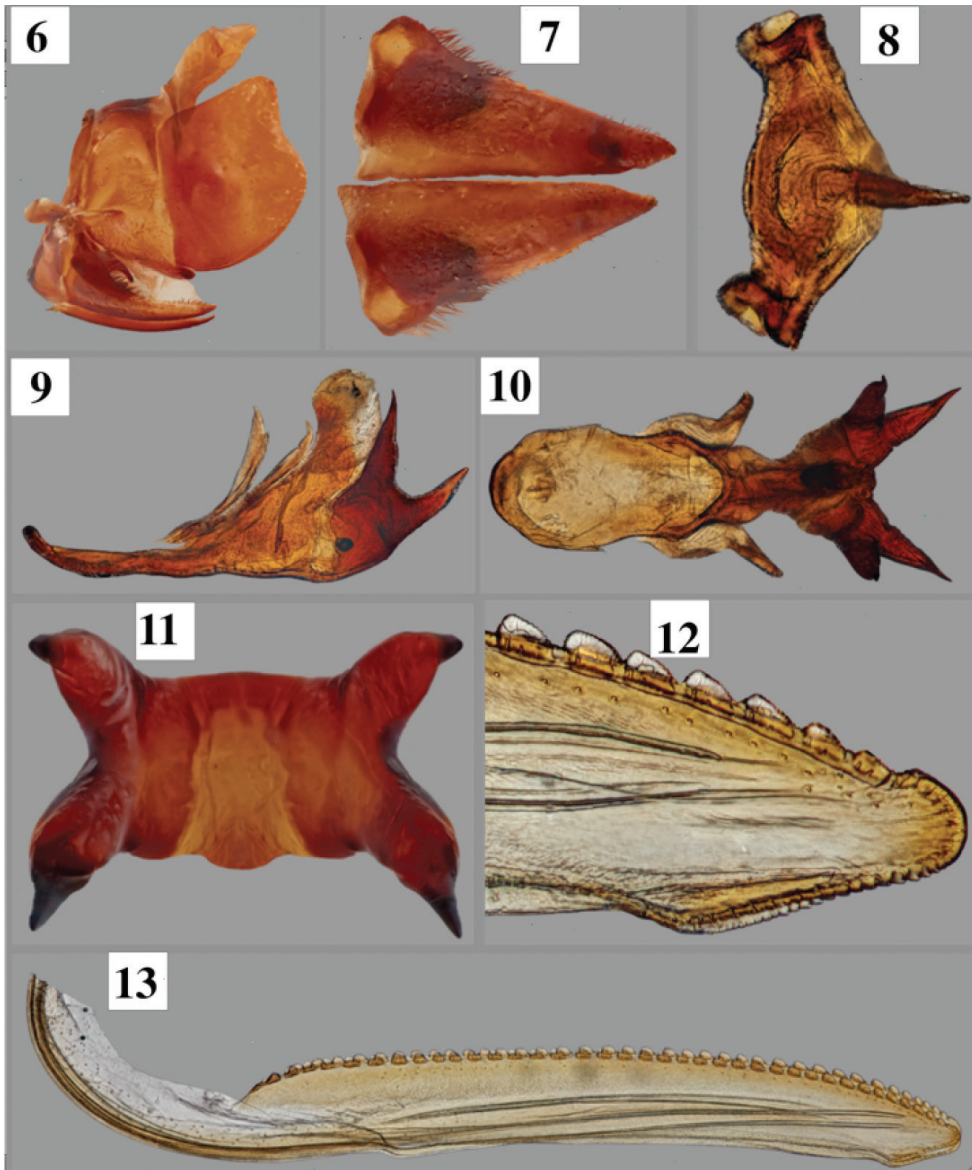
Head (Figs 1–3, 5). Crown maximum length 0.7 times transocular distance and 2.1 times longer than interocular distance in dorsal view; frontoclypeus with deep muscle impressions laterally and planar medially, dorsal surface planar; lateral frontal suture extending onto crown to ocelli. Ocellus located at level of anterior limit of compound eye, distinctly closer to eye than to each other (ratio of distances between eyes vs. between ocelli 2.1). Clypellus anterior margin in lateral view at level of frontoclypeus. Thorax (Figs 1–3, 5). Pronotum maximum width at posterolateral angles 1.1 times wider than transocular distance; maximum length 1.2 times longer than crown length; lateral margins convergent anteriorly, mostly smooth in anterior half, punctate in posterior half; posterior margin transverse; with a pair of suprahumeral processes that are short and directed vertically. Scutellum dorsally smooth, lacking longitudinal carina. Forewing (Figs 1–2, 5) coriaceous; venation with a few extra crossveins between veins R_{4+5} and M_{1+2} . Metathoracic leg with femoral setal formula 2:0:0:0 (AD1 and PD1); tibia with anteroventral row (AV) complete with cucullate (*sensu* Deitz 1975) macrosetae; anterodorsal (AD) and posteroventral (PV) rows complete with uniform non-cucullate macrosetae; posterodorsal (PD) row with smaller, more closely spaced, uniform, noncucullate macrosetae; ratio of length of each individual tarsomere by total tarsus length (excluding pretarsus) equal to 0.5, 0.4 and 0.3, respectively. Coloration. Male unicolorous dark brown throughout. Female unicolorous reddish brown throughout.

Male terminalia. Pygofer (Fig. 6) in lateral view with dorsal margin straight; posterior margin subtruncate. Subgenital plates (Fig. 7) 1.4 times longer than wide at base in ventral view, not fused. Connective (Fig. 8) in dorsal view short (1.5 times wider than long), roughly Y-shaped with anterior arms widely separated and laterally truncate. Style, in dorsal view, without preapical lobe; apex rounded, directed posteriorly beyond connective; ventral margin without preapical dentiform processes. Aedeagus (Figs 9–11) strongly sclerotized, elongate, with 2 pairs of stout spines posteriorly.

Female terminalia. Sternite VII (Fig. 4) transverse, without median emargination of projections; internal sclerotized sternite VIII absent; valvula I (Fig. 14) long, apex acute, lacking spines; valvula II (Figs 12–13) in lateral view serratiform, with 36 teeth, each tooth microserrate on its own dorsal margin; valvula III (Fig. 15) long, broad, apex rounded, basally narrower than distally, lacking spines.

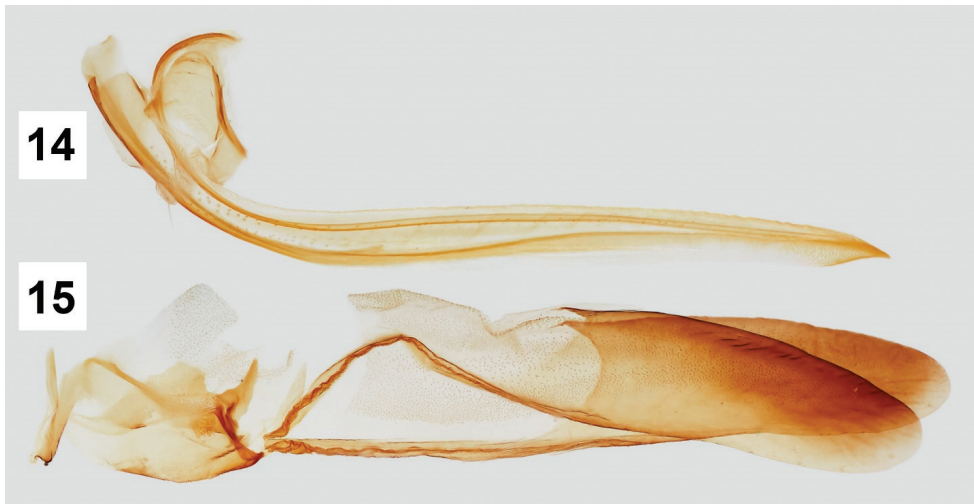
Material examined. 1 male “Costa Rica: | Puntarenas Prov. | Monteverde | 12–21 Apr 1984 | S.McKamey, Coll.” (USNM), 1 female: “Monteverde, Costa Rica | Puntarenas Prov. | 1 July 1981 10:00 am | Stuart McKamey Coll. | flying through foliage | 1/2 way up rd. to Reserve” (USNM).

Distribution. Still known only from Monteverde, Costa Rica, inside and just outside the Reserve. Biology and ecology unknown.



Figures 6–13. Terminalia of *Pseudophera heveli* **6** pygofer, anal segments, and subgenital plates, lateral view **7** subgenital plates, ventral view **8** male connective, dorsal view **9–11** male aedeagus in lateral, dorsal, and posterior views, respectively **12** detail of apex of female valvula II (posterior row of dentae digitally removed) **13** entire valvula II.

Notes. Three species described since Young's (1968) revision reveal that there is more variation in the shape of the posterior margin of the female sternum than indicated in his generic description. Young (1968) described the female sternum VII of *Pseudophera* as "broadly emarginate medially and with a slight convexity within



Figures 14–15. Female valvulae I and III of *Pseudophera heveli* in lateral views, respectively.

the emargination,” based on that of *P. divergens* (Schmidt) and presumably also his new species *P. truncata*, of which he had nine females to examine. Similarly, Emrich’s (1999) illustrations of the female sternum VII indicate that *P. tibialis* Schmidt, *P. contraria* (Walker), *P. heterogena* Schmidt, and *P. paraensis* also have the deep, broad emargination. In contrast, the females of *P. heveli* (Fig. 4), *P. chelicerata* and *P. jimenezi* have the posterior margin of sternum VII transverse, without an emargination or a medial convexity.

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An update of the genera *Idiasta* Foerster and *Rhacalysia* Cameron (Hymenoptera, Braconidae, Alysiinae) and the descriptions of new species from the Neotropical Region

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Abstract

Taxonomic combinations have been made involving the two genera *Idiasta* Foerster and *Rhacalysia* Cameron. Four new species are described from Brazil: *Idiasta rupina* **sp. nov.**, *Rhacalysia ampla* **sp. nov.**, *Rhacalysia jatai* **sp. nov.**, and *Rhacalysia monteiroi* **sp. nov.** Dichotomous identification keys to the Neotropical species of *Idiasta* and *Rhacalysia* are provided. *Phaenocarpa delicata* Papp, 1969 is included in *Rhacalysia* and is a new combination.

Keywords

Alysiini, Brazil, parasitic wasp, parasitoid, taxonomy

Introduction

Idiasta Foerster, 1863 and *Rhacalysia* Cameron, 1910 are both genera of the tribe Alysiini (Braconidae, Alysiinae). Members of *Idiasta* possess the largest set of plesiomorphic characteristics within the *Phaenocarpa* complex (Wharton 2002). The taxon

was revised by Königsman (1969), Papp (1969), Fischer (1975), and Wharton (1980, 2002). The biology of *Idiasta* is poorly known since its members are rarely collected (Wharton 2002). There is a single host record in the literature to *Idiasta euryzona* Wharton, 1980 associated to puparia of *Lispe* flies (Diptera, Muscidae) (Wharton 1984). The genus *Idiasta* is cosmopolitan, currently with 51 described species (Peris-Felipo 2016; Yu et al. 2016), of which three are in the Neotropical Region: *Idiasta euryzona* Wharton, 1980, *I. dixi* Dix, 2010, and *I. maritima* (Haliday, 1838). In the Neotropical Region *Idiasta euryzona* and *I. maritima* are known from Mexico (Wharton 1980), and *I. dixi* from Colombia (Dix 2010). One new species is described and illustrated from Brazil: *Idiasta rupina* sp. nov.

The genus *Rhacalysia* includes four described species: *Rhacalysia congoensis* Fischer, 1993, *R. delicata* (Papp, 1969) comb. nov., *R. profundinigra* Fischer, 1999, and *R. rufobalteata* Cameron, 1910. The biology of *Rhacalysia* is unknown. *Rhacalysia congoensis* is known from Republic of the Congo (Fischer 1993) and *Rhacalysia profundinigra* and *R. rufobalteata* from India (Fischer 1999). Up to now, *Rhacalysia delicata* is the only species of the genus known from the New World and widely distributed in the Neotropical Region. It is reported from Argentina (Papp 1969), Brazil (Arouca and Pentead-Dias 2009), Colombia (Wharton 1980; Dix 2010), Panama, Peru, and Venezuela (Wharton 1980).

The genus *Rhacalysia* was treated as a synonym of *Idiasta* by Shenefelt (1974), Fischer (1967), Bhat (1979), and Marsh (1979), Wharton (1980) considered it at least to be a subgenus, and finally Fischer (1994, 1999), Ray (1999) and Wharton (2002) treated it as a valid genus.

Rhacalysia delicata was originally included in *Phaenocarpa* (Papp, 1969), later attributed to *Idiasta* (Fischer 1975; Wharton 1980), and then transferred to *Rhacalysia* by Fischer (1994) after he examined the male holotype. Peculiarly, *R. delicata* was not included in the key of *Rhacalysia* species by Fischer in 1999. Wharton (2017) pointed to the uncertain generic position of *R. delicata*, but included it in *Idiasta*, as was done by other authors (Braet and van Achterberg 2003; Arouca and Pentead-Dias 2009; Dix 2010). After discovering several additional species reported in this paper, it is obvious that the transfer by Fischer (1994) was correct and we accept the inclusion in *Rhacalysia*. Three new species are described, keyed, and illustrated from Brazil: *Rhacalysia ampla* sp. nov., *R. jatai* sp. nov., and *R. monteiroi* sp. nov.

Materials and methods

Two specimens of *Idiasta* and eight of *Rhacalysia* were studied. *Idiasta rupina* sp. nov. was collected in a grassland environment characterized as rupestrian grassland (campo rupestre) (Fernandes 2016), in a patch of gallery forest, at the Parque Nacional da Serra da Canastra, São Roque de Minas, Minas Gerais, Brazil, at 1317 m. *Rhacalysia ampla* sp. nov. and *R. monteiroi* were collected in the Parque Nacional da Serra dos Órgãos, Teresópolis, Rio de Janeiro, as follows: *Rhacalysia ampla* sp. nov. at 1236 to 1649 m; *Rhacalysia monteiroi* at 252 to 1482 m. In an area of Atlantic forest, the vegetation of

this park is classified as dense ombrophilous forest, and the physiognomies vary according to altitude: low-montane forests occur up to 600–800 m; montane forests are between 600–1600 m; high-montane forests may occur above 1300 m; and altitude fields occur above 1600 m (Rizzini 1979). *Rhacalysia jatai* sp. nov. was collected in Estação Ecológica de Jataí, Luiz Antônio, São Paulo, in a seasonal forest (Coutinho 1978).

Wharton et al. (2017) was used to identify specimens in subfamily and genus. The morphological terminology is based on van Achterberg (1993); terminology for body sculpture follow Eady (1968). The measurements follow Wharton (1977), with additions and modifications by Kula and Zolnerowich (2005, 2008), except for legs, which are as in Peris-Felipo (2016). All the material is deposited in the **DCBU** collection (Departamento de Ecologia e Biologia Evolutiva da Universidade Federal de São Carlos, SP, Brazil).

Digital Scanning Electronic Microscope (SEM) photographs of uncoated specimens were taken with a FEI Quanta 250 SEM in a low vacuum mode. Color digital photographs were taken with a Leica M165C stereomicroscope, using a Leica DFC295 HD camera, LEICA APPLICATION SUITE software version 3.7. ADOBE PHOTOSHOP CS5 Extended version 12.1. was used for minor corrections of images and for the preparation of plates.

Taxonomic accounts

Genus *Idiasta* Foerster, 1863

Type species. *Idiasta (Alysia) maritima* Haliday, 1838

Diagnosis. Mandibles with three teeth, ventral and diagonal ridges well developed. First flagellar segment equal or shorter than second. Fore wing pterostigma broad, discrete, wedge-shaped; 2-SR vein longer than 3-SR. Hind wing with m-cu present, often well developed, M+CU generally equal to or longer than 1-M.

Hosts. Muscidae (Diptera).

Distribution. Cosmopolitan.

Idiasta rupina sp. nov.

<http://zoobank.org/5866B8BE-42BC-4683-84DD-B1F489BC711F>

Figures 1–7

Type material. *Holotype* pinned, female, (DCBU 404791) Brazil, Minas Gerais, São Roque de Minas, Parque Nacional da Serra da Canastra, 20°15'15.29"S, 46°25'14.38"W, alt. 1317 m, 05–07.I.2019, rupestrian grassland, Moericke traps, A. S. Soares col. *Paratype*, male, (DCBU 404792) same data as holotype.

Diagnosis. *Idiasta rupina* is distinct from other Neotropical species in having the eyes glabrous, notauli incomplete, metanotum with high median flange, m-cu of fore wing interstitial, and fore wing cu-a postfurcal.

