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Annotated checklist of the operculated land snails from Thailand (Mollusca, Gastropoda, Caenogastropoda): the family Pupinidae, with descriptions of several new species and subspecies, and notes on classification of *Pupina* Vignard, 1829 and *Pupinella* Gray, 1850 from mainland Southeast Asia

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Abstract

Thailand is located at the crossroads of several biogeographical regions, and boasts a high level of biodiversity, especially among the malacofauna. The most recent checklist of land snail species in Thailand was compiled more than twenty years ago, and so this checklist needs revision and the addition of newly discovered taxa. This study updates the taxonomy and species list of the operculated land snail family Pupinidae from Thailand. This snail family is diverse and abundant, and can be found in various natural habitats in Southeast Asia. Although the taxonomy of some Southeast Asian pupinid genera has been reviewed, studies of *Pupina* Vignard, 1829, which contains the highest number of species, and a lesser-known genus *Pupinella* Gray, 1850 are still lacking. Herein we present an annotated checklist with an up-to-date systematic framework of the Pupinidae in Thailand based on both field investigations and literature surveys, and include the taxonomic treatment of all *Pupina* and *Pupinella* species from mainland Southeast Asia. This annotated checklist contains 30 nominal species and two subspecies from seven genera currently known to occur in Thailand. We describe two species of *Pseudopomatias* (*P. doiangkhangensis* Jirapatrasilp, **sp. nov.** and *P. pallgergelyi* Jirapatrasilp, **sp. nov.**), five species and one subspecies of *Pupina* (*P. bensoni* Jirapatrasilp, **sp. nov.**, *P. bilabiata* Jirapatrasilp, **sp. nov.**, *P. godwinausteni* Jirapatrasilp, **sp. nov.**, *P. latisulci* Jirapatrasilp, **sp. nov.**, *P. stoliczkai* Jirapatrasilp, **sp. nov.**, and *P. dorri isanensis* Jirapatrasilp, **ssp. nov.**) as new to science. New records of *Coptocheilus sumatranus*, *Pupinella mansuyi*, and *Rhaphaulus tonkinensis* are also reported from Thailand. The mainland Southeast Asian *Pupina* species are classified into three species groups (*Pupina artata* group, *Pupina arula* group, and *Pupina aureola* group) based on the distinction of shell teeth and canals, and operculum. Three species formerly in *Pupina* from Vietnam are allocated to *Pupinella* (*P. illustris* **comb. nov.**, *P. sonlaensis* **comb. nov.**, and *P. thaitranbaii* **comb. nov.**) due to the presence of a funnel-like anterior canal.

Keywords

Biodiversity, malacofauna, "prosobranch", systematics, taxonomy

Table of contents

Introduction 4
Materials and methods 6
  Sources 6
  Structure of the list 7
  Terminology of *Pupina* and *Pupinella* shells 8
  Institutional abbreviations 8
  Other abbreviation 8
  Photograph credits 8
  Taxon names 11
Results 12
  Systematics 13
    Family Pupinidae Pfeiffer, 1853 13
    Subfamily Pupinellinae Kobelt, 1902 13
      1. Genus *Coptocheilus* Gould, 1862 13
          Coptocheilus sectilabris (Gould, 1843) 14
          Coptocheilus sumatranus Dohrn, 1881 15
      2. Genus *Pollicaria* Gould, 1856 16
          Pollicaria mouhoti mouhoti (Pfeiffer, 1863) 16
          Pollicaria mouhoti monochroma Kongim & Panha, 2013 18
        Species with uncertain record from Thailand 19
          Pollicaria myersii (Haines, 1855) 19
      3. Genus *Pseudopomatias* Möllendorff, 1885 20
          Pseudopomatias caligosus Páll-Gergely & Hunyadi, 2018 20
          Pseudopomatias doiangkhangensis Jirapatrasilp, sp. nov. 21
          Pseudopomatias pallgergelyi Jirapatrasilp, sp. nov. 22
      4. Genus *Pupinella* Gray, 1850 22
          Pupinella mansuyi (Dautzenberg & Fischer, 1908) 23
        Species from other parts of mainland Southeast Asia not recorded for Thailand 24
          Pupinella illustris (Mabille, 1887) comb. nov. 24
          Pupinella sonlaensis (Do, 2017) comb. nov. 25

Pupinella thaitranbaii (Do, 2017) comb. nov. 26
5. Genus *Rhaphaulus* Pfeiffer, 1856 27
Rhaphaulus lorraini Pfeiffer, 1856 27
Rhaphaulus perakensis Smith, 1898 28
Rhaphaulus ascendens Sykes, 1903 29
Rhaphaulus tonkinensis Páll-Gergely, Hunyadi & Maassen, 2014 29
Species with uncertain record from Thailand 30
Rhaphaulus chrysalis (Pfeiffer, 1853) 30
6. Genus *Tortulosa* Gray, 1847 31
Tortulosa tortuosa (Férussac, 1821) 31
Subfamily Pupininae Pfeiffer, 1853 46
7. Genus *Pupina* Vignard, 1829 46
Group I. *Pupina artata* species group 47
Pupina artata Benson, 1856 48
Pupina pallens Möllendorff, 1894 51
Pupina limitanea Godwin-Austen, 1897 52
Pupina bensoni Jirapatrasilp, sp. nov. 53
Species of group I (*P. artata* species group) from other parts of mainland Southeast Asia not recorded for Thailand 54
Pupina hungerfordiana Nevill, 1878 54
Pupina billeti Fischer, 1898 56
Pupina verneaui Dautzenberg & Fischer, 1906 56
Group II: *Pupina arula* species group 65
Pupina peguensis Benson, 1860 65
Pupina crosseana Morlet, 1883 67
Pupina siamensis Möllendorff, 1902 68
Pupina bilabiata Jirapatrasilp, sp. nov. 69
Pupina godwinausteni Jirapatrasilp, sp. nov. 71
Species of group II (*P. arula* species group) with uncertain record from Thailand 72
Pupina arula Benson, 1856 72
Pupina mouhoti Pfeiffer, 1861 73
Species of group II (*P. arula* species group) from other parts of mainland Southeast Asia not recorded for Thailand 73
Pupina vescoi Morelet, 1862 73
Pupina exclamationis Mabille, 1887 74
Pupina perakensis Möllendorff, 1891 74
Pupina excisa Möllendorff, 1902 75
Group III. *Pupina aureola* species group 84
Pupina aureola Stoliczka, 1872 84
Pupina paviei Morlet, 1883 86
Pupina tchehelensis Morgan, 1885 86
Pupina dorri isanensis Jirapatrasilp, ssp. nov. 87
Pupina latisulci Jirapatrasilp, sp. nov. 88

Pupina stoliczkai Jirapatrasilp, sp. nov. 89
Species of group III (*P. aureola* species group) from other parts of mainland Southeast Asia not recorded for Thailand 90
Pupina lowi Morgan, 1885 90
Pupina dorri dorri Dautzenberg, 1894 91
Pupina tongupensis Godwin-Austen, 1897 92
Pupina anceyi Bavay & Dautzenberg, 1899 92
Pupina laffonti Ancey, 1899 93
Pupina solidula Möllendorff, 1901 94
Pupina brachysoma Ancey, 1904 94
Pupina douvillei Dautzenberg & Fischer, 1906 95
Species from other parts of mainland Southeast Asia with uncertain affiliation 95
Pupina porcellana Rochebrune, 1881 95
Discussion 103
Acknowledgements 103
References 104

Introduction

Thailand boasts a high diversity of both flora and fauna, as the country is located within the Indo-Burma biodiversity hotspot, which is deemed the “crossroads” of three biogeographical regions: southern China in the north, the Indian subcontinent and the Himalayas in the west, and Sundaland in the south (Ashton 1990; Myers et al. 2000; Tordoff et al. 2012). Thailand’s geography can be divided into (i) the hill ranges in the north, (ii) the central plain, (iii) the Khorat Plateau, and (iv) the coastal plains of southeastern Thailand, Kra Isthmus and the Malay Peninsula (Gupta 2005). Each distinct geographical area has unique climatic, geological, and vegetational conditions that provide highly diverse habitats, such as limestone karsts that house several endemic species (e.g., Latinne et al. 2013; Suwannapoom et al. 2018). However, various groups of terrestrial invertebrates have still received less attention compared to their vertebrate counterparts, which have been more frequently and comprehensively inventoried (e.g., amphibians: Chan-ard 2003; Chuaynkern and Chuaynkern 2012; Niyomwan et al. 2019).

Although the terrestrial malacofauna exhibits a particularly high diversity, studies on species diversity in Thailand have only been sporadically published in the past (Suvatti 1938, 1950; Solem 1966; Panha 1996; Hemmen and Hemmen 2001). In the mid-nineteenth century, the earliest study of Thai land snails was done by William A. Haines, who had retrieved specimens from Dr. Samuel R. House, an American missionary (Haines 1855). As Thailand (formerly known as Siam) was never colonised by any Western countries like its neighbours were, there were no prominent naturalists who extensively collected and studied land snails in the country, as Henri Mouhot and Auguste Pavie did in French Indochina (present-day Cambodia, Laos, and Vietnam;

Inkhavilay et al. 2019), and Henry H. Godwin-Austen and several other British naturalists did in Myanmar and Malaysia (Godwin-Austen 1882–1920). However, since the expeditions led by H. Mouhot and A. Pavie surveyed parts of present-day Thailand (Inkhavilay et al. 2019), some Thai land snails were described from the Mouhot collections under Hugh Cuming's legacy, primarily by Louis Pfeiffer (1856a, 1860), and from the Pavie collections by several French and Belgian malacologists (Fischer and Dautzenberg 1904). Later, L. Pfeiffer (1862) also described more new species from Siam. Another important study was done by Eduard von Martens (1867), who worked on the collections from the Prussian Expedition to East Asia during 1859–1862.

Thereafter, and until the twentieth century, studies on Thai land snails were fragmentary and occasionally done by western malacologists who obtained specimens from merchants, naturalists and missionaries visiting Thailand. For example, Otto F. von Möllendorff studied land snails and described new species based on Carl Roebelen's collections from the Samui Islands and based on Hans Fruhstorfer's collections from several localities (von Möllendorff 1894, 1902b). William T. Blanford studied and described two new species from specimens collected by William M. Daly in Lamphun and Phitsanulok (Blanford 1902, 1903). John R. le B. Tomlin studied and described new species from specimens collected by Dr. Arthur Kerr from various parts of Thailand (Tomlin 1929, 1931, 1932a, b), and later Albert E. Salisbury described one new species based on Tomlin's collection (Salisbury 1949). Paul Bartsch described one new species from Kao Sabab, and Fredrik E. Loosjes described one new subspecies from Doi Ang Ka, based on specimens collected by Hugh M. Smith, the Fishery Advisor to the Government (Bartsch 1932; Loosjes 1950). Fritz Haas reported some land snail species collected during the Rush Watkins Zoological Expedition to Siam in 1949 (Haas 1952). Alan Solem studied and described new species and genera based on collections from several Danish expeditions in northern, eastern and western Thailand during 1958–1964 (Solem 1966).

More recently, land snail research in Thailand was boosted after SP began studying Thai land malacofauna in the 1990s (Panha 1996). A number of operculated land snails from the families Alycaeidae, Cyclophoridae and Diplommatinidae were described (Panha and Burch 1998, 2005; Panha and Patamakanthin 2001; Nantarat et al. 2014, 2019; Sutcharit et al. 2014; Jirapatrasilp et al 2021). However, most malacological studies focused on pulmonate land snails, e.g., the families Ariophantidae (Pholyotha et al. 2020; Sutcharit and Panha 2021), Camaenidae (Sutcharit and Panha 2006), Gastrocoptidae (Panha and Burch 2005), and Streptaxidae (Siriboon et al. 2014a, b). The 20-year work of SP and his colleagues has culminated in a recent inventory and book on Thai land snails (BEDO 2017; Sutcharit et al. 2018).

The family Pupinidae Pfeiffer, 1853 belongs to the group of operculated land snails in the superfamily Cyclophoroidea, subclass Caenogastropoda (Bouchet et al. 2017). Although Tielecke (1940) characterised this family by its pupoid shell shape and long bursa copulatrix, several pupinid groups have no pupoid shells, e.g., *Pseudopomatias* and its relatives (Páll-Gergely et al. 2015), and the entire subfamily Liareinae (Powell 1979; Marshall and Barker 2007). The shell shape alone is thus not diagnostic and anatomical information in several groups is still lacking. Approximately 30 extant and ten extinct genera are recognised within this family, the distribution of which ranges from South and East Asia to Southeast Asia, Melanesia, Micronesia and part of Australia (MolluscaBase 2022; see also literature cited in Kongim et al. 2013). Ten pupinid genera have been recorded from mainland Southeast Asia (Kobelt 1902; Páll-Gergely et al. 2015; Thach 2017), where they can be found in various natural habitats and are abundant in limestone areas.

Recently, the taxonomy of some genera has been reviewed; i.e., *Coptocheilus* Gould, 1862 (Páll-Gergely et al. 2019; Bui and Páll-Gergely 2020), *Pollicaria* Gould, 1856 (Kongim et al. 2013), *Rhaphaulus* Pfeiffer, 1856 and *Streptaulus* Benson, 1857 (Páll-Gergely et al. 2014, 2017), and *Pseudopomatias* Möllendorff, 1885 and *Vargapupa* Páll-Gergely, 2015 (Páll-Gergely et al. 2015; Páll-Gergely and Grego 2019). Another land snail genus, *Notharinia* Vermeulen, Phung & Truong, 2007 was originally classified in the Pupinidae based on a set of shell characters shared with *Pseudopomatias*. *Notharinia* also lacks a circular constriction inside the ultimate or penultimate whorl, the presence of which is typical in the Diplommatinidae (Vermeulen et al. 2007; Marzuki and Foon 2016). However, *Notharinia* was later transferred to the Diplommatinidae, due to a similar shell size and shape to *Arinia* H. Adams & A. Adams, 1856, a possession of a distinctly oblique apex which commonly occurs in diplommatinids, and the discovery of *Notharinia* species with a constriction in the spire (Marzuki and Foon 2016; Vermeulen et al. 2019). The studies on *Pupina* Vignard, 1829, which contains the highest number of species, have been restricted to particular geographical areas (Do 2017; Tripathy and Sajan 2019), whereas other, less speciose genera, including *Barnaia* Thach, 2017, *Pupinella* Grey, 1850, and *Tortulosa* Gray, 1847 still remain unexamined.

This study is the first comprehensive work to update the taxonomy and species list of operculated land snails in the family Pupinidae in Thailand, several species of which are recognised as new to science. We also revise the genera *Pupina* and *Pupinella* from mainland Southeast Asia. This paper provides a checklist of species compiled from the literature and based on specimens collected during field surveys throughout the country over the past 28 years (1995–2022). It includes taxonomic updates, illustrations of type specimens (when possible), and photos of newly collected specimens. We hope that this paper will contribute to a better understanding of the operculated land snail biodiversity in Thailand, the knowledge of which can be applied in ecological, agricultural, and pharmaceutical research, and hope to inspire future generations to learn and conserve the country's land snail heritages.

Materials and methods

Sources

The data compiled in this checklist are from two main sources. The first source is the published malacological literature ranging from the nineteenth century until the present (February 2022). These historical works, i.e., the "Proceedings of the Zoological

Society of London", are available online at www.biodiversitylibrary.org and www.archive.org. This list includes all taxa in the family Pupinidae that have their type locality or subsequent localities reported from the area of "Siam" or present-day Thailand. The list also includes all *Pupina* and *Pupinella* species from mainland Southeast Asia, covering Cambodia, Laos, Myanmar, peninsular Malaysia, and Vietnam. The second source of information are field surveys conducted during 1995–2022 (Fig. 1). Land snails in Thailand were collected using direct search techniques throughout the country, including the northern mountainous forests, deciduous forests in the northeast, evergreen forests in the south, limestone areas throughout the country. Surveys included both anthropogenic and plantation areas (Fig. 2).

The direct searching for snails involved all potential land snail microhabitats that could be accessed, such as deep litter beds, decaying tree trunks, rock surfaces and crevices and, especially, limestone cliffs and caves. All sampled locations were recorded. At each locality, land snails were searched for intensively for ca. 1–2 h by three or four well-trained assistants. All living snails were photographed and killed by the two-step method for euthanasia (AVMA 2020) before being preserved in 70% ethanol for anatomical studies, or preserved in 95% (v/v) ethanol for molecular analyses. The handling of animals in this study was approved by Chulalongkorn University Animal Care and Use Committee (CU-ACUC) under the approval number 1723018. Empty shells were air dried in mesh bags for one to two weeks before being sorted. Intact adult shells were measured for whorl number, shell height, and major diameter or shell width using digital Vernier callipers (Mitutoyo, CD-6 CS). Shell spire angle was measured using a goniometer following Kozuch et al. (2017).

Structure of the list

Species identification of specimens is based on the literature and comparisons with the type specimens and/or reference collections from several natural history museums. The classification of the higher taxa in the list is according to Bouchet et al. (2017) and the generic placements mainly follow Kobelt (1902), Clench (1949), Egorov (2013), Kongim et al. (2013), Páll-Gergely et al. (2014, 2015, 2017), Páll-Gergely and Grego (2019), Bui and Páll-Gergely (2020), and MolluscaBase (2022). Under each subfamily, the genera are listed alphabetically whereas the species within each genus are listed chronologically. Within each species or subspecies, the treatment includes the original combination of the taxon name with original spelling, and references to the page(s) and plate and/or figures. The type locality and the localities retrieved from past distribution records that address the occurrences of that particular taxon in Thailand are given verbatim as stated in that respective publication, and when possible, the modern name and/or regional name of those localities is provided in square brackets. In addition, when possible, the type materials with catalogue numbers, the images of the type specimens, and/or the images of newly collected specimens are also provided. Unless specified otherwise, all localities of CUMZ specimen lots are located in Thailand. The species which have an uncertain record from Thailand were not plotted in the distribution maps.

Terminology of *Pupina* and *Pupinella* shells

The terminology of teeth follows those of pupillid snails in Pilsbry (1918), where the upper tooth is called the parietal tooth and the lower tooth is called the columellar tooth (Fig. 3). For the terminology of canals, Egorov (2013) mentioned both 'anterior' and 'posterior' canals, and 'columellar' and 'parietal' canals. The anterior and posterior canals correspond to the columellar and parietal positions, respectively (Fig. 3). Here we adopt the terms 'anterior' and 'posterior' canals following the usages of Stanisic et al. (2010), Do (2017) and Tripathy and Sajan (2019). The terms 'inner' and 'outer' peristomes are adopted based on Liew et al. (2014: fig. 10) and Jirapatrasilp et al. (2021).

Institutional abbreviations

CUMZ	Chulalongkorn University Museum of Zoology, Bangkok;
HNHM	Hungarian Natural History Museum, Budapest;
HNUE	Museum of Biology of Hanoi National University of Education, Hanoi;
MCZ	Museum of Comparative Zoology, Harvard University, Massachusetts;
MNHN	Muséum national d'Histoire naturelle, Paris;
NHMUK	when citing specimen lots deposited in the Natural History Museum, London (NHM);
NMW	National Museum of Wales, Cardiff;
NZSI	The National Zoological Collection of the Zoological Survey of India, Kolkata;
RBINS	Royal Belgian Institute of Natural Sciences, Brussels;
SMF	Forschungsinstitut und Naturmuseum Senckenberg, Frankfurt am Main;
UMZC	Cambridge University Museum of Zoology, Cambridge;
USNM	National Museum of Natural History, Smithsonian Institution, Washington, D.C.;
ZRC	Zoological Reference Collection of Lee Kong Chian Natural History Museum, National University of Singapore.

Other abbreviation

amsl	above mean sea level.

Photograph credits

Photographs of the type specimens from the Molluscs Collection (IM) of MNHN are credited to the museum taken under project E-RECOLNAT: ANR-11-INBS-0004 unless stated otherwise. Photographs of the type specimens and specimens from the other museum collections are credited to each respective museum.

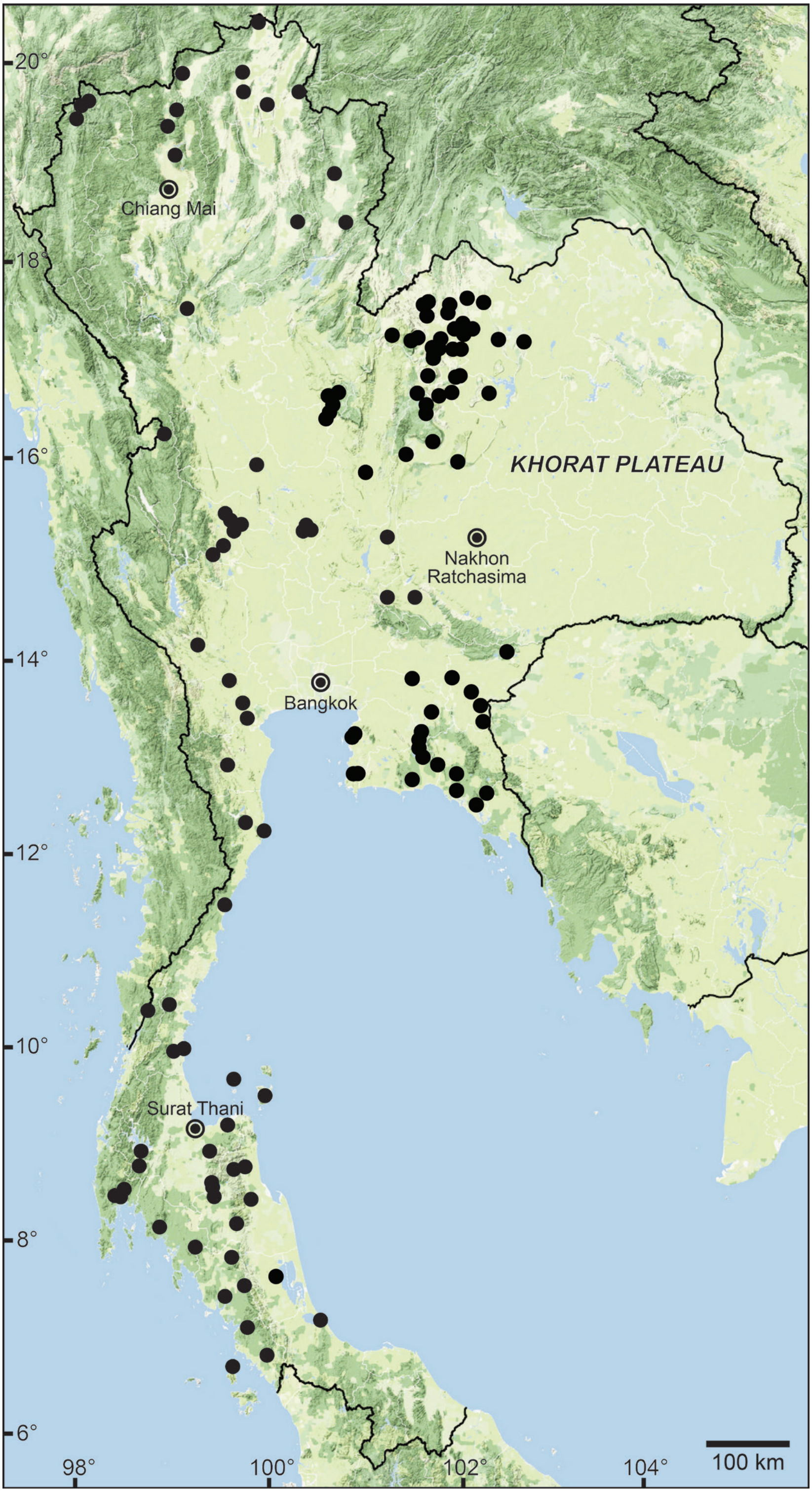

Figure 1. Sampling localities of the Pupinidae in Thailand from field surveys during 1995–2022.

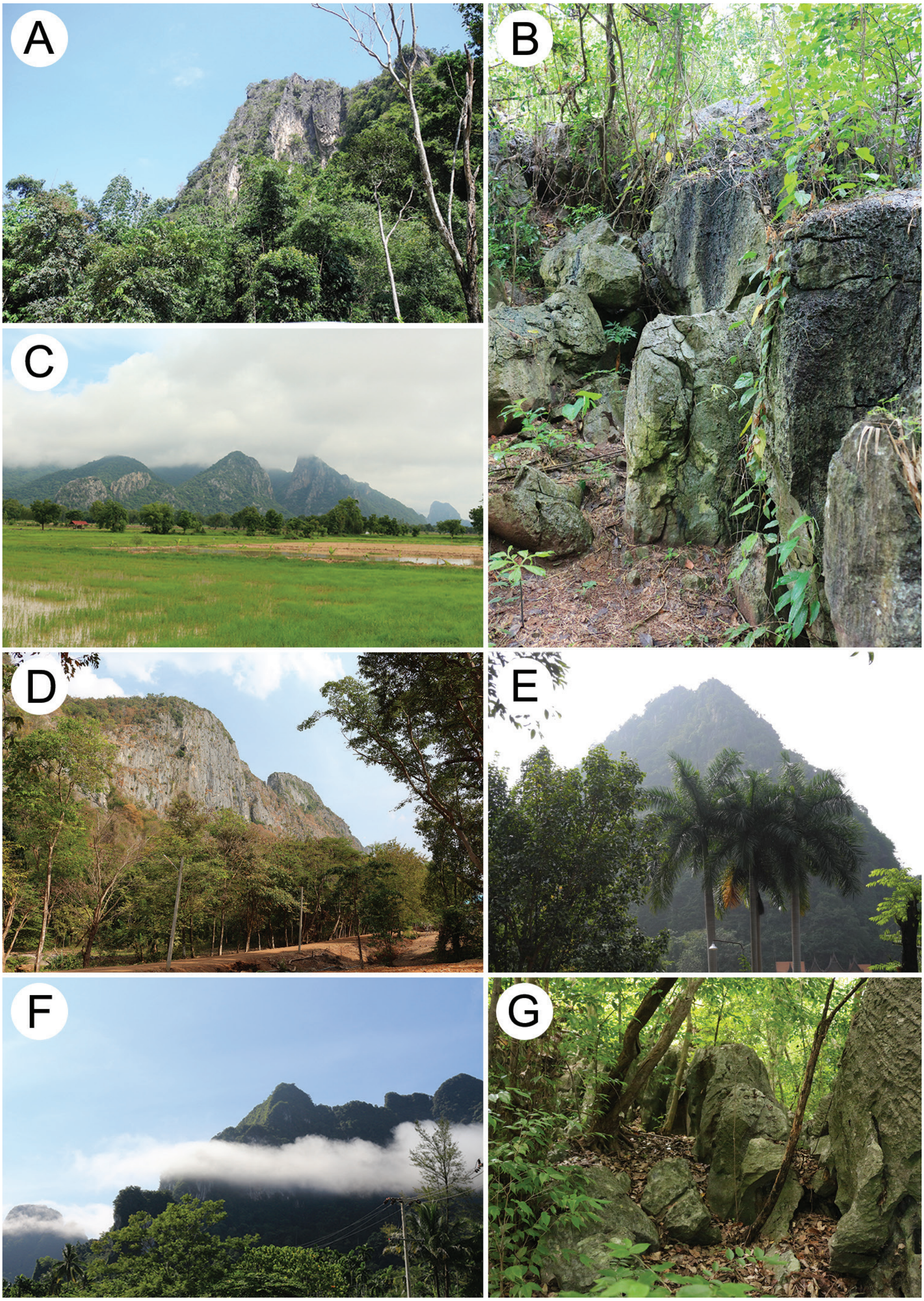

Figure 2. Habitat and vegetation around **A** Luang Cave, Chiang Rai, northern Thailand **B** Wang Daeng Cave, Phitsanulok, central Thailand **C** Tak Fa, Nakhon Sawan, central Thailand **D** Klong Had, Sra Keo, eastern Thailand **E** Khao Wong Cave, Uthai Thani, central Thailand **F** Phanom, Surat Thani, southern Thailand, and **G** Tham Khiriwong Temple, Prachub Kirikhan, western Thailand.

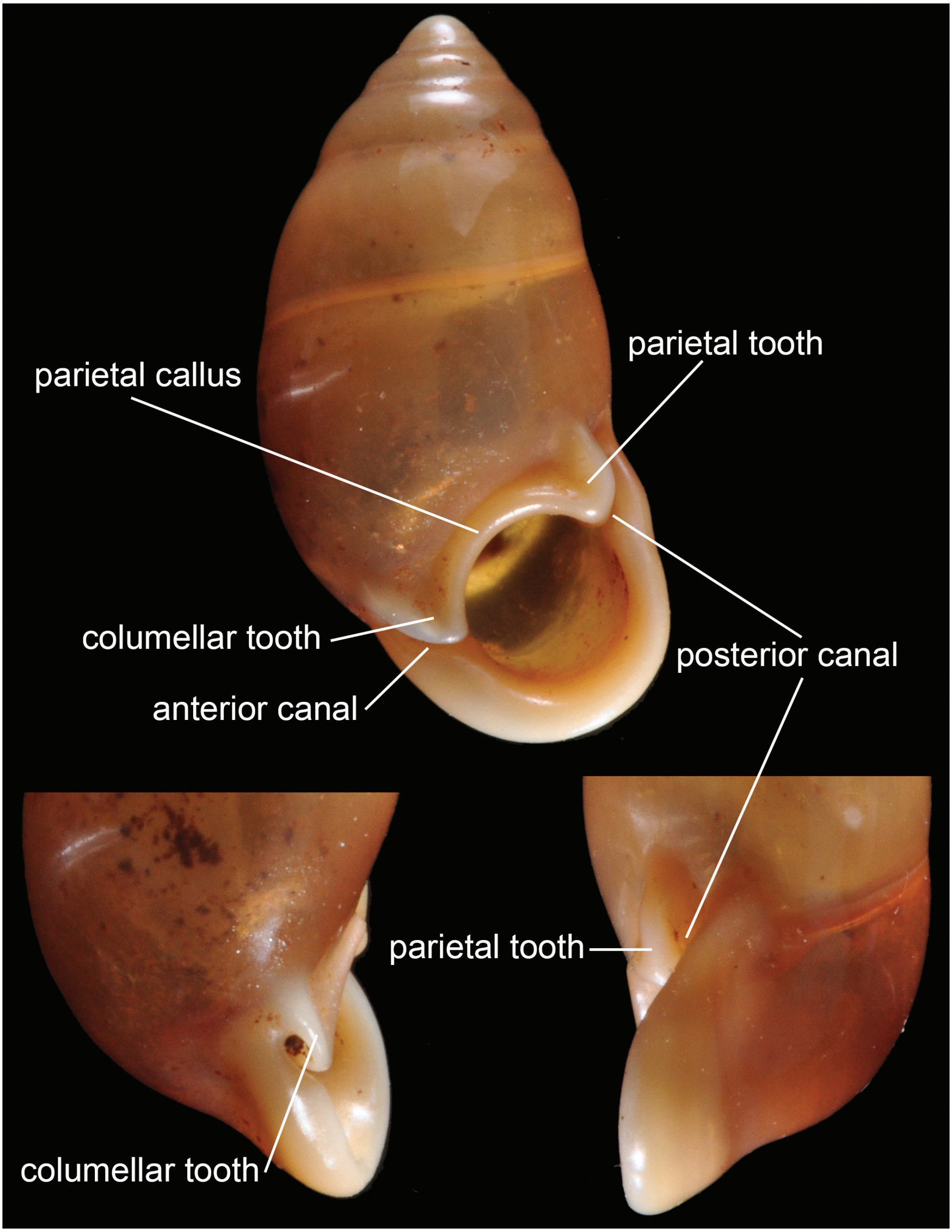

Figure 3. General shell morphology of *Pupina* and its terminology.