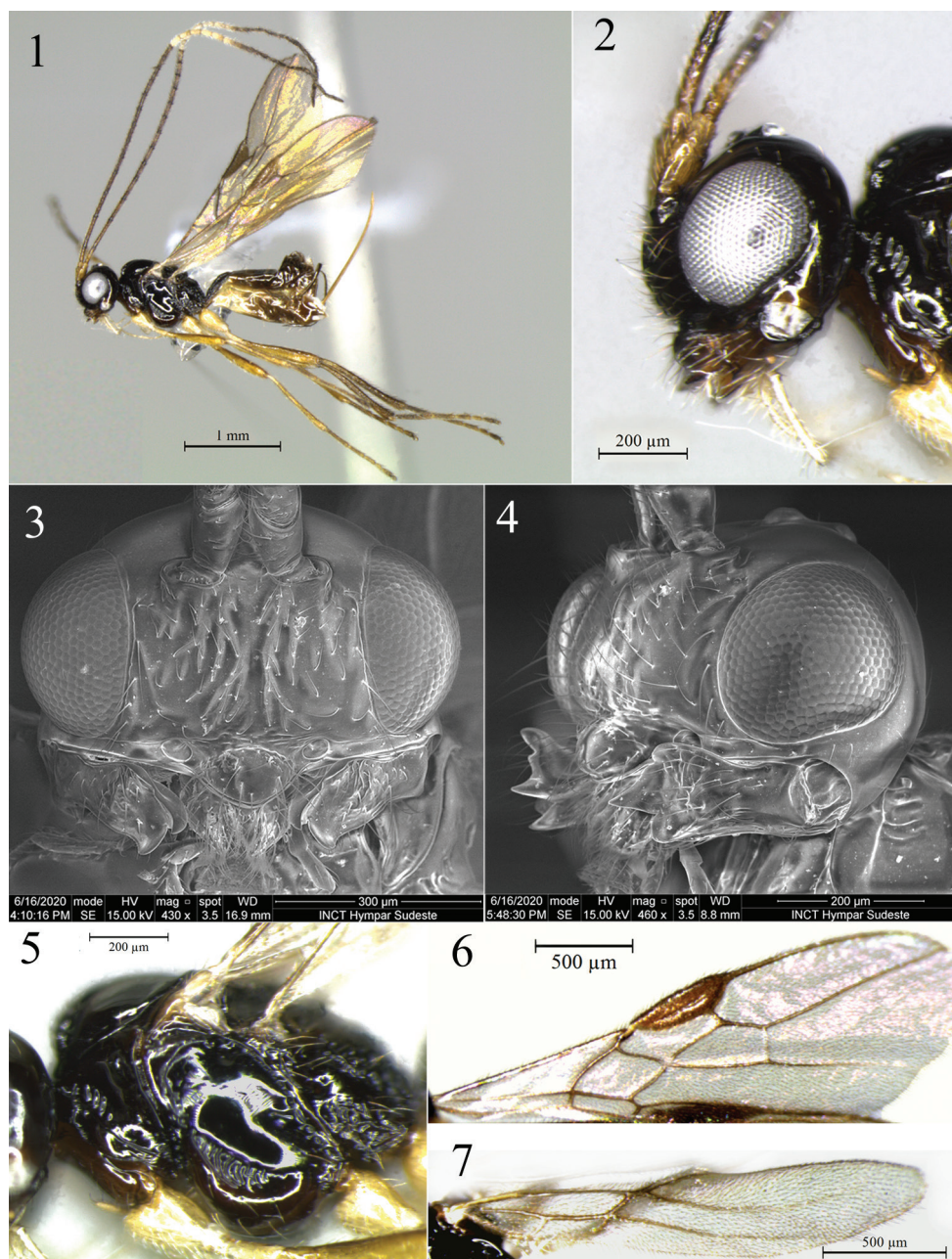
Description. Female (holotype) (Fig. 1). **Length.** Body 2.65 mm; fore wing 2.7 mm; hind wing 1.9 mm.

Head. 1.6× as wide as long; 1.8× as wide as face, 1.6× as wide as mesosoma, 3.3× as wide as apex of first metasomal tergite; slightly wider at eyes than temples in dorsal view. Eye glabrous, 1.2× as high as wide, 2.6× as wide as temple in lateral view (Fig. 2). Occiput, vertex, frons and temples smooth, with some sparse setae. Face 1.7 × as wide as high, setose; slightly rugulose above clypeus (Figs 3, 4). Epistomal sulcus well defined but almost shallow, slightly rugulose. Clypeus protruding, smooth, setose, 1.5× as wide as high; lateral margin of clypeus in contact with paraclypeal fovea (Fig. 3). Malar space ca. 1/10 eye height. Paraclypeal fovea occupying 2/7 of distance between lateral margin of clypeus to eye. Mandible 3-dentate (Fig. 4), 1.9× as long as apical width, slightly wider in apex than base; setose, rugulose antero-medially, punctate; diagonal ridge well developed on apical half of mandible, ventral ridge complete; teeth 1 and 2 connected by flange, incision present but unobtrusive; teeth 1 and 3 approximately equal in size, tooth 2 wider and longer than others. Antenna 1.8× as long as body, with 32 flagellar segments. First flagellar segment 3.3× as long as wide; second flagellar segment 8.2× as long as wide, 2.5× length of first segment; third flagellar segment 6.5× as long as wide, 1.8× length of first. Maxillary palp 1.7× as long as head height.

Mesosoma. 1.4× as long as high, 1.9× as long as wide, 1.7× as high as head. Pronotum in dorsal view with small but distinct pronope, crenulate in posterior margin; in lateral view, crenulate in upper middle area. Mesoscutum 1.1× as wide as long, scattered setae present along notauli. Notauli deep, crenulate anteriorly, absent posteriorly. Mesoscutal pit deep, slightly elongate, occupying a little less than 1/5 extent of mesoscutum. Scutellar sulcus 2.5× as wider as long, with well-developed mid ridge and some weak ridges at posterior margin of lateral areas. Scutellar disc smooth, setiferous; parascutellar area weakly rugulose posteriorly, with setae near scutellar sulcus. Metanotum setiferous anteriorly, in dorsal view rugose medially, depressed lateral fields crenulate; mid ridge complete and two well-developed median lateral ridges; metanotum in lateral view with high median flange. Mesopleuron with scattered setae in ventral area, antero-basal margin crenulate towards anterior subalar area; posterior margin crenulate. Precoxal sulcus deep, long, widely crenulate, separated from posterior margin (Fig. 5). Propodeum with anterior half nearly smooth and median carina; posterior half rugose, including inside areola; areola pentagonal, ca. as long as wide. Metapleuron rugose (except medially) and setose.

Fore wing. Approximately as long as body. Pterostigma 3.4× as long as wide, 2.25× as wide as vein r length; r 0.3× as long as 2-SR, arising distad midpoint of pterostigma; submarginal cell 2.6× as long as high; 2-SR 2.5× as long as r-m, 1.4× as long as 3-SR; 3-SR 2.65× as long as r, 1.8× as long as r-m; SR1 5.15× as long as 3-SR; 2-CU1 1.1× as long as m-cu, this interstitial; cu-a postfurcal by distance less than its length; subdiscal cell closed, nearly parallel-sided; CU1a arising slightly above middle of subdiscal cell (Fig. 6).

Hind wing. With three hamuli, 5.7× as long as wide; vein 1-M 1.15× as long as M+CU, 2.0× as long as 1r-m; m-cu interstitial, spectral (Fig. 7).



Figures 1–7. *Idiasta rupina* sp. nov. (1, 2, 5–7 female, holotype 3 and 4 male, paratype) 1 habitus, lateral view 2 head, lateral view 3 head, anterior view 4 head, lateral view showing mandible 5 mesosoma, lateral view 6 fore wing 7 hind wing.

Legs. Hind femur 6.35× as long as wide. Hind tibia 11.2× as long as its maximum subapical width, 0.9× as long as hind tarsus. First segment of hind tarsus 1.7× as long as second segment.

Metasoma. First metasomal tergite 1.6× as long as apical width; apex 1.5× as wide as base; strongly strigose surface, dorsal carinae convergent and uniting in basal third, continuing as a distinct median carina to apex, dorsope deep. Ovipositor 1.3× as long as hind tibia, 1.45× as long as mesosoma; straight and strongly directed upwards (Fig. 1). Ovipositor sheath setose.

Color. Dark brown to black. Gena and mandibles brown, mandibles lighter in apical third; scape, pedicel, and basal half of first flagellar segment yellow brown; flagellar segments 2–13 brown, 14–19 white, 20–32 dark brown. Propleuron, ventral mesopleuron, and tegulae brown. Second and third metasomal tergites brownish yellow. Legs yellow, gradually darkening towards apex; coxa and trochanter pale yellow; hind tibia and hind tarsus brown. Wings hyaline, venation and pterostigma brown.

Male. Similar to female but body length 2.4 mm; hind wing 2.0 mm; head 3.0× as wide as apex of first metasomal tergite; antenna with 36 flagellar segments; first flagellar segment 3.9× as long as wide; second flagellar segment 7.95× as long as wide, 1.8 × length of first segment; third flagellar segment 7.0× as long as wide, 1.4× length of first segment; maxillary palp 2.4× as long as head height. Mesoscutum slightly longer than wide; scutellar sulcus 2.25× as wide as long. Fore wing with 2-SR vein 1.9× as long as r-m, 1.6× as long as 3-SR; 3-SR 1.2× as long as r-m. Hind wing 1-M 0.8× as long as M+CU, 2.6× as long as 1r-m. Hind femur 5.15× as long as wide; first segment of hind tarsus 1.5× as long as second segment. Antenna brown except yellowish basal half of first flagellar segment; wing venation and pterostigma light brown.

Etymology. The species name refers to the ecosystem from which the studied material was collected.

Distribution. Brazil, State of Minas Gerais, São Roque de Minas, rupestrian grassland.

Comments. *Idiasta rupina* and *I. dixi* are related Neotropical species and share the notauli absent posteriorly, fore wing cu-a postfurcal, and hind wing m-cu not tubular. The color pattern of the body is also similar. However, *Idiasta rupina* can be differentiated by the glabrous eye (with sparse setae in *I. dixi*), high median flange of the metanotum (absent in *I. dixi*), fore wing m-cu interstitial (slightly antefurcal in *I. dixi*). Additionally, *Idiasta rupina* differ in the following quantitative ratios: eye 2.5 × as wide as temple (3.1× in *I. dixi*); maxillary palp ca. twice as long as head height (1.4 × in *I. dixi*); sulcus scutellar 2.5× as wide as long (1.4× in *I. dixi*); fore wing vein 3-SR 2.6 × as long as r (3.5× in *I. dixi*); SR1 5.1× as long as 3-SR (4.5× in *I. dixi*); ovipositor 1.4× as long as mesosoma (ca. 1.0× in *I. dixi*).

Genus *Rhacalsia* Cameron, 1910

Type species. *Rhacalsia rufobalteata* Cameron, 1910

Diagnosis. Enlarged paraclypeal fovea extending to eye. First flagellar segment shorter than second. Fore wing venation complete; 2-RS vein longer than 3-SR, m-cu

antefurcal to interstitial. Metasomal terga unsculptured beyond the first tergite, not forming a carapace.

Hosts. Unknown.

Distribution. Afrotropical, Asian, and Neotropical Regions.

***Rhacalysia ampla* sp. nov.**

<http://zoobank.org/543C6C87-1523-4941-8513-26A6C4D42200>

Figures 8–18

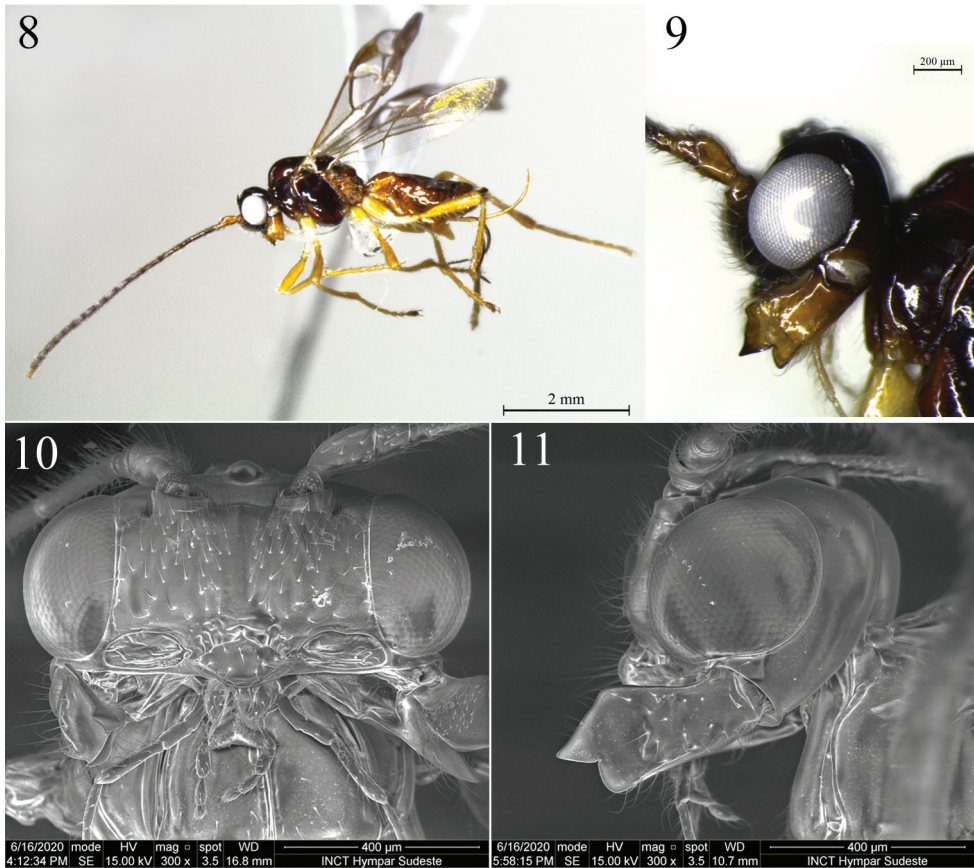
Type material. *Holotype* pinned, female (DCBU 361839) Brazil, Rio de Janeiro, Teresópolis, Parque Nacional da Serra dos Órgãos, 22°26'57"S, 43°00'13"W, alt. 1236 m, XI.2015, dense ombrophilous forest, Malaise trap, R. F. Monteiro col. *Paratypes*, females (3), (DCBU 358123) 22°26'57"S, 43°00'13"W, alt. 1236 m, III.2015, Malaise trap, R. F. Monteiro col.; (DCBU 360613) 22°27'03"S, 43°00'54"W, alt. 1649 m, IV.2015, Malaise trap, R. F. Monteiro col.; (DCBU 404793) 22°27'03"S, 43°00'54"W, alt. 1649 m, I.2015, Malaise trap, R. F. Monteiro col.

Diagnosis. *Rhacalysia ampla* can be differentiated from other species of genus by the notauli incomplete, precoxal sulcus sculptured only in anterior fourth, fore wing with m-cu interstitial, CU1a arising below middle of subdiscal cell, and hind wing with three hamuli.

Description. Female (Fig. 8). **Length.** Body 3.1–4.0 mm; fore wing 3.4–4.4 mm; hind wing 2.8–3.45 mm.

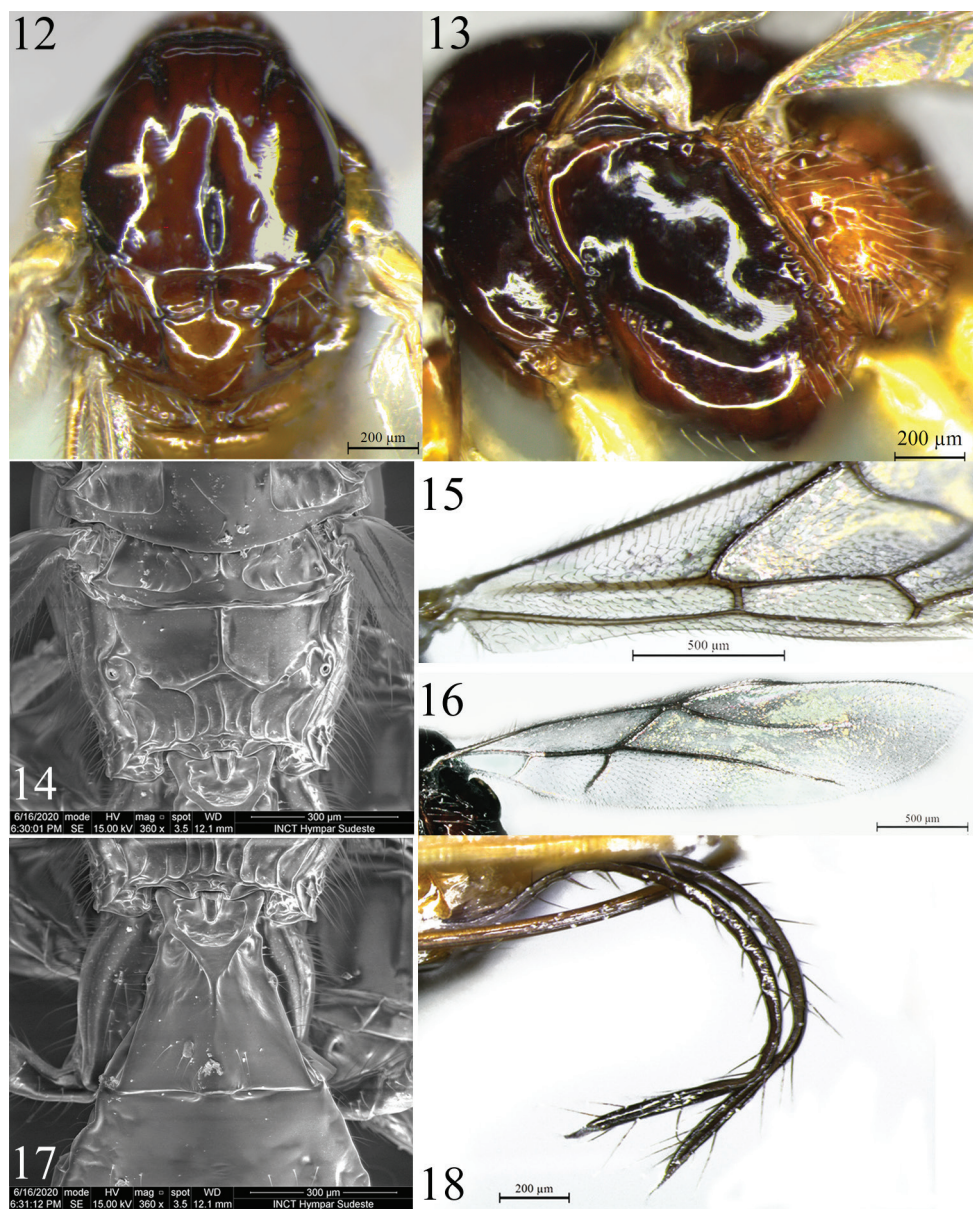
Head. 1.5–1.85× as wide as long; 1.7× as wide as face, 1.5–1.6× as wide as mesosoma, ca. 2.2× as wide as apex of first metasomal tergite; slightly wider at eyes than temples in dorsal view. Eye glabrous, 1.0–1.1× as high as wide, 2.9–3.0× as wide as temples in lateral view (Fig. 9). Occiput, vertex, and temples smooth, with some sparse setae. Frons occasionally with weak pit mesally. Face 2.1–2.2× as wide as high, setose; low mid ridge dorsally, rugulose above clypeus (Fig. 10). Epistomal sulcus deep, crenulate. Clypeus protruding, smooth to rugulose, setose (setae as long as wide clypeus), 1.6–2.0× as wide as high; lateral margin of clypeus does not contact with paraclypeal fovea. Malar space short, 1/13 eye height. Paraclypeal fovea enlarged to form broad groove extending to eye (Fig. 10).

Mandible 3-dentate (Figs 9, 11), 1.7–1.9× as long as apical width, apex 1.2–1.3× as wide as base; setose, slightly rugose antero-medially; diagonal ridge well developed on apical half of mandible, relatively displaced to ventral margin, and ventral carina present in basal half; teeth 1 and 2 connected by flange, indistinct incision; tooth 3 wider than tooth 1; tooth 2 wider and longer than others. Antenna 1.7× as long as body, with 38 flagellar segments (holotype). First flagellar segment 3.5–3.8× as long as wide; second flagellar segment 6.3–6.9× as long as wide, 1.7–2.0× length of first segment; third flagellar segment 5.4–5.9× as long as wide, 1.5–1.8× length of first segment. Maxillary palp 1.9–2.0× as long as head height.



Figures 8–11. *Rhacalysia ampla* sp. nov. (females, paratypes) **8** habitus, lateral view **9** head, lateral view **10** head, anterior view **11** head, lateral view showing mandible.

Mesosoma. 1.3–1.4× as long as high, 1.9–1.95× as long as wide, 2.0–2.4× as high as head. Pronotum in dorsal view with distinct pronope, crenulate laterally; smooth in lateral view. Notauli deep, narrow, crenulate anteriorly, absent posteriorly (Fig. 12). Mesoscutum 1.05–1.1× as wide as long, scattered setae present along notauli. Scutellar sulcus 2.2–2.7× as wide as long, with well-developed mid ridge and smooth lateral areas. Mesoscutal pit deep, slightly elongate, occupying 1/6 to 1/5 extent of mesoscutum (Fig. 12). Scutellar disc smooth, setiferous; parascutellar area smooth to rugose posteriorly, with setae near scutellar sulcus. Metanotum setiferous anteriorly, in dorsal view smooth to rugose medially and very weakly crenulate near posterior margin of depressed lateral fields; mid ridge well-developed anteriorly, absent posteriorly, lateral ridges absent (Fig. 14); metanotum in lateral view without high median flange. Mesopleuron with some setae in posterior area below, antero-basal margin crenulate towards anterior subalar area; posterior margin crenulate. Precoxal sulcus deep, crenulate weakly on anterior fourth of mesopleuron, mostly smooth (Fig. 13). Propodeum smooth, except for some rugae



Figures 12–18. *Rhacalyisia ampla* sp. nov. (females, paratypes) **12** mesoscutum and scutellar sulcus, dorsal view **13** mesosoma, lateral view **14** metanotum and propodeum, dorsal view **15** fore wing **16** hind wing **17** first metasomal tergite, dorsal view **18** ovipositor sheaths.

inside areola; anterior half with median carina, posterior half with pentagonal areola ca. as long as wide (Fig. 14). Metapleuron rugose posteriorly and setose.

Fore wing. 0.9–1.1× as long as body. Pterostigma 3.6–3.75× as long as wide, 1.9–2.2× as wide as vein r length; r 0.2–0.3× as long as 2-SR, arising distad midpoint of

pterostigma; submarginal cell $2.5\text{--}2.7\times$ as long as high; 2-SR $2.5\text{--}2.7\times$ as long as r-m, $1.1\text{--}1.3\times$ as long as 3-SR; 3-SR $3.1\text{--}3.5\times$ as long as r, $2.1\text{--}2.3\times$ as long as r-m; SR1 $3.5\text{--}4.0\times$ as long as 3-SR; 2-CU1 $1.3\text{--}1.4\times$ as long as m-cu, this interstitial; cu-a post-furcal by distance ca. equal to its length; subdiscal cell closed, expanded distally, CU1a arising below middle of subdiscal cell (Fig. 15).

Hind wing. With three hamuli, $1.3\text{--}1.4\times$ as long as wide; vein 1-M $1.2\times$ as long as M+CU, $1.3\text{--}1.6\times$ as long as 1r-m; m-cu antefurcal, strongly nebulous for most of its length, tubular basally near its insertion, nearly reaching wing margin (Fig. 16).

Legs. Hind femur $5.7\text{--}6.1\times$ as long as wide. Hind tibia $11.4\text{--}12.1\times$ as long as its maximum subapical width, $1.0\text{--}1.1\times$ as long as hind tarsus. First segment of hind tarsus $1.5\text{--}1.7\times$ as long as second segment.

Metasoma. First metasomal tergite ca. as long as apical width; apex $2.0\text{--}2.1\times$ as wide as base; smooth surface, dorsal carinae strongly convergent, uniting in basal third, continuing as distinct median carina but not reaching to apex; dorsope deep (Fig. 17). Ovipositor $1.0\text{--}1.25\times$ as long as hind tibia, $1.1\text{--}1.4\times$ as long as mesosoma; strongly curved upwards (Fig. 8). Ovipositor sheath setose (Fig. 18).

Color. Mostly dark brown. Mandibles light brown to yellow, darker at base. Clypeus, scape, pedicel, scutellum, and metanotum brown to light brown. Flagellar segment 17–20 whitish (holotype). Mesonotum brown to reddish brown. Propodeum and metapleuron yellowish to dark orange. First metasomal tergite orange to yellowish orange, base of terga 2 sometimes orange, other tergites brown. Tegula, ovipositor, and most of legs yellow. Trochanter and troncantellus pale yellow, telotarsus darkened; hind leg with distal tibia and tarsus brown. Wings hyaline; venation and pterostigma light brown to brown.

Male. Unknown.

Etymology. The species name refers to the form of the paraclypeal fovea.

Distribution. Brazil, State of Rio de Janeiro, Teresópolis, dense ombrophilous forest.

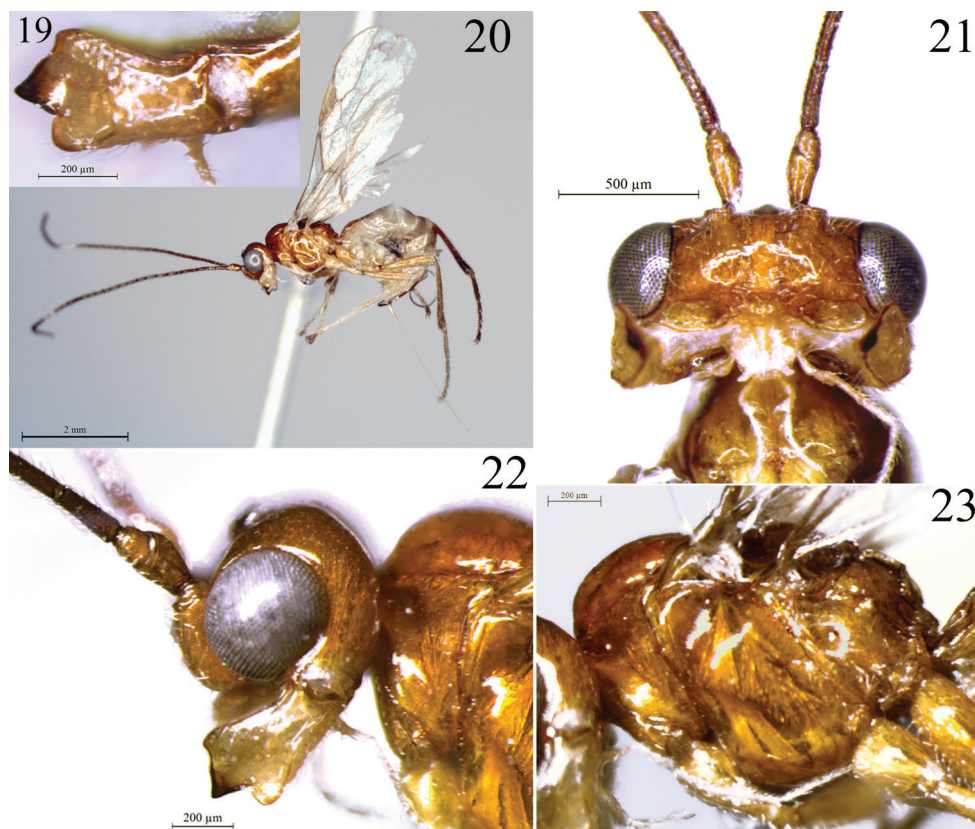
Comments. *Rhacalysia ampla* is similar morphologically to *R. delicata*, with which it shares many characteristics. Members *Rhacalysia ampla* can be differing by the precoxal sulcus weakly sculptured only in the anterior fourth of mesopleuron (Fig. 13) (sculpture shallow but long in *R. delicata*), vein CU1a of fore wing arising below middle of subdiscal cell (Fig. 15) (at middle in *R. delicata*), and the following quantitative ratios: eye ca. $3.0\times$ as wide as temples ($2.2\times$ in *R. delicata*); mesosoma $2.0\text{--}2.4\times$ as high as head ($1.7\times$ in *R. delicata*); pterostigma $1.9\text{--}2.2\times$ as wide as vein r length ($3.0\times$ in *R. delicata*); hind femur $5.7\text{--}6.1\times$ as long as wide ($5.0\times$ in *R. delicata*); and ovipositor $1.0\text{--}1.2\times$ as long as hind tibia ($2.0\times$ in *R. delicata*).

Rhacalysia jatai sp. nov.

<http://zoobank.org/0D1B38F5-B74A-46DE-A61D-B56D95A28905>

Figures 19–27

Type material. *Holotype* pinned, female, (DCBU 408525) Brazil, São Paulo, Luiz Antônio, Estação Ecológica do Jataí, $21^{\circ}36'S$, $47^{\circ}47'W$, 9.XI.2006, seasonal forest,



Figures 19–23. *Rhacalysia jatai* sp. nov. (female, holotype) **19** mandible, lateral view **20** habitus, lateral view **21** head and basal antennae, anterior view **22** head and pronotum, lateral view **23** mesosoma, lateral view.

Malaise trap, N. W. Periotto col. Original label: “Luiz Antonio/SP, EE. Jataí, 9/11/06, Col. N. Periotto”.

Diagnosis. *Rhacalysia jatai* can be recognizable by the notauli and precoxal sulcus entirely smooth, fore wing with m-cu interstitial, CU1a arising at middle of subdiscal cell, hind wing with four hamuli; ovipositor 2.2× as long as mesosoma, body yellow (without brown parts).

Description. Female (holotype) (Fig. 20). Length. Body 3.8 mm; fore wing 4.0 mm; hind wing 2.9 mm.

Head. 1.7× as wide as long; 1.7× as wide as face, 1.6× as wide as mesosoma; 1.9 × as wide as apex of first metasomal tergite; slightly wider at eyes than temples in dorsal view. Eye glabrous, ca. as high as wide, 2.5× as wide as temple in lateral view (Fig. 22). Occiput, vertex, and temples smooth, with some sparse setae. Frons with weak pit mesally. Face 2.3× as wide as high, setose; low mid ridge dorsally and some weak transverse striae just above epistomal sulcus (Fig. 21). Epistomal sulcus deep, crenulate. Clypeus protruding, smooth, setose (setae as long as clypeus width), 1.6× as wide as high; lateral margin of clypeus does not contact with paraclypeal fovea. Malar space ca. 1/12 eye height. Paraclypeal fovea enlarged to form broad groove reaching to eye (Fig. 21).

Mandible 3-dentate (Fig. 19), 1.6× as long as apical width, apex 1.5× as wide as base; setose, slightly rugulose medially; diagonal ridge well developed on apical half of mandible, ventral carina present on basal third of mandible; teeth 1 and 2 connected by flange, indistinct incision; tooth 3 rounded, slightly wider than tooth 1; tooth 2 wider and longer than others. Antenna with apical flagellar segments missing, 31 flagellar segments present. First flagellar segment 3.5× as long as wide; second flagellar segment 5.6× as long as wide, 1.6× length of first segment; third flagellar segment 4.9× as long as wide, 1.4× length of first segment. Maxillary palp ca. twice as long as head height.

Mesosoma. 1.3× as long as high, 2.0× as long as wide, 2.2× as high as head. Pronotum smooth (Fig. 22); in dorsal view, with some setae mesally, pronope absent. Notauli deep anteriorly but smooth, absent posteriorly (Fig. 24). Mesoscutum as wide as long, with scattered setae. Mesoscutal pit shallow, lightly elongate, occupying ca. 2/7 extent of mesoscutum. Scutellar sulcus 3.0× as wide as long, with well-developed mid ridge and some weak ridges at posterior margin of lateral areas. Scutellar disc and parascutellar area smooth, setiferous. Metanotum smooth, setiferous anteriorly; depressed lateral fields weakly crenulate in the posterior margin; mid ridge complete, lateral ridges absent; metanotum in lateral view with median flange slightly higher than scutellar disc. Mesopleuron smooth, with some sparse setae. Precoxal sulcus deep, entirely smooth (Fig. 23). Propodeum with median carina anteriorly; posterior half with pentagonal areola ca. as long as wide; rugulose inside areola, smooth remaining. Metapleuron smooth, setose.

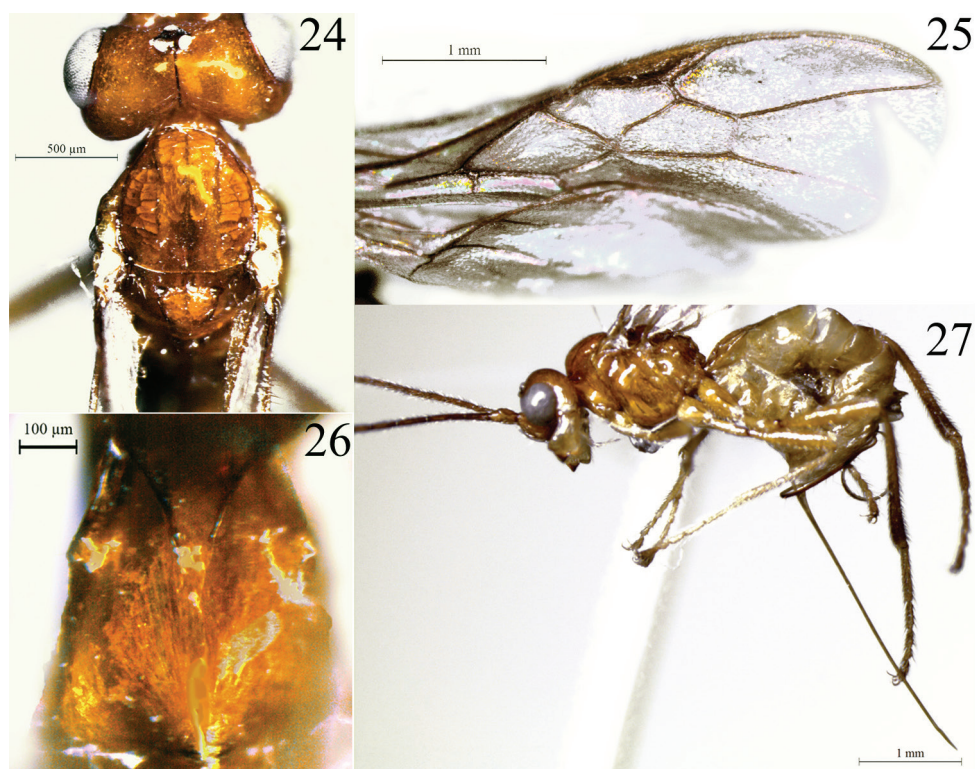
Fore wing. 1.05× as long as body. Pterostigma 4.0× as long as wide, 2.2× as wide as vein r length; r 0.2× as long as 2-SR, arising distad midpoint of pterostigma; submarginal cell 2.25× as long as high; 2-SR 2.4× as long as r-m, 1.3× as long as 3-SR; 3-SR 3.8× as long as r, 1.8× as long as r-m; SR1 3.8× as long as 3-SR; 2-CU1 1.2 × as long as m-cu; m-cu interstitial; cu-a postfurcal by distance slightly shorter than its length (Fig. 25); subdiscal cell closed, slightly expanded distally, CU1a arising near middle of subdiscal cell.

Hind wing. With four hamuli, 4.4× as long as wide; vein 1-M 0.9× as long as M+CU, 1.6× as long as 1r-m; m-cu antefurcal, nebulous but heavily pigmented.

Legs. Hind femur 5.2× as long as wide. Hind tibia 11.2× as long as its maximum subapical width, 1.1× as long as hind tarsus. First segment of hind tarsus 1.95× as long as second segment.

Metasoma. First metasomal tergite 0.9× as long as apical width; apex 2.0× as wide as base; smooth surface, dorsal carinae converging anteriorly but not extending as median carina (Fig. 26); dorsoplate deep. Ovipositor 2.0× as long as hind tibia, 2.2× as long as mesosoma, straight (Fig. 27). Ovipositor sheath setose.

Color. Yellow. Ocellar field and epicranial suture dark brown (Fig. 24); mandibles, fore coxae, and metasoma (except first metasomal tergite) pale yellow. Flagellum light brown, except flagellar segments 19–21 whitish (holotype). Mesosoma dorsally and first metasomal tergite yellow-orange. Legs with telotarsus light brown; hind leg from tibia to apex and ovipositor sheath brown. Wings hyaline, venation and pterostigma light brown.



Figures 24–27. *Rhacalysia jatai* sp. nov. (female, holotype) **24** head, mesoscutum, and scutellar sulcus, dorsal view **25** fore wing **26** first metasomal tergite, dorsal view **27** habitus, lateral view showing ovipositor.

Male. Unknown.

Etymology. The name of species refers to locality of collection of material for study.

Distribution. Brazil, State of São Paulo, Luiz Antônio, seasonal forest.

Comments. *Rhacalysia jatai* is morphologically similar to *R. monteiroi* and both species shares the hind wing with four hamuli, as well as several other features. *Rhacalysia jatai* can be differentiated by the follow quantitative ratios: third flagellar segment 4.9× as long as wide (4.5–4.6× in *R. monteiroi*), 1.4× length of first segment (1.0–1.1 × in *R. monteiroi*); eye 2.5× as wide as temple (1.5–2.0× in *R. monteiroi*); vein 3-SR of fore wing 3.8× as long as r (3.0–3.1× in *R. monteiroi*); hind femur 5.2 × as long as wide (6.2–6.7× in *R. monteiroi*); hind tibia 11.1× as long as its maximum apical width (12.2–12.7× in *I. monteiroi*); ovipositor 2.0× as long as hind tibia (1.3–1.5 × in *R. monteiroi*), 2.2× as long as mesosoma (1.4–1.7× in *R. monteiroi*). In addition, in *Rhacalysia jatai* the body is entirely yellowish (Figs 24, 27), while in *R. monteiroi* the color pattern of mesosoma and metasoma is mixed between yellowish and distinctly brown parts (Figs 28, 35–38).