Taxon names

All the nominal species and subspecies names described as new to science in this work are attributed to the first author (Jirapatrasilp). Thus, a complete citation of the authors is "Jirapatrasilp in Jirapatrasilp et al., 2022"

Results

A total of 195 voucher specimen lots was collected over the entire survey period and represented in this study. In total, 30 nominal species with two subspecies from seven genera are currently known to occur in Thailand. Two species of *Pseudopomatias*, and five species plus one subspecies of *Pupina* are described herein as new to science (Table 1). The taxonomic treatment of 15 *Pupina* species and three *Pupinella* species from mainland Southeast Asia are also included, together with the images of type specimen(s) where possible.

Table 1. List of species of the family Pupinidae recorded from Thailand.

Subfamily	Genus (and species group)	Species with recently collected material	Species not recently collected but based on literature and museum collections	Species with uncertain record from Thailand, based on literature only
Pupinellinae	*Coptocheilus*	*C. sectilabris*	*C. sumatranus*	–
	Pollicaria	*P. mouhoti monochroma* *P. mouhoti mouhoti*	–	*P. myersii*
	Pseudopomatias	*P. caligosus* *P. doiangkhangensis* Jirapatrasilp, sp. nov. *P. pallgergelyi* Jirapatrasilp, sp. nov.	–	–
	Pupinella	*P. mansuyi*	–	–
	Rhaphaulus	*R. lorraini* *R. tonkinensis*	*R. ascendens* *R. perakensis*	*R. chrysalis*
	Tortulosa	*T. tortuosa*	–	–
Pupininae	*Pupina*			
	Pupina artata species group	*P. artata* *P. limitanea* *P. pallens* *P. bensoni* Jirapatrasilp, sp. nov.	–	–
	Pupina arula species group	*P. crosseana* *P. peguensis* *P. siamensis* *P. bilabiata* Jirapatrasilp, sp. nov. *P. godwinausteni* Jirapatrasilp, sp. nov.	–	*P. arula* *P. mouhoti*
	Pupina aureola species group	*P. aureola* *P. paviei* *P. tchehelensis* *P. dorri isanensis* Jirapatrasilp, ssp. nov. *P. latisulci* Jirapatrasilp, sp. nov. *P. stoliczkai* Jirapatrasilp, sp. nov.	–	–
Total	7	25	3	4

Systematics

Class Gastropoda Cuvier, 1795
Subclass Caenogastropoda Cox, 1960
Grade Architaenioglossa Haller, 1892
Superfamily Cyclophoroidea Gray, 1847

Family Pupinidae Pfeiffer, 1853

Remarks. Currently, there are three subfamilies within the family Pupinidae: Pupininae, Liareinae Powell, 1946, and Pupinellinae Kobelt, 1902 (Bouchet et al. 2017). The subfamily Liareinae was endemic to New Zealand, originally established as a family (Powell 1946), and this familial assignment was adopted by Egorov (2013). Later, Ponder and Warén (1988) treated this taxon as a subfamily of the Pupinidae; this classification scheme was adopted by Bouchet et al. (2017) and MolluscaBase (2022).

The subfamily Pupinellinae was originally established as a section under the Pupinidae, and the only diagnostic character that distinguished this subfamily from the Pupininae is the shell surface (Kobelt 1902). The Pupininae has a shell surface covered by glaze, which is glossy and completely smooth, whereas the shell surface of the Pupinellinae is without glaze, being either striated, matt or silky-shiny (Kobelt 1902; Egorov 2013). Whether this character is a subfamilial synapomorphy needs further confirmation because at least one *Pupina* species has a matt surface (e.g., *P. arula*) and some *Pupinella* species have a somewhat glossy surface (e.g., *P. mansuyi*, *P. illustris*).

Subfamily Pupinellinae Kobelt, 1902

Remarks. There are a total of six genera with 12 species and one subspecies of pupinellinid known to occur in Thailand, and two additional species have uncertain records.

1. Genus *Coptocheilus* Gould, 1862

Coptocheilus Gould, 1862: 282.
Schistoloma Kobelt, 1902: 278. Egorov 2013: 14.

Type species. *Cyclostoma altum* Sowerby I, 1842, by original designation.

Diagnosis. Shell high conical to elongate ovate. Sculpture mostly smooth, rarely ribbed. Periumbilical keel either present or absent. Aperture round without any tubes or apparent slits, sometimes with a slight angular indentation at peristome upper junction. Operculum thin, flat, closely coiled.

Differential diagnosis. Shell size and matt surface of *Coptocheilus* are more similar to *Tortulosa* than other genera in this subfamily. However, *Coptocheilus* is different from *Tortulosa* in having a round aperture without any tubes or apparent slits, but sometimes with a slight angular indentation at the upper junction of peristome. In addition, *Coptocheilus* has a thin, flat operculum, and does not have a periumbilical keel (Kobelt 1902).

Remarks. For the resurrection of *Coptocheilus* Gould, 1862 over *Schistoloma* Kobelt, 1902 and the list of all *Coptocheilus* species, see Bui and Páll-Gergely (2020). The distribution of *Coptocheilus* species in Thailand is provided in Fig. 4.

Coptocheilus sectilabris (Gould, 1843)

Fig. 5A–C

Cyclostoma sectilabrum Gould, 1843: 140. Type locality: Tavoy [Dawei, Dawei Township, Dawei District, Tanintharyi Region, Myanmar]. Gould 1844: 459, pl. 24, fig. 10. Pfeiffer 1848: pl. 24, figs 17, 18. Pfeiffer 1849: 164, 165. Johnson 1964: 147.

Megalomastoma sectilabre—Theobald 1858[1857]: 247, Yanglaw, on the Tenasserim [Tanintharyi Region, Myanmar].

Megalomastoma sectilabrum—Sowerby I 1866: Pupinidae, pl. 1 (pl. 263), *Pollicaria* and *Megalomastoma*, sp. 19, fig. 24. Hanley and Theobald 1870: 4, pl. 7, fig. 3. Reeve 1878: Pupinidae, pl. 10, sp. 88. Crosse 1879: 339. de Morgan 1885: 412, 413.

Megalomastoma (*Coptocheilus*) *sectilabrum*—Nevill 1878: 297.

Megalomastoma (*Coptochilus*) *sectilabrum*—von Martens 1886: 161, King Island [Kadan Island or Kadan Kyun, Kyunsu Township, Myeik District, Tanintharyi Region, Myanmar]. von Möllendorff 1887[1886]: 314, Tenasserim.

Schistoloma sectilabrum—Kobelt 1902: 280. Gude 1921: 170, 171. Zilch 1957: 42. Maassen 2001: 43. Tumpeesuwan and Panha 2008: 65, 66, fig. 1a–c, Kaeng Krachan National Park, Phetchaburi Province, Thailand. Egorov 2013: 14, fig. 22d–g. BEDO 2017: 97. Sutcharit et al. 2018: 157, figs 5–11e, 5–13m. Páll-Gergely et al. 2019: 325, 326.

Type material examined. ***Lectotype*** MCZ 169361 (Fig. 5A) from Tavoy. Paralectotype MCZ 87934 (1 shell) from Tavoy.

Other material examined. SMF 109813 (1 shell; Fig. 5B) from Tavoy. CUMZ OLM-0111 (1 shell; Fig. 5C) from Kaeng Krachan District, Phetchaburi Province, 20 Sept. 1998.

Diagnosis. Shell elongate conical without any periumbilical keel. Aperture round with a slight angular indentation at upper junction of peristome.

Differential diagnosis. *Coptocheilus sectilabris* is different from *C. sumatranus* in having a slight angular indentation at the upper junction of the peristome.

Distribution. Myanmar and western Thailand (Tumpeesuwan and Panha 2008).

Remarks. As the original description did not explicitly state that the description of this species was based on a single specimen (nor could this be inferred), the designation of a holotype by Johnson (1964) in fact constitutes a lectotype designation (ICZN 1999: Art. 74.6). Several records of *C. sectilabris* from southern Thailand and peninsular Malaysia should be recognised as *C. sumatranus* (see below). The occurrence of *C. sectilabris* in Vietnam (Thach 2016) is dubious and needs further confirmation (Páll-Gergely et al. 2019).

Coptocheilus sumatranus **Dohrn, 1881**

Fig. 5D–F

Coptocheilus sumatranus Dohrn, 1881: 65. Type locality: Sumatra, Singalang [Mount Singgalang, West Sumatra].

Megalomastoma sectilabrum [in part]—Stoliczka 1872: 268, pl. 10, fig. 13, Penang hill [Penang Island, Penang State, Malaysia]. Crosse 1879: 339, Perak [Malaysia]. de Morgan 1885: 412, 413.

Megalomastoma (*Coptocheilus*) *sectilabrum* [in part]—Nevill 1878: 297.

Megalomastoma (*Coptochilus*) *sectilabrum* [in part]—von Martens 1886: 161. von Möllendorff 1887[1886]: 314; Larut [Bukit Larut, Perak State, Malaysia].

Coptochilus sectilabrum [non Gould]— von Möllendorff 1891: 346.

Schistoloma sectilabrum [in part]—Kobelt 1902: 280. Gude 1921: 170, 171.

Coptocheilus perakensis Fulton, 1903: 102, pl. 9, fig. 3. Type locality: Perak.

Schistoloma perakense—Laidlaw 1928: 33.

Schistoloma sectilabrum [non Gould]—Sykes 1903: 197, Ulu Selama, Perak. Laidlaw 1928: 33, Ulu Selama, Perak; Lampan Patalung [Phatthalung Province, Thailand]. Foon et al. 2017: 41, fig. 16b, Perak, forested slope behind the village at Gunung Pondok.

Schistoloma sumatranum—Kobelt 1902: 281. van Benthem Jutting 1949: 55, 56, Kuala Legap, Plus Valley, Perak; Maxwell's Hill, Perak; Gunong Kledang, Perak; Taiping Perak; Dusun Tua, Selangor [Malaysia]. Davison 1995: 236, Sungai Halong and Sungai Emban, Temengor Forest Reserve, Perak, Malaysia. Chan 1998a: 4, Ipoh, Perak. Maassen 2001: 43, 44. Páll-Gergely et al. 2019: 327.

Schistoloma perakensis—Berry 1963: pl. 6, fig. 29.

Type material examined. ***Syntype*** of *Coptocheilus perakensis* NHMUK 1903.11.20.33 (1 shell; Fig. 5D) from Perak.

Other material examined. SMF 262529/1 "*Schistoloma siamensis* Brandt" (1 shell; Fig. 5E) from Thailand: an den Tanto-Fällen bei Ban Nong Star; Yala Provinz [Than To Waterfall Forest Park, Bannang Sata District, Yala Province, Thailand]. NHMUK 1986.4.19.14 "*Coptocheilus sectilabrum* var." (1 shell; Fig. 5F) from Larut near Perak.

Diagnosis. Shell elongate conical without any periumbilical keel. Apertural round without any indentation.

Differential diagnosis. *Coptocheilus sumatranus* is different from *C. sectilabris* in having a round aperture without any indentation.

Distribution. Peninsular Malaysia, Sumatra Island, and southern Thailand (Laidlaw 1928; van Benthem Jutting 1949; Foon et al. 2017).

Remarks. No material of this species was found during this survey. Although *C. sumatranus* only differs from *C. sectilabris* by an absence of an indentation in the peristome (van Benthem Jutting 1949), we do not synonymise *C. sumatranus* with *C. sectilabris* because of the lack of DNA data and that there are too few specimens to verify whether specimens collected from the same localities of *C. sectilabris* eventually lack an angular indentation in the peristome. *Coptocheilus perakensis* was retrieved as a junior subjective synonym of *C. sumatranus* because there are no distinct differences in shell form and size between them (*C. sumatranus*: shell height 19–24 mm, diameter 8–9 mm; *C. perakensis*: shell height 23 mm, diameter including peristome 11 mm; van Benthem Jutting 1949).

The name "*Schistoloma siamensis* Brandt" given to two samples (SMF 262529 = holotype" and SMF 262530 = "paratypes") from Than To Waterfall Forest Park, Bannang Sata District, Yala Province, Thailand was never published and so is not available. These specimens are larger, more elongated, and have a darker shell colour but the other diagnostic characters conform to those found in the syntype of '*C. perakensis*'. Thus, Brandt's specimens are herein identified as *C. sumatranus*.

2. Genus *Pollicaria* Gould, 1856

Pollicaria Gould, 1856: 14. Kobelt 1902: 288, 289. Egorov 2013: 15, 16.

Type species. *Cyclostoma pollex* Gould, 1856 (junior synonym of *Megalomastoma gravidum* Benson, 1856), by monotypy.

Diagnosis. Shell of great size (up to 50 mm in shell height); pupoid shape with shallow posterior angled groove at palatal edge as breathing device; with or without parietal declining shoulder inside the peristome.

Differential diagnosis. *Pollicaria* can be distinguished from all other genera in this subfamily by a greater shell size, and a shallow posterior angled groove at palatal edge as a breathing device (Kongim et al. 2013; Minton et al. 2017).

Remarks. The taxonomic history of *Pollicaria* was reviewed in Kongim et al. (2013) and Minton et al. (2017). The juvenile shell of this genus (Fig. 6A) does not develop the large last whorl seen in adults (Fig. 6B), making its shell shape similar to the pulmonated ariophantid snails, which might lead to a misidentification [see the case of *Ariophanta huberi* Thach, 2018 and *P. rochebruni* (Mabille, 1887) in Páll-Gergely and Hunyadi (2018a)]. The distribution of *Pollicaria* species in Thailand from Kongim et al. (2013) and this study is provided in Fig. 7.

Pollicaria mouhoti mouhoti (Pfeiffer, 1863)

Figs 6C–E, 8A, B

Hybocystis mouhoti Pfeiffer, 1863b [1862]: 276, pl. 36, fig. 13. Type locality: Lao Mountains, Camboja [Cambodia or Laos]. Pfeiffer 1863a: 227, 228, pl. 59, figs 5–8. Nevill 1878: 298, Siam (?). Fischer 1891: 108. Fischer and Dautzenberg 1904: 432.

Pollicaria mouhoti—Sowerby I 1866: Pupinidae, pl. 1 (pl. 263), *Pollicaria* and *Megalomastoma*, sp. 3, fig. 9. Reeve 1878: Pupinidae, pl. 8, sp. 67. Sutcharit et al. 2018: 156, figs 5–11c, 5–12a–g, 5–13a. Inkhavilay et al. 2019: 28, fig. 15a, Thailand, probably in both Cambodia and Laos.

Megalomastoma (*Hybocystis*) *mouhoti*— von Martens 1867: 67.

Pollicaria myersii [non Haines]—Habe 1965: 114, 115, pl. 2, fig. 3, Phukae Botanical Garden, Sara Buri [Province], Thailand (limestone region).

Pollicaria mouhoti mouhoti—Kongim et al. 2013: 31, 32, figs 2b, 3a–e, 4h, i, 6b. BEDO 2017: 86. Thach 2018: 96 (figure caption), figs 124, 125.

Pollicaria nicoarlingi Thach, 2021: 17, 18, figs 53–55, 57, 58. Type locality: Konsan District, Chaiyaphum Province, Thailand. Syn. nov.

Type material examined. ***Lectotype*** of *Hybocystis mouhoti* NHMUK 20130071/1 (Fig. 6C) and paralectotypes NHMUK 20130071/2–3 (2 shells) from Lao Mountains, Camboja. ***Holotype*** of *Pollicaria nicoarlingi* MNHN-IM-2000-37277 (Fig. 6D) from Konsan District, Chaiyaphum Province, Thailand.

Other material examined. CUMZ 12166 (5 shells and 5 specimens in ethanol; Figs 6E, 8A) from Wang Daeng Cave, Noen Maprang District, Phitsanulok Province, 17 Mar. 2017. CUMZ 12175 (3 specimens in ethanol; Fig. 8B) from Wang Daeng Cave, Noen Maprang District, Phitsanulok Province, 8 June 2017. CUMZ 12176 (6 adult shells and 1 juvenile shell) from Phu Wiang District, Khon Kaen Province, 8 July 1995. CUMZ 12177 (1 shell) from Phraya Nakkharaj Cave, Chum Phae District, Khon Kaen Province, 21 July 2020. CUMZ 12178 (8 shells and 4 specimens in ethanol) from Tad Tone Waterfall, Mueang Chaiyaphum District, Chaiyaphum Province, 20 July 2020. CUMZ 12179 (9 shells) from Pa Mamuang Bureau of Monks, Noen Maprang District, Phitsanulok Province, 3 Aug. 2020. CUMZ 12180 (1 shell) from Tham Phrommalok Temple, Chai Badan District, Lopburi Province, 24 Aug. 2020. CUMZ 12181 (1 shell) from Tham Badan Temple, Muak Lek District, Saraburi Province, 3 Aug. 2020.

Diagnosis. Shell height 35–40 mm. Last whorl and penultimate whorl purple to black; spire and apex distinct yellow to bright orange. Dorsal side of last whorl with bold wrinkles. Aperture round, without apertural groove; apertural lip expanded, bright orange to red. Umbilicus subumbilicate.

Differential diagnosis. *Pollicaria mouhoti mouhoti* is similar to *P. myersii* and *P. m. monochroma* in shell shape, but different from *P. myersii* by a smaller shell size with purplish shell colour, bright orange spire, expanded bright orange to red apertural lip and bold wrinkles on the dorsal side of last whorl, and different from *P. m. monochroma* by a larger shell size, yellow to bright orange spire and apex, and a distinct karyotype pattern of (6m+4sm+2st+1t) (Kongim et al. 2009, 2010, 2013).

Distribution. Phetchabun Range in central and northeastern Thailand, and probably in both Cambodia and Laos (Kongim et al. 2013; Inkhavilay et al. 2019).

Remarks. Pain (1974) treated *P. mouhoti* as a subjective synonym of *P. myersii*, whereas Kongim et al. (2013) regarded *P. mouhoti* as valid because these two species are distinct in several shell characters and karyotype pattern. Thus, the distribution range of *P. myersii* is restricted to limestone areas of Vientiane to Luang Prabang, Laos, and probably to the northern part of Thailand, whereas *P. mouhoti* mostly occurs in central and northeastern Thailand (Kongim et al. 2013).

One differential diagnostic character of *P. nicoarlingi* is "special sculpture with many large, broad, and deep holes on dorsal side" (Thach 2021). This character is not unique because all the type specimens and recently collected specimens of *P. m. mouhoti* have this kind of shell sculpture, although to a different degree. The "special colour" of a very red columellar outer lip and parietal wall, and an orange spire and apex of *P. nicoarlingi* conform to the type specimens of *P. m. mouhoti*, although there is variation in the spire and apex colour from dark brown to bright orange. Other differences in shell shape, apertural lip, columella and sculpture of umbilicus between *P. nicoarlingi* and *P. m. mouhoti* as stated by Thach (2021) are possibly due to different shell condition and infraspecific variation. Moreover, *P. nicoarlingi* is described from the same vicinity of *P. m. mouhoti* specimens examined in this study. Therefore, *P. nicoarlingi* is regarded herein as a junior subjective synonym of *P. m. mouhoti*.

Pollicaria mouhoti monochroma **Kongim & Panha, 2013**

Figs 6A, B, 8C

Pollicaria myersii [non Haines]—Solem 1966: 13, on limestone outcrops 20 km. east of Wang Sapung [District] near Loei [Province], Thailand.

Pollicaria mouhoti monochroma Kongim & Panha in Kongim et al. 2013: 32, 33, figs 2c, 4j, k, 6c. Type locality: limestone outcrop with dry forest at Wat Tam Pha Bing, Wungsapoong District, Loei Province, Thailand. BEDO 2017: 86. Sutcharit et al. 2018: 156.

Type material examined. ***Holotype*** CUMZ 1577 and ***paratypes*** CUMZ 1548 (9 shells) figured in Kongim et al. (2013: figs 4j, k). ***Paratypes*** CUMZ 1562 (85 shells and 10 specimens in ethanol; Figs 6B, 8C) from Tam Pha Bing Temple, Wungsapoong District, Loei Province, 11 June 2013.

Other material examined. CUMZ 12182 (3 juvenile shells; Fig. 6A) from Tham Suea Lueang Temple, Mueang Loei District, Loei Province, 1 Sept. 2020. CUMZ 12183 (4 shells) from Tham Pha Poo, Mueang Loei District, Loei Province, 1 Sept. 2020. CUMZ 12184 (3 adult shells and 2 juvenile shells) from Phu Pha Lom, Mueang Loei District, Loei Province, 1 Sept. 2020. CUMZ 12185 (3 adult shells and 7 juvenile shells) from Tham Pha Phung Temple, Wang Saphung District, Loei Province, 2 Sept. 2020. CUMZ 12186 (3 adult shells and 3 juvenile shells) from Pa Phaya Temple, Suwannakhuha District, Nong Bua Lam Phu Province, 31 Aug. 2020.

Diagnosis. Shell height < 35 mm. Shell entirely black to purple. Dorsal side of last whorl with bold wrinkles. Aperture almost round, shallow posterior angled groove present; apertural lip expanded, yellow to pale orange. Umbilicus narrow.

Differential diagnosis. This subspecies is different from the nominotypical subspecies by a smaller shell size, an entirely black to purple shell, and a distinct karyotype pattern of (7m+3sm+2st+1t) (Kongim et al. 2009, 2013).

Distribution. Loei and Nong Bua Lam Phu provinces, northeastern Thailand (Kongim et al. 2013).

Remarks. DNA data are required to demonstrate whether *P. m. monochroma* is distinct from the nominotypical subspecies and should be elevated to specific status.

Species with uncertain record from Thailand

Pollicaria myersii (Haines, 1855)

Fig. 6F

Cyclostoma myersii Haines, 1855: 157, pl. 5, figs 9–11. Type locality: Siam [Thailand].

Pollicaria myersi [sic]—Sowerby I 1866: Pupinidae, pl. 1 (pl. 263), *Pollicaria* and *Megalomastoma*, sp. 2, fig. 11. von Martens 1867: 67. Reeve 1878: Pupinidae, pl. 8, sp. 69.

Hybocystis myersi [sic]—Fischer 1891: 108. Fischer and Dautzenberg 1904: 432.

Pollicaria myersii—Pain 1974: 175, 176, pl. 6, figs 2, 5. Hemmen and Hemmen 2001: 39. Kongim et al. 2013: 30, figs 2a, 4f, g, 6a, limestone areas of Vientiane to Luang Prabang, Laos, and probably the northern part of Thailand. BEDO 2017: 87. Sutcharit et al. 2018: 156, fig. 5–13b. Inkhavilay et al. 2019: 28, figs 15b, 18g, Ban Phone Can village, Yommalath District, Khammouan Province, Laos. Páll-Gergely et al. 2020: 40.

Pollicaria huberi Thach, 2018: 20, 21, figs 116–123. Type locality: Thakhek, Laos.

Type material examined. ***Holotype*** of *Pollicaria huberi* NHMUK 20180253 (Fig. 6F) from Thakhek, Laos.

Other material examined. NHMUK 20090242 from Siam figured in Kongim et al. (2013: fig. 4f). CUMZ 1531, 1572 figured in Kongim et al. (2013: fig. 4g), 1591 from Pahom, Vang Vieng, Laos.

Diagnosis. Shell height > 40 mm. Shell elongated, reddish brown to bright orange or red. Dorsal side of last whorl with very fine wrinkles. Aperture round, without apertural groove; apertural lip expanded, yellow to pale orange. Umbilicus narrow.

Differential diagnosis. *Pollicaria myersii* is different from *P. m. mouhoti* by having an elongated purple to pale orange shell with thin periostracum, a rounded aperture, very fine wrinkles on the dorsal part of the last whorl, and a distinct karyotype pattern of (4m+6sm+2st+1t). This species also differs from *P. gravida*, *P. rochebruni* and *P. crossei* by having a larger shell, no apertural groove, and noticeable wrinkles on last whorl (Kongim et al. 2010, 2013).

Distribution. Laos and an uncertain record from northern Thailand (Kongim et al. 2013; Inkhavilay et al. 2019).

Remarks. No material of this species was found during this survey, and the record in Thailand needs further confirmation. The type material of this species was presumably lost (Kongim et al. 2013). Páll-Gergely et al. (2020) treated *P. huberi* as a junior subjective synonym of *P. myersii* because the shell shape and colour, and the aperture shape of *P. huberi* agree with those of *P. myersii*, which also occurs in Laos.

3. Genus *Pseudopomatias* Möllendorff, 1885

Pseudopomatias Möllendorff, 1885: 164. Kobelt 1902: 272. Egorov 2013: 12.

Type species. *Pseudopomatias amoenus* Möllendorff, 1885, by monotypy.

Diagnosis. Shell turriform or spindle-shaped, rather regularly ribbed, without additional groove above the suture, and without basal keel. Aperture rather round with slight columellar-parietal and more angled parietal-palatal transitions.

Differential diagnosis. *Pseudopomatias* is similar to *Hedleya* Cox, 1892, *Nodopomatias* Gude, 1921, *Vargapupa* Páll-Gergely, 2015 and *Csomapupa* Páll-Gergely, 2015 in shell shape and ribbing, but different from *Hedleya* by an absence of two canals in the aperture, different from *Nodopomatias* and *Vargapupa* by an absence of a basal keel, and different from *Csomapupa* by the lack of an additional line (groove) above the suture (Páll-Gergely et al. 2015).

Remarks. The taxonomic history of *Pseudopomatias* was reviewed and its systematic position in the family Pupinidae was confirmed by Páll-Gergely et al. (2015). The distribution of all *Pseudopomatias* species in Thailand is provided in Fig. 7.

Pseudopomatias caligosus Páll-Gergely & Hunyadi, 2018

Fig. 9A, B

Pseudopomatias caligosus Páll-Gergely & Hunyadi, 2018b: 64, fig. 3. Type locality: Mae Hong Son Province, 9.1 km from Ban Soppong towards Mae Hong Son, left side of road # 1095, Thailand. Páll-Gergely and Grego 2019: 588, fig. 2a–h, 169.5 km milestone, 36 km west towards Taungoo, Demoso, Kayah State, Myanmar.

Type material examined. ***Holotype*** HNHM 100176 (Fig. 9A) and ***paratypes*** HNHM 100442 (17 shells) from the type locality.

Other material examined. CUMZ 12191 (1 shell; Fig. 9B) from Pa Tham Wua Temple, Mueang Mae Hong Son District, Mae Hong Son Province, 18 Jan. 2015.

Diagnosis. Shell slender turriform; ca. 9 whorls, with regular strong ribs. Area between ribs with very fine spiral striation mostly on upper whorls. Peristome reflected.

Differential diagnosis. *Pseudopomatias caligosus* is most similar to *P. peguensis* (Theobald, 1864) and *P. shanensis* Páll-Gergely, 2015 in shell size and bulging whorls, but different from *P. peguensis* by a less glossy shell, much stronger ribs, and a reflected peristome, and different from *P. shanensis* by more bulging whorls, a less expanded peristome, and less-packed ribs with indistinct spiral striation between them (Páll-Gergely et al. 2015; Páll-Gergely and Hunyadi 2018b).

Distribution. Mae Hong Son Province and Kayah State, Myanmar (Páll-Gergely and Hunyadi 2018b; Páll-Gergely and Grego 2019).

Remarks. Although the apex of the CUMZ specimen is broken, the other remaining characters conform to those of the holotype of *P. caligosus*. The collecting locality is in the same vicinity as the type locality.

Pseudopomatias doiangkhangensis **Jirapatrasilp, sp. nov.**

https://zoobank.org/C419E00F-438D-4A5C-BC61-8AD63F0828E0

Fig. 9C, D

Type material. ***Holotype*** CUMZ 12165/1 (Fig. 9C), 24 Oct. 2015, coll. C. Sutcharit, R. Srisonchai, A. Pholyotha, T. Seesamut. Measurement: shell height 8.6 mm, shell width 4.3 mm and 7½ whorls. ***Paratypes*** CUMZ 12165/2–6 (5 shells), NHMUK 20210331 (2 shells), same data as holotype; CUMZ 5219, 5221, 16 Mar. 2000, coll. C. Sutcharit, S. Panha (2 shells; Fig. 9D) from the type locality.

Type locality. Doi Ang Khang, Fang District, Chiang Mai Province, Thailand, 19°52'09.6"N, 99°03'17.4"E, 1341 m amsl.

Diagnosis. Shell ovate to ovate conical, widest at penultimate whorl; ca. 7½ whorls, with regular weak ribs. Area between ribs with very fine radial striation. Outer peristome expanded and reflected.

Differential diagnosis. *Pseudopomatias doiangkhangensis* sp. nov. is similar to the ovate-shaped *P. harli* Páll-Gergely, 2015 (Páll-Gergely et al. 2015), but differs in having more whorls, weaker ribs, and a wider apertural lip. In addition, the shell is widest at its penultimate whorl, compared to *P. harli* that is widest at its last whorl.

Description. Shell height 8.8–9.2 mm; shell width 4.4–4.6 mm. Shell ovate to ovate conical, widest at penultimate whorl, solid, semi-transparent, pale orange. Whorls ca. 7½ with sutures deep. Protoconch ca. 2 whorls (slightly eroded), first ca. 1½ whorl very finely granulated; remaining whorls and teleoconch very finely, regularly ribbed every 0.2 mm; ribs weak and 0.1 mm wide. Area between ribs with very fine radial lines, visible only under high magnification (> 20×), getting weaker in earlier whorls. Last whorl with 28–30 ribs. Apex obtuse. Spire angle ca. 50°. Aperture rounded with very slightly angled columellar-parietal transition and more sharply angled parietal-palatal transition; outer peristome expanded and reflected (0.4–0.5 mm wide and 0.3 mm thick), white to pale pinkish in colour. Umbilicus closed. Operculum unknown.

Etymology. The specific epithet is named after Doi Ang Khang, the type locality of this species.

Distribution. Known only from the type locality.

Remarks. This species exhibits infraspecific variation in shell shape from ovate to ovate conical (Fig. 9C, D).

Pseudopomatias pallgergelyi Jirapatrasilp, sp. nov.

https://zoobank.org/804C66C4-EA2C-4692-9BFE-3D7E612B9616
Fig. 9E, F

Type material. ***Holotype*** CUMZ 12167/1 (Fig. 9E), 18 Jan. 2015, coll. C. Sutcharit, P. Jirapatrasilp, W. Siriwut, R. Srisonchai, T. Seesamut. Measurement: shell height 14.5 mm, shell width 4.9 mm and 11 whorls. ***Paratypes*** CUMZ 12167/2–4 (3 shells; Fig. 9F) and NHMUK 20210332 (1 shell), same data as holotype.

Type locality. Pha Daeng Cave, Mueang Mae Hong Son District, Mae Hong Son Province, Thailand, 19°25'23.9"N, 97°59'03.1"E, 270 m amsl.

Diagnosis. Shell elongate turriform; ca. 11 whorls, with regular strong ribs separated by wide space. Area between ribs with very fine spiral striation. Outer peristome expanded and strongly reflected.

Differential diagnosis. *Pseudopomatias pallgergelyi* sp. nov. can be distinguished from *P. caligosus* and *P. shanensis* by a more slender shell shape with more whorls that are less bulging, stronger ribs that are nearly twice as widely spaced, and a more expanded and strongly reflected outer peristome.

Description. Shell height 14.0–14.6 mm; shell width 4.8–5.1 mm. Shell elongate turriform, widest at its base, solid, semi-transparent, whitish to pale pinkish. Whorls ca. 11 with sutures deep. Protoconch ca. 2 whorls (slightly eroded), first ca. 1½ whorl very finely granulated; remaining whorls and teleoconch very finely, regularly ribbed every 0.4–0.5 mm; ribs strong 0.1 mm wide, triangular in cross section. Area between ribs with very fine spiral lines, visible only under high magnification (> 20×). Last whorl with 20–26 ribs. Apex obtuse. Spire angle ca. 30°. Aperture rounded with very slightly angled columellar-parietal transition and more sharply angled parietal-palatal transition appearing as indentation; outer peristome expanded and strongly reflected (0.5–0.6 mm wide and 0.5 mm thick), white to pale pinkish in colour. Umbilicus closed. Operculum unknown.

Etymology. The specific epithet is dedicated to B. Páll-Gergely, a Hungarian malacologist who extensively studies the taxonomy and systematics of Southeast Asian land snails, especially revising the taxonomy of the genus *Pseudopomatias*.

Distribution. Known only from the type locality.

4. Genus *Pupinella* Gray, 1850

Pupinella Gray, 1850: 33. Kobelt 1902: 291. Egorov 2013: 9.

Type species. *Cyclostoma pupiniforme* Sowerby I, 1842, by original designation.

Diagnosis. Shell with funnel- or gutter-like [= umbilical passage in Varga and Páll-Gergely (2017)] anterior canal forming a tube opening at both ends, appearing as a slit when observed from apertural view that is widened or slightly widened on outer margin.

Differential diagnosis. *Pupinella* is most similar to *Pupina* in shell shape and the presence of both teeth and canals, but differs in having an umbilical passage or a funnel-like anterior canal forming a tube opening at both ends (Fig. 10A; Varga and Páll-Gergely 2017). The comparison of the umbilical, columellar, and parietal views between *Pupinella* and *Pupina* is illustrated in Fig. 10.

Remarks. The most comprehensive compilation of members of this genus could be traced back to Kobelt (1902). This genus has two subgenera, the nominotypical subgenus and *Pupinopsis* H. Adams, 1866 (Kobelt 1902; Egorov 2013). The subgenus *Pupinopsis* is diagnosed with a presence of a posterior canal, as in the type species *Pupinella swinhoei* H. Adams, 1866 (see Hwang 2014: fig. 1g, h). On the other hand, the posterior canal is absent in the subgenus *Pupinella*, as in the type species *Pupinella pupiniformis* (Sowerby, 1842) (see Varga and Páll-Gergely 2017: fig. 1a–c). The taxonomic works on *Pupinella* are sporadic (e.g., van Benthem Jutting 1963; Ueng and Chiou 2004) and there has been no taxonomic revision of this genus since then. Three species formerly in *Pupina* from Vietnam are now allocated to this genus (see below), and all four species from mainland Southeast Asia would belong to the subgenus *Pupinopsis*. A synoptic view of all four *Pupinella* species is given in Fig. 11 to provide the comparative size.

***Pupinella mansuyi* (Dautzenberg & Fischer, 1908)**

Figs 10A, 11A–G, 12A–C

Eupupina mansuyi Dautzenberg & Fischer, 1908: 207, 208, pl. 6, figs 12–15. Type locality: Deux-Ponts [in northeastern Vietnam]; Quang-Huyen [Quang Uyen, Cao Bang Province, Vietnam].

Pupina mansuyi—Saurin 1953: 113, environs du village méo de Pah Hia, à 100 kilomètres au Sud de Xieng-Khouang, chef-lieu de la province du Tran Ninh, Laos [probably refers to Ban Namthong, Longchaeng District, Xaisomboun Province, Laos]. Fischer 1963: 33.

Pupinella mansuyi—Do et al. 2015: 128, fig. 7c, Son La Province, Vietnam. Inkhavilay et al. 2019: 46, 47, fig. 16d.

Pupinella frednaggsi Thach & Huber in Thach, 2017: 19, 20, figs 124–130. Type locality: suburb of Luang Phrabang, Laos. Inkhavilay et al. 2019: 46, figs 16b, c, 18h, Tam Phatok Cave, Ngoy District, Luang Phrabang Province. Páll-Gergely et al. 2020: 41, Nam Wu, Ban Pak Ou, Luang Phrabang Province. Syn. nov.

Pupinella franzhuberi Thach, 2020: 21, figs 161–165. Type locality: Luang Prabang, Laos. Syn. nov.

Type material examined. ***Syntype*** of *Eupupina mansuyi* MNHN-IM-2000-30756 from Deux-Ponts (1 shell; Fig. 11A, Inkhavilay et al. 2019: fig. 16d). ***Syntypes*** of *Eupupina mansuyi* MNHN-IM-2000-36067 (10 shells; Fig. 11B) from Deux-Ponts. ***Syntypes*** of *Eupupina mansuyi* MNHN-IM-2000-36068 (5 shells; Fig. 11C) from Quang-Huyen. ***Syntypes*** of *Eupupina mansuyi* RBINS MT970/1 (5 shells; Figs 11D, 12A) from Quang-Huyen. ***Holotype*** of *Pupinella frednaggsi* NHMUK 20170285 (Fig. 11E, Inkhavilay et al. 2019: fig. 16b). ***Holotype*** of *Pupinella franzhuberi* MNHN-IM-2000-35510 figured in Thach (2020: figs 161–165).

Other material examined. CUMZ 12148 (38 shells; Figs 10A, 11F, 12B) from Pha Chu, Na Noi District, Nan Province, 12 Jan. 2008. CUMZ 12149 (3 specimens in ethanol; Figs 11G, 12C) from Pha Tub Cave, Mueang Nan District, Nan Province, 11 Oct. 2009. CUMZ 12150 (15 specimens in ethanol) from Pha Tub Cave, Mueang Nan District, Nan Province, 24 Aug. 2014. CUMZ 12151 (1 shell) from Pha Tub Cave, Mueang Nan District, Nan Province, 22 Feb. 2019. CUMZ 12152 (2 shells) from Tham Phajarui Temple, Pa Daet District, Chiang Rai Province, 25 Oct. 2008. CUMZ 12153 (66 shells) from Tham Phra Bamphen Bun Temple, Phan District, Chiang Rai Province, 29 Nov. 2009.

Diagnosis. Shell fusiform; last whorl ca. 60% of shell height. Apertural lip highly expanded and reflected; inner peristome thickened and cord-like; apertural lip when observed from lateral view almost straight. Parietal callus thickened and cord-like. Parietal tooth fin-shaped, highly thickened, covering posterior canal. Anterior canal funnel-like. Umbilicus closed.

Differential diagnosis. *Pupinella mansuyi* can be distinguished from all other species in mainland Southeast Asia by a highly expanded and reflected apertural lip with a thickened, cord-like inner peristome. Comparing to *P. sonlaensis* and *P. thaitranbaii*, this species has a thicker and more cord-like parietal callus as well as a thicker fin-shaped parietal tooth.

Distribution. Northern Vietnam (Do et al. 2015), Luang Phrabang Province, Laos (Inkhavilay et al. 2019; Páll-Gergely et al. 2020), Nan and Chiang Rai provinces, northern Thailand.

Remarks. Upon examining the type specimens of *P. mansuyi*, *P. frednaggsi*, and *P. franzhuberi*, the holotypes of *P. frednaggsi* and *P. franzhuberi* agree well with all the type specimens of *P. mansuyi* in having a fusiform shell shape, a highly expanded and reflected apertural lip with a thickened cord-like peristome, parietal callus, and a highly thickened, fin-shaped, parietal tooth covering the posterior canal. Moreover, the distinctions of *P. frednaggsi* and *P. franzhuberi* from *P. mansuyi* as indicated in the original descriptions should be treated as infraspecific variation. Thus, *P. frednaggsi* and *P. franzhuberi* are regarded herein as junior subjective synonyms of *P. mansuyi*. The absence of a columellar tooth in the syntype of *Eupupina mansuyi* from Deux-Ponts (Fig. 11A) is likely due to teratological conditions. This species has a wide distribution range from northern Vietnam to northern Thailand. The distribution of this species in Thailand is provided in Fig. 7.

Species from other parts of mainland Southeast Asia not recorded for Thailand

Pupinella illustris (Mabille, 1887) comb. nov.

Figs 11I–L, 12D, E

Pupina illustris Mabille, 1887: 136, 137. Type locality: Tonkin. Fischer 1891: 107. Fischer and Dautzenberg 1904: 431.

Pupina tonkiniana Bavay & Dautzenberg, 1899: 54, 55, pl. 3, fig. 6, 6a (as *Pupina tonkiana* in the original description). Type locality: Entre Lang-Son [Lang Son Province, Vietnam] et That-Khé [That Ke, Lang Son Province, Vietnam]. Syn. nov.

Pupina (*Tylotoechus*) *illustris*—Kobelt 1902: 314, 315.

Pupina (*Tylotoechus*) *tonkiniana*—Kobelt 1902: 323, 324. Zilch 1957: 48.

Pupina tonkiniana—Fischer and Dautzenberg 1904: 432. Fischer-Piette 1950: 167. Do et al. 2015: 126, fig. 6b, Son La Province, Vietnam. Raheem et al. 2017: 5 (plate figure).

Type material examined. ***Syntypes*** of *Pupina illustris* MNHN-IM-2000-35842 (9 shells; Figs 11I, J, 12D) from Tonkin. ***Lectotype*** of *Pupina tonkiniana* MNHN-IM-2000-35838 (Fig. 11K) from Lang-Son et That-Khé. Paralectotypes of *Pupina tonkiniana* SMF 109932/10 (10 shells; Figs 11L, 12E) from Tonkin: That-khé. Paralectotypes of *Pupina tonkiniana* RBINS MT976/2 (14 shells) from Lang Son et That-khé.

Diagnosis. Shell elongate fusiform; last whorl ca. 55–60% of shell height. Apertural lip expanded and slightly reflected; apertural lip when observed from lateral view almost straight. Parietal callus absent. Parietal tooth pointily sharp, located next to wide posterior canal. Anterior canal funnel-like. Umbilicus closed.

Differential diagnosis. *Pupinella illustris* can be distinguished from all other species in mainland Southeast Asia by an elongate fusiform shell shape, an absence of parietal callus and a pointily sharp parietal tooth located next to a wide posterior canal.

Distribution. Northern Vietnam (Do et al. 2015; Raheem et al. 2017).

Remarks. This taxon is allocated to the genus *Pupinella* due to the presence of a funnel-like anterior canal, which is the diagnostic character of this genus. In the original description of *Pupina tonkiniana*, two ways of spelling were shown: the spelling '*tonkiana*' in the description, and '*tonkiniana*' in the plate caption. Later, Kobelt (1902) acted as the First Reviser (ICZN 1999: Art. 24.2.3) in selecting '*tonkiniana*' as the correct original spelling. As the original description did not explicitly state that the description of *P. tonkiniana* was based on a single specimen (nor could this be inferred), the designation of a holotype by Fischer-Piette (1950) in fact constitutes a lectotype designation (ICZN 1999: Art. 74.6).

Upon examining the type specimens of both *P. illustris* and *P. tonkiniana*, the type series of *P. tonkiniana* agree well with all the syntypes of *P. illustris* in having an elongate fusiform shell shape, an expanded and slightly reflected apertural lip without a parietal callus, and a sharp, tooth-like, parietal tooth located next to a wide posterior canal. Thus, *P. tonkiniana* is regarded herein as a junior subjective synonym of *P. illustris*.

Pupinella sonlaensis **(Do, 2017) comb. nov.**

Figs 11H, 12F

Pupina sonlaensis Do, 2017: 300, 302, figs 2a, 3a. Type locality: limestone karst in Muong Bu Commune, Muong La District, Son La Province, Vietnam.

Type material examined. ***Holotype*** HNUE-OC 00108 figured in Do (2017: figs 2a, 3a). ***Paratypes*** ZRC.MOL.9377 (3 shells; Figs 11H, 12F) from the type locality.

Diagnosis. Shell ovate-fusiform; last whorl ca. 60% of shell height. Apertural lip slightly expanded and reflected, thickened cord-like peristome absent; apertural lip when observed from lateral view almost straight. Parietal callus somewhat distinct and cord-like. Parietal tooth sharp with wide base, thickened and covering posterior canal. Anterior canal funnel-like, appearing as a slit on the inside, widened on outer margin, bordered by a thickened columellar margin. Umbilicus closed.

Differential diagnosis. *Pupinella sonlaensis* is most similar to *P. mansuyi* in shell size, but differs in having an ovate-fusiform shell shape with a less thickened parietal tooth, as well as a less thickened, expanded, and reflected apertural lip without a thickened cord-like inner peristome.

Distribution. Muong La District, Thuan Chau District, and Van Ho District, Son La Province, Vietnam (Do 2017).

Remarks. This taxon is allocated to the genus *Pupinella* due to the presence of a funnel-like anterior canal, which is the diagnostic character of this genus. The paratype figured in this study is similar to *P. mansuyi* in having a triangular parietal tooth covering the posterior canal and an expanded and reflected apertural lip with somewhat cord-like inner peristome, although with less thickening, and the shell has a less elongate shape. However, the holotype of *P. sonlaensis* figured in Do (2017: figs 2a, 3a) has an ovate-fusiform shell with a thickened, wide-based parietal tooth not covering the posterior canal, and a slightly expanded and reflected apertural lip without a thickened cord-like inner peristome. A thorough examination of the specimens would clarify whether the type series contain more than one taxon or whether the validity of this taxon should be reassessed.

Pupinella thaitranbaii (Do, 2017) comb. nov.

Pupina thaitranbaii Do, 2017: 302, 303, figs 2b, 3b. Type locality: limestone forest in Pa Cop Village, Van Ho Commune, Van Ho District, Son La Province, Vietnam.

Type material examined. ***Holotype*** HNUE-OC 00109 figured in Do (2017: figs 2b, 3b).

Diagnosis. Shell ovate-fusiform; last whorl ca. two-thirds of shell height. Apertural lip expanded and slightly reflected; apertural lip curved when observed from lateral view. Parietal callus somewhat thickened and cord-like. Parietal tooth thickened, fin-shaped, covering posterior canal. Anterior canal forming a long gutter, extending into a spike-like protrusion. Umbilicus open and deep.

Differential diagnosis. *Pupinella thaitranbaii* can be distinguished from all other species in mainland Southeast Asia by having an anterior canal forming a long gutter and extending into a spike-like protrusion, a curved apertural lip when observed from lateral view, and an open and deep umbilicus.

Distribution. Known only from the type locality (Do 2017).

Remarks. This taxon is allocated to the genus *Pupinella* due to the presence of a funnel-like anterior canal, which is the diagnostic character of this genus.

5. Genus *Rhaphaulus* Pfeiffer, 1856

Rhaphaulus Pfeiffer, 1856b: 75. Kobelt 1902: 274, 275. Egorov 2013: 12.

Type species. *Anaulus bombycinus* Pfeiffer, 1855, by monotypy.

Diagnosis. Shell pupoid, with large penultimate whorl dominating the shell, being almost as wide as upper whorls combined when observed from apertural view. Peristome continuous, with parietal callus well-developed. Aperture shifting to the right side of the shell. Inner tube or breathing device short (of c. 0.25 whorl). Outer tube not perforated and varies in direction, never running strictly along the suture.

Differential diagnosis. *Rhaphaulus* is most similar to *Streptaulus* Benson, 1857 and *Barnaia* Thach, 2017 in shell shape and size (8–19 mm) and a thin operculum. Both *Rhaphaulus* and *Streptaulus* have two portions of a breathing tube: an inner portion starting from the peristome and running internally and posteriorly under the suture to its inner opening within the body whorl, and an outer portion extending from the parieto-palatal junction of the peristome to the outer opening, whereas *Barnaia* lacks this outer portion. However, *Rhaphaulus* differs from *Streptaulus* in having a continuous peristome with well-developed parietal callus, and an outer tube without holes on side wall, whereas *Streptaulus* has an interrupted peristome with weak parietal callus, as well as several circular holes along the tube's wall when the outer tube is present (Páll-Gergely et al. 2014, 2017).

Remarks. Pfeiffer (1855) proposed a monotypic genus *Anaulus* with '*A. bombycinus*' as the type species. However, this generic name was occupied by *Anaulus* Ehrenberg, 1844 (a diatom genus in the phylum Ochrophyta), hence *Anaulus* Pfeiffer, 1855 became a junior homonym. Later, Pfeiffer (1856b), under the remark of '*Rhaphaulus lorraini* Pfr.', stated that the generic name *Rhaphaulus* was to replace the junior homonym *Anaulus* Pfeiffer, 1855. The distribution of *Rhaphaulus* species in Thailand is provided in Figs 4, 7.

Rhaphaulus lorraini Pfeiffer, 1856

Fig. 13A, B

Rhaphaulus lorraini Pfeiffer, 1856a: 36. Type locality: Pulo Penang [Penang Island, Penang State, Malaysia]. Pfeiffer 1856b: 75, pl. 20, figs 21, 22. von Martens 1867: 155. de Morgan 1885: 413. Smith 1898: 18, figs 3, 4. Kobelt 1902: 276. Laidlaw 1928: 33, Penang. Maassen 2001: 42, West Malaysia. Páll-Gergely et al. 2014: 572, fig. 9. BEDO 2017: 96.

Rhaphaulus lorainii [sic]—Sowerby I 1866: Pupinidae, pl. 2 (pl. 264), *Rhaphaulus*, fig. 5. Reeve 1878: Pupinidae, pl. 10, sp. 96.

Rhaphaulus lorrainii [sic]—Habe 1965: 115, 116, pl. 2, fig. 12, as a synonym of *Rhaphaulus chrysalis*, Khao Chong, Trang Province, peninsular Thailand.

? *Rhaphaulus chrysalis*—Maassen 2001: 42, West Malaysia.

Type material examined. ***Syntypes*** NHMUK 20130454 (3 shells; Fig. 13A) from Pulo Penang.

Other material examined. CUMZ 12162 (1 shell; Fig. 13B) from Kiriwong (Tham Kope) Temple, Thap Put District, Phang Nga Province, 16 Jan. 2009.

Diagnosis. Shell ovate; body whorls bulging. Tube cylindrical, pointing upward and forward.

Differential diagnosis. *Rhaphaulus lorraini* can be distinguished from all other species from mainland Southeast Asia by a cylindrical tube pointing upward and forward.

Distribution. Malaysia and southern Thailand (Laidlaw 1928; Páll-Gergely et al. 2014).

Remarks. It is possible that *R. chrysalis* sensu Habe (1965) from Khao Chong, Trang Province, southern Thailand is *R. lorraini*. This species is distributed in the Malay Peninsula and is disjunct from *R. chrysalis*, which is distributed in northeastern India and Myanmar. See also remarks in *R. ascendens*.

Rhaphaulus perakensis **Smith, 1898**

Fig. 13C

Rhaphaulus perakensis Smith, 1898: 17, figs 1, 2. Type locality: Maxwell's Hill, Larut [Bukit Larut], Perak. Kobelt 1902: 276, 277. Laidlaw 1928: 32, 33. van Benthem Jutting 1949: 57, Kuala Kenering; Maxwell's Hill, Perak; Dusun Tua, Selangor [Malaysia]. Habe 1965: 115, 116, as a synonym of *Rhaphaulus chrysalis*. Hemmen and Hemmen 2001: 40, Thailand. Páll-Gergely et al. 2014: 572, fig. 12, western Malaysia. BEDO 2017: 97.

Rhaphaulus perakensis var. *jalorensis* Sykes, 1903: 197, pl. 20, figs 9, 10. Type locality: Bukit Bisar, on the borders of Jalor [Khao Yai National Reserved Forest, Namtok Sai Khao National Park, Mueang Yala District, Yala Province, Thailand].

Rhaphaulus perakensis var. *ialorensis* [sic]—Laidlaw 1928: 33.

Rhaphaulus perakensis jalorensis—Maassen 2001: 42.

Rhaphaulus perakensis perakensis—Maassen 2001: 42.

Rhaphaulus jalorensis —Páll-Gergely et al. 2014: 572, western Malaysia. BEDO 2017: 96. Sutcharit et al. 2018: 157, fig. 5–13l.

Type material examined. ***Syntypes*** of *Rhaphaulus perakensis* NHMUK 1897.3.15.41–2 (2 shells; Fig. 13C) from Larut, Perak.

Diagnosis. Shell elongate ovate; body whorls slightly bulging. Tube cylindrical, pointing diagonally downward and backward.

Differential diagnosis. *Rhaphaulus perakensis* can be distinguished from all other species from mainland Southeast Asia by a cylindrical tube pointing diagonally downward and backward.

Distribution. Northern Peninsular Malaysia and southern Thailand (Maassen 2001; Páll-Gergely et al. 2014).

Remarks. No material of this species was found during this survey. Maassen (2001) treated *R. perakensis jalorensis* as a junior subjective synonym of *R. p. perakensis* without apparent reason, whereas Páll-Gergely et al. (2014) listed this subspecies as a valid species following the opinion of Sykes (1903).

Rhaphaulus ascendens Sykes, 1903

Fig. 13D

Rhaphaulus ascendens Sykes, 1903: 196, 197, pl. 20, figs 11, 12. Type locality: Patalung [Phatthalung Province, Thailand]. Laidlaw 1928: 33. Hemmen and Hemmen 2001: 40. Páll-Gergely et al. 2014: 572. Thach 2018: 21, figs 126–129, Phang Nga District, South Thailand. BEDO 2017: 95. Sutcharit et al. 2018: 157, figs 5–11d, 5–13k.

Type material examined. ***Syntype*** UMZC I.100025 (1 shell; Fig. 13D) from Patalung, Malay Peninsula.

Diagnosis. Shell ovate; body whorls not bulging. Tube cylindrical and pointing straight upward.

Differential diagnosis. *Rhaphaulus ascendens* can be distinguished from all other species from mainland Southeast Asia by having body whorls that are not bulging and a cylindrical tube pointing straight upward.

Distribution. Southern Thailand (Páll-Gergely et al. 2014; Thach 2018).

Remarks. No material of this species was found during this survey. Laidlaw (1928) treated *R. ascendens* as a junior subjective synonym of *R. lorraini*. However, by comparing the type specimens of both species, the body whorls of *R. ascendens* are not bulging, whereas the distribution ranges tend to overlap. Thus, the validity of *R. ascendens* needs further confirmation.

Rhaphaulus tonkinensis Páll-Gergely, Hunyadi & Maassen, 2014

Figs 13E, F, 14A

Rhaphaulus tonkinensis Páll-Gergely et al. 2014: 567, 569, fig. 1. Type locality: rocky wall, left side of the road nr. 6, 156 km towards Moc Chau, Ha Noi, Son La Province, Vietnam. Do et al. 2015: 128, fig. 7d, Son La Province, Vietnam. Páll-Gergely et al. 2017: fig. 1a–e. Raheem et al. 2017: 6 (plate figure).

Type material examined. ***Holotype*** HNHM 98757 from Ha Noi, Son La Province, Vietnam (Fig. 13E).

Other material examined. CUMZ 12163 (4 shells; Figs 13F, 14A) from Luang Cave, Mae Sai District, Chiang Rai Province, 23 Oct. 2015. CUMZ 12164 (2 shells) from Pha Mee Cave, Mae Sai District, Chiang Rai Province, 23 Oct. 2015.

Diagnosis. Shell elongated ovate; body whorls slightly bulging. Tube thick and flat, turning first straight upward then abruptly downward, highly widening and extending to nearly the entire last whorl height.

Differential diagnosis. *Rhaphaulus tonkinensis* can be distinguished from all other species from mainland Southeast Asia by a distinctive tube that is thick and flat, turning first straight upward then abruptly downward, greatly widening and extending to nearly the entire last whorl height.

Distribution. Northern Vietnam (Do et al. 2015) and Chiang Rai Province, northern Thailand.

Remarks. The tube of one specimen from Tham Luang, Mae Sai District, Chiang Rai Province when turning downward does not adhere to the apertural margin (Fig. 13F). However, the tube of another specimen from the same locality adheres to the apertural margin (Fig. 14A), identical to the holotype (Páll-Gergely et al. 2014). Thus, the extent of tube adherence to the apertural margin is treated as an infraspecific variation.

Species with uncertain record from Thailand

Rhaphaulus chrysalis (Pfeiffer, 1853)

Fig. 14B–D

Cyclostoma chrysalis Pfeiffer, 1853: 239, pl. 31, figs 23, 24. Type locality: Arva [Mandalay Region, Myanmar]. Pfeiffer 1854: 158.

Rhaphaulus chrysalis—Theobald 1858[1857]: 247, Maulmein [Mawlamyine, Mawlamyine Township, Mawlamyine District, Mon State, Myanmar]. Sowerby I 1866: Pupinidae, pl. 2 (pl. 264), *Rhaphaulus*, figs 6, 7, Siam. Hanley and Theobald 1875: 53, pl. 133, fig. 7. Nevill 1878: 301. Reeve 1878: Pupinidae, pl. 10, sp. 95. Godwin-Austen 1886: 200, 201, pl. 47, fig. 1, 1a. Tapparone-Canefri 1889: 310. Smith 1898: 19. Kobelt 1902: 275, 276. Gude 1921: 165, 166, fig. 24. Páll-Gergely et al. 2014: 572, fig. 11, north-eastern India and Myanmar. BEDO 2017: 95. Sutcharit et al. 2018: 157.

Raphaulus [sic] *chrysalis*—Stoliczka 1871: 151, farm caves, near Moulmein, Myanmar.

Type material examined. ***Possible syntype*** NHMUK 2013.04.16 (1 shell; Fig. 14B) from Siam.

Other material examined. NHMUK 1871.9.23.52 (1 shell; Fig. 14C) from Burma. NHMUK 1903.7.1.3073 (2 shells; Fig. 14D) from Molmein.

Diagnosis. Shell ovate; body whorls slightly bulging. Tube cylindrical, pointing upward and backward.

Differential diagnosis. *Rhaphaulus chrysalis* is most similar to *R. lorraini* in shell shape, but differs in having a cylindrical tube pointing upward and backward, instead of forward as in *R. lorraini*.

Distribution. Northeastern India, Myanmar, and an uncertain record from Thailand (Páll-Gergely et al. 2014).

Remarks. No material of this species was found during this survey, and the record in Thailand needs further confirmation. The type locality on the label of the possible type specimen is "Siam", which is different from that reported in the original description as "Arva". A lack of a tube in a possible syntype NHMUK 2013.04.16 (Fig. 14B) is possibly due to damage.

6. Genus *Tortulosa* Gray, 1847

Tortulosa Gray, 1847: 177. Kobelt 1902: 281. Egorov 2013: 14.

Type species. *Turbo tortuosus* Férussac, 1821, by original designation.

Diagnosis. Shell elongated ovate. Periumbilical keel present. Aperture almost round; basal edge of peristome with a canal or indentation extending below into periumbilical keel. Operculum moderately thick to thick, corneous, circular, flat or cylindrical, closely coiled, multi-layer.

Differential diagnosis. *Tortulosa* can be distinguished from all other genera in this subfamily, especially *Coptocheilus* which has a similar shell size and matt surface, by a canal or indentation at a basal edge of peristome extending below into a periumbilical keel, and a thick, multi-layer operculum (Kobelt 1902; Raheem et al. 2014).

Remarks. This genus comprises two subgenera: the nominotypical subgenus and *Eucataulus* Kobelt, 1902. The subgenus *Tortulosa* possesses a detached last whorl and contains only one species, *Tortulosa tortuosa*. At present, the subgenus *Eucataulus* contains 29 species, all of which are distributed in Western Ghats, India, and Sri Lanka (Kobelt 1902; Raheem et al. 2014, 2018).

Tortulosa tortuosa (Férussac, 1821)

Figs 8D, 15, 16

Turbo tortuosus—Chemnitz 1795: 158, 159, pl. 195, figs 1882, 1883. Type locality: Nicobarischen Eylanden [Nicobar Islands]. Unavailable name.

Helix (*Cochlodina*) *tortuosa* Férussac, 1821: 61.

Pupa tortuosa—Gray 1825: 413.