***Rhacalysia monteiroi* sp. nov.**

<http://zoobank.org/C9B2CD68-89AF-434D-87DF-03BEEC3B3303>

Figures 28–38

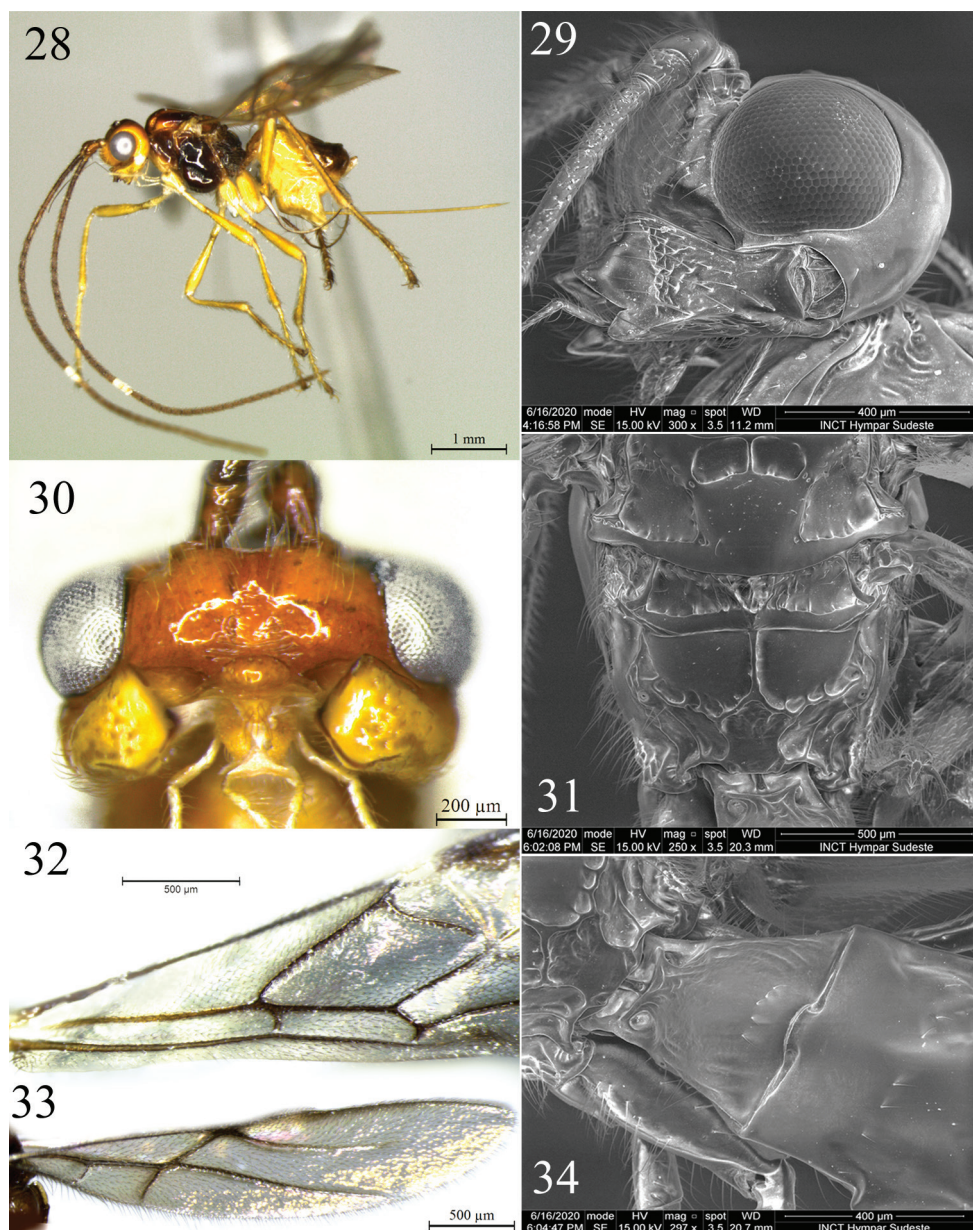
Type material. *Holotype* pinned, female, (DCBU 404794) Brazil, Rio de Janeiro, Teresópolis, Parque Nacional da Serra dos Órgãos, 22°26'54"S, 43°00'49"W, alt. 1482 m, XII.2014, dense ombrophilous forest, Malaise trap, R. F. Monteiro col. *Paratypes* females (2), (DCBU 374756) 22°28'11"S, 43°00'05"W, alt. 868 m, VII.2015, Malaise trap, R. F. Monteiro col.; (DCBU 361820) 22°31'00"S, 43°00'23"W, alt. 252 m, XI.2015, Malaise trap, R. F. Monteiro col.

Diagnosis. *Rhacalysia monteiroi* can be recognized by the notauli incomplete, fore wing with m-cu interstitial, CU1a arising at middle or slightly below middle of subdiscal cell, hind wing with four hamuli, hind femur 6.2–6.7× as long as wide, coloration of body mixed between yellowish and brown parts.

Description. Female (Fig. 28). **Length.** Body 3.4–4.1 mm; fore wing 3.9–4.2 mm; hind wing 2.6–3.0 mm.

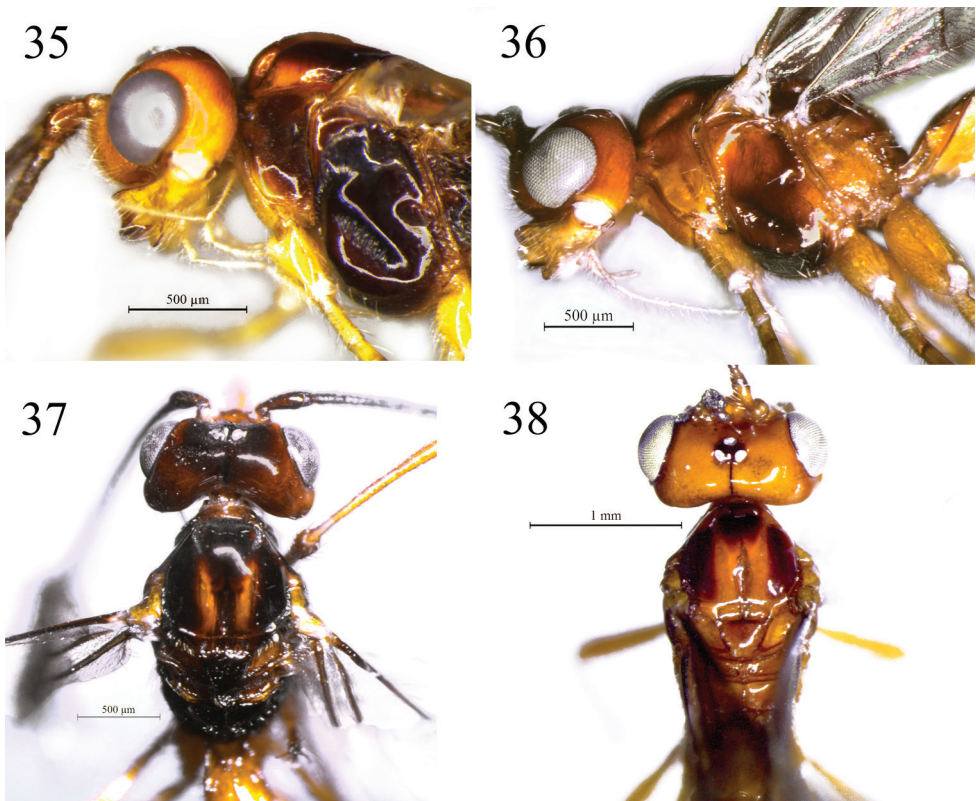
Head. 1.7–1.9× as wide as long; 1.7–1.9× as wide as face, 1.4–1.6× as wide as mesosoma; 2.1× as wide as apex of first metasomal tergite; slightly wider at eyes than temples in dorsal view. Eye glabrous, 1.1–1.2× as high as wide, 1.5–2.0× as wide as temples in lateral view (Figs 35, 36). Occiput, vertex and temples smooth, with some sparse setae. Frons smooth or with weak pit mesally. Face 2.0–2.5× as wide as high, setose; low mid ridge dorsally, with rugulose pair of grooves near clypeus or some transversal striae just above epistomal sulcus (Fig. 30). Epistomal sulcus deep, crenulate. Clypeus protruding, smooth, setose (setae as long as clypeus width), 1.6–1.8× as wide as high; lateral margin of clypeus does not contact paraclypeal fovea. Malar space ca. 1/10 eye height. Paraclypeal fovea enlarged to form broad groove extending to eye. Mandible 3-dentate (Fig. 29), 1.6–1.7× as long as apical width, apex 1.4× as wide as base; setose, rugulose medially; diagonal ridge well developed on apical half of mandible, ventral carina not visible; teeth 1 and 2 connected by flange, indistinct incision; tooth 2 wider and longer than others. Antenna 1.9× as long as body, with 40 flagellar segments (holotype). First flagellar segment 3.3–3.8× as long as wide; second flagellar segment 5.2–5.8× as long as wide, 1.3× length of first segment; third flagellar segment 4.5–4.6× as long as wide, 1.0–1.1× length of first segment. Maxillary palp 2.25–2.55× as long as head height.

Mesosoma. 1.3–1.4× as long as high, 1.9× as long as wide, 2.4× as high as head. Pronotum with pronope relatively large, slightly crenulate laterally and with some setae in dorsal view; smooth to slightly crenulate in lateral view. Mesoscutum 1.1× as wide as long, scattered setae, smooth to weakly crenulate in postero-lateral margins. Notauli deep, smooth to weakly crenulate anteriorly, absent posteriorly (Figs 37, 38). Mesoscutal pit deep, elongate, occupying 1/4 to 1/3 extent of mesoscutum. Scutellar sulcus 2.6–3.0× as wide as long, with well-developed mid ridge and smooth lateral areas. Scutellar disc smooth, setiferous; parascutellar area smooth,



Figures 28–34. *Rhacalysia monteiroi* sp. nov. (females; **28** and **32** holotype, others paratypes) **28** habitus, lateral view **29** head, lateral view **30** head, anterior view **31** metanotum and propodeum, dorsal view **32** fore wing **33** hind wing **34** first metasomal tergite, posterior view.

with setae near scutellar sulcus. Metanotum setose anteriorly, in dorsal view rugose to rugulose medially, smooth to slightly crenulate near anterior and posterior margins of depressed lateral fields (Fig. 31); anterior mid ridge complete, some



Figures 35–38. *Rhacalysia monteiroi* sp. nov. (females; **35** holotype, **36–38** paratypes) **35** head and mesosoma, lateral view, precoxal sulcus crenulate **36** head and mesosoma, lateral view, precoxal sulcus smooth **37** head and mesosoma, dorsal view **38** head and mesosoma, dorsal view.

lateral carinae incomplete to absent; metanotum in lateral view with median flange slightly higher than scutellar disc. Mesopleuron with some setae postero-ventrally and subalar area; antero-basal margin weakly crenulate towards anterior subalar area; posterior margin crenulate. Precoxal sulcus deep, crenulate, separated from posterior margin (Fig. 35) or almost entirely smooth (Fig. 36). Propodeum with median carina anteriorly, posterior half with pentagonal areola ca. as long as wide (Fig. 31); smooth to slightly rugose near to carinae and inside areola. Metapleuron rugose posteriorly and setose.

Fore wing. 1.0–1.2× as long as body. Pterostigma 3.6–4.1× as long as wide, 2.1–2.3× as wide as vein r length; r 0.2–0.25× as long as 2-SR, arising distad mid-point of pterostigma; submarginal cell 2.5–3.5× as long as high; 2-SR 2.4–2.7× as long as r-m, 1.3–1.6× as long as 3-SR; 3-SR 3.0–3.1× as long as r, 1.7–2.0× as long as r-m; SR1 3.8–4.0× as long as 3-SR; 2-CU1 1.0–1.35× as long as m-cu, this inter-

stitial; cu-a postfurcal by distance ca. equal to its length; subdiscal cell closed, slightly expanded distally, CU1a arising at middle to slightly below middle of subdiscal cell (Fig. 32).

Hind wing. With four hamuli, 4.1–4.9× as long as wide; vein 1-M 1.0–1.2× as long as M+CU, 1.4–1.7× as long as 1r-m; m-cu antefurcal, heavily nebulous, tubular basally or not, almost reaching wing margin (Fig. 33).

Legs. Hind femur 6.2–6.7× as long as wide. Hind tibia 12.2–12.7× as long as its maximum subapical width, 1.1–1.2× as long as hind tarsus. First segment of hind tarsus 1.7–1.8× as long as second segment.

Metasoma. First metasomal tergite 1.0–1.1× as long as apical width; apex 1.8–1.9 × as wide as base, strigose to slightly strigose; dorsal carinae converging in basal third, extending posteriorly as median carina incomplete or median carina absent (Fig. 34); dorsope deep. Ovipositor 1.35–1.5× as long as hind tibia, 1.45–1.7× as long as mesosoma; straight. Ovipositor sheath setose.

Color. Body parts vary between dark brown to yellow (Figs 35–38). Head mostly yellow, vertex yellow to brown, ocellar field and epicranial suture dark brown; mandible light yellow. Flagellar segments brown to dark brown, except 18–19 whitish (holotype). Propleuron yellow; mesonotum yellow-orange, with more or less developed lateral and antero-medial spots brown, other parts of mesosoma varying from yellow-orange to dark brown. Legs yellowish to orange; telotarsus brown; hind leg with tibia and tarsus darker. Metasoma yellow except for metasomal tergites 4 towards to apex and ovipositor sheaths brown. Wings hyaline to dusky, venation and pterostigma light brown to dark brown.

Male. Unknown.

Etymology. The species is named in honor of Ricardo Ferreira Monteiro, the collector of the studied material.

Distribution. Brazil, State of Rio de Janeiro, Teresópolis, dense ombrophilous forest.

Comments. *Rhacalysia monteiroi* shares many morphological characteristics with *R. jatai*; both species can be differentiated by the coloration pattern of body, relative length of the ovipositor, and relative length/wide of the posterior femur (see above).

The three specimens of *R. monteiroi* studied here vary considerably in some characteristics. In short, the sculpturing of face (striate or rugulose above the clypeus), notauli (smooth or weakly crenulate), precoxal sulcus (smooth or crenulate), and first metasomal tergite (with or without median carina); the coloration of vertex, pronotum, metanotum, propodeum, and metapleuron yellowish or brown (Figs 35–38). Despite this, the observed variations were not significant to consider them as different species.

Members of the genera *Idiasta* and *Rhacalysia* can be morphologically differentiated as follows: paraclypeal fovea not extending to eye in *Idiasta* (Fig. 3); paraclypeal fovea enlarged to form broad groove extending to eye in *Rhacalysia* (Figs 10, 21).

Key to the Neotropical species of the genus *Idiasta*

- 1 Fore wing patterned with several dark spots or bands, M+CU1 of fore wing very weak, not, or only weakly, pigmented for much of its length; notauli complete to mesoscutal pit; metanotum with high flange. Body length 3.0–5.0 mm. Mexico, Holarctic.....*I. maritima* (Haliday) (♀♂)
- Fore wing either hyaline or dusky but never patterned with spots or bands; M+CU1 of fore wing well-developed, usually strongly pigmented throughout; variable development of notauli; metanotum with or without high flange.....2
- 2 Notauli complete and rugose; fore wing with CU1a arising well below middle of first subdiscal cell, cu-a interstitial or postfurcal; metanotum with high flange. Body length 2.5–4.0 mm. Mexico*I. euryzona* Wharton (♀♂)
- Notauli incomplete, not reaching mesoscutal pit (as Fig. 12); fore wing with CU1a arising at middle or slightly above middle of subdiscal cell, cu-a postfurcal; metanotum with or without high flange3
- 3 Eye with scattered setae, maxillary palp 1.4× as long as head height; scutellar sulcus 1.4× as wide as long; metanotum without high flange; 3-SR of fore wing 3.4× as long as r, m-cu slightly antefurcal (2-SR+M present); ovipositor ca. as long as mesosoma. Colombia.....*I. dixi* Dix (♀)
- Eye glabrous; maxillary palp 2.0–2.4× as long as head height; scutellar sulcus 2.2–2.5× as wide as long; metanotum with high flange; 3-SR of fore wing 2.6× as long as r, m-cu interstitial (2-SR+M absent); ovipositor 1.45× as long as mesosoma. Body length 2.4–2.7 mm. Brazil (Figs 1–7)*I. rupina* sp. nov. (♀♂)

Key to the species of the genus *Rhacalysia**

- 1 Fore wing with vein CU1a interstitial. Body length 2.4 mm. Republic of the Congo.....*R. congoensis* Fischer (♀♂)
- Fore wing with variable CU1a insertion but not interstitial2
- 2 Notauli complete and heavily sculptured; face with two wide and sculptured longitudinal sulcus lateral to mid ridge. Body length 4.3 mm. India.....*R. rufobalteata* Cameron (♀♂)
- Notauli smooth or incomplete (Figs 12, 37, 38); face without long and sculptured sulcus (Figs 10, 21, 30).....3
- 3 Clypeus slightly wider than high; vein m-cu of fore wing antefurcal; scutellar sulcus with 7 longitudinal ridges; first metasomal tergite longitudinally striate, median carinae present; body entirely black. Body length 5.0 mm. India.....*R. profundinigra* Fischer (♀♂)
- Clypeus 1.6–2.0× as wide as long; vein m-cu of fore wing interstitial (Fig. 25); scutellar sulcus with mid ridge, lateral carina absent (Fig. 12); first metasomal

* Modified from Fischer 1999.

- tergite smooth to strigose, with or without median carinae; body color variable.....4
- 4 Hind wing with three hamuli; metanotum without high flange; body color mostly brown.....5
- Hind wing with four hamuli; metanotum with high flange; body yellowish or at least with distinctly yellow-orange parts.6
- 5 Eye 2.0–2.2× as wide as temple; mesosoma 1.7× as high as head; hind femur ca. 5.0× as long as wide; fore wing with pterostigma 3.0× as wide as vein r length, cu-a slightly postfurcal, CU1a arising at middle of subdiscal cell; ovipositor ca. twice as long as hind tibia. Body length 3.5–5.4 mm. Argentina, Brazil, Colombia, Mexico, Panama, Peru, and Venezuela..... ***R. delicata* (Papp)** (♀♂)
- Eye ca. 3.0× as wide as temple; mesosoma 2.0–2.4× as high as head; hind femur 5.7–6.1× as long as wide; fore wing with pterostigma 1.9–2.4× as wide as vein r length, cu-a postfurcal by distance ca. equal to its length, CU1a arising below of subdiscal cell; ovipositor 1.0–1.2× as long as hind tibia. Body length 3.1–4.2 mm. Brazil (Figs 8–18) ***R. ampla* sp. nov.** (♀)
- 6 Vein 3-SR of fore wing 3.8× as long as r; hind femur 5.2× as long as wide; hind tibia 11.2× as long as its maximum subapical width; ovipositor 2.0× as long as hind tibia, 2.2× as long as mesosoma; body color yellowish. Body length 3.8 mm. Brazil (Figs 19–27). ***R. jatai* sp. nov.** (♀)
- Vein 3-SR of fore wing 3.0–3.1× as long as r; hind femur 6.2–6.7× as long as wide; hind tibia 12.2–12.7× as long as its maximum subapical width; ovipositor 1.4–1.5× as long as hind tibia, 1.5–1.7× as long as mesosoma; mesosoma with distinctly brown parts. Body length 3.4–4.1 mm. Brazil (Figs 28–38) ..
..... ***R. montei* sp. nov.** (♀)

Discussion

The wing venation pattern of *Idiasta* is widely maintained in *Rhacalysia*. The morphological support for the retention of the generic status of *Rhacalysia* has been the enlarged paraclypeal fovea (Fischer 1967, 1994; Wharton 1980, 2002). However, although it is decidedly an apomorphic character within Alysiniinae, it is not clear that all species with the enlarged paraclypeal fovea form a monophyletic group (Wharton 2002).