Cyclostoma tortuosum—Sowerby I 1843: 152, pl. 28, figs 185, 186. Pfeiffer 1848: pl. 24, figs 19, 20. Pfeiffer 1849: 165, 166.

Tortulosa tortuosa—Adams and Adams 1856: 285, pl. 86, fig. 2, 2a, b. Gude 1921: 190, ?Nicobars; India: Trevandrum. van Benthem Jutting 1960: 11, 12, limestone hill Kaki Bukit, near kampong Wang Tangga, Perlis [Malaysia]. Berry 1963: pl. 6, fig. 31. Hemmen and Hemmen 2001: 40, fig. 7, Wat Thum Sua, Nation Valley, near Krabi. Maassen 2001: 44. Sutcharit and Panha 2008: 50, 51, with figs, Khao Nan National Park, Nakhon Si Thammarat, Thailand. Egorov 2013: 14, 15, fig. 23. Raheem et al. 2014: 53, figs 9e, 30b, c. BEDO 2017: 98. Sutcharit et al. 2018: 159, figs 5–11f, 5–13n. Thach 2018: 97 (figure caption), figs 139, 140. Meksuwan et al. 2020: 249, fig. 2, Tonsai Waterfall, Thalang District, Phuket Province. Páll-Gergely et al. 2020: 41.

Cataulus (*Tortulosa*) *tortuosus*—Sowerby I 1866: Pupinidae, pl. 2 (pl. 264), *Cataulus*, fig. 1.

Cataulus tortuosus—Reeve 1878: Pupinidae, pl. 6, sp. 49. Nevill 1881: 149.

Tortulosa (*Tortulosa*) *tortuosa*—Kobelt 1902: 288, fig. 64.

Perlisia tweediei Tomlin, 1948: 225, 226, pl. 11, fig. 6. Type locality: Kaki Bukit, Perlis [Malaysia]. Páll-Gergely et al. 2020: 41, fig. 3.

Tortulosa tweediei—BEDO 2017: 98.

Tortulosa huberi Thach, 2018: 21, 22, figs 133–138. Type locality: Krabi, South Thailand. Páll-Gergely et al. 2020: 41, fig. 5.

Tortulosa schileykoi Thach & Huber in Thach, 2018: 22, figs 142–146. Type locality: Phang Nga, South Thailand. Páll-Gergely et al. 2020: 41, fig. 4.

Type material examined. ***Lectotype*** of *Perlisia tweediei* NHMUK 1948.10.2.6 (Fig. 15A) from Kaki Bukit, Perlis. ***Holotype*** of *Tortulosa huberi* MNHN-IM-2000-34054 (Fig. 15B) from Krabi Province, Thailand. ***Holotype*** of *Tortulosa schileykoi* MNHN-IM-2000-34055 (Fig. 15C) from Phang Nga Province, Thailand.

Material examined. NHMUK 20100643/1–2 (2 shells) from the Nicobar Islands figured in Raheem et al. (2014: figs 30b, c). CUMZ 12154 (1 shell) from Nai-Chong Silvicultural Research Station, Mueang Krabi District, Krabi Province, 16 Jan. 2009. CUMZ 12166 (> 500 shells; Figs 15D, 16) from Tham Suea Temple, Mueang Krabi District, Krabi Province, 10 May 2010. CUMZ 12155 (12 specimens in ethanol; Fig. 8D) from Tham Suea Temple, Mueang Krabi District, Krabi Province, 9 July 2017. CUMZ 12156 (2 specimens in ethanol) from Phung Chang Cave, Mueang Phang Nga District, Phang Nga Province, 8 Aug. 2016. CUMZ 12157 (1 shell) from Phung Chang Cave, Mueang Phang Nga District, Phang Nga Province, 31 July 2018. CUMZ 12188 (2 shells) from Nam Phut Cave, Mueang Phang Nga District, Phang Nga Province, 7 Oct. 2010. CUMZ 12158 (1 specimen in ethanol) from Ban Yai, Phanom District, Surat Thani Province, 7 Aug. 2016. CUMZ 12159 (18 specimens in ethanol) from Khiri Rat Phatthana Temple, Wiang Sa District, Surat Thani Province, 4 July 2017. CUMZ 12189 (3 shells) from Natural Trail, Ratchaprapha Dam, Ban Ta Khun District, Surat Thani Province, 8 Dec. 2008. CUMZ 12160 (3 specimens in ethanol; Fig. 15E–H) from Tham Kanlayanamit Temple, Tham Phannara District, Nakhon Si Thammarat Province, 4 July 2017. CUMZ 12161 (3 specimens in ethanol) from Ton Din Cave, Khuan Don District, Satun Province, 7 July 2017.

Diagnosis. Shell rounded, spindle-shaped, translucent whitish to brown. Whorls 7, convex; third to penultimate whorls broader; last whorl narrower, detached, brought forward, with a filiform basal keel broader at the mouth. Aperture almost circular, always with basal indentation; palatal indentation obvious in specimens with thicker shell. Operculum thick cylindrical, corneous, multi-layer, spring-like when extended by force; inner operculum (attached to dorsal side of posterior body) translucent yellow, convex with crater within and conical protrusion in the middle; outer operculum (free surface) dark brown and usually eroded.

Differential diagnosis. *Tortulosa tortuosa* can be distinguished from other species in this genus by a narrower last whorl that is detached from the penultimate whorl and brought forward, a shallower basal indentation, and the presence of a palatal indentation (Raheem et al. 2014).

Distribution. Northern Peninsular Malaysia and southern Thailand. The type locality of this species is still controversial while the occurrences in India and Nicobar Islands need further confirmation (Sutcharit and Panha 2008; Raheem et al. 2014, 2018; Páll-Gergely et al. 2020).

Remarks. The name *Turbo tortuous* Chemnitz, 1795 was published prior to Férussac's name, but it is unavailable (Raheem et al. 2018). See Raheem et al. (2014, 2018) and Páll-Gergely et al. (2020) for the notes on taxonomy and type specimen of this species. Currently, this is the only extant species in the subgenus *Tortulosa*. One extinct species, *T. naggsi* Raheem & Schneider, 2017 in Raheem et al. (2018) was discovered from Son La Province, Northern Vietnam. This species exhibits a terminal part of the body whorl that is fully attached to the penultimate whorl, and thus corresponds more to the subgenus *Eucataulus* from South Asia (Raheem et al. 2018).

Maassen (2001) treated *P. tweediei*, and Páll-Gergely et al. (2020) treated both *T. huberi* and *T. schileykoi* as junior subjective synonyms of *T. tortuosa*. We agree on those synonymisations because the specimens we collect from the same locality exhibit a high infraspecific variation in the length of the detached part of the body whorl relative to the shell height, also in shell shape from ovate to elongate, and shell colour from translucent whitish to brown (Fig. 16). All the specimens in Fig. 16 were found together with hundreds of other specimens inside the same decaying log at Tham Suea Temple, Krabi Province, southern Thailand. The distribution of this species in Thailand is provided in Fig. 4.

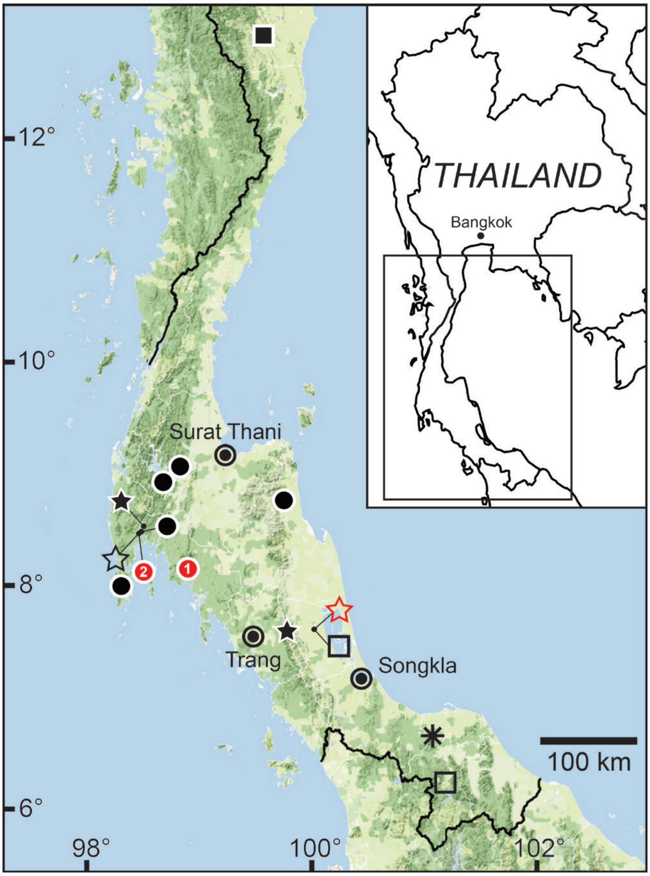

Figure 4. Map of southern Thailand showing the distribution of *Coptocheilus sectilabris* (filled square), *Coptocheilus sumatranus* (open square), *Rhaphaulus lorraini* (filled star), *Rhaphaulus ascendens* (open star), *Rhaphaulus perakensis* (asterisk), and *Tortulosa tortuosa* (circle). Each red symbol indicates the type locality of its respective taxon. Red circles indicate the type localities of *Tortulosa huberi* (1) and *Tortulosa schileykoi* (2).

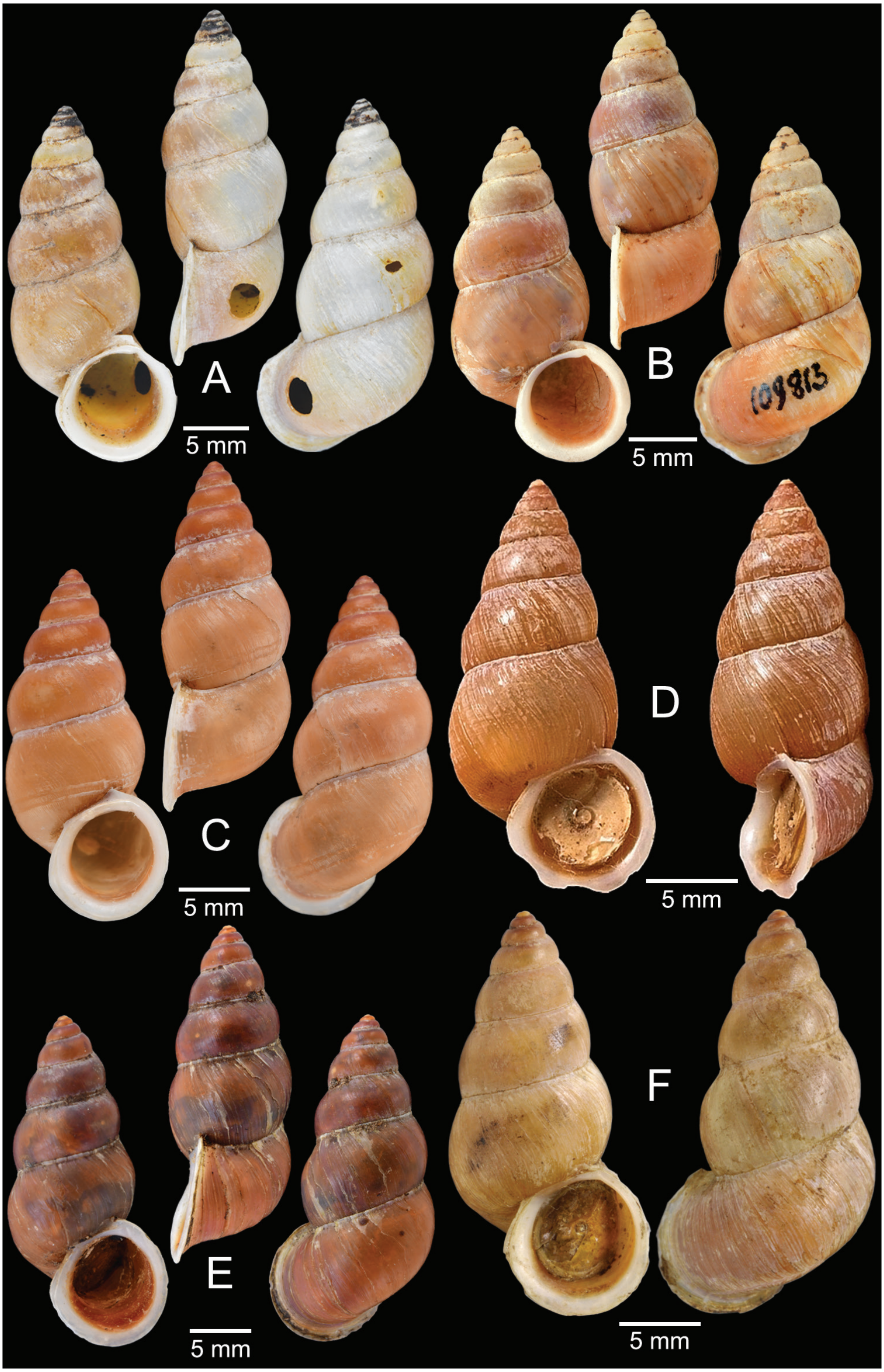

Figure 5. A–C *Coptocheilus sectilabris*: **A** lectotype MCZ 169361 from Tavoy **B** specimen SMF 109813 from Tavoy, and **C** specimen CUMZ OLM-0111 from Kaeng Krachan, Phetchaburi **D–F** *Coptocheilus sumatranus*: **D** syntype of *Coptocheilus perakensis* NHMUK 1903.11.20.33 from Perak **E** specimen SMF 262529/1 "*Schistoloma siamensis* Brandt" from Thailand: an den Tanto-Fällen bei Ban Nong Star; Yala Provinz, and **F** specimen NHMUK 1986.4.19.14 "*Coptocheilus sectilabrum* var." from Larut near Perak.

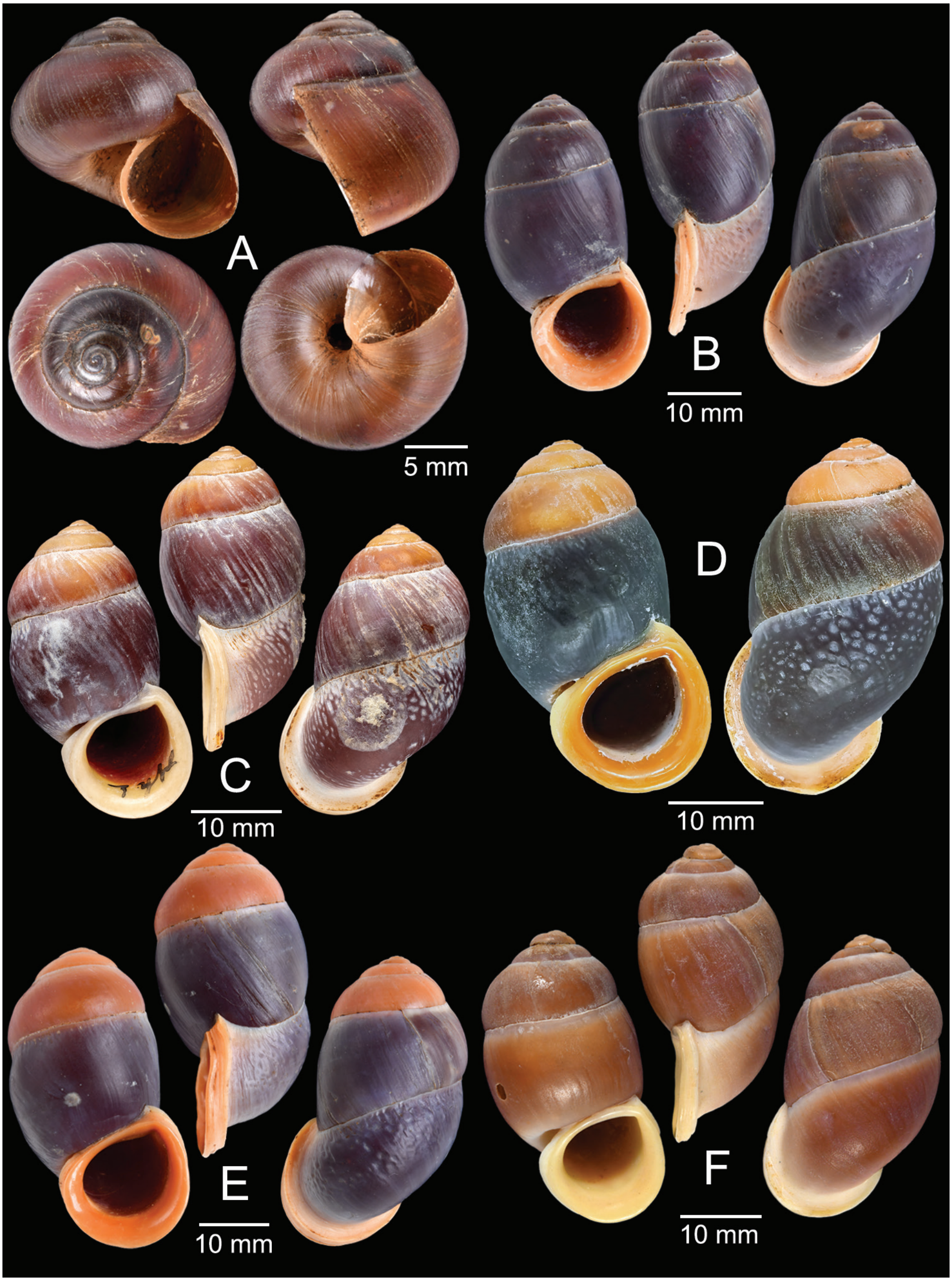

Figure 6. A, B *Pollicaria mouhoti monochroma*: **A** juvenile specimen CUMZ 12182 from Tham Suea Lueang Temple, Loei and **B** paratype CUMZ 1562 from Tam Pha Bing Temple, Loei **C–E** *Pollicaria mouhoti mouhoti* **C** lectotype of *Hybocystis mouhoti* NHMUK 20130071/1 from Lao Mountains, Camboja **D** holotype of '*Pollicaria nicoarlingi*' MNHN-IM-2000-37277, and **E** specimen CUMZ 12166 from Wang Daeng Cave, Phitsanulok **F** *Pollicaria myersii*, holotype of '*Pollicaria huberi*' NHMUK 20180253. Photo: F. Prugnaud, MNHN (**D**).

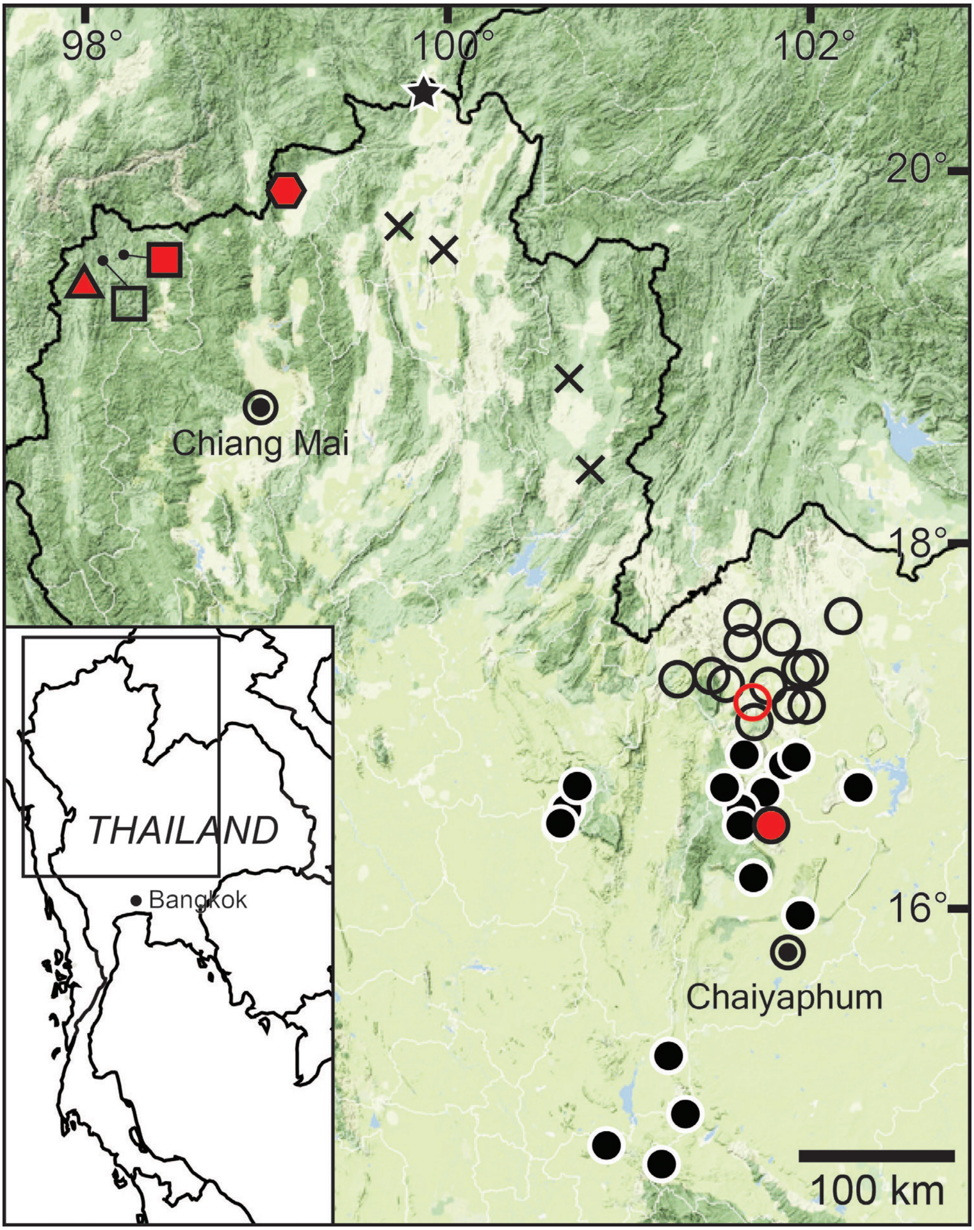

Figure 7. Map of northern Thailand showing the distribution of *Pollicaria mouhoti mouhoti* (filled circle), *Pollicaria mouhoti monochroma* (open circle), *Pseudopomatias caligosus* (square), *Pseudopomatias doiangkhangensis* sp. nov. (hexagon), *Pseudopomatias pallgergelyi* sp. nov. (triangle), *Pupinella mansuyi* (cross), and *Rhaphaulus tonkinensis* (star). Each red symbol indicates the type locality of its respective taxon. The red filled circle denotes the type locality of *Pollicaria nicoarlingi*.

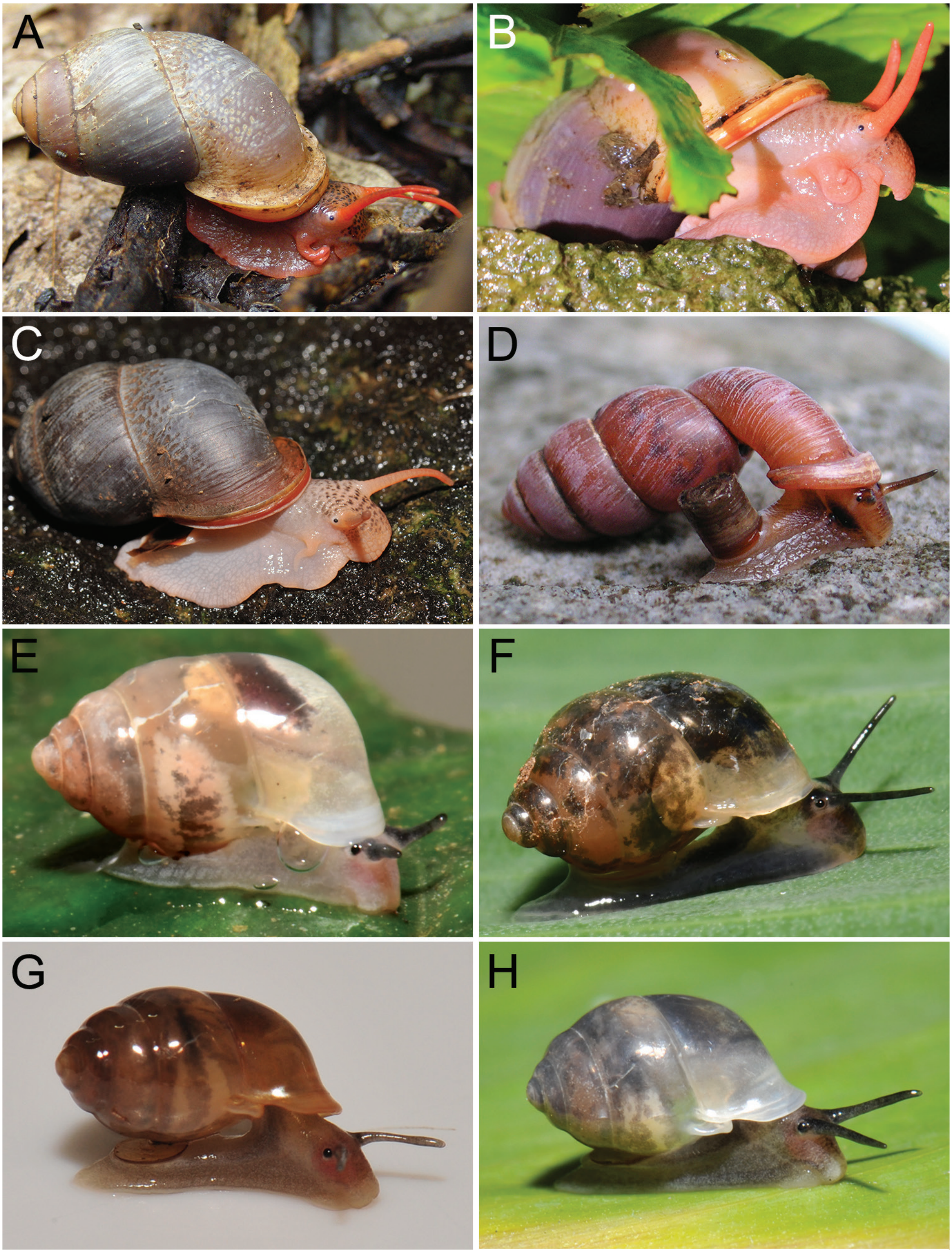

Figure 8. Live specimens of **A, B** *Pollicaria mouhoti mouhoti*: specimens **A** CUMZ 12166 and **B** CUMZ 12175 from Wang Daeng Cave, Phitsanulok **C** *Pollicaria mouhoti monochroma*, paratype CUMZ 1562 from Tam Pha Bing Temple, Loei **D** *Tortulosa tortuosa*, specimen CUMZ 12155 from Tham Suea Temple, Krabi **E–H** *Pupina artata*: specimens of **E** CUMZ 12006 from Pha Daeng Cave, Mae Hong Son **F** CUMZ 12008 from Tham Nam Pha Pha Ngam Temple, Lampang, and **G, H** CUMZ 12029 from Khao Tham Raet Temple, Chachoengsao showing the brown (**G**) and grey (**H**) shell morphs; All not to scale.

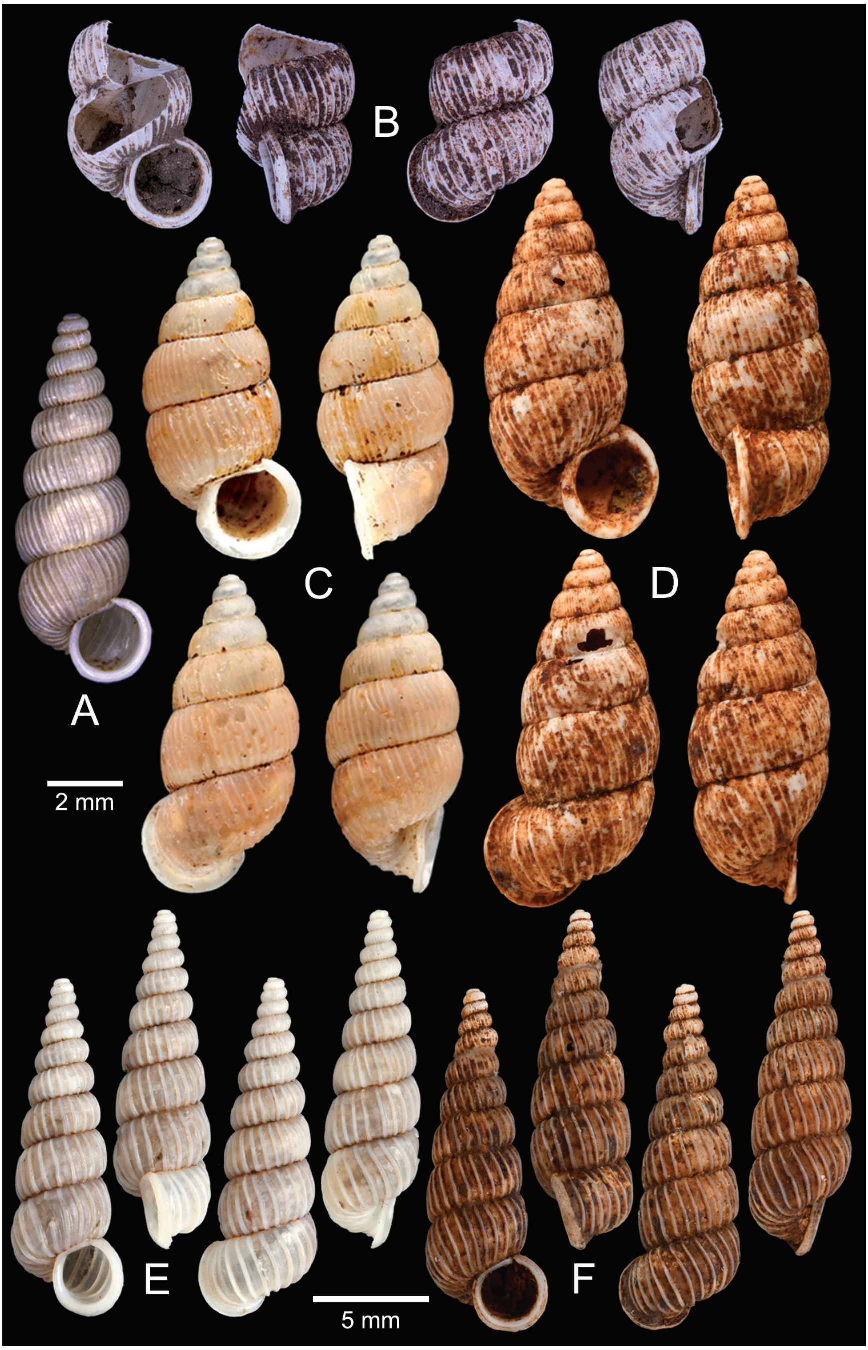

Figure 9. A, B *Pseudopomatias caligosus*: **A** holotype HNHM 100176 and **B** specimen CUMZ 12191 from Pa Tham Wua Temple, Mae Hong Son **C, D** *Pseudopomatias doiangkhangensis* sp. nov. **C** holotype CUMZ 12165/1 and **D** paratype CUMZ 5219 from Doi Ang Khang, Chiang Mai **E, F** *Pseudopomatias pallgergelyi* sp. nov. **E** holotype CUMZ 12167/1 **F** paratype CUMZ 12167/2 from Pha Daeng Cave, Mae Hong Son. Photo: B. Páll-Gergely (**A**).

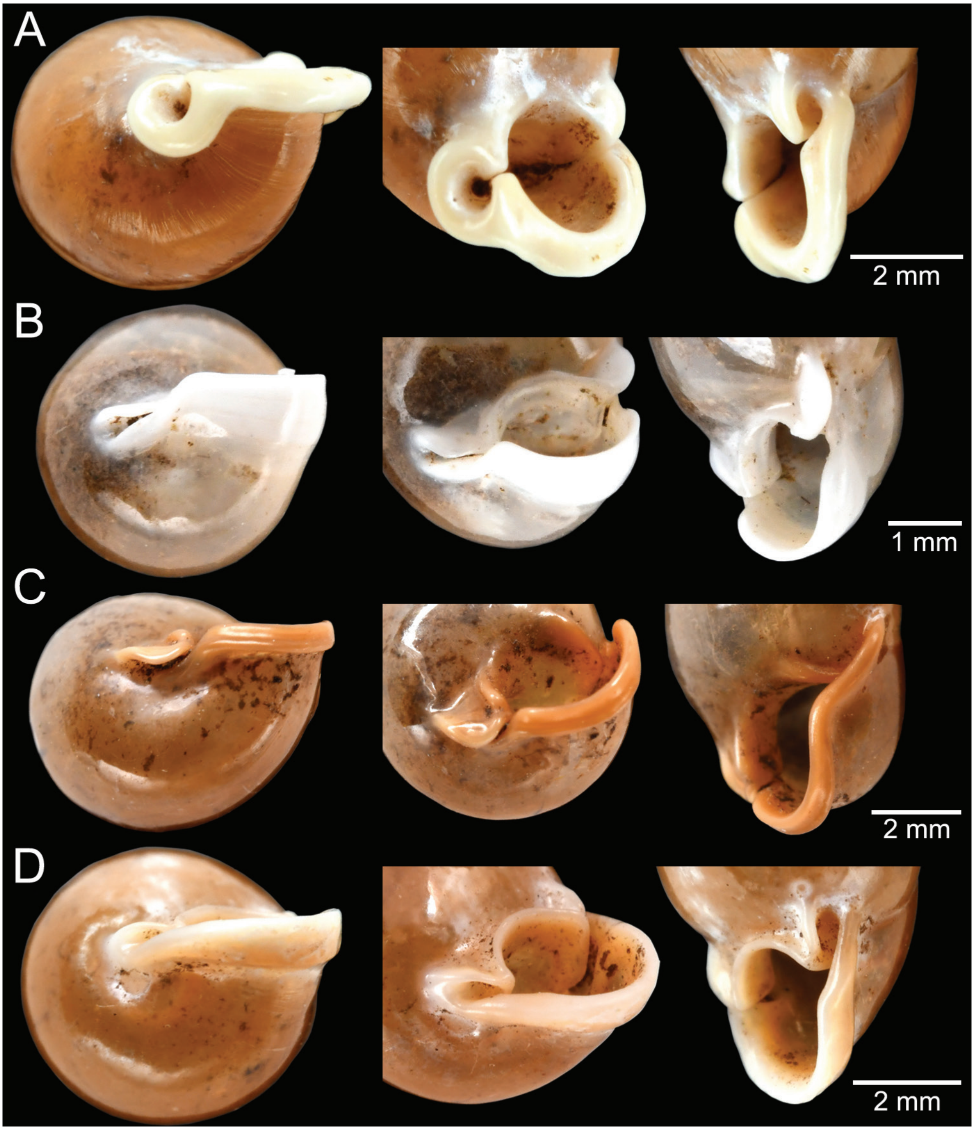

Figure 10. Umbilical, columellar and parietal views of **A** *Pupinella mansuyi*, specimen CUMZ 12148 from Pha Chu, Nan **B** *Pupina artata* from the *Pupina artata* species group, specimen CUMZ 12003 from Ban Ping Khong, Chiang Mai **C** *Pupina godwinausteni* sp. nov. from the *Pupina arula* species group, holotype CUMZ 12090/1 **D** *Pupina aureola* from the *Pupina aureola* species group, specimen CUMZ 12130 from Sra Morakot, Krabi.

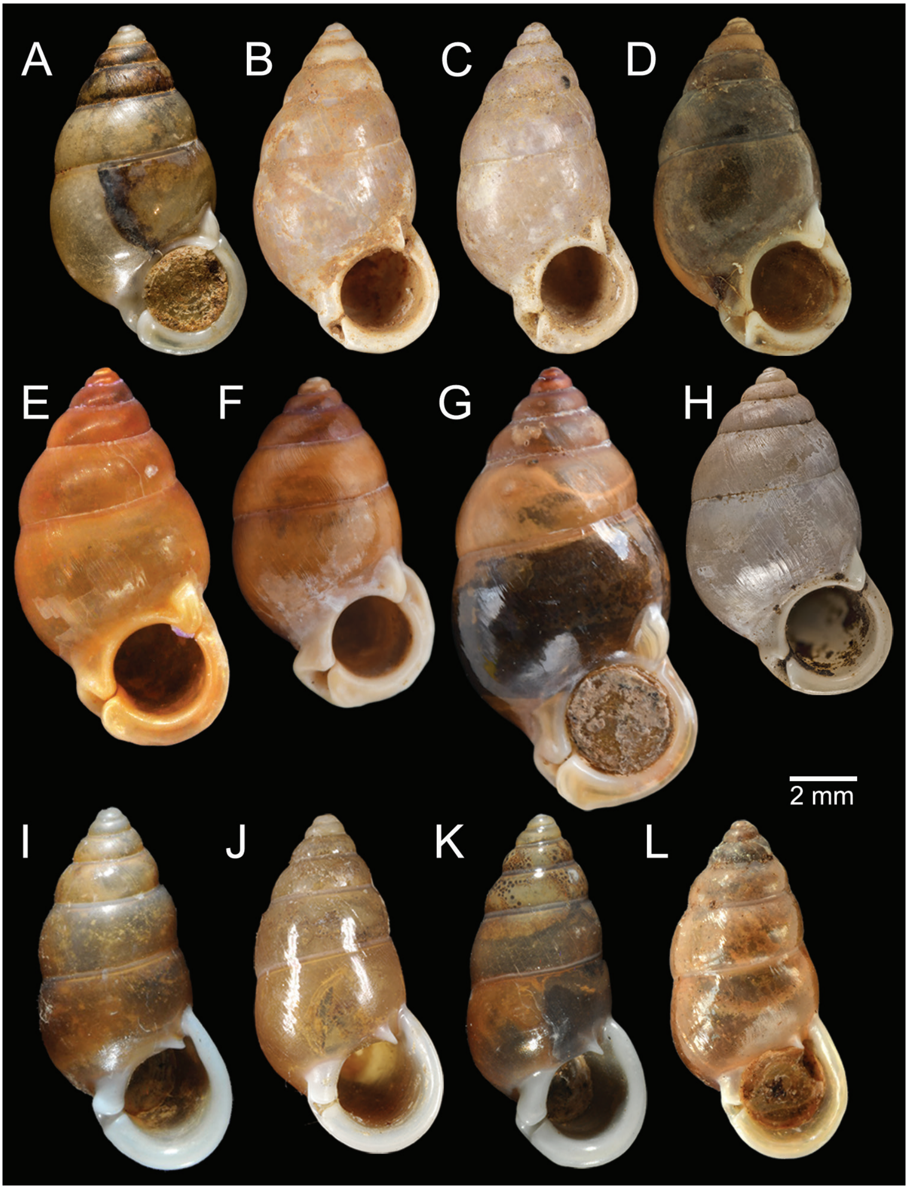

Figure 11. Shells of *Pupinella* species from mainland Southeast Asia. **A–G** *Pupinella mansuyi*: **A** syntype of *Eupupina mansuyi* MNHN-IM-2000-30756 from Deux-Ponts **B** syntype of *Eupupina mansuyi* MNHN-IM-2000-36067 from Deux-Ponts **C** syntype of *Eupupina mansuyi* MNHN-IM-2000-36068 from Quang-Huyen **D** syntype of *Eupupina mansuyi* RBINS MT970/1 from Quang-Huyen **E** holotype of *Pupinella frednaggsi* NHMUK 20170285 **F** specimen CUMZ 12148 from Pha Chu Mount, Nan, and **G** specimen CUMZ 12149 from Pha Tub Cave, Nan **H** *Pupinella sonlaensis*, paratype ZRC.MOL.9377 **I–L** *Pupinella illustris* **I, J** syntypes of *Pupina illustris* MNHN-IM-2000-35842 from Tonkin **K** lectotype of *Pupina tonkiniana* MNHN-IM-2000-35838 from Lang-Son et Thať-Khé, and **L** paralectotype of *Pupina tonkiniana* SMF 109932/10 from Tonkin: That-khé. Photo: A. Lardeur, P. Maestrati, MNHN (**A–C, I–K**), F. Trus, RBINS (**D**), S.K. Tan, ZRC (**H**).

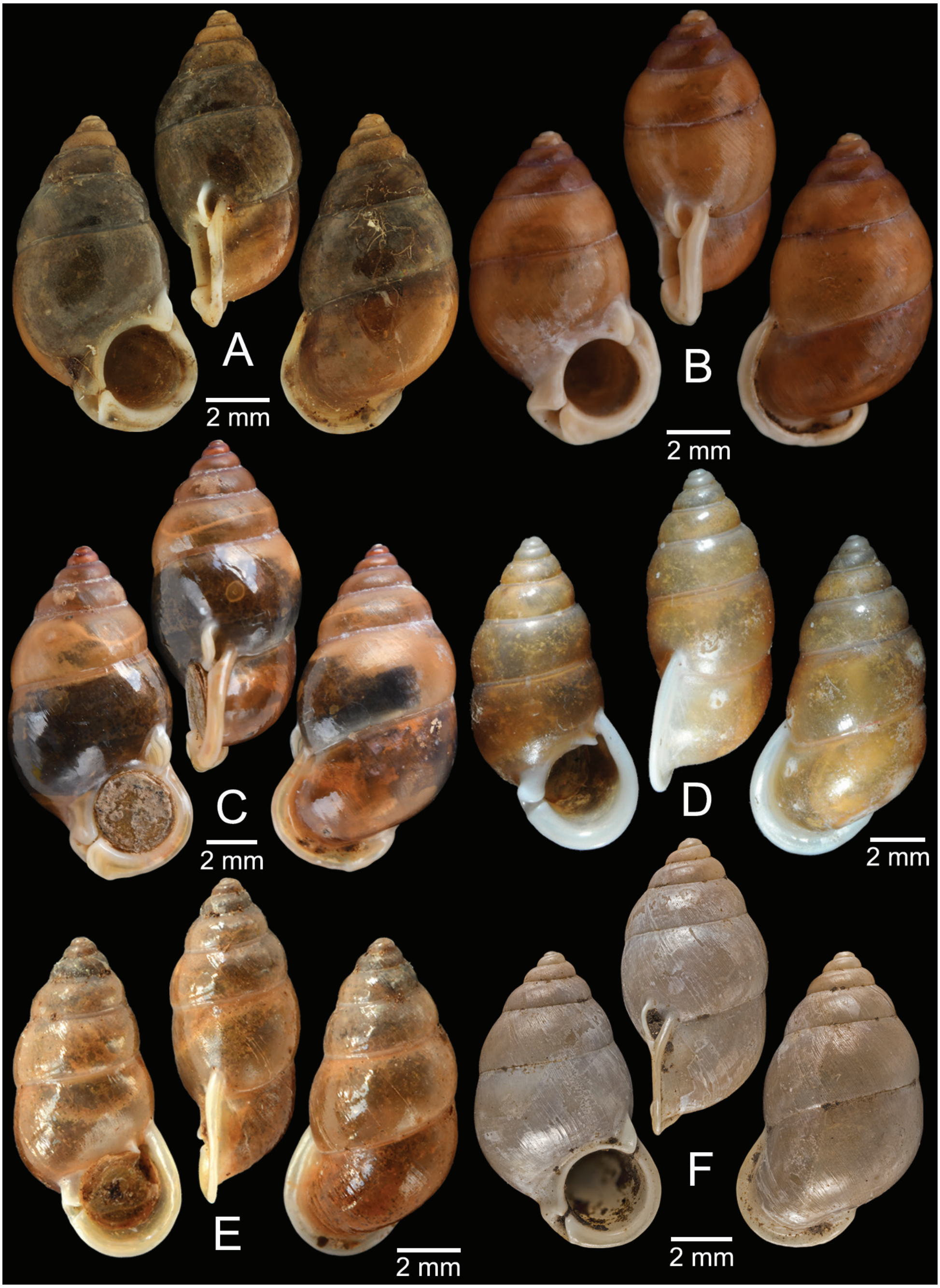

Figure 12. A–C *Pupinella mansuyi*: **A** syntype of *Eupupina mansuyi* RBINS MT970/1 from Quang-Huyen **B** specimen CUMZ 12148 from Pha Chu Mount, Nan, and **C** specimen CUMZ 12149 from Pha Tub Cave, Nan. **D, E** *Pupinella illustris* **D** syntype of *Pupina illustris* MNHN-IM-2000-35842 from Tonkin and **E** paralectotype of *Pupina tonkiniana* SMF 109932/10 from Tonkin: That-khé **F** *Pupinella sonlaensis*, paratype ZRC.MOL.9377. Photo: F. Trus, RBINS (**A**), P. Maestrati, MNHN (**D**), S.K. Tan, ZRC (**F**).

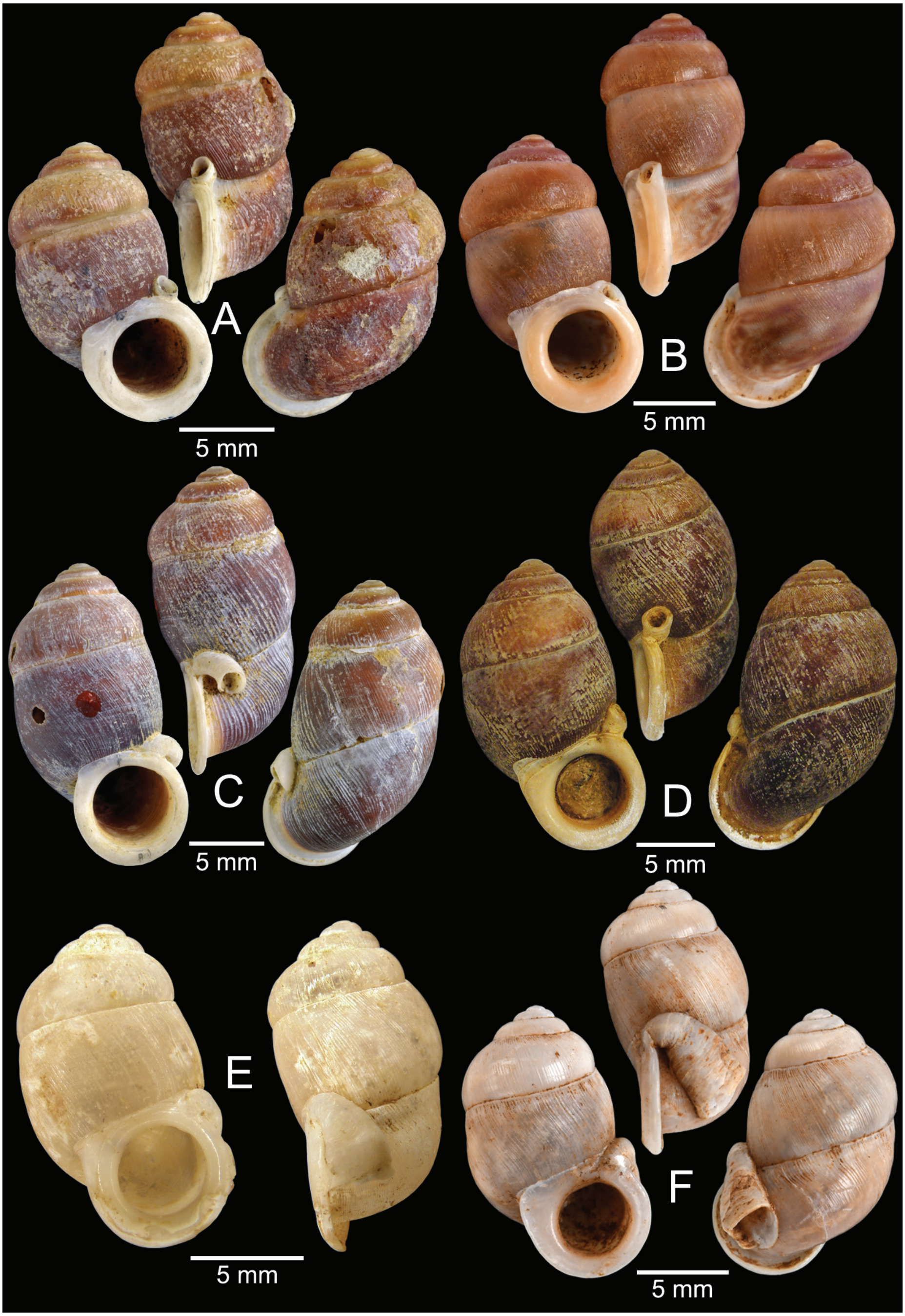

Figure 13. A, B *Rhaphaulus lorraini*: **A** syntype NHMUK 20130454 from Pulo Penang and **B** specimen CUMZ 12162 from Kiriwong (Tham Kope) Temple, Phang Nga **C** *Rhaphaulus perakensis*, syntype NHMUK 1897.3.15.41 from Larut, Perak **D** *Rhaphaulus ascendens*, syntype UMZC I.100025 from Patalung, Malay Peninsula **E, F** *Rhaphaulus tonkinensis* **E** holotype HNHM 98757 and **F** specimen CUMZ 12163/1 from Luang Cave, Chiang Rai. Photo: B. Páll-Gergely (**E**)

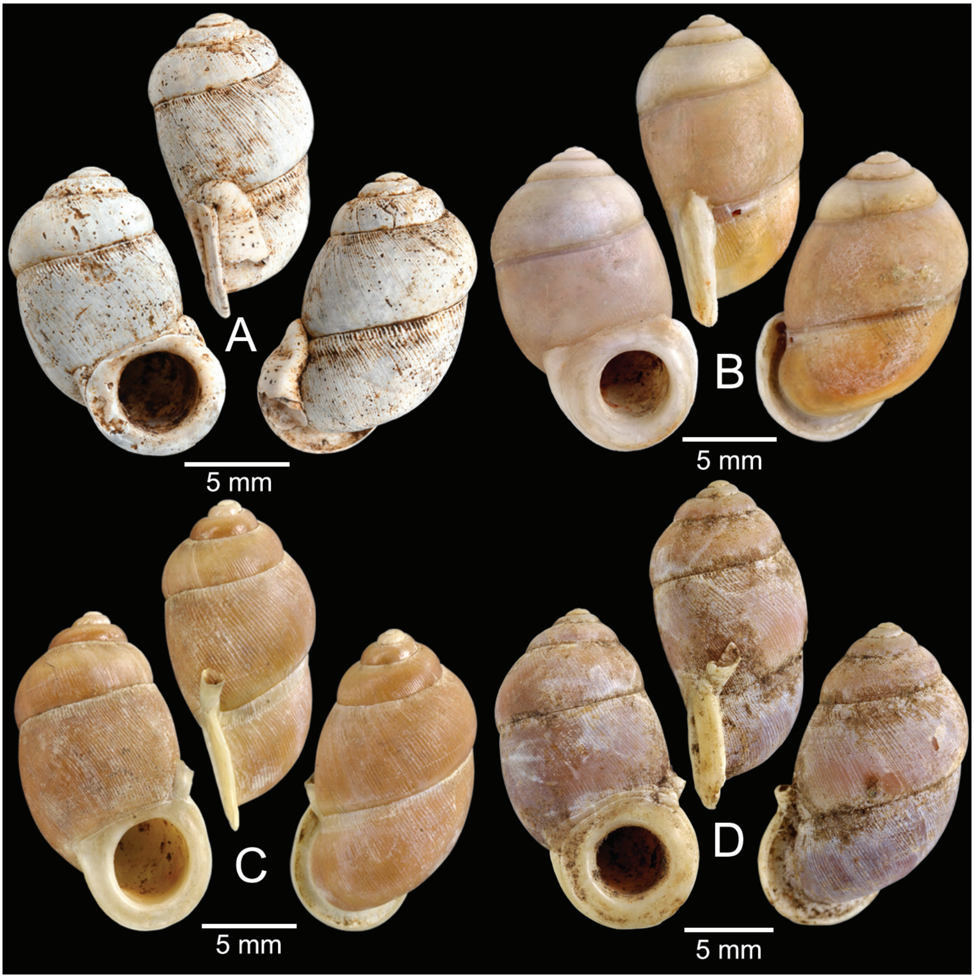

Figure 14. A *Rhaphaulus tonkinensis*, specimen CUMZ 12163/2 from Luang Cave, Chiang Rai. **B–D** *Rhaphaulus chrysalis* **B** possible syntype NHMUK 2013.04.16 from Siam **C** specimen NHMUK 1871.9.23.52 from Burma, and **D** specimen NHMUK 1903.7.1.3073 from Molmein.

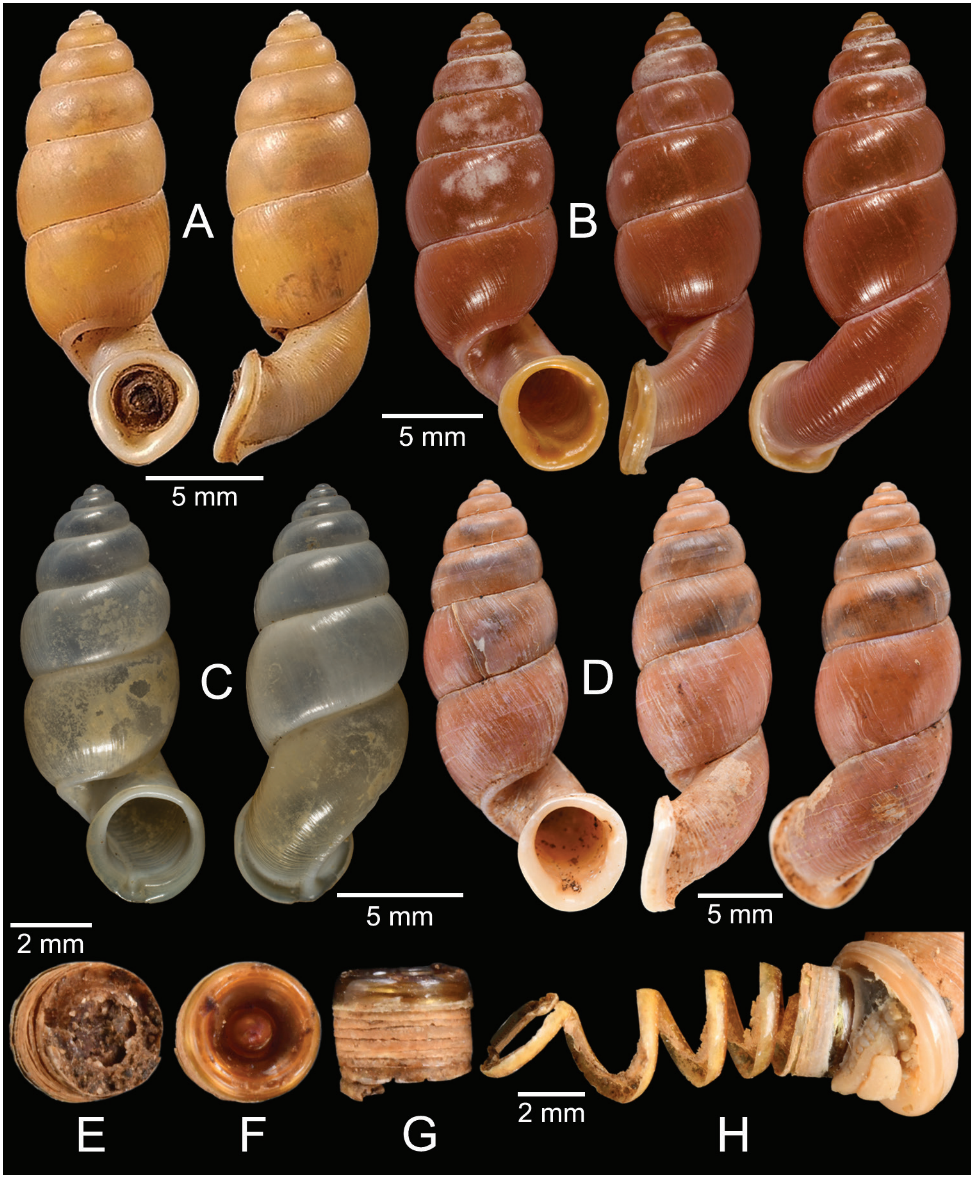

Figure 15. *Tortulosa tortuosa* **A** lectotype of *Perlisia tweediei* NHMUK 1948.10.2.6 from Kaki Bukit, Perlis **B** holotype of *Tortulosa huberi* MNHN-IM-2000-34054 from Krabi **C** holotype of *Tortulosa schileykoi* MNHN-IM-2000-34055 from Phang Nga **D** specimen CUMZ 12166 from Tham Suea Temple, Krabi, and **E–H** operculum of specimen CUMZ 12160 from Tham Kanlayanamit Temple, Nakhon Si Thammarat, showing **E** outer operculum **F** inner operculum **G** side view (inner surface up), and **H** spring-like inner operculum when extended by force. Photo: M. Caballer, MNHM (**B, C**).

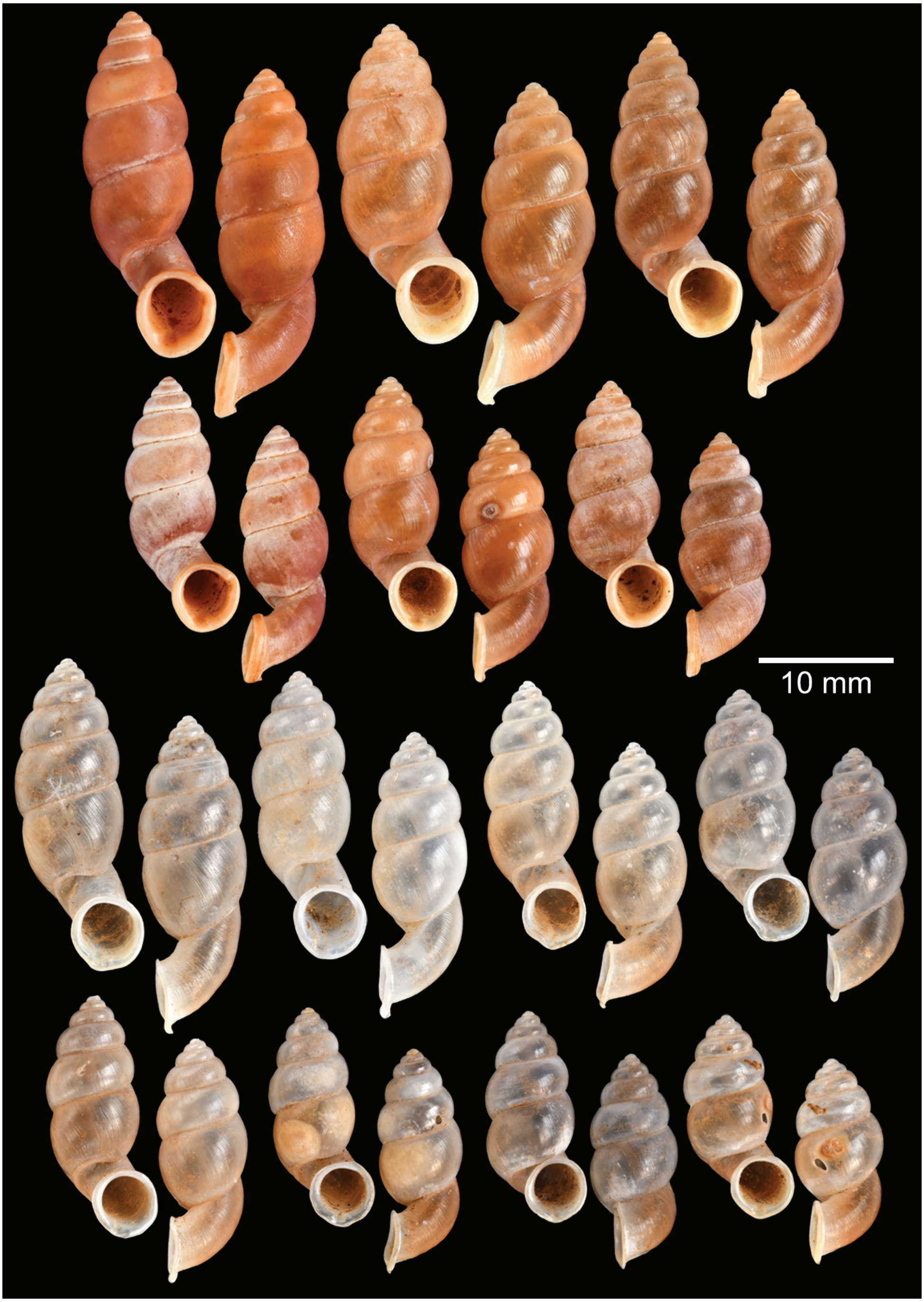

Figure 16. Infraspecific variation of shell shape and colour found in the same collecting locality of *Tortulosa tortuosa*, CUMZ 12166 from Tham Suea Temple, Krabi.