The insertion antefurcal of vein m-cu of fore wing (and therefore 2-SR+M present) was considered diagnostic characteristic of *Idiasta* by Wharton (2002), supposedly differing from the trend observed in *Rhacalysia* species (this vein less antefurcal). Indeed, m-cu of fore wing is interstitial in most known *Rhacalysia* species but is antefurcal in *R. congoensis* and *R. profundinigra*. Moreover, this vein is interstitial in *I. rupina* (Fig. 6) and postfurcal in *Apiasta* Wharton, 2002, a subgenus of *Idiasta* known from Australian Region and considerably similar to *Rhacalysia* in morphology (Wharton 2002). It has also been argued that the density of setae on the ovipositor sheath is typically higher in *Idiasta* than *Rhacalysia* (Wharton 1980, 2002). Here, we observed that the setae ovipositor

sheath in *R. ampla*, *R. jatai*, and *R. monteiroi* are separated by a distance shorter than its length (Fig. 18), although sparser than *I. rupina*. Thus, this feature must be used carefully.

In addition to the enlarged paraclypeal fovea, all known species of *Rhacalysia* shares the follow characteristics: fore wing with pterostigma distinct and wide, vein r arising from its distal middle, vein r shorter than pterostigma width, cu1 postfurcal (Figs 15, 25, 32); mid ridge present on face (at least weakly developed); and first metasomal tergite widened towards to apex (apical width ca. twice the basal) (Fig. 17). Furthermore, the vein CU1a of fore wing not interstitial, m-cu of hind wing well-developed, and indistinct incision between mandibular teeth 1 and 2 (Figs 11, 19, 29), are characteristics shared by all species except *R. congoensis*, with relatively distinct morphology, in which the CU1a of fore wing is interstitial, m-cu of hind wing absent, and there is well defined incision between teeth 1 and 2.

Studies covering more *Rhacalysia* specimens in the future, should provide a clearer and more conclusive morphological delineation in relation to the genus *Idiasta*, especially if together the analysis of molecular data. Nevertheless, as well as Fischer (1994) and Wharton (2002), we maintain the genus position of *Rhacalysia*, and consider *R. delicata* part of it, based on the new species described here.

Considering our records, the distribution of *Idiasta* is slightly altered: the genus is no longer recorded from Argentina, Peru, and Venezuela. In turn, considering *delicata* species as *Rhacalysia*, the genus *Rhacalysia* is now known from many countries of the Neotropical Region.

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Description and biological notes of the larva of *Cionus olivieri* Rosenschold, 1838 (Coleoptera, Curculionidae), with a comparison with other species of the tribe Cionini

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Abstract

The mature larva of *Cionus olivieri* Rosenschold, 1838 is described and illustrated in detail for the first time. It is compared with those known from the same genus and other genera in the tribe Cionini and with those of the hypothesized sister tribe Mecinini in the Curculioninae. The larvae of *Cionus* have three distinctive diagnostic features: the reduced number of setae on the epicranium (only two or three *des* and one or two *fs*) and on the epipharyngeal lining (only two *als*, two *ams*, and no *mes*); i.e., distinctly fewer than the most frequent number of setae in weevils, and mandibles dentate or angulate internally near the base. If considered together with *Stereonychus* Suffrian, 1854, the other genus of Cionini with larvae studied in detail, it is preliminarily suggested that mature larvae of this tribe might be characterized by six main diagnostic features: (1) labial palpi one-segmented, (2) labral rods absent, (3) pedal areas swollen to form large lobes or prolegs, (4) mandible with sharp apical teeth, (5) reduced number of *fs* on frons, only one or two *fs*, and (6) reduced number of epipharyngeal setae (two or three *als* and two or three *ams*, but no *mes*). It was noticed that *C. helleri* Reitter, 1904 from Japan, a very distinct species in the genus for some characters of the adult, also possesses distinctive characters in the larva which are uncommon among known cionines. New biological data on *C. olivieri* with the discovery of its host plant, *Verbascum songaricum* (Scrophulariaceae), in central Asia are also reported.

Keywords

biology, Curculioninae, ecology, immature stages, *Verbascum songaricum*, weevils

Introduction

The tribe Cionini Schoenherr, 1825 in the subfamily Curculioninae Latreille, 1802 (Curculionidae) currently comprises seven genera occurring predominantly in the Palearctic region (Alonso-Zarazaga et al. 1999). The largest genus is *Cionus* Clairville, 1798, which is also represented in the Afrotropical and Oriental regions, whereas the other genera include fewer than ten species (*Cleopus* Dejean, 1821; *Nanomicrophytes* Pic, 1908; *Stereonychus* Suffrian, 1854) or are monotypic (*Cionellus* Reitter, 1904; *Patialus* Pajni, Kumar & Rose, 1991; *Stereonychidius* Morimoto, 1962). Based on the Palearctic species, Caldara and Korotyaev (2002) delimited the tribe as a monophyletic group identified by several synapomorphies in character states of the head, antennae, abdomen, and genitalia. Moreover, they also analyzed the phylogenetic relationships of the genera, based mainly on the presence of a rostral prosternal canal and tibial unci. Recently, after the revision of the Palearctic species of *Cionus* based also on a preliminary study of species of other regions, Košťál and Caldara (2019) realized that some genera seem to be paraphyletic and that most of the characters currently used to distinguish them are conflictive and need to be reassessed. On the other hand, they did not find new adult morphological characters potentially phylogenetically informative. The study of immature stages appears very important to provide additional morphological evidence.

Adults of *Cionus olivieri* Rosenschold, 1838 are clearly distinguished from other species of *Cionus* by the following features taken together: body size on average large (♂♂ 3.80–5.40 mm, ♀♀ 3.90–5.95 mm); rostrum in lateral view stout, almost evenly curved, approximately of the same width from base to apex, its apical part in dorsal view with parallel sides, not narrower in midlength; antennal insertion in males closer to rostrum midlength; pronotum with almost conically narrowed sides; elytra with sub-rounded sides, short (length/width ratio usually less than 1.25), with the integument concealed by densely distributed scales, without rows of erect setae-like scales; anterior onychia in males of normal length, at most as long as tarsomeres 1 to 3 combined (Košťál and Caldara 2019).

This is a widespread species in central and southern Europe and Asia. Its distribution extends from Portugal and Spain to Anatolia, Transcaucasus, Middle East, central Asia, western China (Xinjiang), Afghanistan, and Pakistan. *Cionus olivieri* does not occur in northern Europe, northern and eastern Asia, or North Africa (Alonso-Zarazaga et al. 2017, Košťál and Caldara 2019).

Host plants of Palearctic *Cionus* usually include *Verbascum*, *Scrophularia*, *Buddleja* (Scrophulariaceae) and *Limosella* (Plantaginaceae) (Hoffmann 1958; Read 1977; Räther 1989; Košťál and Caldara 2019). Larvae are ectophagous, feeding exposed on aerial parts, leaves and stems, of the plants; pupation takes place inside a cocoon built on the same host plant or in the soil (Hoffmann 1958; Smreczyński 1976; Košťál

and Caldara 2019). It is known that *Cionus olivieri* lives on many *Verbascum* species: *V. thapsus* L., *V. nigrum* L., *V. sinuatum* L., *V. densiflorum* Bertol., *V. phlomoides* L., *V. longifolium* Ten. (Hoffmann 1958; Smreczyński 1976; Košťál and Caldara 2019). In Turkey, Kazakhstan, and Kyrgyzstan it was collected on a large number of *Verbascum* species (M. Košťál, pers. obs.).

The aim of the present study is to describe the larva of *C. olivieri* in detail for the first time, in order to provide further characters for the identification of this taxon, and to compare this larva with the larvae of other species of *Cionus*, Cionini, and the apparent sister tribe Mecinini Gistel, 1848.

Materials and methods

Sampling

Fifteen mature larvae from Kyrgyzstan (Beshtash, Talas State, 42.391391°N; 72.279285°E, 1546 m, *Verbascum songaricum*, 2-VII-2018, leg. Chunyan Jiang) and 6 mature instar larvae from Kazakhstan (Altyn Emel Conservation Area, 44.18862°N; 78.51847°E, 1577 m, *Verbascum songaricum*, 12-VIII-2018, leg. Chunyan Jiang).

Morphological description

All described specimens were fixed in 75% ethanol and examined under a Nikon SMZ 1500 optical stereomicroscope with calibrated oculars. To prepare microscope slides, we made dissections as in May (1994): a larva was decapitated, and the head was cleared in a 10% potassium hydroxide (KOH) for three minutes by heating in a 70 °C water bath and then rinsed in distilled water. After clearing, the mouthparts were separated from the head capsule. We used nail polish as mounting medium, which contains a mixture of butyl acetate, ethyl acetate, multipolymer of adipic acid, neopentyl glycol, trimellitic acid, and acetyl tributyl citrate. All slides together with the adult specimens are deposited at the Museum of the Institute of Zoology, Chinese Academy of Sciences (IOZ, CAS).

The observations and measurements were conducted using a compound microscope with calibrated ocular lenses (Leica DM 2500). The following dimensions were measured for each larva and provided in the Description: head width and length, body length (larvae fixed in a C-shape were measured in segments), and body width in the widest place (i.e., metathorax or abdominal segments I–IV). The relative lengths of all setae can be seen in the figures. Transparent structures were stained with Chlorazol Black E for further examination.

Photos of larvae were taken with a Canon-5D camera mounted on the microscope. Images of adults were photographed with a CCD Qimaging MicroPublisher 5.0 RTV mounted on a Zeiss SteREO Discovery. V12 microscope. Images from microscopic slides were taken with a Nikon CoolPix 5400. Photographs in the field were taken with Canon G15 camera.

Drawings were made from the original photographs using the software Adobe Illustrator CS6. The numbers of setae in bilateral structures are given for one side only.

We used the terms and abbreviations for the setae of the mature larvae found in May (1994) and Marvaldi (1999).

Results

Cionus olivieri Rosenschoeld, 1838

Cionus olivieri Rosenschoeld, 1838: 725. Hoffmann 1958: 1222. Smreczyński 1976: 58. Košťál and Caldara 2019: 68.

Description of mature larva. Figures 1–12. *Measurements* (in mm). Body length: 9.00–9.75 ($N = 18$). Body width: 2.50–3.00 ($N = 18$, abdominal segment III–V). Head width (in front view): 0.68–0.74 ($N = 10$); length: 0.70–0.78 ($N = 10$).

General. Body subcylindrical, C-shaped, weakly curved, extremely soft, declivous and attenuate posteriorly (Figs 1, 13).

Coloration. Head dark brown, very strongly sclerotized (Figs 1, 13). All thoracic and abdominal segments yellow, pronotum partly pigmented and sclerotized (Figs 1, 13).

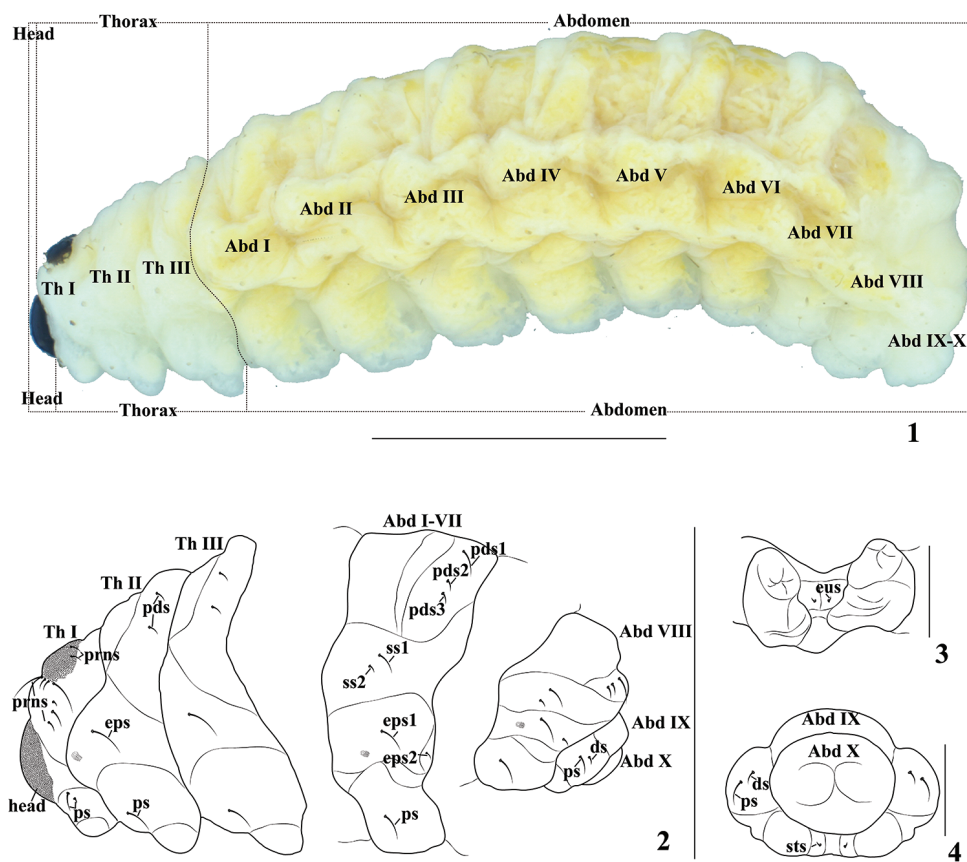
Vestiture. Thoracic and abdominal segments with some minute and relatively long setae, cuticle minutely spiculate, pleural lobes distinct.

Head capsule (Figs 5, 6). Head suboval and slightly rounded laterally, cranial suture undivided, wide, half-length of head. Frontal suture distinct, not extending to mandibular membrane. Endocarinal line present, reaching to half of frons. Anterior and posterior stemmata (st) present, projecting, anterior one located below stripe at side, externally close to antenna, posterior one located laterally. Setae on head piliform, varying in length, from very long to minute. Dorsal epicranium with three *des*; *des*₁ and *des*₄ reduced to a basal sensillum; *des*₂ approximately as long as one-third length of *des*₃; very long *des*₃ located anteriorly on epicranium close to frontal suture; *des*₅ located anterolaterally, as long as two-thirds length of *des*₃. Frons only with one *fs*; *fs*₁, *fs*₂, *fs*₃, and *fs*₅ reduced to basal sensilla; long *fs*₄ located near epistoma. Epicranium with only one *les* as long as *des*₁. Ventral epicranium with two, minute *ves*. Posterior epicranium with four, minute *pes*_{1–4} and one sensillum. Postoccipital condyles distinct, hypopharyngeal bracon distinct. Tentorial bridge narrow, membranous in middle and half base of sides, strongly sclerotized at sides, with two pairs of acute auricular anterior projections.

Antenna (Fig. 7) located at the end of the frontal suture on each side, with one segment; sensory appendage (sensorium) three times as long as wide, circular in cross section, contiguous with frontal suture, with four conical sensillae.

Chypeus (Fig. 10) transverse-shaped, strongly sclerotized, with one sensillum and two *cls* of the same length, all in one line.