Subfamily Pupininae Pfeiffer, 1853

Remarks. Only one genus, *Pupina*, with a total of 14 species and one subspecies belonging to three species groups, is known to occur in Thailand, and two additional species have an uncertain record.

7. Genus *Pupina* Vignard, 1829

Pupina Vignard, 1829: 439, 440. Kobelt 1902: 302. Egorov 2013: 4, 5.

Type species. *Pupina keraudrenii* Vignard, 1829, by monotypy.

Diagnosis. Shell elongate ovate, smooth, with a shining enamel-like coating. Peristome with two canals; posterior canal at the suture; anterior canal oblique at the middle of columellar margin. Parietal callus normally thickened, and bordered by two teeth; parietal tooth located near or covering posterior canal; lower columellar tooth located near or covering anterior canal (Figs 3, 10B–D).

Differential diagnosis. *Pupina*, especially the *Pupina artata* species group (see below), is most similar to *Signepupina* Iredale, 1937 and *Cordillerapina* Stanisic, 2010 in having fin-shaped teeth. However, *Signepupina* tends to have a more elongated or turriform shell shape and *Cordillerapina* has a non-glossy surface with axial ribs (Stanisic et al. 2010).

Remarks. *Pupina* is the oldest taxon as well as the type genus of the family Pupinidae, and the only genus from the subfamily Pupininae occurring in mainland Southeast Asia. The three original subgenera, namely *Pupina* s. s., *Tylotoechus* Kobelt & Möllendorff, 1897, and *Siphonostyla* Kobelt, 1897 (Kobelt and von Möllendorff 1897) were adopted by later authors (Gude 1921; Egorov 2013). The subgenus *Siphonostyla* is diagnosed with a specialised anterior canal, which is lengthened into an ascending tube (Kobelt 1902; Egorov 2013), as in the type species *Pupina longituba* Kobelt, 1897 (see Egorov 2013: fig. 6).

Various diagnoses between *Pupina* s. s. and *Tylotoechus* had been proposed by different authors (Table 2). *Tylotoechus* was originally established by Kobelt and von Möllendorff (1897) apparently to replace *Mesostoma* Heude, 1886 [non Dugès, 1830]. The type species had been subsequently designated as *Pupina destructa* Heude, 1885 by Gude (1921), which agreed well with the original proposal by Heude (1886), in that *P. destructa* being monotypic in *Mesostoma*. Later, Clench (1949) elevated *Tylotoechus* to the generic level, and stated that many *Tylotoechus* species recognised by Kobelt (1902) should belong to *Pupina* s. s. Upon examining the type specimen figure of *P. destructa* in Heude (1885: pl. 24, fig. 15) and the specimen in the Heude Collection deposited in the National Museum of Natural History, Smithsonian Institution (USNM 472296, from the type locality, Tchen-k'eou, China; Fig. 17), we found that the parietal tooth is weak and does not extend up onto the body whorl, in contrast to the diagnostic stated in Kobelt (1902) and Clench (1949) (Table 2). It is not certain whether Heude (1885), Kobelt (1902) and Clench (1949) recognised the diagnostic characters of *Tylotoechus* in the same fashion or not.

Table 2. Diagnoses of the subgenera *Pupina* s. s. and *Tylotoechus* from different authors.

Author and citation	*Pupina* Vignard, 1829 Type species: *Pupina keraudrenii* Vignard, 1829	*Tylotoechus* Kobelt & Möllendorff, 1897 Type species: *P. destructa* Heude, 1885
P.M. Heude (Heude 1885: pl. 24, fig. 15; Heude 1890: 130)	–	… interrupted peristome; columella cloven, right margin intact, parietal callus with tooth and slit. … The aperture is rather that of *Pupina* than *Registoma*. The columellar fissure is that of the latter, while the fissure on the right edge is missing. The parietal callus does not reach the edge, remains inwards and is rather weak, while simulating the opening of the *Pupina*, Seems to belong to the same group as *Pupina japonica* Martens. (as of *Mesostoma* Heude, 1886, non *Mesostoma* Ehrenberg, 1835 [rhabdocoel flatworm])
W. Kobelt (Kobelt 1902: 302, 306, figs 70, 71)	Canal simple, formed by a tongue-like projecting callus on the apertural wall.	Upper canal formed by a tongue detached from the callus and the edge of the mouth.
W.J. Clench (Clench 1949: 31, 44, figs 17b, c, 18c, d)	Possessing a well-developed parietal tooth within margin of aperture; possessing a columellar notch cut parallel with face of aperture.	Possessing a well-developed parietal tooth extending outward and up onto body whorls; possessing a columellar notch. The single character upon which the genus is based is only the extension of the parietal tooth outward and upward as a tongue-like process on the body whorl in *Tylotoechus*, the parietal tooth remaining within the margin of the aperture in *Pupina*, s. s. Extremes in both cases are easily placed, but many species are exceedingly close to either of the two genera.
R. Egorov (Egorov 2013: 5–7, figs 3, 7)	Parietal canal simple, formed by tongue-shaped projecting callus, sometimes reduced. Parietal tooth differently developed.	Parietal canal formed by apertural margin and tongue-shaped projected in front process separated from callus.

Clench (1949) also established three new *Pupina*-related genera based on differences of columellar tooth from the Pacific Islands, namely *Pupinoa*, *Pupinesia*, and *Kanapa*. The current elevation of *Tylotoechus* and *Siphonostyla* to generic level, and the treatment of *Pupinoa*, *Pupinesia*, and *Kanapa* at subgeneric level (Bank 2017; MolluscaBase 2022) needs a further comprehensive revision, especially the examination of all type specimens of nominal taxa within each subgenus and the results from molecular phylogenetic analyses. As the validity of each subgenus within *Pupina* is still uncertain, this work adopts the genus *Pupina* in a wide sense, and does not apply the subgeneric classification or the elevation of those subgenera to the generic level.

Based on the distinction of shell teeth, canals (Figs 10, 18), and operculum (Fig. 19), the mainland Southeast Asian *Pupina* could be classified into three species groups, namely *P. artata* group, *P. arula* group, and *P. aureola* group. These species groups, however, might not reflect DNA-based reciprocal monophyly.

Group I. *Pupina artata* species group

Figs 10B, 18A, 19A

This species group is characterised by a triangular or fin-shaped parietal tooth covering a posterior canal. A columellar tooth is less thickened, never ear-shaped and mostly fin-shaped, located next to or covering an anterior canal. When observed from apertural view, the anterior canal mostly appears slit-like and the posterior canal is not visible. An apertural lip is straight or slightly curved when observed from lateral view. An operculum is round, thin, multispiral, yellowish, transparent corneous, and with a smooth edge.

The *Pupina artata* species group highly resembles the Australian genus *Signepupina* (type species: *Pupinella macgillivrayi* Cox, 1864 [= *Signepupina meridionalis* (Pfeiffer, 1864)]). Both groups possess a triangular or fin-shaped parietal tooth covering the posterior canal, and the columellar tooth is mostly fin-shaped, located next to the anterior canal, making the anterior canal slit-like. However, *Signepupina* tends to have a more elongated or turriform shell shape. As the relationship between *Pupina* and *Signepupina* is still uncertain, we do not allocate the *Pupina artata* species group from mainland Southeast Asia to *Signepupina*.

This species group from mainland Southeast Asia contains seven species, including three nominal species and one new species (*P. bensoni* sp. nov.) from Thailand. The distribution of the *P. artata* species group in Thailand is provided in Fig. 20. A synoptic view of all species within the *P. artata* species group from mainland Southeast Asia is given in Fig. 21 to provide the comparative size.

***Pupina artata* Benson, 1856**

Figs 8E–H, 10B, 18A, 21A–M, 22, 23, 24A, 25A–C

Pupina artata Benson, 1856: 230. Type locality: Moulmein [Mawlamyine, Mawlamyine Township, Mawlamyine District, Mon State, Myanmar]. Theobald 1858 [1857]: 247, 248. Pfeiffer 1860: 142, pl. 37, figs 10–12. Sowerby I 1866: Pupinidae, pl. 3 (pl. 265), *Pupina*, figs 1, 2. Hanley and Theobald 1870: 4, pl. 7, fig. 5. Stoliczka 1871: 151, 152. Nevill 1878: 299, 300, Ava [Mandalay Region, Myanmar]; Moulmein; Buket Pondong [Gunung Pondok, Perak State, Malaysia]. Reeve 1878: Pupinidae, pl. 1, sp. 3. Crosse 1879: 340. de Morgan 1885: 413, Boukit Pondong, Pérak; Java [doubtful]; Moulmein; Lahat, Ipoh, Gôping, Kinta [Perak State, Malaysia]. von Möllendorff 1894: 155, the Samui Islands, Gulf of Siam [Samui Island, Surat Thani Province, Thailand]. Godwin-Austen 1897: 38, 39, pl. 69, fig. 6, 6a, b. Fischer and Dautzenberg 1904: 431, Ile Samui, golfe de Siam [Samui Island, Surat Thani Province, Thailand]. van Benthem Jutting 1960: 12, a hill near the hot springs, near Tandjong Rambutan, N.E. of Ipoh, Perak. Solem 1966: 12, Chieng Dao, Doi Sutep [Chiang Dao District and Doi Suthep Mountain, Chiang Mai Province, Thailand]. Davison 1995: 236, 237, limestone island C, Temengor dam, Perak, Malaysia. Chan 1998b: 2, Ipoh, Perak. Maassen 2001: 39, 40. BEDO 2017: 87. Sutcharit et al. 2018: fig. 5–13d.

Pupina artata var. *blanfordiana* Nevill, 1878: 300. Type locality: Thyet Myo [Thayetmyo, Magway Region, Myanmar]; Akoutong [Akauk Taung, Pyay District, Bago Region, Myanmar]; Kamah Hill, Tongoop, & c., Arakan [Toungup, Thandwe District, Rakhine State, Myanmar]; Prome [Pyay, Bago Region, Myanmar].

Pupina peguensis [non Benson]—Godwin-Austen 1897: 40, pl. 69, fig. 3, 3a–d, Kama on the right bank of the Irrawaddy, Pegu [Kamma Township, Thayet District, Magway Region, Myanmar]. BEDO 2017: 93.

Pupina (*Tylotoechus*) *artata*—Kobelt 1902: 306, 307. Gude 1921: 193. Laidlaw 1928: 33.
Pupina (*Pupina*) *artata*—Hemmen and Hemmen 2001: 39.
Pupina blanfordi [non Theobald]—BEDO 2017: 89.
Pupina limitanea [non Godwin-Austen]—BEDO 2017: 90. Sutcharit et al. 2018: fig. 5–13g.
Pupina sp.—Sutcharit et al. 2018: fig. 5–11a.

Type material examined. ***Syntype*** UMZC I.102960.A (1 shell; Figs 21A, 22A) from the R. McAndrew collection, labelled "Bens. col., Moulmein".

Other material examined. NHMUK 1906.4.4.28 (6 shells; Figs 21J, 22B) from Moulmein, Myanmar. CUMZ 12001 (7 shells; Figs 21H, 22C) from Khao Tham Phra Temple, Mueang Chiang Rai District, Chiang Rai Province, 9 Jan. 2008. CUMZ 12002 (1 shell) from Luang Cave, Mae Sai District, Chiang Rai Province, 23 Oct. 2015. CUMZ 12003 (21 shells; Figs 10B, 18A, 21I, 22D) from Ban Ping Khong, Chiang Dao District, Chiang Mai Province, 8 Oct. 2008. CUMZ 12193 (4 shells) from Ban Ping Khong, Chiang Dao District, Chiang Mai Province, 21 Nov. 2012. CUMZ 12190 (3 shells) from Chiang Dao Cave, Chiang Dao District, Chiang Mai Province, 25 Oct. 2015. CUMZ 12004 (4 specimens in ethanol) from Bua Tong Cave, Mae Tang District, Chiang Mai Province, 8 Oct. 2017. CUMZ 12168 (4 shells) from Doi Ang Khang, Fang District, Chiang Mai Province, 24 Oct. 2015. CUMZ 12005 (43 shells) from Pha Daeng Cave, Mueang Mae Hong Son District, Mae Hong Son Province, 18 Jan. 2015. CUMZ 12006 (17 shells and 1 specimen in ethanol; Fig. 8E) from Pha Daeng Cave, Mueang Mae Hong Son District, Mae Hong Son Province, 3 Dec. 2020. CUMZ 12007 (7 shells) from Tham Nam Pha Pha Ngam Temple, Mae Phrik District, Lampang Province, 7 Jan. 2008. CUMZ 12008 (3 shells and 4 specimens in ethanol; Fig. 8F) from Tham Nam Pha Pha Ngam Temple, Mae Phrik District, Lampang Province, 8 Oct. 2020. CUMZ 12009 (12 shells; Figs 21G, 22E) from Phu Sang Waterfall, Phu Sang District, Phayao Province, 24 Oct. 2008. CUMZ 12010 (5 shells) from Phu Sang Waterfall, Phu Sang District, Phayao Province, 19 Nov. 2012. CUMZ 12011 (12 shells and 7 specimens in ethanol; Figs 21B, 22F) from Thep Sathaporn Temple, Banphot Phisai District, Nakhon Sawan Province, 17 July 2008. CUMZ 12012 (17 shells) from Khao Chuak Charoentham Temple, Ban Rai District, Uthai Thani Province, 8 July 2009. CUMZ 12013 (3 shells) from Khao Chuak Charoentham Temple, Ban Rai District, Uthai Thani Province, 27 Aug. 2016. CUMZ 12014 (1 shell) from Khao Chuak Charoentham Temple, Ban Rai District, Uthai Thani Province, 5 Dec. 2020. CUMZ 12015 (14 shells; Figs 21F, 23A) from Khao Wong Phrommachan Temple, Ban Rai District, Uthai Thani Province, 8 July 2009. CUMZ 12016 (5 shells) from Tham Prathat Mueang Thep Temple, Ban Rai District, Uthai Thani Province, 5 Dec. 2020. CUMZ 12017 (13 shells) from Krasae Cave, Sai Yok District, Kanchanaburi Province, 10 Dec. 2006. CUMZ 12173 (14 shells) from Tham Charoentham Temple, Mueang Kanchanaburi District, Kanchanaburi Province, 19 Aug. 2020. CUMZ 12192 (1 shell) from Ban Tapoepu-Wakruko, Umphang District, Tak Province, 30 June 2015. CUMZ 12018 (68 shells and 10 specimens in ethanol; Figs 21M, 23B) from Tham Khao Thalu Temple, Chom Bueang District, Ratchaburi Province, 9 Dec. 2006. CUMZ 12019 (21 shells) from Tham Khao Thalu Temple, Chom Bueang District, Ratchaburi Province, 9 Dec. 2009. CUMZ 12020 (4 shells and 6 specimens in ethanol; Fig. 25A) from Buri Ratchawanaram Temple, Pak Tho District, Ratchaburi Province, 8 May 2017. CUMZ 12021 (20 shells and 1 specimen in ethanol) from Buri Ratchawanaram Temple, Pak Tho District, Ratchaburi Province, 18 Aug. 2020. CUMZ 12022 (5 specimens in ethanol; Fig. 25B) from Golden Dragon Cave, Pak Tho District, Ratchaburi Province, 18 Aug. 2019. CUMZ 12023 (17 shells; Figs 21C, 23C) from Tham Khiriwong Temple, Bang Saphan District, Prachub Kirikhan Province, 21 Apr. 2007. CUMZ 12024 (147 shells) from Tham Khiriwong Temple, Bang Saphan District, Prachub Kirikhan Province, 29 July 2019. CUMZ 12169 (10 shells) from Tham Thep Nimit Temple, Pak Chong District, Nakhon Ratchasima Province, 24 Aug. 2020. CUMZ 12025 (28 shells) from Tham Khao Cha Ang On Temple, Bo Thong District, Chonburi Province, 13 Mar. 2006. CUMZ 12026 (28 shells and 23 specimens in ethanol; Figs 21E, 23D) from Tham Khao Cha Ang On Temple, Bo Thong District, Chonburi Province, 17 Aug. 2006. CUMZ 12028 (34 shells) from Bo Thong District, Chonburi Province, 9 May 2008. CUMZ 12027 (2 specimens in ethanol) from Phromawat Temple, Si Racha District, Chonburi Province, 19 Sept. 2020. CUMZ 12174 (1 shell) from Tham Khao Loi Temple, Khao Chamao District, Rayong Province, 23 Oct. 2010. CUMZ 12029 (85 shells and 10 specimens in ethanol; Fig. 8G, H) from Khao Tham Raet Temple, Tha Takiap District, Chachoengsao Province, 21 May 2012. CUMZ 12030 (3 shells) from Khao Tham Raet Temple, Tha Takiap District, Chachoengsao Province, 1 Mar. 2018. CUMZ 12031 (43 shells; Figs 21L, 23E) from Tham Khao Chakan Temple, Khao Chakan District, Sa Kaeo Province, 7 Apr. 2000. CUMZ 12032 (7 specimens in ethanol) from Tham Khao Chakan Temple, Khao Chakan District, Sa Kaeo Province, 25 Feb. 2018. CUMZ 12033 (2 shells) from Tham Khao Maka Temple, Mueang Sa Kaeo District, Sa Kaeo Province, 2 Nov. 2008. CUMZ 12034 (2 shells) from Khao Pha Pheung Temple, Klong Had District, Sra Keo Province, 21 May 2018. CUMZ 12035 (1 specimen in ethanol) from Na Mueang Waterfall, Ko Samui District, Surat Thani Province, 4 Mar. 2007. CUMZ 12036 (10 shells) from Wua Ta Lap Island, Ko Samui District, Surat Thani Province, 5 Mar. 2007. CUMZ 12037 (1 shell and 2 specimens in ethanol; Figs 21K, 23F, 25C) from Wua Ta Lap Island, Ko Samui District, Surat Thani Province, 6 June 2009. CUMZ 12038 (4 shells; Figs 21D, 24A) from Tham Suea Temple, Mueang Krabi District, Krabi Province, 6 Oct. 2006. CUMZ 12039 (4 shells) from Khao Noi Phothiyan Temple, Mueang Satul District, Satul Province, 31 Aug. 2015. CUMZ 12040 (1 shell) from Khao Rup Chang, Mueang Songkhla District, Songkhla Province, 23 Jan. 2007.

Diagnosis. Shell ovate; last whorl ca. three quarters of shell height. Apertural lip slightly thickened, not expanded. Both parietal and columellar teeth fin-shaped and slightly thickened; parietal tooth covering posterior canal; columellar tooth next to slit-like anterior canal.

Differential diagnosis. *Pupina artata* is most similar to *P. pallens* and *P. limitanea* in shell shape, but different from *P. pallens* in that the basal position of the apertural lip is not widened, and different from *P. limitanea* by a longer last whorl, and parietal and columellar teeth and apertural lip less thickened.

Distribution. Peninsular Malaysia, Myanmar (Laidlaw 1928; Solem 1966), and throughout Thailand except in the northeastern region.

Remarks. The type specimen of *P. artata blanfordiana* could not be located, so the validity of this subspecies is still unknown. The specimen identified as *P. peguensis* and figured in Godwin-Austen (1897: pl. 69, fig. 3, 3a–d) from Kama on the right bank of the Irrawaddy River, Pegu is different from the holotype of *P. peguensis* (see Tripathy and Sajan 2019), but similar to the type specimen of *P. artata*. Thus, this specimen is herein identified as *P. artata*.

The specimen of *P. artata* figured in Maassen (2002: text-fig. 3) from Sumatra should constitute a different species as it is different from the syntype figured here in having a smaller, sharper parietal tooth revealing the posterior canal and an ear-lobe-shaped columellar tooth covering the anterior canal. Thus, those specimens should belong to the *P. arula* species group instead (see below).

All specimens from Thailand with a slightly thickened, fin-shaped parietal tooth covering the posterior canal are herein identified as *P. artata*. However, these specimens exhibit a variable shell size (smaller with shell height 5.4 mm, shell width 3.5 mm, to larger with shell height 8.4 mm; shell width 5.9 mm; Fig. 21A–M). The shell shape is also variable from ovate which is similar to the syntype (Fig. 21A), to more globose (Fig. 21F) or more elongate (Fig. 21L). In addition, these specimens exhibit a variation in length, outer curvature and thickness of the parietal tooth, and body colour. There is also a case of different shell colour morphs (brown and grey) within the same population (Fig. 8G, H). Therefore, DNA data is needed to reveal the extent of genetic differentiation or cryptic diversity within the *P. artata* morphotype.

Pupina pallens **Möllendorff, 1894**

Figs 21N, O, 24B, C

Pupina pallens Möllendorff, 1894: 155, pl. 16, figs 27, 28. Type locality: Samui Islands, Gulf of Siam [Samui Island, Surat Thani Province, Thailand]. Fischer and Dautzenberg 1904: 431. BEDO 2017: 92. Sutcharit et al. 2018: fig. 5–13i.

Pupina (*Tylotoechus*) *pallens*—Kobelt 1902: 318, 319. Laidlaw 1928: 34. Zilch 1957: 47, pl. 2, fig. 16. Hemmen and Hemmen 2001: 39.

Type material examined. ***Lectotype*** SMF 109951 (Figs 21N, 24B) and paralectotypes SMF 109952 (4 shells), SMF 109953 (2 shells) from Golf von Siam: Koh Samui.

Other material examined. CUMZ 12041 (1 shell) from Bang Phu Temple, Sam Roi Yot District, Prachuap Khiri Khan Province, 19 Oct. 2020. CUMZ 12042 (14 shells; Figs 21O, 24C) from Suan Wiwek Bureau of Monks, Sam Roi Yot District, Prachuap Khiri Khan Province, 21 Oct. 2020.

Diagnosis. Shell ovate; last whorl ca. three quarters of shell height. Apertural lip slightly thickened, not expanded; basal position widened. Both parietal and columellar teeth fin-shaped and slightly thickened; parietal tooth covering posterior canal; columellar tooth next to slit-like anterior canal.

Differential diagnosis. *Pupina pallens* can be distinguished from all other species in the *P. artata* species group from mainland Southeast Asia by the widened basal position of the apertural lip.

Distribution. The type locality (Laidlaw 1928) and Prachuap Khiri Khan Province, western Thailand.

Remarks. von Möllendorff (1894) stated that this species is different from *P. arula* in having "the more obtuse spire, the more distorted last whorl, and consequently the aperture placed more to the right and protracted at the base, the thinner outer peristome, the broader columella, the broad triangular parietal lamella, and the narrower lower incision". More sampling of this species, with both morphometric and molecular phylogenetic analyses, are needed to resolve the relationship between *P. pallens* and other species in the *P. artata* species group.

Pupina limitanea **Godwin-Austen, 1897**

Figs 21P–R, 24D–F

Pupina limitaneus [sic] Godwin-Austen, 1897: 40, pl. 69, fig. 4, 4a, b. Type locality: Eastern frontier of Burmah and Siam; Eastern Shan Plateau [Shan State, Myanmar].

Pupina (*Tylotoechus*) *limitanea*—Kobelt 1902: 316, 317. Gude 1921: 196. Hemmen and Hemmen 2001: 39.

Pupina brachysoma [non Ancey]—Inkhavilay et al. 2019: 29, fig. 15f, Nam Ork Roo, Ban Nathong village, Namo District, Oudomxay Province.

Type material examined. ***Syntypes*** NHMUK 1903.7.1.2967 (10 shells; Figs 21P, Q, 24D, E) from East of Burma & Siam.

Other material examined. CUMZ 12043 (1 specimen in ethanol) from Pha Tub Cave, Mueang Nan District, Nan Province, 11 Oct. 2009. CUMZ 12171 (1 shell) from Luang Sakoen Cave, Song Khwae District, Nan Province, 19 Jan. 2017. CUMZ 12044 (2 shells; Figs 21R, 24F) from Mae Lana junction, Pang Mapha District, Mae Hong Son Province, 18 Jan. 2015.

Diagnosis. Shell ovate; last whorl ca. 60% of shell height. Apertural lip highly thickened, not expanded. Both parietal and columellar teeth fin-shaped and very thickened; parietal tooth always covering posterior canal; columellar tooth either next to or covering slit-like anterior canal.

Differential diagnosis. *Pupina limitanea* is most similar to *P. artata* in shell shape, but differs in having parietal and columellar teeth and apertural lip thickened, and a shorter last whorl.

Distribution. Eastern Myanmar, Laos (Godwin-Austen 1897; Inkhavilay et al. 2019), and Nan Province, northern Thailand.

Remarks. The specimen of *P. brachysoma* from Oudomxay Province, Laos figured in Inkhavilay et al. (2019: fig. 15f) is different from the type materials of *P. brachysoma* (see below) in having a thick and large parietal tooth covering the posterior canal, whereas *P. brachysoma* has a sharp triangular parietal tooth which is not thickened, making the posterior canal visible. Therefore, the specimen from Oudomxay Province, Laos is herein identified as *P. limitanea* of the *P. artata* species group, whereas *P. brachysoma* belongs to the *P. aureola* species group.

As this species is highly similar to *P. artata*, more sampling of this species, with both morphometric and molecular phylogenetic analyses, are needed to resolve the relationship between these two species.

Pupina bensoni **Jirapatrasilp, sp. nov.**

https://zoobank.org/B493C554-4B2C-4910-809C-33297E1A6005
Figs 19A, 21W, X, 24G, 25D, E, 26A

Type material. ***Holotype*** CUMZ 12045/1 (Figs 21W, 24G), 5 June 2017, coll. C. Sutcharit, R. Srisonchai, A. Pholyotha. Measurement: shell height 8.5 mm, shell width 5.9 mm and 5½ whorls. ***Paratypes*** CUMZ 12045/2–10 (7 shells and 2 specimens in ethanol; Fig. 25D) and NHMUK 20210333 (2 shells), same data as holotype; CUMZ 12046, 5 Dec. 2020, coll. P. Jirapatrasilp, C. Sutcharit, A. Pholyotha (14 shells and 2 specimens in ethanol; Figs 21X, 26A), from the type locality.

Type locality. Khao Wong Cave, Ban Rai District, Uthai Thani Province, Thailand, 15°01'53.1"N, 99°27'21.0"E, 246 m asl.

Other material examined. CUMZ 12047 from Tham Namthip Bureau of Monks, Lan Sak District, Uthai Thani Province, 28 July 2016 (8 shells and 12 specimens in ethanol; Figs 19A, 25E). CUMZ 12048 from Tham Namthip Bureau of Monks, Lan Sak District, Uthai Thani Province, 5 Dec. 2020 (7 shells and 7 specimens in ethanol).

Diagnosis. Shell ovate; last whorl ca. two thirds of shell height. Apertural lip thickened, not expanded to slightly expanded; with a furrow between inner and outer peristomes; inner peristome thickened and cord-like. Parietal tooth thickened, long trapezoid shaped, reaching beyond the middle of last whorl, outer border nearly straight, always covering posterior canal; columellar tooth thickened, curvedly triangular shaped, located next to slit-like anterior canal.

Differential diagnosis. *Pupina bensoni* sp. nov. is most similar to *P. hungerfordiana* in having a long parietal tooth reaching beyond the middle of last whorl, but differs in the long, trapezoid shape of parietal tooth, with the outer border nearly straight, and a furrow between inner and outer peristomes, with the inner peristome thickened and cord-like.

Description. Shell height 7.0–8.6 mm; shell width 4.0–6.0 mm. Shell ovate, solid, semi-transparent, whitish to brown, devoid of prominent sculpture on glazed smooth surface. Apex obtuse. Growth lines on shell surface inconspicuous. Whorl

5½–6, last whorl large ca. two-thirds of shell height. Spire angle ca. 90°; somewhat extended. Sutures slightly impressed, but shallow. Aperture circular; lip thickened with paler colour (ca. 0.2–0.3 mm wide and 0.5–0.6 mm thick), not expanded to slightly expanded. Apertural lip with a furrow between inner and outer peristomes, with inner peristome thickened and cord-like. Parietal callus sharply defined and thickened with paler colour. Peristome interrupted by two canals; posterior canal ca. 1.5 mm long and 0.3 mm at its widest, continuing slightly obliquely forming narrow groove bordered by parietal tooth and extended part of apertural lip; anterior canal curved and slit-liked continuing horizontally ca. 1.7 mm. Parietal tooth thickened, long trapezoid shaped (ca. 2.0 mm high, 0.7 mm wide and 0.3 mm thick), outer border somewhat straight, located at angular corner of aperture, extending beyond apertural lip and reaching beyond the middle of last whorl, always covering posterior canal. Columellar tooth somewhat thickened, curvedly triangular shaped (ca. 0.9 mm high, 2.2 mm long and 0.3 mm thick), located next to anterior canal. Umbilicus closed. Operculum round, yellowish, transparent corneous with smooth edge.

Etymology. The specific epithet is dedicated to W.H. Benson, an Irish malacologist, who made large collections of molluscs and described numerous species from India and Myanmar, especially the two oldest *Pupina* species from this region.

Distribution. This new species is found from Uthai Thani Province, central Thailand.

Species of group I (*P. artata* species group) from other parts of mainland Southeast Asia not recorded for Thailand

Pupina hungerfordiana Nevill, 1878

Figs 21U, V, 26B

Pupina hungerfordiana Nevill, 1878: 300, 301. Type locality: Hsaddan Koo, Salween Valley [Hasaddan Koo, the cave on the limestone hill south of Hpa-An in Ein Du Village, Hpa-An Township, Hpa-An District, Kayin State, Myanmar]. Nevill 1881: 148, pl. 6, fig. 6.

Pupina hungerfordi [sic]—Godwin-Austen 1897: 41, 42, pl. 69, fig. 7, 7a.

Pupina (*Tylotoechus*) *hungerfordiana*—Kobelt 1902: 314. Gude 1921: 194, 195.

Type material examined. ***Holotype*** of *Pupina hungerfordiana* figured in Nevill (1881: pl. 6, fig. 6).

Other material examined. NHMUK 91.3.14.686–7 (2 shells; Figs 21U, V, 26B) from Hsaddan Koo.

Diagnosis. Shell ovate; last whorl ca. two thirds of shell height. Apertural lip thickened. Parietal tooth thickened, long fin-shaped, reaching beyond the middle of last whorl, outer border curved, covering posterior canal; columellar tooth somewhat thickened, curvedly triangular shaped, located next to slit-like anterior canal.

Figure 17. Specimen of *Pupina destructa*, the type species of *Tylotoechus*, USNM 472296. Photo: USNM.

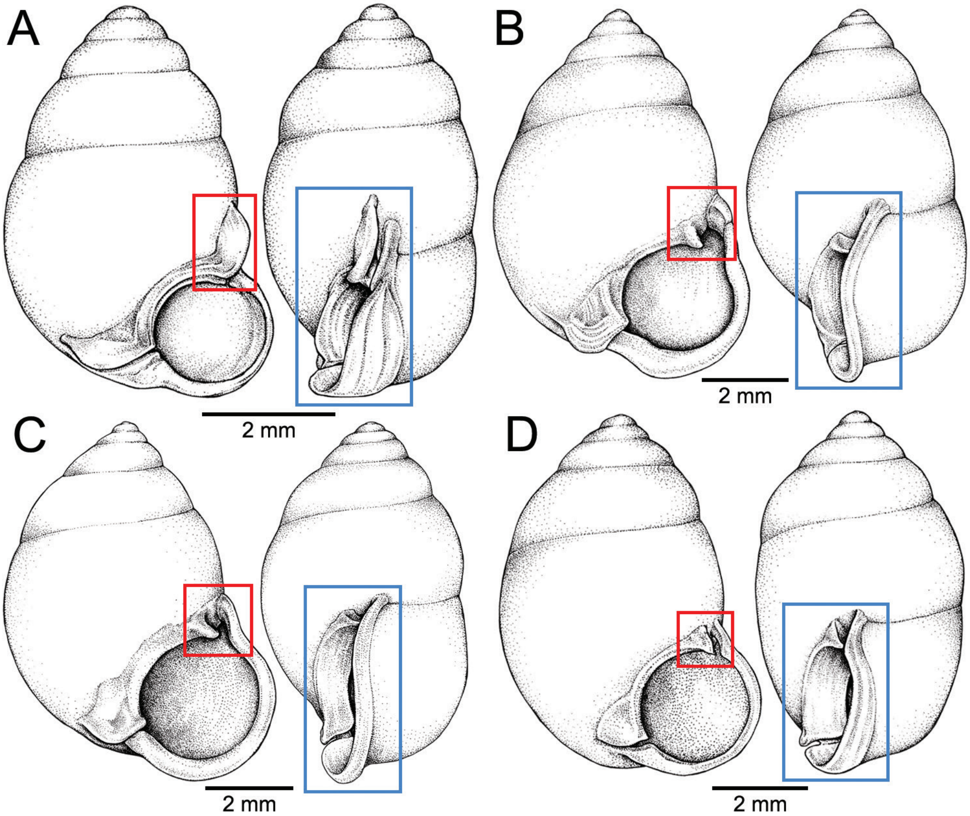

Figure 18. External shell morphology of three mainland Southeast Asian *Pupina* species groups **A** *Pupina artata* from the *Pupina artata* species group, CUMZ 12003 from Ban Ping Khong, Chiang Mai **B** *Pupina peguensis* from the *Pupina arula* species group, CUMZ 12094 from Khao Tham Phra Temple, Chiang Rai **C** *Pupina siamensis* from the *Pupina arula* species group, CUMZ 12052 from Sri Thong Cave, Sra Keo, and **D** *Pupina tchehelensis* from the *Pupina aureola* species group, CUMZ 12136 from limestone mountain, Phang Nga. Red frames focus on the parietal tooth and posterior canal; blue frames focus on the curvature of the apertural lip when observed from lateral view.

Differential diagnosis. *Pupina hungerfordiana* is most similar to *P. artata* and *P. bensoni* sp. nov. in shell shape, but different from *P. artata* by the long, thickened, fin-shaped parietal tooth, reaching beyond the middle of last whorl, and different from *P. bensoni* sp. nov. by the lack of furrow between the inner and outer peristomes.

Distribution. Known only from the type locality (Gude 1921).

Remarks. As *P. hungerfordiana* was described based on a single specimen as explicitly stated in the original description, that specimen is the holotype fixed by monotypy (ICZN 1999: Art. 73.1.2).

Pupina billeti **Fischer, 1898**

Figs 21S, 26C

Pupina billeti Fischer, 1898: 333, 334, pl. 18, figs 38–41. Type locality: Rochers calcaires Déo-Ma-Phuc [limestone areas around Ma Phuc Pass, Tra Linh District, Cao Bang Province, Vietnam]. Fischer and Dautzenberg 1904: 431, Bac-Kan, Tonkin [Bac Kan Province, Vietnam].

Pupina (*Tylotoechus*) *billeti*—Kobelt 1902: 309.

Type material examined. ***Holotype*** MNHN-IM-2000-35841 (Figs 21S, 26C) from Deo-Ma-Phuc.

Diagnosis. Shell ovate; last whorl ca. 70% of shell height. Apertural lip extremely thickened; with a furrow between inner and outer peristomes; inner peristome thickened and cord-like; parietal callus distinct. Both parietal and columellar teeth extremely thickened; parietal tooth covering posterior canal; columellar tooth next to slit-like anterior canal.

Differential diagnosis. *Pupina billeti* can be distinguished from all other species in the *P. artata* species group from mainland Southeast Asia by having the thickest parietal and columellar teeth and apertural lip, and a distinct parietal callus.

Distribution. Northern Vietnam (Fischer and Dautzenberg 1904).

Remarks. As *P. billeti* was described based on a single specimen as explicitly stated in the original description, that specimen is the holotype fixed by monotypy (ICZN 1999: Art. 73.1.2).

Pupina verneaui **Dautzenberg & Fischer, 1906**

Figs 21T, 26D

Pupina verneaui Dautzenberg & Fischer, 1906 [1905]: 440, 441, pl. 10, figs 13–15. Type locality: Ha-Giang [Ha Giang Province, Vietnam]. Fischer 1963: 34. Do et al. 2015: 126, fig. 6c, Son La Province, Vietnam.

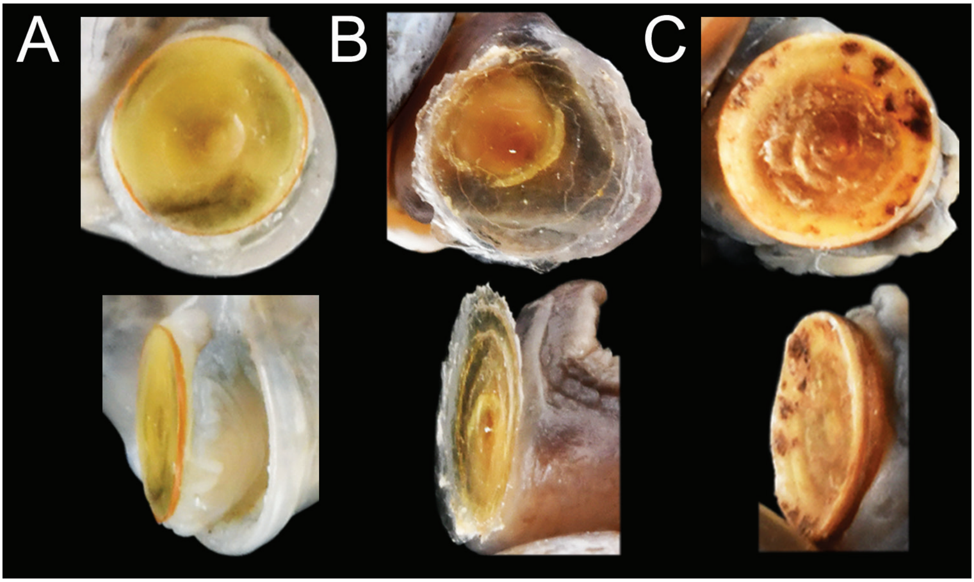

Figure 19. Opercula of three mainland Southeast Asian *Pupina* species groups **A** *Pupina bensoni* sp. nov. from the *Pupina artata* species group, specimen CUMZ 12047 **B** *Pupina siamensis* from the *Pupina arula* species group, specimen CUMZ 12067, and **C** *Pupina aureola* from the *Pupina aureola* species group, specimen CUMZ 12116. All not to scale.

Eupupina verneaui—Dautzenberg and Fischer 1908: 208, 209, Mo-Xat [west of Quang Uyen, Cao Bang Province, Vietnam]; Quang-Huyen [Quang Uyen, Cao Bang Province, Vietnam].

Type material examined. ***Syntypes*** MNHN-IM-2000-35843 (Figs 21T, 26D) from Ha-Giang, Tonkin.

Diagnosis. Shell ovate-fusiform; last whorl ca. 70% of shell height; suture very shallow. Apertural lip somewhat thickened, not expanded. Both parietal and columellar teeth fin-shaped and thickened; parietal tooth somewhat covering posterior canal; columellar tooth next to slit-like anterior canal.

Differential diagnosis. *Pupina verneaui* is most similar to *P. artata* in having fin-shaped and thickened teeth, but differs in having a more ovate-fusiform shell shape and a rather shallower suture.

Distribution. Northern Vietnam (Do et al. 2015).

Remarks. The specimen of *P. verneaui* figured in Inkhavilay et al. (2019: fig. 16a) from Ban Nong Kham village, Kasy District, Vientiane Province, Laos should constitute a different species as it is different from the syntype figured here in having a wider spire, a more bulging last whorl and a thinner and sharper parietal tooth.

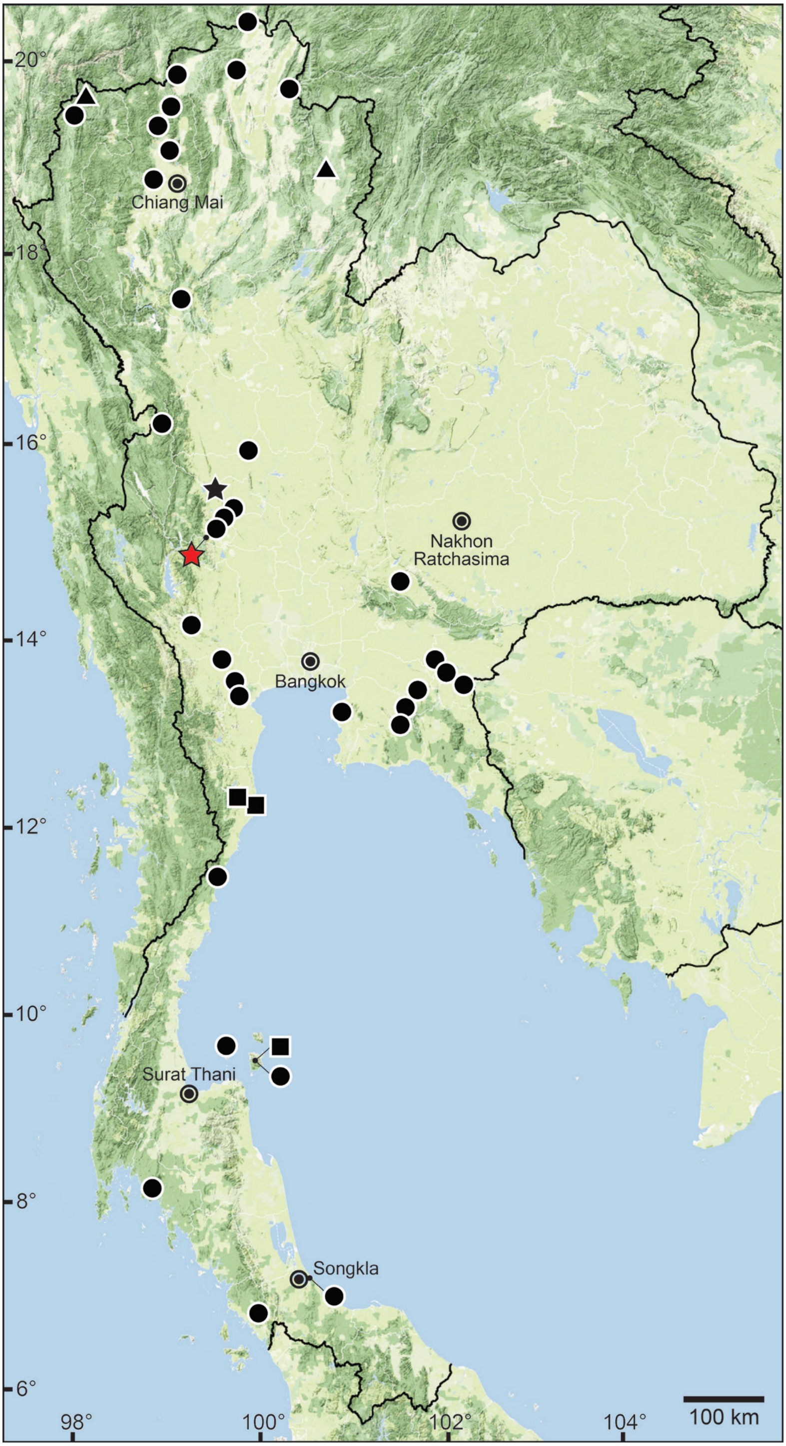

Figure 20. Distribution map of the *Pupina artata* species group: *Pupina artata* (circle), *Pupina limitanea* (triangle), *Pupina pallens* (square), and *Pupina bensoni* sp. nov. (star) with a red star indicating the type locality.

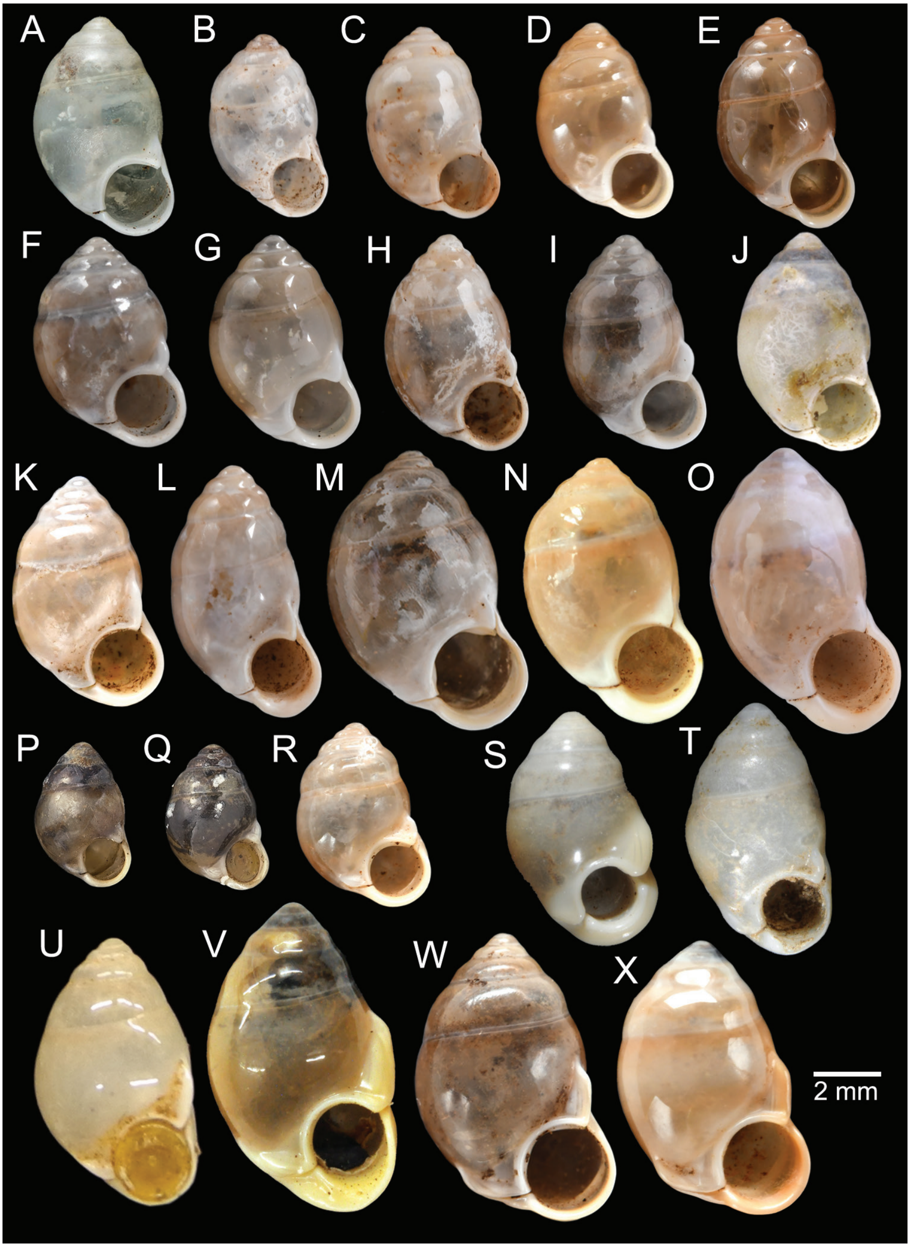

Figure 21. Shells of *Pupina artata* species group from mainland Southeast Asia **A–M** *Pupina artata* **A** syntype UMZC I.102960.A and specimens **B** CUMZ 12011 **C** CUMZ 12023 **D** CUMZ 12038 **E** CUMZ 12026 **F** CUMZ 12015 **G** CUMZ 12009 **H** CUMZ 12001 **I** CUMZ 12003 **J** NHMUK 1906.4.4.28 **K** CUMZ 12037 **L** CUMZ 12031, and **M** CUMZ 12018 **N, O** *Pupina pallens* **N** lectotype SMF 109951 and **O** specimen CUMZ 12042 **P–R** *Pupina limitanea* **P, Q** syntypes NHMUK 1903.7.1.2967 and **R** specimen CUMZ 12044 **S** *Pupina billeti*, holotype MNHN-IM-2000-35841 **T** *Pupina verneaui*, syntype MNHN-IM-2000-35843 **U,V** *Pupina hungerfordiana*, specimens NHMUK 91.3.14.686–7 **W, X** *Pupina bensoni* sp. nov. **W** holotype CUMZ 12045/1 and **X** paratype CUMZ 12046/1. Photo: H. Taylor, NHM (**A, P, Q**), P. Maestrati, MNHN (**S,T**).

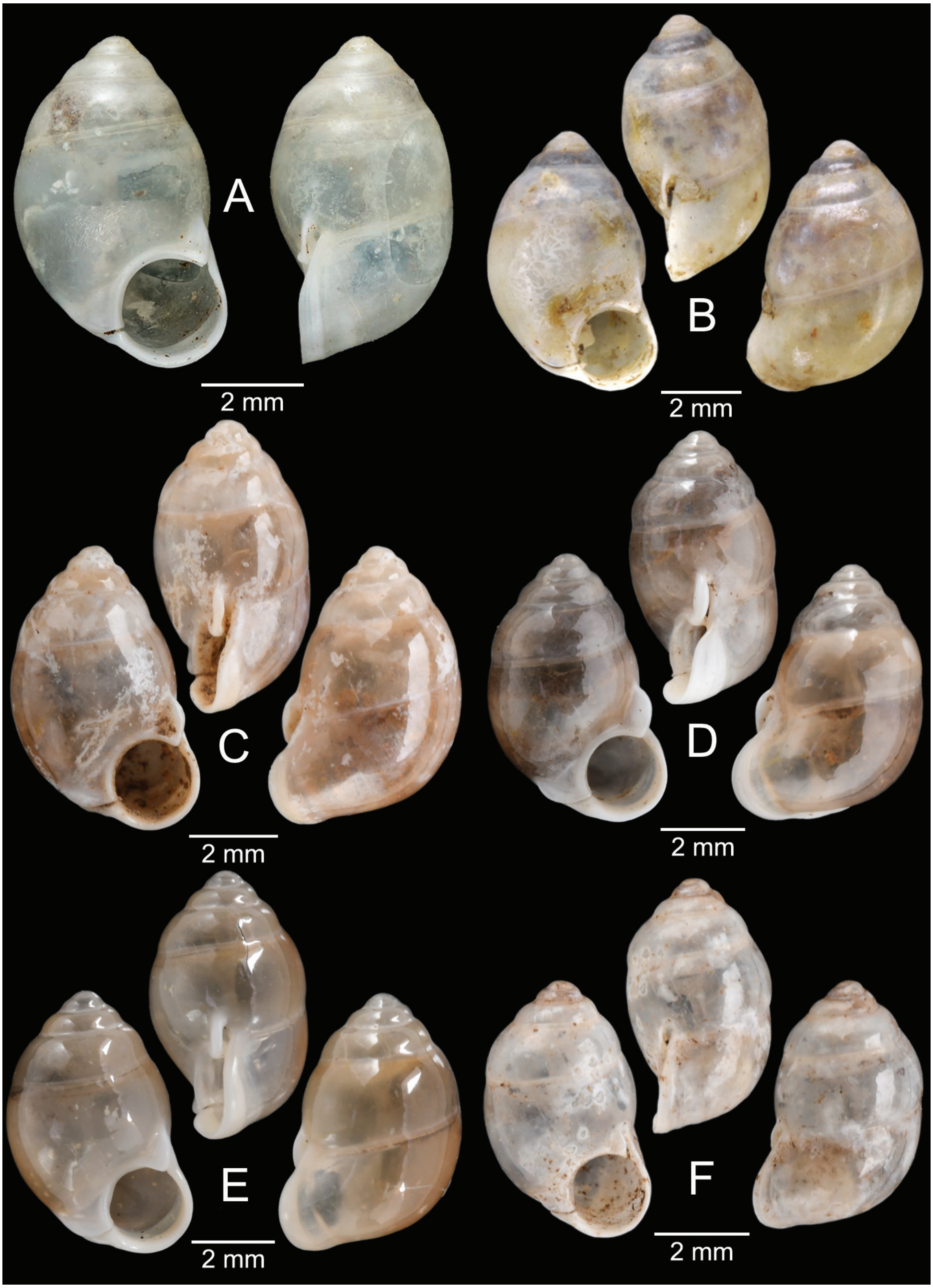

Figure 22. *Pupina artata* **A** syntype UMZC I.102960.A from Moulmein **B** specimen NHMUK 1906.4.4.28 from Moulmein **C** specimen CUMZ 12001 from Khao Tham Phra Temple, Chiang Rai **D** specimen CUMZ 12003 from Ban Ping Khong, Chiang Mai **E** specimen CUMZ 12009 from Phu Sang Waterfall, Phayao, and **F** specimen CUMZ 12011 from Thep Sathaporn Temple, Nakhon Sawan. Photo: H. Taylor, NHM (**A**).

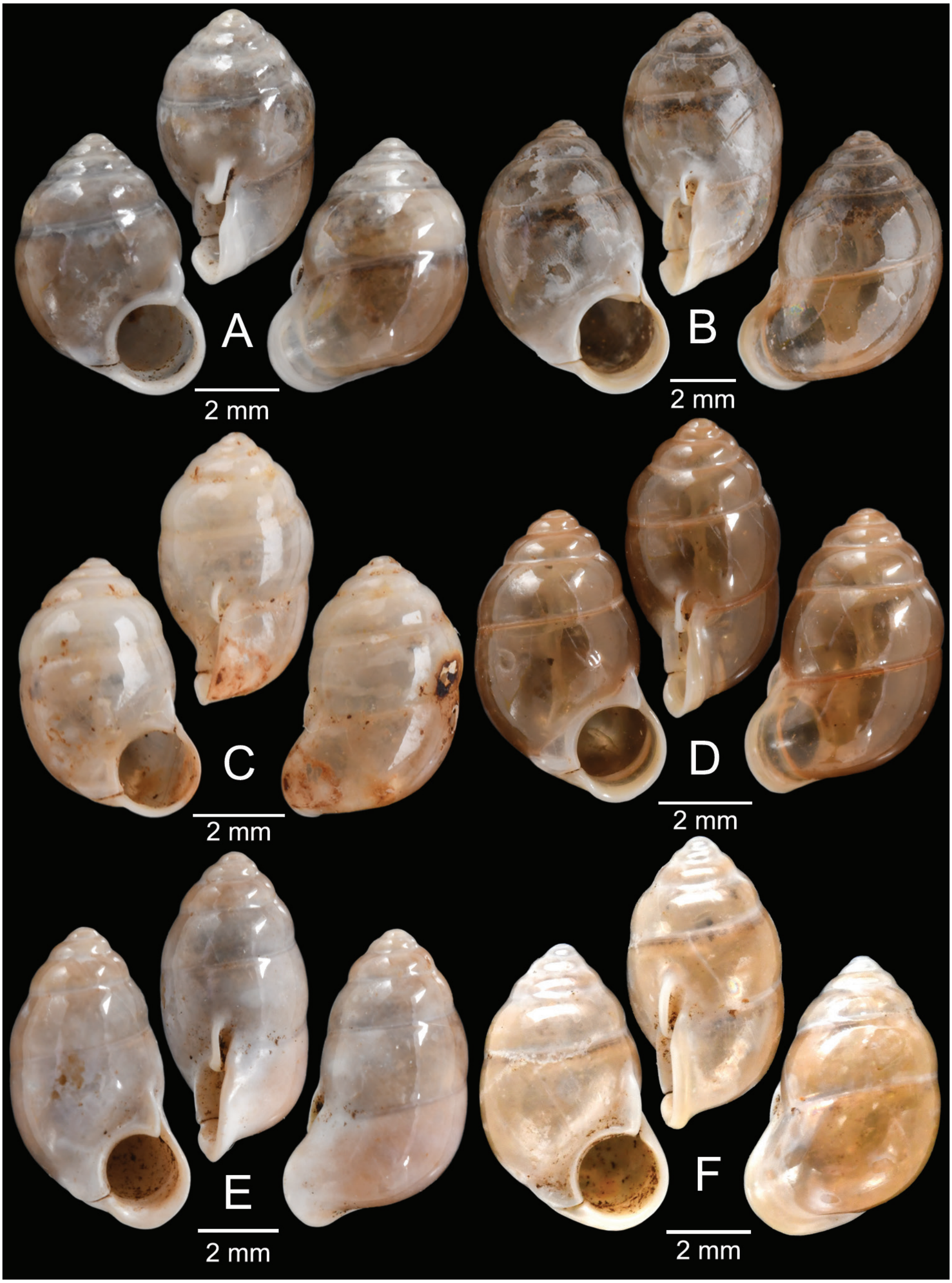

Figure 23. *Pupina artata*: specimens **A** CUMZ 12015 from Khao Wong Phrommachan Temple, Uthai Thani **B** CUMZ 12018 from Tham Khao Thalu Temple, Ratchaburi **C** CUMZ 12023 from Tham Khiriwong Temple, Prachub Kirikhan **D** CUMZ 12026 from Tham Khao Cha Ang On Temple, Chonburi **E** CUMZ 12031 from Tham Khao Chakan Temple, Sa Kaeo, and **F** CUMZ 12037 from Wua Ta Lap Island, Surat Thani.

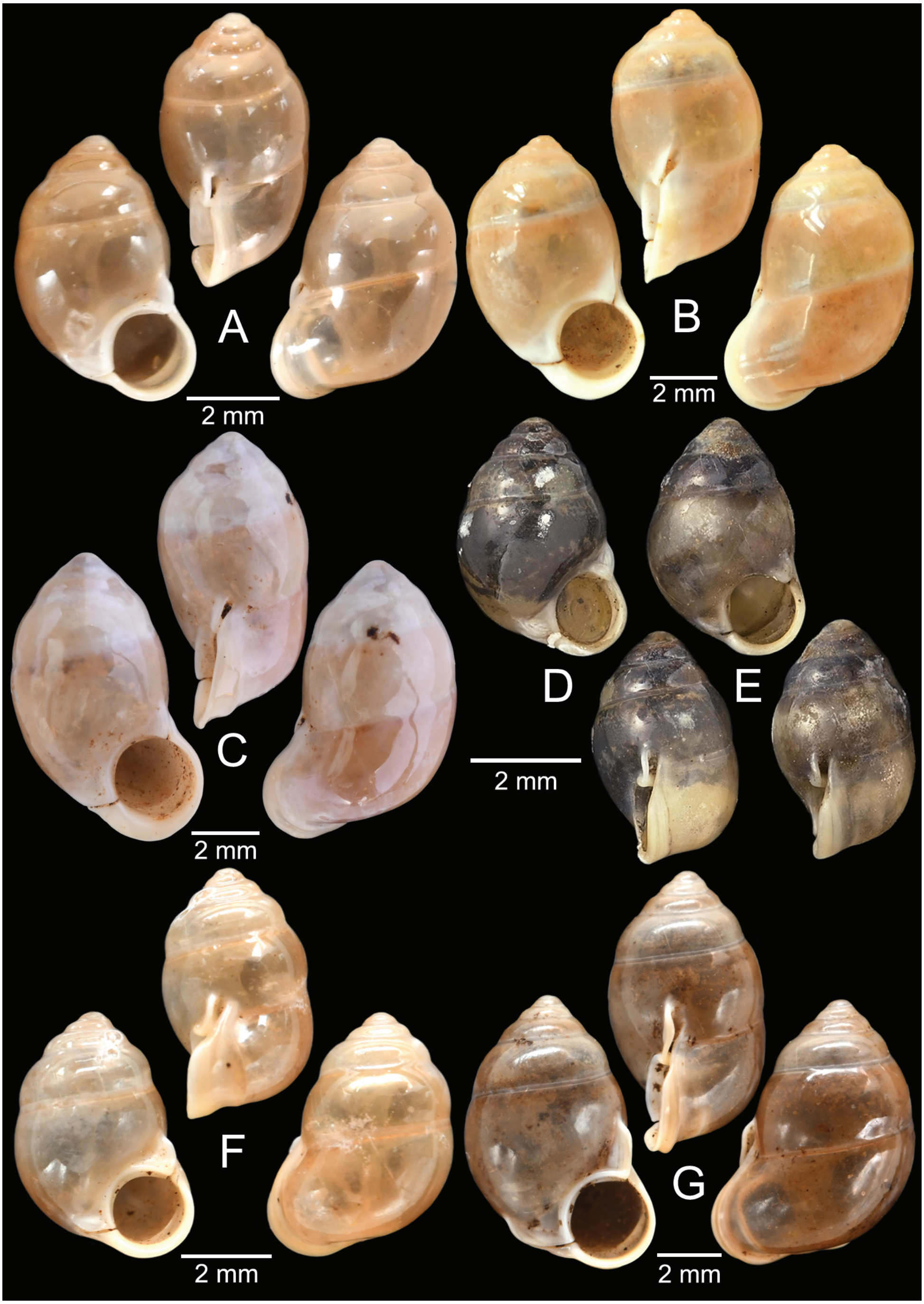

Figure 24. A *Pupina artata*, specimen CUMZ 12038 from Tham Suea Temple, Krabi **B, C** *Pupina pallens* **B** lectotype SMF 109951 and **C** specimen CUMZ 12042 from Suan Wiwek Bureau of Monks, Prachuap Khiri Khan **D–F** *Pupina limitanea* **D, E** syntypes NHMUK 1903.7.1.2967 from East of Burma & Siam and **F** specimen CUMZ 12044 from Mae Lana junction, Mae Hong Son **G** *Pupina bensoni* sp. nov., holotype CUMZ 12045/1. Photo: H. Taylor, NHM (**D, E**).