Mouthparts (Figs 9–12). Labrum (Fig. 10) transverse-shaped, strongly sclerotized, deeply concave in the middle at apex, with three *lms*, very short *lms*₁ as long



Figures 1–4. *Cionus olivieri*, mature larva: **1** habitus, lateral view **2** thoracic segments, abdominal segment I, and abdominal segments VIII–X, lateral view **3** pedal area, ventral view **4** anus (ThI–III, numbers of thoracic segments; AbdI–X, numbers of abdominal segment. Setae: *ds* dorsal s., *eps* epipleural s., *eus* eusternal s., *pds* postdorsal s., *prns* pronotal s., *ps* pleural s., *ss* spiracular s., *sts* sternal s.). Scale bars: 2 mm (**1, 2**), 1 mm (**3, 4**).

as *lms*₃, and as long as half-length of short *lms*₂, all localized centrally. Epipharynx (Fig. 11) with two small, stout, apically rounded *ams*; two relatively long, stout, apically rounded *als*; two epipharyngeal sensilla; *mes* and labral rods absent. Mandibles (Fig. 9) symmetrical, incisor section with two apical teeth and moderately rounded flange posterior to dorsal tooth, with many small teeth on inner side of anterior tooth, with one acute projection at base; molar section with two *mds*; *mds*₂ moderately long, *mds*₁ minute. Maxillae (Fig. 12) with maxillary palpi (*mvp*) two-segmented, basal segment with one tiny *mvp*₁, two clavate accessory appendages and one sensillum; distal segment sclerotized, with one sensillum, apex flattened with dense short irregular spiculate setae. Mala with four dorsal robust *dms*, gradually reducing in length; with three short, more acute *vms*. Stipes with one *stps*, two *pfs*, one *mbs* and one sensillum, very long *stps* located submedially on venter of base, *mbs* minute, long *pfs*₁ three times

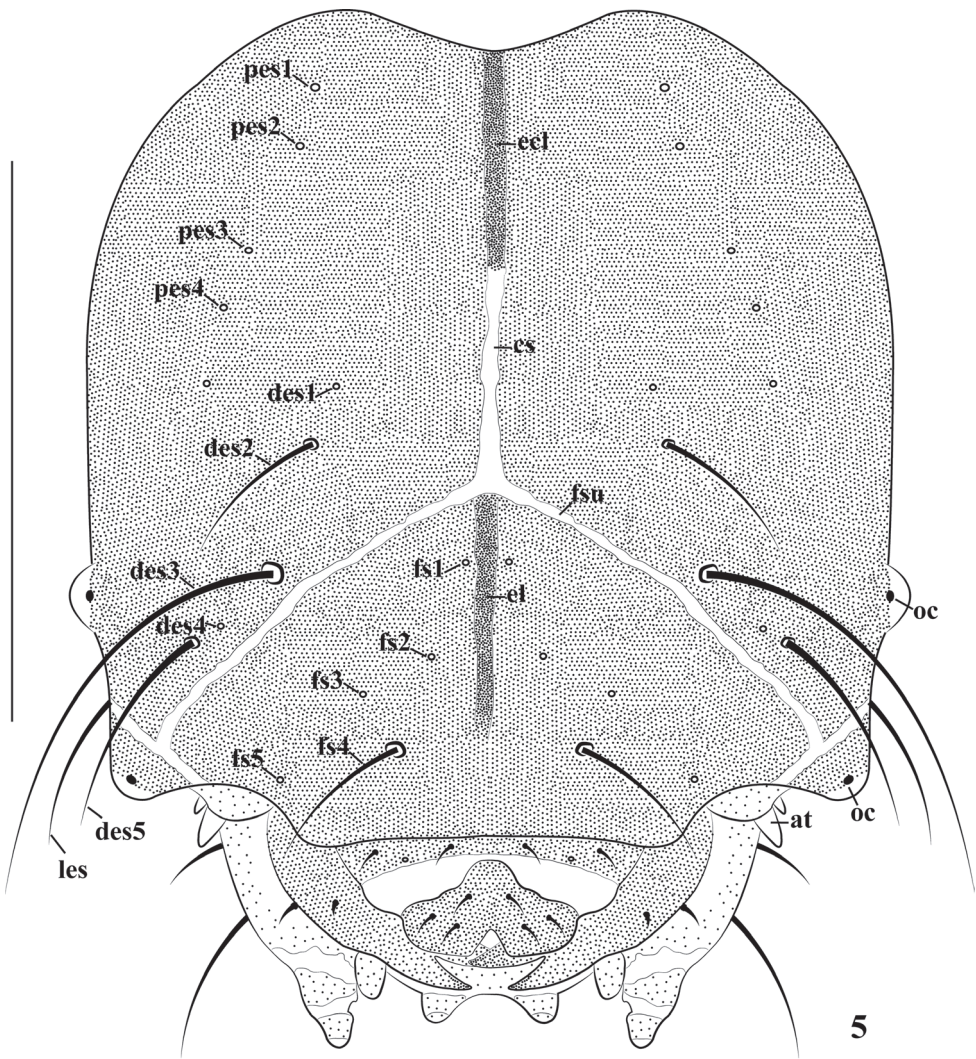
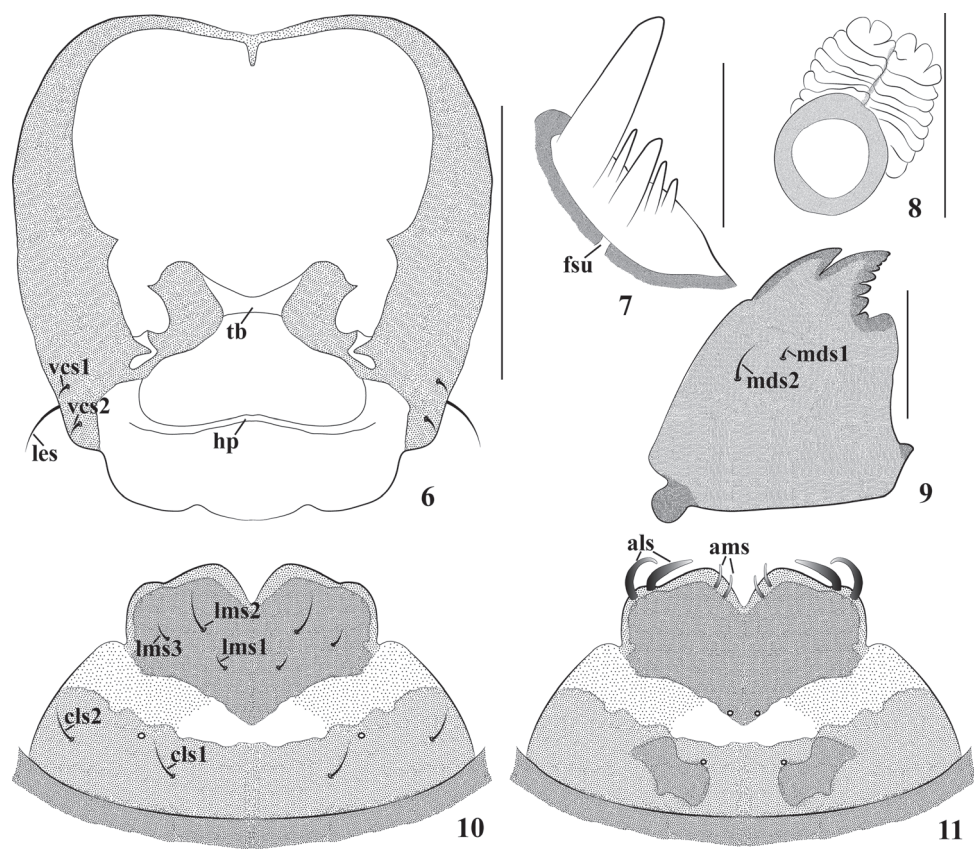


Figure 5. *Cionus olivieri*, mature larva, head, frontal view (at antenna, st stemmata, cs cranial suture, ecl eccysial line, fsu frontal suture). Setae: *des* dorsal epicranial, *fs* frontal epicranial, *les* lateral epicranial, *pes* postero-epicranial). Scale bar: 0.5 mm.

longer than pf_2 . Labium (Fig. 12) membranous excepting the premental sclerite; labial palpi with one segment, longer than wide, slightly globular at base, apex of palpi flattened with short, dense, irregular, spiculate setae, and one sensillum. Prelabium (*prm*) with sclerite distinctly dilated posteriorly and laterally, without posterior extension, cup-like, with one sensillum and one short *prms*; ligula with one tiny *ligs*. Postlabium (*plb*) with M-shaped sclerotization, with three *plbs* on sclerotized area, all setae separated from each other by about the same distance; short $plbs_1$ and $plbs_3$ as long as one-third length of $plbs_2$.



Figures 6–11. *Cionus olivieri* mature larva. **6** head, ventral view **7** antenna **8** spiracle **9** mandible **10** labrum and clypeus **11** epipharynx (*hp* hypopharyngeal bracon, *fsu* frontal suture, *tb* tentorial bridge). Seta(e): *als* anterolateral s., *ams* anteromedial s., *cls* clypeal s., *lms* labral s., *les* lateral epicranial s., *mds* mandible dorsal s., *ves* ventral epicranial s.). Scales bars: 0.5 mm (**6**), 0.25 mm (**10**, **11**), 0.1 mm (**8**, **9**), 0.025 mm (**7**).

Thorax (Fig. 2). Prothorax with pronotal shield partly sclerotized on dark brown smooth plate; with nine *prns*: two short ones on sclerotized area, two long and two short ones placed anteriorly, and three placed more medially; bicameral spiracle intersegmental between pro- and mesothorax, air-tube subequal to diameter of circular peritreme; pleural lobe with two *ps*; pedal area without setae; eusternum with one *eus*. Mesonotum with two folds, prodorsum without seta, postdorsum with two transversally aligned *pds* of the same length; epipleurum with one long *eps*; pleurum with one long *ps*; setae of pedal area and eusternum identical to that of prothorax. Chaetotaxy of metathorax identical to that of mesothorax.

Abdomen (Figs 2–4). Abdominal segments I–VII of almost equal lengths, remaining abdominal segments gradually decreasing in width posteriad. Tergites on abdominal segments I–VII with three folds, prodorsum wide and flat, mesodorsum narrow, with soft protuberance, postdorsum with soft protuberance; tergite on abdominal seg-

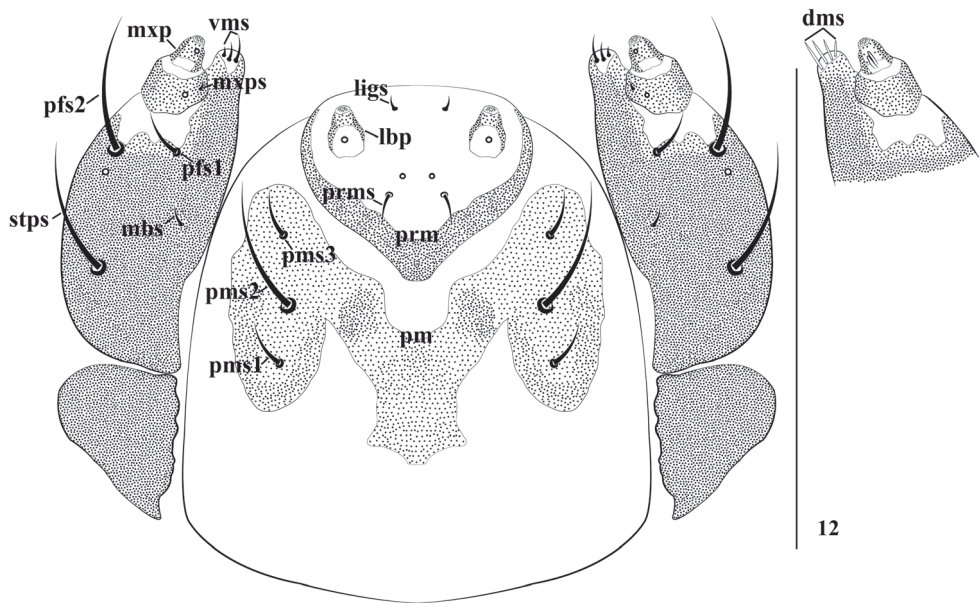


Figure 12. *Cionus olivieri* mature larva, maxillolabial complex, ventral view (lbp labial palpus, pm postmentum, prm prementum). Setae: *dms* dorsal malar s., *ligs* ligular s., *mbs* basoventral s., *mxps* maxillary palps s., *pfs* palpiferal s., *pms* postmental s., *prms* premental s., *stps* stipital s., *vms* ventral malar s.). Scale bar 0.25 mm.

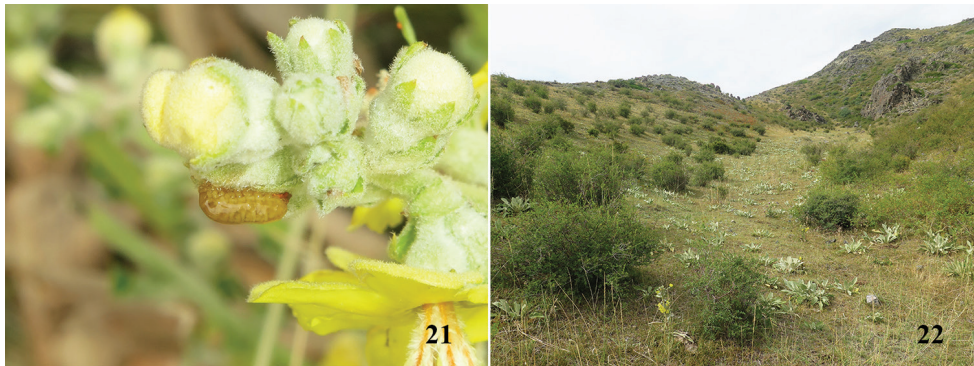
ment VIII with two folds, and on abdominal segment IX with no folds. Abdominal segment X reduced to four anal lobes of unequal size. Anus located subterminally. Spiracles (Fig. 8) bicameral, the eight abdominal spiracles located more ventrally up to ventral side of epipleurum, close to the anterior margin of abdominal segments I–VIII, size similar, each with two annulated air-tubes, pointing posteriad, air-tube subequal to diameter of circular peritreme. Abdominal segments I–VIII with three *pds*, located in one line, long *pds*₁, two times longer than *pds*₂, *pds*₂ as long as *pds*₃; with two *ss*, long *ss*₁, short *ss*₂, located in small indefinitely folds; with two *eps*, transversally aligned, long *eps*₁, short *eps*₂ as long as one-third length of *eps*₁; with one long *ps*; and with one *eus*. Abdominal segment IX with one short *ds*, one slight long *ps* and one, minute *sts*. Abdominal segment X without setae.

Biological notes

The biology of this species was studied on *Verbascum sinuatum* in southern France by Hoffmann (1958), where it has two generations, in June and August. The ectophagous larva digs a deep groove on the underside surface of a leaf. When mature, it builds a cocoon, where pupation takes place, on the same plant. The adults of the second generation hibernate in the soil. The same behavior was reported in other species of *Cionus* feeding either on *Verbascum* (Grandi 1929; Ruffo 1937; Hoffmann 1958) or *Scrophularia* (Read 1977; R  ther 1989).



Figures 13–20. Biology of *Cionus olivieri* from Kyrgyzstan **13** larva on flower **14** habitat **15** seeds of host plant **16** flowering host plant **17** larva on feeding **18** feeding holes **19** damage on host plant by larva **20** copulating adults.



Figures 21–22. Biology of *Cionus olivieri* from Kazakhstan. **21** larva on bud **22** habitat.

We collected larvae of *Cionus olivieri* (Fig. 13) from *Verbascum songaricum* Schrenk in early July in mountain slopes at 1546 m altitude (Fig. 14) in Kyrgyzstan. This plant, widely distributed in the temperate zone of Eurasia including the Caucasus, central Asia, and Tacheng, Xinjiang, China, was never previously reported as host of *Cionus*. Two-thirds of the host plants had already produced seeds (Fig. 15), while the remaining parts were still blooming (Fig. 16). Larvae were eating on the flower buds, with head, thorax, and part of the abdomen burrowed into the ovary and leaving red excrement, with a layer of clear mucus on the surface of the body (Fig. 17). The feeding holes were regular circles (Fig. 18). The most serious damage by the larvae reached 90% of one branch (Fig. 19), and most of the damaged buds could not bloom. We also observed many adults, more than 50% of which were mating (Fig. 20) and most of them were in the middle part of the host plants.

Later, we collected larvae of *Cionus olivieri* (Fig. 21) from the same host plant species in mid-August in mountain slopes at 1577 m altitude (Fig. 22) in Kazakhstan. Damage of the larvae were similar to those in Kyrgyzstan. However, we did not find adults mating. Bearing in mind Hoffmann's observations, we can assume that we probably collected the first generation in Kyrgyzstan and the second generation in Kazakhstan. However, in both situations, we did not find any cocoons on the plants (Fig. 15). This fact might be explained in two ways: both our observations were made before pupation or pupation happened in the soil. This second is unusual in *Cionus* but has been observed in *Cionus alauda* (Herbst, 1784) by Read (1977) and *Cleopus pulchellus* (Herbst, 1795) by R  ther (1989).

Discussion

Comparison with larvae of other *Cionus* species

The larvae of eight *Cionus* taxa have been previously described (Grandi 1929, 1938; Scherf 1964; Lee and Morimoto 1988b). Unfortunately, comparing descriptions of

some previously described *Cionus* species is problematic because of missing details on the chaetotaxy and/or the absence of quality drawings. Only the descriptions of four species were partly useful for comparison – *Cionus helleri* Reitter, 1904 (Lee and Morimoto 1988b), *C. hortulanus* (Geoffroy, 1785) (Grandi 1929), *C. olens* (Fabricius, 1792), and *C. scrophulariae* (Linnaeus, 1758) (Grandi 1938) – whereas the descriptions of another four – *C. alauda* (Herbst, 1784), *C. tuberculosus* (Scopoli, 1763), *C. olivieri*, and *C. thapsus* (Fabricius, 1792) (Scherf 1964) – were almost completely useless because they were very lacking in details. In particular, the morphological description of *Cionus olivieri* larva by Scherf (1964) is scant, and there are only a few details; which can be easily compared with our detailed descriptions. There are only a few useful characters, e.g., body length, number of folds on thoracic and abdominal segments, but no valuable information about chaetotaxy (actually he presents two *des* and two *fs*, and not three *des* and one *fs*).

The mature larvae of the genus *Cionus* are probably characterized by three diagnostic features: the reduced number of setae (1) on the epicranium (only two or three *des* and one or two *fs*), and (2) on the epipharyngeal lining (only two *als*, two *ams*, and no *mes*), i.e., distinctly fewer than the most frequent number of setae in weevils, and (3) mandibles dentate or angulate internally near the base (for details, see Grandi 1929, 1938; Scherf 1964; Lee and Morimoto 1988a). The unique exception of the first two diagnostic features is the larva of *Cionus helleri*, which has the standard number of setae as in other weevils, i.e., five *des* and five *fs* (vs. two or three *des* and one or two *fs*); and eight epipharyngeal setae (vs. four epipharyngeal setae, two *als*, and two *ams*). This fact appears particularly interesting. Indeed, Košťál and Caldara (2019) recently noticed that *C. helleri* is unique in Palearctic *Cionus* in having three tubercles on the pronotum, and mucronate apices of the meso- and metatibiae in males as well as spines on the anterior tarsomere 1. The first two character states are particularly interesting from a taxonomic and phylogenetic point of view because tubercles on the pronotum are possessed only by several species of Afrotropical *Cionus* and some Oriental *Cleopus* (M. Košťál and R. Caldara, pers. obs.), whereas the presence of tibial unci in male is a plesiomorphic condition shared in other genera of Cionini, i.e., *Nanomicrophyes*, *Cleopus*, and *Stereonychidius* (Caldara and Korotyaev 2002). Therefore, in the light of the data on immatures, the systematic placement of *C. helleri* is presently problematic and interpretation and comparison of the distinctive larval characters is crucial and worthy of further study.

The count of setae on the epipharynx (especially *ams* and *mes*) in Curculionidae has not been completely resolved, but this has been discussed in previous papers (e.g., Tychiini: Skuhrovec et al. 2014, 2015; Gosik et al. 2017). In our case, the setae on the labrum and epipharynx can be easily confused due to the lack of resolution in most compound microscopes. Compared to the setae on the epipharynx of *Cionus helleri* (Lee and Morimoto 1988b) with eight epipharyngeal setae, there are only two very tiny *als*, two *ams*, and no *mes* in *C. olivieri* as listed also in other *Cionus* descriptions (Grandi 1929, 1938; Scherf 1964). We were not able to establish whether the difference is due to their being different species or they are erroneous observations. It is

possible (C. Jiang and R. Zhang, pers. obs.) that the setae on the labrum and the edge part of epipharynx are more easily distinguishable by a scanning electron microscope.

The abdominal spiracles in Curculionidae are located mainly on the spiracular area, but we observed their position more ventrally up to the ventral side of the epipleurum in *Cionus olivieri*. A similar position of the spiracle in *Cionus* species is also shown on the drawings of Scherf (1964: figs 356, 366) and Lee and Morimoto (1988b: fig. 14B), but we have a different point of view on the status of setae around spiracles. Lee and Morimoto (1988b) reported them as *ss* setae, and setae above them as *pds*₄ and *pds*₅. In our opinion, “our” *ss* setae are on a distinct lobe which is normally accepted as the spiracular area, and spiracles are placed more ventrally on epipleurum, known also for some Brachycerinae taxa (May 1993, 1994). The drawings by Scherf (1964: figs 356, 366) do not show any other setae above the abdominal spiracles.

Comparison with larvae of related genera and tribes

With regard to the other genera of the tribe Cionini, only the immatures of three species were previously described, one belonging to *Cleopus* and two to *Stereonychus* (Scherf 1964; Lee and Morimoto 1988b). Unfortunately, as already emphasized for *Cionus*, two descriptions by Scherf (1964) for *Cleopus solani* (Fabricius, 1792) and *Stereonychus fraxini* (DeGeer, 1775) are problematic due to missing details on chaetotaxy, and it is almost impossible to compare it with *Cionus* species. Only a detailed larval description, that of *Stereonychus thoracicus* Faust, 1887 published by Lee and Morimoto (1988b), was useful. The mature larva of this species has similar chaetotaxy on the head (one *fs*, and no *mes*) as *Cionus* species, but there are some differences: *Stereonychus* has five *des* (in *Cionus* at most three), three *als* and three *ams* (in *Cionus* at most two *als* and two *ams*). It seems that mature larvae of *Cionus* (excluding *C. helleri*) + *Stereonychus* are characterized by six main diagnostic features: (1) labial palpi one-segmented, (2) labral rods absent, (3) pedal areas swollen to form large lobes or prolegs, (4) mandible with sharp apical teeth, (5) reduced number of *fs*, only one or two *fs*, on epicranium, and (6) reduced number of epipharyngeal setae (two or three *als* and two or three *ams*, but no *mes*), i.e., fewer than the most frequent number of setae recorded in weevils (for details, see Grandi 1929, 1938; Scherf 1964; Lee and Morimoto 1988a, 1988b). The first four diagnostic features in Cionini larvae are identical with *C. helleri* and also with Hyperini larvae (Lee and Morimoto 1988a, 1988b; Skuhrovec and Bogusch 2016), but this similarity with Hyperini is probably only due to the same ectophagous lifestyle.

Since it was hypothesized by a phylogenetic study based on morphological characters of imagos that the tribe Cionini might be the sister group of the tribe Mecinini (Caldara 2001) we also tried to compare the larvae of these two tribes. We found several distinct differential features: (1) bicameral spiracles in Cionini (vs. unicameral or bicameral spiracles in Mecinini); (2) dorsum of epicranium with two or three *des* (vs. five *des*); (3) frons with one or two *fs* (vs. three to five *fs*); (4) epipharynx without *mes* (vs. with one or two *mes*); and (5) mala with three to five *dms* and two to five *vms* (vs.

six or seven *dms* and four or five *vms*). The count of palpomeres on the labial palpi was confirmed as one of the most important morphological characters of larvae in the tribe Mecinini (van Emden 1938; Skuhrovec et al. 2018; Gosik et al. 2020), but the larvae in the tribe Cionini have no variability in this character, and the labial palpi have only one palpomere.

We realize that a thorough study of the immatures of the genus *Cionus* and related genera and tribes is still impossible because of limited available knowledge. However, it is clear that a detailed description of immature stages is of primary importance for further studies on generic and intergeneric taxonomic relationships within Cionini and/or Curculioninae, as done in other groups of Curculioninae, such as Tychiini (Gosik et al. 2017) and Mecinini (Jiang and Zhang 2015; Skuhrovec et al. 2018; Gosik et al. 2020).

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Taxonomic study of genus *Peucela* Ragonot, 1891 (Lepidoptera, Pyralidae) in China, with descriptions of three new species

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Abstract

The genus *Peucela* Ragonot, 1891 from China is revised. Three species are described as new to science, *P. acutivalva* **sp. nov.**, *P. baishanzuensis* **sp. nov.**, and *P. nigra* **sp. nov.** In addition, *P. olivalis* **comb. nov.** is newly combined. Photographs of adults, and male and female genitalia are provided. A key to the species of *Peucela* in China is also provided.

Keywords

key, morphology, Pyralinae, Pyraloidea

Introduction

The genus *Peucela* Ragonot, 1891 (Pyralidae, Pyralinae) was described with *Pyralis pallivittata* Moore, 1888 from India as the type species. Warren (1896) described *P. fumosalis* and *P. rubrifuscalis* from India. Later, the same author, Warren (1897) described *P. zonalis* from South Africa. Viette (1951) and Marion (1955) described *P. bourgini* and *P. ignealis* from Madagascar, respectively. Leraut (2010) established the new genus *Goateria* Leraut, 2010 and transferred *P. bourgini* to this genus. Leraut (2011) transferred *P. ignealis* to the genus of *Zitha* Walker, 1865. To date, the genus *Peucela* is

comprised of three valid species, which occur in South Africa and Asia (Moore 1888; Warren 1896, 1897; Nuss et al. 2020). In this study, the genus *Peucela* from China is reviewed, including descriptions of three new species and one new combination. The generic characters of *Peucela* are given in detail, and a key to Chinese species based on male genitalia characters is provided.

Material and methods

The examined specimens were collected with light traps and the dissections of genitalia were prepared by following the methods introduced by Li (2002). Wing venation preparations were carried out by following the protocol of Li and Zheng (1996). Specimens were examined using an Olympus SZX16 stereomicroscope. Images of adults and genitalia were captured with a Leica M205A stereomicroscope and a Leica DM750 microscope plus Leica Application suite 4.2 software. Terminology follows Slamka (2006) and Li and Li (2009). All specimens examined, including the types of the new species, are deposited in the Insect Collection of Nankai University (NKU), Tianjin, China.

Taxonomy

Genus *Peucela* Ragonot, 1891

Peucela Ragonot, 1891: 47. Type species: *Pyralis pallivittata* Moore, 1888.

Generic characters. Adult. Wingspan 19.0–26.5 mm. Frons rounded. Vertex covered with erect scales. Labial palpus upturned, third segment short and slightly porrect (Figs 1, 2). Maxillary palpus with three segments, usually as long as third segment of labial palpus and extending beyond its first segment. Antenna with scape dilated or ovate, flagellum filiform. Forewing ground color yellowish brown or grayish brown, with basal and terminal areas darker than median area. Hindwing concolorous with forewing, ante- and postmedial lines conspicuous. Venation (Fig. 3): forewing with 12 veins, R_3 and R_4 stalked from 2/5 length of R_3 , R_5 stalked with R_{3+4} at basal 1/4, R_{3+4+5} and M_1 connate at upper angle of cell, M_2 and M_3 connate at lower angle of cell, 1A+2A furcated at base; hindwing with 10 veins, Sc+ R_1 and Rs adjacent at middle of Sc+ R_1 , Rs and M_1 shortly stalked at upper angle of cell, M_2 and M_3 connate at lower angle of cell.

Male genitalia. Uncus trapezoidal or at least nearly trapezoidal basally. Gnathos with lateral arms bandlike, sinuous or straight; distal process short and hooked; two free basal extensions from base of gnathos, rod-shaped or band-shaped, sometimes enlarged or distally lobe-shaped. Valva broadest at base, narrowed towards apex; sacculus well developed. Juxta oval or shield-shaped. Saccus U-shaped, rounded at apex. Phallus medially curved, with basal part slightly enlarged, distal part cylindrical and granular on inner surface; cornutus thorn-shaped, sometimes basally or medially furcate.

Female genitalia. Papillae anales ovate. Apophyses posteriores shorter than apophyses anteriores. Antrum sclerotized; colliculum usually sclerotized, folded laterally. Ductus bursae slim, several times as long as corpus bursae, usually granular on inner surface anteriorly. Corpus bursae rounded, signum present or absent.

Diagnosis. The genus *Peucela* superficially resembles *Fujimacia* Marumo, 1939 in having a similar wing pattern. It can be distinguished from *Fujimacia* by having the uncus without a basolateral process at the base (with one basolateral process on each side at base in *Fujimacia*), the gnathos having two rod-shaped or band-shaped basal extensions (without basal extension in *Fujimacia*), and the valva without a spine-like process at the apex (with a small spine-like process at the apex) in the male genitalia. *Peucela* is also similar to *Maradana* Moore, 1884, but it can be distinguished by having the uncus basally trapezoidal (conical in *Maradana*), the distal process of the gnathos rather tiny and hooked (distal process of gnathos usually about half as long as lateral arms in *Maradana*), and the phallus slightly enlarged basally (evenly cylindrical in *Maradana*) in the male genitalia.

Key to the species of *Peucela* in China based on male genitalia

- 1 Valva distally curved; basal extension of gnathos not enlarged or lobe-shaped distally **2**
- Valva distally not curved; basal extension of gnathos enlarged or lobe-shaped distally **3**
- 2 Uncus trapezoidal; gnathos with lateral arms about half as long as basal extensions; valva rounded at apex (Fig. 9) ***P. baishanzuensis* sp. nov.**
- Uncus basally trapezoidal; gnathos with lateral arms as long as basal extensions; valva triangular at apex (Fig. 8) ***P. acutivalva* sp. nov.**
- 3 Uncus with apex about 1/3 width of basal width; lateral arms of gnathos as long as its basal extension (Fig. 10) ***P. nigra* sp. nov.**
- Uncus with apex about 1/2 width of basal width; lateral arms of gnathos about 1.5 times as long as its basal extension (Fig. 11) ***P. olivalis***

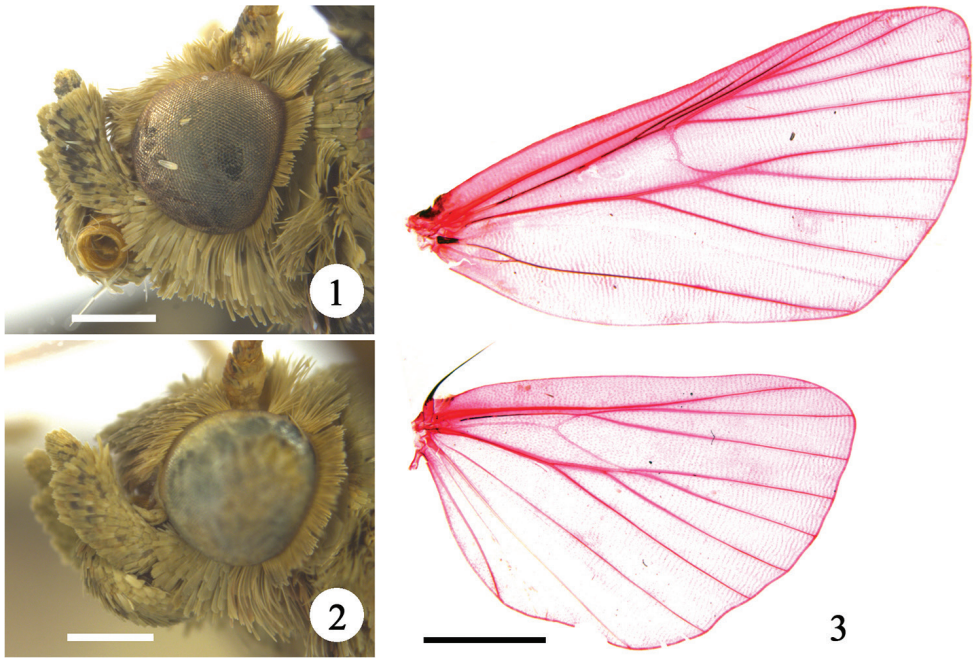
Peucela acutivalva Qi & Li, sp. nov.

<http://zoobank.org/04E42A7F-C659-4545-B026-0A2C8C05F3B1>

Figs 1, 2, 4, 8, 12

Type material. China, Tibet: **Holotype**, ♂, Langjiu Village (28.40°N, 85.35°E), Gyirong County, 2772 m, 11.VII.2019, leg. Mujie Qi, Jiaqi Deng, genitalia slide No. QMJ19027.

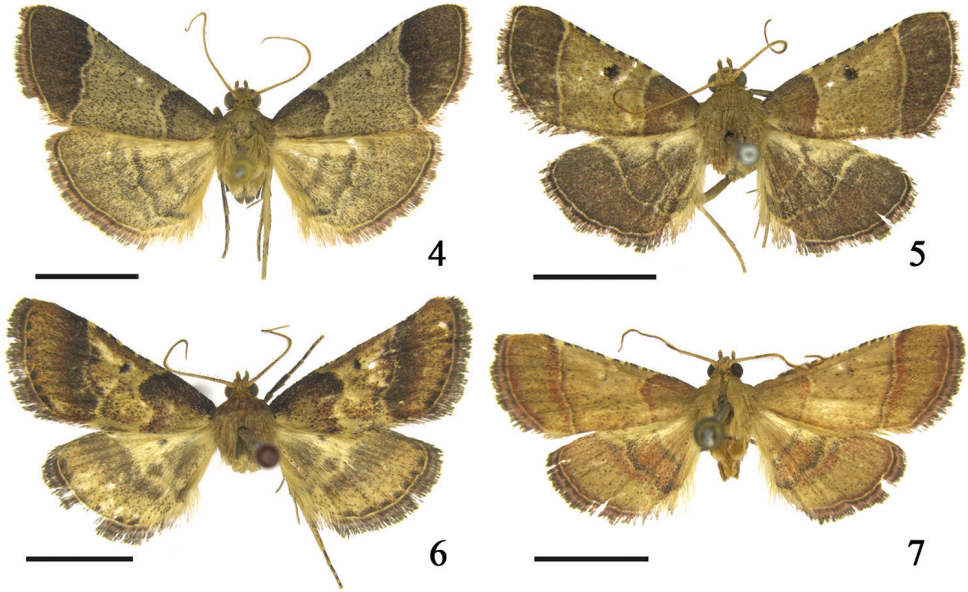
Paratypes: 2 ♂♂, 2 ♀♀, same data as holotype, genitalia slides No. QMJ19024♂, QMJ19038♂, QMJ19045♀, QMJ19047♀; 2 ♂♂, 1 ♀, Zhangmu Town (27.98°N, 85.97°E), Nyalam County, 1961 m, 5–8.VII.2019, leg. Mujie Qi, Jiaqi Deng, genitalia slide No. QMJ19023♂, QMJ19050♂, QMJ19048♀; 1 ♀, Chongse Village (28.38°N, 85.36°E), Gyirong County, 2640 m, 14.VII.2019, leg. Mujie Qi, Jiaqi Deng, genitalia slide No. QMJ19039.



Figures 1–3. Morphology of *Peucela* spp. **1** head of *P. acutivalva*, sp. nov., ♂ **2** head of *P. acutivalva*, sp. nov., ♀ **3** venation of *P. nigra* sp. nov., slide No. QMJ15128w. Scale bars: 0.5 mm (**1**, **2**); 2.5 mm (**3**).

Diagnosis. This species is similar to *P. pallivittata* (Moore, 1888) in the male genitalia, but it can be distinguished from the latter by the valva sharp at apex, the gnathos with the basal extension as long as the lateral arms, and the cornutus furcated at basal 1/3. In *P. pallivittata*, the valva is rounded at apex, the basal extension of the gnathos is about half the length of the lateral arms, and the cornutus is not furcated basally.

Description. Adult (Fig. 4). Wingspan 22.0–23.5 mm. Frons and vertex yellowish brown. Labial palpus yellowish brown, slightly mixed with fuscous scales; first segment about 1/3 length of second; second segment upturned; third segment as long as first. Maxillary palpus with first segment as long as third; second segment with constriction medially, extending strongly beyond first segment of labial palpus; concolorous with labial palpus. Male antenna with scape ovate, flagellum ventrally ciliate. Patagium and regula yellowish brown. Forewing grayish brown; basal area fuscous except for grayish brown at posterior half; terminal area fuscous, slightly mixed with reddish brown scales; costal margin fuscous except for median area interrupted with pale grayish brown spots; antemedial line pale grayish brown, from basal 1/4 of costa to basal 1/3 of dorsum, anterior half arched outwardly, posterior half concave inwardly; postmedial line concolorous with antemedial, edged with fuscous line on inner side, from distal 2/5 of costa to distal 1/8 of dorsum sinuously, with a distinct pointed convex between vein M_1 and M_2 ; median area sparsely suffused with fuscous scales, distal discoidal

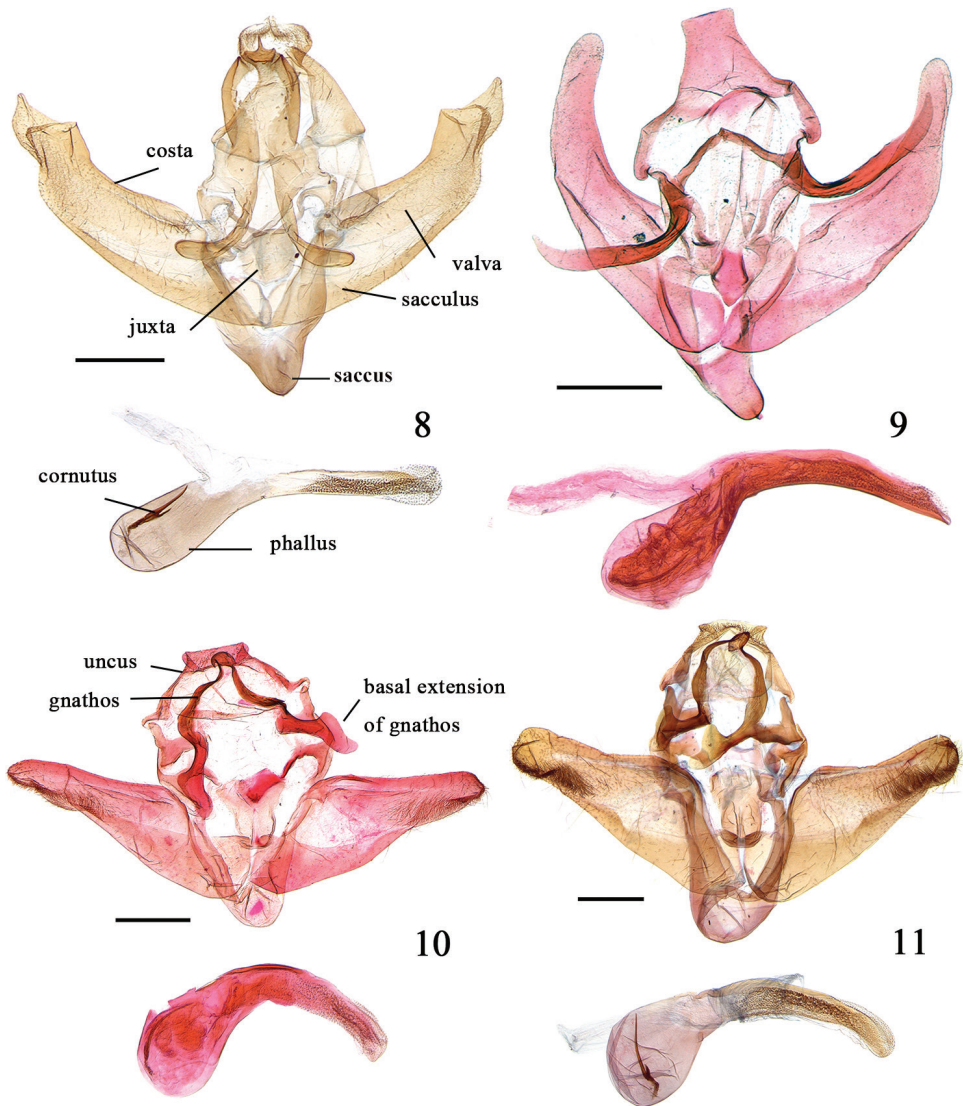


Figures 4–7. Adults of *Peucela* spp. **4** *P. acutivalva*, sp. nov., holotype, ♂ **5** *P. baishanzuensis*, sp. nov., holotype, ♂ **6** *P. nigra* sp. nov., holotype, ♂ **7** *P. olivalis*, ♂. Scale bars: 5.0 mm.

stigma fuscous; cilia fuscous at basal half, reddish brown at distal half. Hindwing concolorous with median area of forewing; ante- and postmedial lines pale grayish brown, both arched outwardly, outer side of antemedial and inner side of postmedial lines edged with fuscous lines; cilia fuscous at base, reddish brown distally. Foreleg fuscous except for tibia slight mixed with yellowish brown and each tip of tarsomere yellowish brown; midleg fuscous except for distal tibia and each apex of tarsomere yellowish brown; hindleg with femur fuscous, tibia and tarsus fuscous suffused with yellowish-brown scales, tarsus with scattered yellowish-brown scales, each tarsomere with apex yellowish brown.

Male genitalia (Fig. 8). Uncus with basal 3/5 trapezoidal, distal 2/5 oblong, with tiny triangular process at apex. Gnathos basally crescent-shaped, with a slim and up-turned hook apically about 1/10 as long as uncus; basal extension rod-shaped, as long as lateral arms, slightly inflated distally. Valva broad basally, gradually narrowed towards triangular apex, ventral margin curved at apex, dorsal margin with flat triangular projection at distal 1/4 of valva. Sacculus broad at base, gradually tapered distally, about 3/5 as long as valva. Juxta shield-shaped. Saccus U-shaped, distal 1/4 slightly narrowed. Phallus with basal half oval, distal half cylindrical and granular; cornutus about 1/4 length of phallus, furcated at basal 1/3, furcated part about 1/5 as long as cornutus.

Female genitalia (Fig. 12). Papillae anales ovate. Apophyses anteriores gradually tapered toward apex, about 3 times as long as apophyses posteriores. Antrum sclerotized, as long as apophyses anteriores; colliculum well sclerotized, slightly folded



Figures 8–11. Male genitalia of *Peucela* spp. **8** *P. acutivalva*, sp. nov., paratype, slide No. QMJ19023 **9** *P. baishanzuensis*, sp. nov., holotype, slide No. LJ17121 **10** *P. nigra* sp. nov., holotype, slide No. LJ17056 **11** *P. olivalis*, slide No. QMJ19029. Scale bars: 0.5 mm.

laterally, about as long as or slightly shorter than antrum. Ductus bursae with basal half wrinkled, anterior half granular on inner side, about 3 times as long as corpus bursae. Corpus bursae rounded; signum absent.

Etymology. The specific name is derived from the Latin *acutatus* (tapered) and *valva* (valva), in reference to the shape of the valva at the apex in the male genitalia.

Distribution. China (Tibet).

***Peucela baishanzuensis* Qi & Li, sp. nov.**

<http://zoobank.org/EC73F1FE-785F-4EB0-8F0A-456C41A975B1>

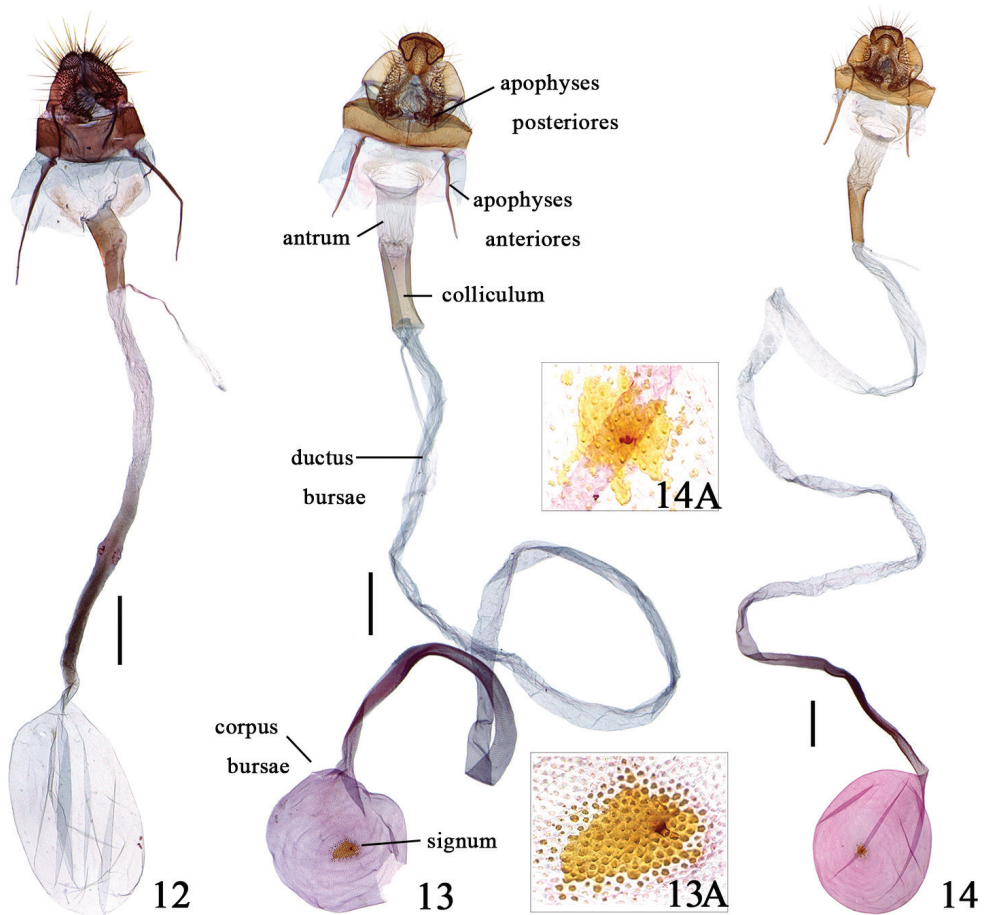
Figs 5, 9

Type material. China, Zhejiang Province: *Holotype*, ♂, Baishanzu Nature Reserve (27°44'N, 119°10'E), Qingyuan County, 1149 m, 15.VIII.2016, leg. Qingyun Wang, Meiqing Yang, Ping Liu, genitalia slide No. LJ17121.

Diagnosis. This species is superficially most similar to *P. olivalis*, but the male genitalia can be distinguished from that species in having the trapezoidal uncus not folded laterally at the apex, and the short and straight lateral arms of the gnathos about half as long as the basal extension, which is sharp and lacks an inflated triangular lobe distally. In *P. olivalis*, the uncus is basally semicircular, distally rectangular, and laterally folded at the apex; the lateral arms of the gnathos are arched and as long as the basal extension, which is inflated and distally lobe-shaped, and rounded at the apex.

Description. Adult male (Fig. 5). Wingspan 25.0 mm. Frons and vertex yellowish brown. Labial palpus yellowish brown; first segment as long as third, about 1/4 length of second. Maxillary palpus yellowish brown, as long as third segment of labial palpus; extending slightly beyond first segment of labial palpus. Antenna of male with scape dilated; flagellum ventrally with cilia. Patagium and tegula pale grayish brown. Forewing grayish brown; basal area with anterior 1/3 fuscous along costa, posterior 2/3 pale reddish brown except basal area pale brown; median area pale brown, with scattered fuscous scales; terminal area fuscous, mixed with reddish brown scales; costal margin fuscous, interrupted by yellowish-brown spots at median area; antemedial line pale yellowish brown, arched outwardly from basal 1/4 of costa to basal 1/3 of dorsum; postmedial line concolorous with antemedial line, edged with fuscous line both on inner and outer sides, from distal 1/4 of costa to distal 1/6 of dorsum sinuously; distal discoidal stigma fuscous; cilia fuscous at base, distally reddish brown. Hindwing fuscous mixed with reddish brown scales; ante- and postmedial lines yellowish brown and sinuous; postmedial line with posterior half incurved inwardly, approximated to antemedial line at dorsum; cilia same as that in forewing. Foreleg fuscous except each apex of tarsomere yellowish brown; midleg with femur fuscous, tibia yellowish brown except basal half and apex fuscous, tarsus yellowish brown, suffused basally with fuscous scales; hindleg yellowish brown, femur suffused with fuscous scales, basal of spurs and tarsomere fuscous.

Male genitalia (Fig. 9). Uncus trapezoidal, flat at apex, laterally concave at distal 1/3. Gnathos with lateral arms slim and straight; distal process tiny and rhombic; basal extension upturned at basal 1/4, about twice as long as lateral arms of gnathos, knife-shaped at apex. Valva broad basally, gradually narrowed towards rounded apex; clasper flat, at below base of costa; sacculus gradually tapered distally, about 3/5 length of valva. Juxta with basal part sclerotized and rhombic, apical part membranous and rectangular. Saccus U-shaped, rounded at apex, about 1/3 length of sacculus. Phallus with basal part oval; distal part about 1.2 times as long as basal part, distally with granules; cornutus about 1/5 length of phallus.



Figures 12–14. Female genitalia of *Peucela* spp. **12** *P. acutivalva*, sp. nov., paratype, slide No. QMJ19048 **13** *P. nigra* sp. nov., paratype, slide No. QMJ15128 **13A** Enlarged signum **14** *P. olivalis*, slide No. QMJ15152 **14A** Enlarged signum. Scale bars: 0.5 mm.

Female. Unknown.

Etymology. The specific name is derived from the type locality, Baishanzu Nature Reserve in Qingyuan County, Zhejiang Province.

Distribution. China (Zhejiang).

***Peucela nigra* Qi & Li, sp. nov.**

<http://zoobank.org/7C7F8047-04B4-4E42-BE04-7C0A915BBF5B>

Figs 6, 10, 13

Type material. China, Yunnan Province: **Holotype:** ♂, Mt. Jizu (25.96°N, 100.39°E), Dali City, 2228 m, 27.VII.2014, leg. Kaijian Teng, Wei Guan, Xiuchun Wang, Shurong Liu, genitalia slide No. LJ17056.

Paratypes: 2 ♀♀, same data as holotype, genitalia slides No. QMJ15128, LJ17057; 1 ♀, Lingbaoshan Forestry Park, Nanjian County, 2338 m, 25.VIII.2015, leg. Kaili Liu, Jingxia Zhao, genitalia slide No. QMJ19026.

Diagnosis. This species is similar to *P. olivalis* in the male and female genitalia, but it can be distinguished in the male genitalia by the uncus with the apical width about $1/3$ of the basal width and the lateral arms of the gnathos as long as the basal extension and knife-shaped at apex; and in the female genitalia by the antrum as long as the colliculum and the corpus bursae about $1/10$ as long as the ductus bursae. In *P. olivalis*, the apex of the uncus is about $1/2$ width of its basal width, the lateral arms of the gnathos is 1.5 times as long as its basal extension, and is rounded at apex (Fig. 11); the antrum is longer than the colliculum and the corpus bursae is about $1/8$ the length of ductus bursae (Fig. 14).

Description. Adult (Fig. 6). Wingspan 23.0–26.5 mm. Frons and vertex covered with yellowish-brown scales. Labial palpus yellowish brown; second and third segments mixed ventrally with fuscous scales; first segment as long as third; second segment about 5 times as long as first; third segment porrect. Maxillary palpus yellowish brown, slightly shorter than third segment of labial palpus, extending slightly beyond first segment of labial palpus. Antenna with scape ovate, flagellum ventrally with cilia in male. Patagium reddish brown, with scattered fuscous scales; tegula grayish brown. Forewing yellowish brown; basal area with anterior half fuscous, mixed with reddish brown, posterior half grayish brown except for outer margin reddish brown and slightly mixed with fuscous; terminal area with basal half fuscous, outer margin reddish brown, apical half brown, slightly mixed with reddish brown and fuscous; terminal line fuscous with interrupted by reddish brown spots; costal margin fuscous except apex brown, interrupted by yellowish brown spots at median area; antemedial line pale yellowish brown, from basal $2/5$ of costa to basal $1/3$ of dorsum sinuously; postmedial line bounded by slim, fuscous line on inner side, waved from distal $2/5$ of costa to distal $1/3$ of dorsum; median area with scattered fuscous and reddish-brown scales, distal discoidal stigma fuscous; cilia fuscous except yellowish brown at base. Hindwing pale grayish brown, terminal area yellowish brown; ante- and postmedial lines yellowish brown, both sinuous; median area with anterior half yellowish brown, posterior half pale grayish brown, interrupted by yellowish-brown spots; cilia concolorous with forewing. Foreleg fuscous except each apex of tarsomere brown; midleg fuscous except behind spur and apex of tarsomere brown; hindleg fuscous, femur slightly mixed with yellowish scales, basal of tibia suffused with brown scales, each distal half of tarsomere brown.

Male genitalia (Fig. 10). Uncus with basal $4/5$ semicircular; distal $1/5$ rectangular, flat at apex, dorsally setose, ventrally with lobe-shaped process. Gnathos with lateral arms sinuous, distal process beaklike; basal extension as long as lateral arms, basal half straight, distal half dorsally with triangular dilatation. Valva basally broad, gradually narrowed towards truncated apex, setose at distal $2/5$ of ventral margin of valva. Sacculus near subtriangular, about $2/3$ as long as valva. Juxta with basal half ovate, distal part inverted trapezoidal. Saccus U-shaped, about $1/4$ length of sacculus. Phallus with basal $1/3$ oval; distal part about twice as long as base, apically gradually narrowed, with granules at distal $4/5$; cornutus about $1/3$ length of phallus.

Female genitalia (Fig. 13). Papillae anales with anterior 4/5 ovate, posterior 1/5 diamond-shaped. Apophyses anteriores gradually tapered toward apex, about 3 times as long as apophyses posteriores. Antrum about 4/5 length of apophyses anteriores; colliculum well sclerotized, laterally folded, about as long as apophyses anteriores. Ductus bursae about 10 times as long as corpus bursae, anterior 1/3 scobinate on inner surface. Corpus bursae rounded, scobinate on inner surface; signum consisting of numeral spinules, with short thorn at middle.

Etymology. The specific name is derived from the Latin *niger* (black) in reference to the dark belt in the distal area of the forewing.

Distribution. China (Yunnan).

***Peucela olivalis* (Caradja, 1927), comb. nov.**

Figs 7, 11, 14

Bostra olivalis Caradja, 1927: 44. TL: China.

Arppara indicator marginata (Walker, 1865): Leraut 2013: 60.

Material examined. **Fujian:** 1 ♂, 1 ♀, Guadun, Mt. Wuyi, 1100 m, 28.VII.2008, leg. Weichun Li, Yongling Sun, Haiyan Bai, genitalia slide No. QMJ17021♂, QMJ17022♀; **Guangxi:** 1 ♂, Yangchang Forestry center, Leye County, 1160 m, 26.VII.2004, leg. Jiasheng Xu, genitalia slide No. QMJ16004; **Hainan:** 1 ♀, Mt. Diaoluo, 940 m, 31.V.2007, leg. Zhiwei Zhang, Weichun Li, genitalia slide No. LJ17086; 1 ♂, Jianfengling Nature Reserve (18.44°N, 108.52°E), Ledong County, 770 m, 29.V.2015, leg. Peixin Cong, Wei Guan, Sha Hu, genitalia slide No. QMJ19030; **Hunan:** 1 ♂, Zhangjiajie, 650 m, 7.VII.2001, leg. Houhun Li, Xinpu Wang, genitalia slide No. QMJ15197. **Sichuan:** 1 ♂, 2 ♀♀, Caoping Village (30.95°N, 103.32°E), Wenchuan County, 1557 m, 9–12.VII.2014, leg. Kaijian Teng, Wei Guan, Xiuchun Wang, Shurong Liu, genitalia slide No. QMJ16005♂, LJ17081♀, LJ16041♀; 3 ♀♀, Labahe Nature Reserve, Tianquan County, 1300 m, 28–29.VII.2004, leg. Yingdang Ren, genitalia slide No. LJ17078, QMJ15152, LJ17080; **Yunnan:** 1 ♂, Taiyanghe Nature Reserve, 1450m, 2.IX.2014, leg. Zhengguo Zhang, genitalia slide No. LJ16024; **Zhejiang:** 1 ♂, Chanyuansi, Mt. Tianmu, 350 m, 15.VIII.1999, leg. Houhun Li et al., genitalia slide No. WSS02136.

Diagnosis. This species shares most of the diagnostic characters of the genus as follows: in male genitalia, gnathos with two free basal extensions at base and phallus medially curved, with basal part enlarged slightly; in female genitalia, colliculum cylindrical and sclerotized and ductus bursae several times as long as rounded corpus bursae and granular anteriorly. Adult (Fig. 7) with wingspan 19.5–22.0 mm. This species is superficially most similar to *P. baishanzuensis* sp. nov., and the differences between them are stated under *P. baishanzuensis* sp. nov. In addition, it resembles *P. nigra* sp. nov. in the male and female genitalia, and the differences between them are stated in the diagnosis of *P. nigra* sp. nov.

Distribution. China (Fujian, Guangxi, Hainan, Hunan, Sichuan, Yunnan, Zhejiang).

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