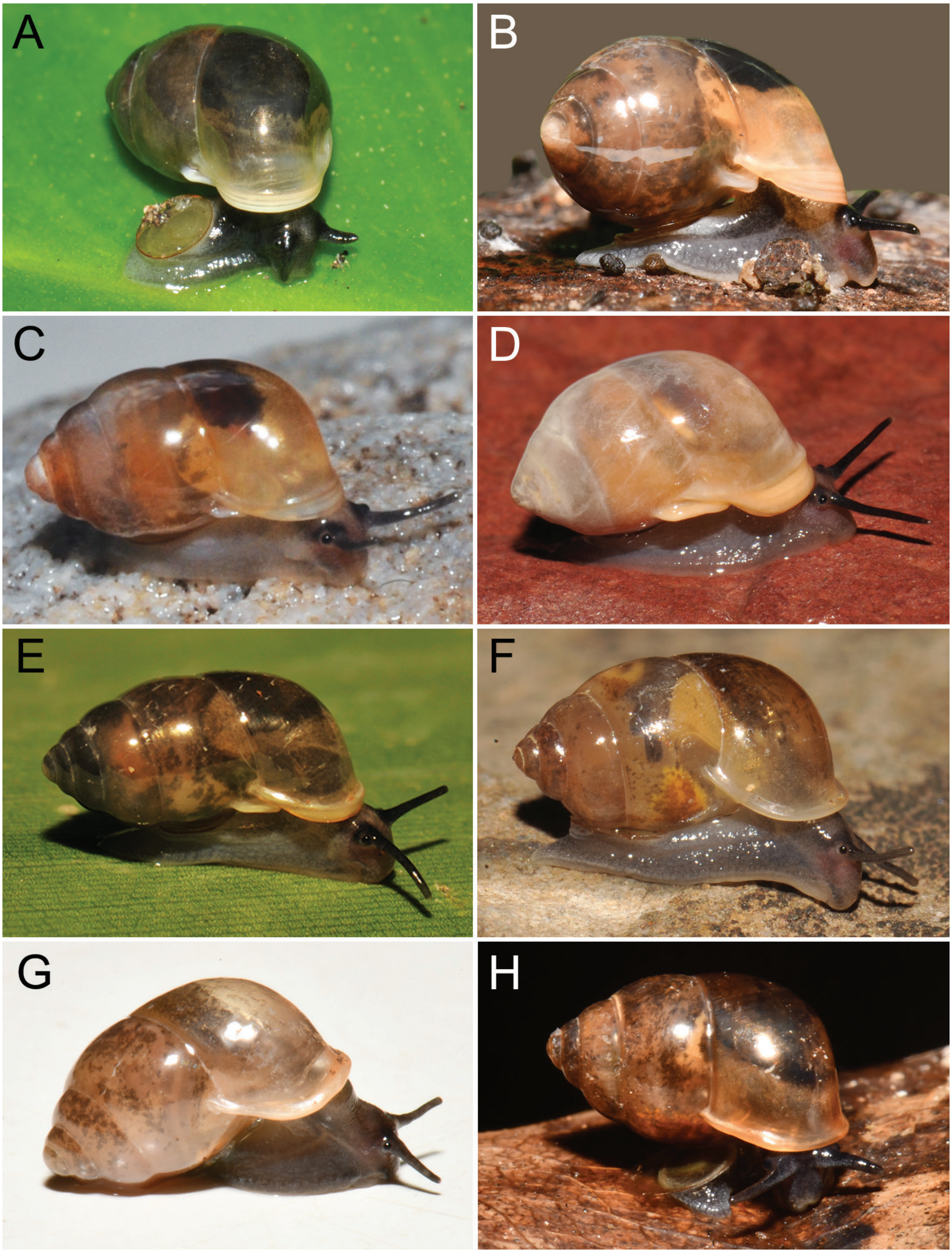

Figure 25. Live specimens of **A–C** *Pupina artata*: specimens **A** CUMZ 12020 from Buri Ratchawanaram Temple, Ratchaburi **B** CUMZ 12022 from Golden Dragon Cave, Ratchaburi, and **C** CUMZ 12037 from Wua Ta Lap Island, Surat Thani **D, E** *Pupina bensoni* sp. nov. **D** paratype CUMZ 12045/2 from Khao Wong Cave, Uthai Thani and **E** specimen CUMZ 12047 from Tham Namthip Bureau of Monks, Uthai Thani **F, G** *Pupina peguensis*: specimens **F** CUMZ 12050 from Chai Thong Wararam Temple, Nakhon Sawan and **G** CUMZ 12051 from Tham Saeng Wiset Bureau of Monks, Nakhon Sawan **H** *Pupina siamensis*, specimen CUMZ 12069 from Khao Chi Chan Buddha Image, Chonburi. All not to scale.

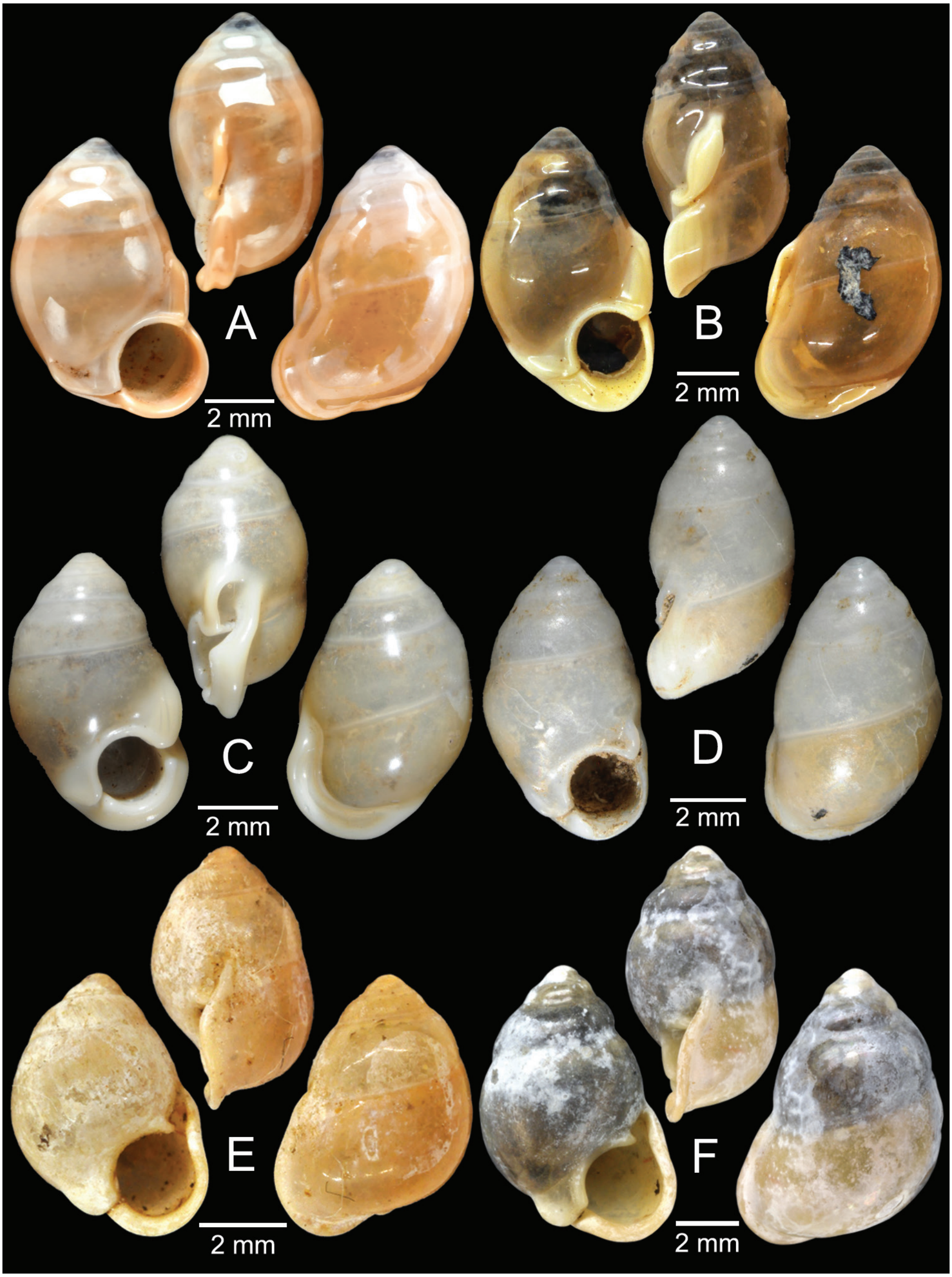

Figure 26. A *Pupina bensoni* sp. nov., paratype CUMZ 12046/1 from Khao Wong Cave, Uthai Thani **B** *Pupina hungerfordiana*, specimen NHMUK 91.3.14.686–7 from Hsaddan Koo **C** *Pupina billeti*, holotype MNHN-IM-2000-35841 **D** *Pupina verneaui*, syntype MNHN-IM-2000-35843 from Ha-Giang, Tonkin **E, F** *Pupina peguensis* **E** syntype of *Pupina blanfordi* NHMUK 1888.12.4.100 from Pegu and **F** specimen NHMUK ex. Cuming coll. from Lao Mountains, Camboja. Photo: P. Maestrati, MNHN (**C, D**).

Group II: *Pupina arula* species group

Figs 10C, 18B, C, 19B

This species group is characterised by an indistinct to thick parietal tooth, extending from a parietal callus. When observed from lateral view, the parietal tooth continues horizontally. A columellar tooth is fin-shaped, or the outer margin is curved downward appearing as an earlobe shape covering an anterior canal. The anterior canal is either not visible or appears slit-like when observed from apertural view, where the anterior canal is as long as the apertural lip width. A posterior canal is always wide and curved outward, bulging at the outer margin, sometimes slit-like. An outer apertural lip is slightly curved (Fig. 18C) to sharply bent when observed from lateral view (Fig. 18B). An operculum is round, thin, multispiral, yellowish, transparent corneous, and sometimes with uneven edge.

This species group from mainland Southeast Asia contains 10 species, including five nominal species and two new species (*P. bilabiata* sp. nov. and *P. godwinasuteni* sp. nov.) from Thailand. The distribution of the *Pupina arula* species group in Thailand is provided in Fig. 27. A synoptic view of all species within the *P. arula* species group from mainland Southeast Asia is given in Figs 28, 29 to provide the comparative size.

Pupina peguensis Benson, 1860

Figs 18B, 25F, G, 26E, F, 28A–G, 30A–D

Pupina peguensis Benson, 1860: 192, 193. Type locality: Pegu [Bago Region, Myanmar]. Nevill 1878: 300, Shuay-Gheen, Burma [Shwegyin, Bago Region, Myanmar]; Zwagabin [Zwekabin Taung mountain, Hpa-An District, Kayin State, Myanmar]. Tripathy and Sajan 2019: 508, fig. 1.

Pupina blanfordi Theobald, 1864: 247, 248. Type locality: Pegu. Hanley and Theobald 1870: 4, pl. 7, fig. 6. Reeve 1878: Pupinidae, pl. 1, sp. 6. Godwin-Austen 1897: 41, pl. 69, fig. 2, 2a, b. Syn. nov.

Pupina (*Tylotoechus*) *blanfordi*—Kobelt 1902: 309, 310. Gude 1921: 194.

Pupina (*Tylotoechus*) *peguensis*—Kobelt 1902: 319. Gude 1921: 197.

Pupina mouhoti [non Pfeiffer]—BEDO 2017: 91. Sutcharit et al. 2018: figs 4–2–7, 5–13h. Inkhavilay et al. 2019: 46, fig. 15g, Ngoy Town, Ngoy District, Luang Phrabang Province, Laos.

Type material examined. ***Holotype*** of *Pupina peguensis* NZSI M.32940/9 from 'Shuay-Gheen', Burma figured in Tripathy and Sajan (2019: fig. 1). ***Syntype*** of *Pupina blanfordi* NHMUK 1888.12.4.100 (1 shell; Figs 26E, 28A) from Pegu.

Other material examined. Specimen NHMUK ex. Cuming coll. (1 shell; labelled as *Pupina mouhoti*, Pfeiffer; Figs 26F, 28E) from Lao Mountains, Camboja. CUMZ 12050 (78 shells and 73 specimens in ethanol; Figs 25F, 28C, 30A) from Chai Thong Wararam Temple, Tak Fa District, Nakhon Sawan Province, 9 June 2017. CUMZ 12051 (170 shells and 125 specimens in ethanol; Fig. 25G) from

Tham Saeng Wiset Bureau of Monks, Tak Fa District, Nakhon Sawan Province, 6 Dec. 2020. CUMZ 12105 (2 shells; Figs 28B, 30B) from Thep Phithak Punnaram Temple, Pak Chong District, Nakhon Ratchasima Province, 18 Sept. 2017. CUMZ 12107 (1 specimen in ethanol) from Tham Wua Daeng Temple, Phakdi Chumphon District, Chaiyaphum Province, 3 Sept. 2020. CUMZ 12108 (8 shells; Figs 28G, 30C) from Tham Thep Bandan Temple, Wichian Buri District, Phetchabun Province, 21 Oct. 2007. CUMZ 12109 (1 shell) from Tham Pha Ta Phon, Noen Maprang District, Phitsanulok Province, 3 Aug. 2020. CUMZ 12110 (1 shell) from Tham Wang Na Bureau of Monks, Noen Maprang District, Phitsanulok Province, 8 June 2017. CUMZ 12172 (15 shells) from Tham Pet Tham Thong Forest Park, Takhli District, Nakhon Sawan Province, 1 Dec. 2009. CUMZ 12094 (12 shells; Figs 18B, 28F, 30D) from Khao Tham Phra Temple, Mueang Chiang Rai District, Chiang Rai Province, 9 Jan. 2008. CUMZ 12095 (1 shell) from Tham Phajarui Temple, Pa Daet District, Chiang Rai Province, 25 Oct. 2008. CUMZ 12096 (9 shells) from Luang Cave, Mae Sai District, Chiang Rai Province, 23 Oct. 2015. CUMZ 12097 (3 shells) from Tham Phra Bamphen Bun Temple, Phan District, Chiang Rai Province, 29 Nov. 2009. CUMZ 12098 (1 shell) from Mae Lana checkpoint, Pang Mapha District, Mae Hong Son Province, 6 Oct. 2017. CUMZ 12099 (5 shells) from Mae Lana junction, Pang Mapha District, Mae Hong Son Province, 18 Jan. 2015. CUMZ 12100 (6 shells) from Pha Daeng Cave, Mueang Mae Hong Son District, Mae Hong Son Province, 18 Jan. 2015. CUMZ 12101 (1 specimen in ethanol) from Pha Daeng Cave, Mueang Mae Hong Son District, Mae Hong Son Province, 5 Oct. 2017. CUMZ 12102 (6 shells) from Pha Daeng Cave, Mueang Mae Hong Son District, Mae Hong Son Province, 3 Dec. 2020. CUMZ 12187 (2 shells) from Doi Ang Khang, Fang District, Chiang Mai Province, 24 Oct. 2015. CUMZ 12103 (3 specimens in ethanol; Fig. 28D) from Pha Tub Cave, Mueang Nan District, Nan Province, 11 Oct. 2009. CUMZ 12104 (24 shells) from Tham Pha Nang Khoi Temple, Rong Kwang District, Phrae Province, Thailand, 9 Oct. 2007.

Diagnosis. Shell globose to ovate-fusiform; last whorl ca. 75–80% of shell height. Apertural lip thickened but not expanded; apertural lip curved when observed from lateral view. Columellar tooth fin-shaped or curved downward like an earlobe.

Differential diagnosis. *Pupina peguensis* is similar to *P. arula* in shell shape and a curved apertural lip when observed from lateral view, but differs in having a glossy shell surface. This species is also similar to *P. exclamationis* in having a glossy surface and a curved apertural lip when observed from lateral view, but differs in having a more ovate shell shape and a more distinct parietal callus.

Distribution. Myanmar (Benson 1860; Theobald 1864), Luang Phrabang Province, Laos (Inkhavilay et al. 2019), northern, northeastern, and central Thailand.

Remarks. Given that the holotype of *P. peguensis* and the syntype of *P. blanfordi* are highly similar in shell shape and size, and their type localities belong to the same area, *P. blanfordi* is regarded herein as a junior subjective synonym of *P. peguensis*. This species was previously identified as *P. mouhoti* (BEDO 2017; Sutcharit et al. 2018).

However, compared to the type specimens of *P. mouhoti*, *P. peguensis* has a longer and wider posterior canal. In addition, the apertural lip when observed from lateral view of *P. peguensis* is curved and its columellar tooth is curved downward like an earlobe.

All specimens in the *Pupina arula* species group from Thailand with an ovate shell shape and a curved apertural lip when observed from lateral view are herein identified as *P. peguensis* (Fig. 28A–G). However, these specimens exhibit a variable shell size (smaller with shell height 6.1 mm, shell width 4.6 mm; Fig. 28A, to larger with shell height 9.6 mm; shell width 7.1 mm; Fig. 28G). The shell shape is also variable from globose as in the type material (see Tripathy and Sajan 2019: fig. 1), to more ovate and ovate-fusiform. As this species is also similar to *P. exclamationis*, more sampling, with both morphometric and molecular phylogenetic analyses, are needed to resolve the relationship between these two species and reveal the extent of genetic differentiation or cryptic diversity within the *P. peguensis* morphotype.

***Pupina crosseana* Morlet, 1883**

Figs 28H–J, 30E, F, 31A

Pupina crosseana Morlet, 1883: 108, 109, pl. 4, fig. 5. Type locality: Cambodge [Cambodia]. Morlet 1889: 152, Pnom-Rohan (Cambodge) [Phnum Roung, Kampong Thom Province, Cambodia]; Ajuthia (Siam) [Phra Nakhon Si Ayutthaya Province, Thailand]. Fischer 1891: 107. Morlet 1904: 371, pl. 20, fig. 14, 14a. Fischer and Dautzenberg 1904: 431. Fischer-Piette 1950: 153. Fischer 1973: 48. BEDO 2017: 89.

Pupina (*Tylotoechus*) *crosseana*—Kobelt 1902: 310, 311. Hemmen and Hemmen 2001: 39.

Type material examined. ***Lectotype*** MNHN-IM-2000-35834 (Figs 28H, 30E) from Cambodge. Paralectotype RBINS MT966/10591 (1 shell; Figs 28I, 30F) from Phnom-Rohan, Cambodge.

Other material examined. CUMZ 12049 (16 shells; Figs 28J, 31A) from Khao Jedee Temple, Ta Kli District, Nakhon Sawan Province, 25 Oct. 2005.

Diagnosis. Shell fusiform; last whorl ca. three quarters of shell height. Apertural lip somewhat thickened, but not expanded; apertural lip when observed from lateral view somewhat curved. Columellar tooth fin-shaped.

Differential diagnosis. *Pupina crosseana* is most similar to *P. perakensis* in having a fusiform shell shape, but differs in having the parietal callus and parietal tooth less thickened, a less curved apertural lip when observed from lateral view, and a fin-shaped columellar tooth.

Distribution. Cambodia and central Thailand (Fischer and Dautzenberg 1904).

Remarks. As the original description did not explicitly state that the description of this species was based on a single specimen (nor could this be inferred), the designation of a holotype by Fischer-Piette (1950) in fact constitutes a lectotype designation (ICZN 1999: Art. 74.6).

Pupina siamensis Möllendorff, 1902

Figs 18C, 19B, 25H, 28K, L, 31B, C, 32A

Pupina (*Tylotoechus*) *siamensis* Möllendorff, 1902b: 160. Type locality: "Bangkok" [see Remarks]. Zilch 1957: 47, pl. 2, fig. 15. Hemmen and Hemmen 2001: 39.

Pupina siamensis—Fischer and Dautzenberg 1904: 432, Muok-Lek, Siam [Muak Lek District, Saraburi Province, Thailand]. Boonngam et al. 2008: 258, Chonburi Province, Thailand. Chanyapate et al. 2008: 2116, with text fig., Sakaerat Biosphere Reserves, Nakhon Ratchasima Province. Chidchua and Dumrongrojwattana 2010: 164, fig. 2, Klaeng District, Rayong Province and Kaenghangmaew District, Chanthaburi Province. Dumrongrojwattana 2016: 17, 18, fig. 4–4, Kaeng Hin Poeng, Thap Lan National Park, Prachin Buri Province. BEDO 2017: 94. Sutcharit et al. 2018: fig. 5–13j.

Type material examined. ***Lectotype*** SMF 109948 (Figs 28K, 31B) from "Bangkok", Thailand.

Other material examined. CUMZ 12052 (15 shells; Figs 18C, 28L, 31C) from Sri Thong Cave, Klong Had District, Sra Keo Province, 25 Nov. 2006. CUMZ 12053 (3 shells) from Liam Cave, Klong Had District, Sra Keo Province, 25 Nov. 2006. CUMZ 12054 (7 shells and 9 specimens in ethanol) from Khao Pha Pheung Temple, Klong Had District, Sra Keo Province, 21 May 2012. CUMZ 12055 (12 shells and 1 specimen in ethanol) from Tham Khao Maka Temple, Mueang Sa Kaeo District, Sa Kaeo Province, 2 Nov. 2008. CUMZ 12056 (9 shells) from Tham Khao Chakan Temple, Khao Chakan District, Sa Kaeo Province, 7 Apr. 2000. CUMZ 12057 (9 specimens in ethanol) from Tham Khao Chakan Temple, Khao Chakan District, Sa Kaeo Province, 25 July 2018. CUMZ 12058 (3 specimens in ethanol) from Khao Chakan, Khao Chakan District, Sa Kaeo Province, 22 May 2012. CUMZ 12059 (1 shell) from Makok Waterfall, Khlung District, Chanthaburi Province, 10 Aug. 2014. CUMZ 12060 (2 specimens in ethanol) from Phlio Waterfall, Mueang Chanthaburi District, Chanthaburi Province, 20 Oct. 2010. CUMZ 12061 (3 specimens in ethanol) from Khao Sukim Temple, Tha Mai District, Chanthaburi Province, 9 Aug. 2011. CUMZ 12062 (2 specimens in ethanol) from Tham Krong Thip Bureau of Monks, Tha Mai District, Chanthaburi Province, 24 July 2018. CUMZ 12063 (2 specimens in ethanol) from Tham Khao Wong Temple, Kaeng Hang Maeo District, Chanthaburi Province, 4 Aug. 2016. CUMZ 12064 (8 shells) from Tham Khao Charoensuk Temple, Phanom Sarakham District, Chachoengsao Province, 2 Jan. 2008. CUMZ 12065 (18 shells and 3 specimens in ethanol) from Tham Khao Cha Ang On Temple, Bo Thong District, Chonburi Province, 17 Aug. 2006. CUMZ 12066 (5 shells) from Bo Thong District, Chonburi Province, 9 May 2008. CUMZ 12194 (2 specimens in ethanol) from Khao Ha Yot Temple, Bo Thong District, Chonburi Province, 6 Feb. 2022. CUMZ 12067 (2 shells and 20 specimens in ethanol; Fig. 19B) from Phromawat Temple, Si Racha District, Chonburi Province, 19 Sept. 2020. CUMZ 12068 (10 specimens in ethanol) from Pa Lilaiyawan Temple, Si Racha District, Chonburi Province, 19 Sept. 2020.

CUMZ 12069 (1 shell and 9 specimens in ethanol; Fig. 25H) from Khao Chi Chan Buddha Image, Sattahip District, Chonburi Province, 19 Sept. 2020. CUMZ 12070 (1 shell and 8 specimens in ethanol) from Ban Klong Wan Pen, Sattahip District, Chonburi Province, 19 Sept. 2020. CUMZ 12071 (10 specimens in ethanol; Fig. 32A) from Tham Khao Loi Temple, Khao Chamao District, Rayong Province, 5 Sept. 2008. CUMZ 12072 (1 specimen in ethanol) from Khao Hin Tang Bureau of Monks, Klaeng District, Rayong Province, 9 June 2019.

Diagnosis. Shell globose; last whorl ca. 80% of shell height. Apertural lip thickened, but not expanded; apertural lip when observed from lateral view almost straight. Columellar tooth fin-shaped.

Differential diagnosis. *Pupina siamensis* is most similar to *P. mouhoti* in having an almost straight apertural lip when observed from lateral view, but differs in having a more globose shell shape and a thicker, more distinct, parietal tooth.

Distribution. Eastern and northeastern Thailand (Boonngam et al. 2008; Chanyapate et al. 2008; Chidchua and Dumrongrojwattana 2010; Dumrongrojwattana 2016).

Remarks. As the original description did not explicitly state that the description of this species was based on a single specimen (nor could this be inferred), the designation of a holotype by Zilch (1957) in fact constitutes a lectotype designation (ICZN 1999: Art. 74.6).

The type locality of this species in Bangkok, the capital city of Thailand, as designated by von Möllendorff (1902b) is dubious. This species was described based on a collection made by the butterfly collector, H. Fruhstorfer, who made an expedition in Thailand (Lamas 2005). The type locality "Bangkok" is probably not the location where the type specimen was collected. The probable type locality would be "Muok-Lek" [Muak Lek District, Saraburi Province, Thailand] as indicated in Fischer and Dautzenberg (1904), and several butterfly specimens were also collected from this site by H. Fruhstorfer. This locality is in the same vicinity as recent records and our collecting localities of *P. siamensis*.

Pupina bilabiata **Jirapatrasilp, sp. nov.**

https://zoobank.org/E970A73C-E3EE-4DDA-B7C8-1B9D7960E3EF

Figs 28M–P, 31D–F, 32B–D, 33A

Type material examined. ***Holotype*** CUMZ 12073/1 (Figs 28M, 31D), 31 July 2019, coll. C. Sutcharit, A. Pholyotha. Measurement: shell height 7.4 mm, shell width 5.0 mm and 5½ whorls. ***Paratypes*** CUMZ 12073/2–13 (12 specimens in ethanol; Fig. 32B) and NHMUK 20210334 (2 shells), same data as holotype.

Type locality. Banpot Pisai Temple, Lang Suan District, Chumphon Province, Thailand, 9°56'05.0"N, 99°08'56.7"E, 20 m amsl.

Other material examined. CUMZ 12074 (11 shells) from Bat Cave, Phu Pha Man District, Khon Kaen Province, 20 Oct. 2007. CUMZ 12075 (9 shells and 7 specimens in ethanol) from Phraya Nakharaj Cave, Phu Pha Man District, Khon Kaen Province, 21 July 2020. CUMZ 12076 (4 shells) from Tham Pha Pu Temple, Mueang Loei District, Loei Province, 28 Oct. 2018. CUMZ 12077 (1 shell and 17 specimens in ethanol) from Tham Pha Pu Temple, Mueang Loei District, Loei Province, 1 Sept. 2020. CUMZ 12078 (3 shells) from Phu Pha Lom, Mueang Loei District, Loei Province, 1 Sept. 2020. CUMZ 12079 (2 shells; Figs 28N, 31E) from Tham Pha Ya Temple, Na Duang District, Loei Province, 28 Oct. 2018. CUMZ 12080 (2 specimens in ethanol) from Hin Pha Ngam Park, Nong Hin District, Loei Province, 2 Sept. 2020. CUMZ 12081 (13 shells; Figs 28O, 31F) from Pha Jor Cave, Na Wang District, Nong Bua Lam Phu Province, 15 Oct. 2007. CUMZ 12082 (15 shells and 9 specimens in ethanol; Fig. 32C) from Pha Jor Cave, Na Wang District, Nong Bua Lam Phu Province, 31 Aug. 2020. CUMZ 12083 (2 shells) from Tham Suwannakhuha Temple, Suwannakhuha District, Nong Bua Lam Phu Province, 31 Aug. 2020. CUMZ 12084 (8 shells) from Pa Pha Ya Temple, Suwannakhuha District, Nong Bua Lam Phu Province, 31 Aug. 2020. CUMZ 12085 (2 specimens in ethanol) from Phu Thong Thep Nimit Temple, Nong Saeng District, Udon Thani Province, 30 Aug. 2020. CUMZ 12086 (2 shells; Figs 28P, 33A) from Na San Temple, Ban Na San District, Surat Thani Province, 3 July 2017. CUMZ 12087 (2 specimens in ethanol; Fig. 32D) from Ban Yai, Phanom District, Surat Thani Province, 7 Aug. 2016. CUMZ 12088 (2 shells) from Tham Nam Lod Thepnimit Bureau of Monks, Sawi District, Chumphon Province, 30 July 2019. CUMZ 12089 (1 specimen in ethanol) from Tham Kanlayanamit Temple, Tham Phannara District, Nakhon Si Thammarat Province, 4 July 2017.

Diagnosis. Shell ovate-fusiform to fusiform; last whorl ca. three quarters of shell height. Apertural lip highly thickened, slightly expanded; with a furrow between inner and outer peristomes; inner peristome thickened, cord-like; apertural lip curved when observed from lateral view. Columellar tooth curved downward like an earlobe.

Differential diagnosis. *Pupina bilabiata* sp. nov. is similar to *P. peguensis* in shell shape, but differs in having a furrow between inner and outer peristomes, with an inner peristome thickened and cord-like. This furrow also appears in *P. godwinausteni* sp. nov. and *P. stoliczkai* sp. nov., but *P. godwinausteni* sp. nov. is larger and more globose, and the apertural lip when observed from lateral view is more angled than that of *P. bilabiata* sp. nov., whereas *P. stoliczkai* sp. nov. belongs to the *P. aureola* species group.

Description. Shell height 4.0–8.4 mm; shell width 4.4–5.7 mm. Shell ovate-fusiform to fusiform, solid, semi-transparent, whitish to pale brown, devoid of prominent sculpture on glazed smooth surface. Apex obtuse. Growth lines on shell surface inconspicuous. Whorls 5½–6, last whorl large (ca. three quarters of shell height) and bulging slightly. Spire angle ca. 80°, somewhat extended. Sutures slightly impressed, but shallow. Aperture circular; lip thickened to highly thickened (ca. 0.5–0.6 mm wide and 0.3–0.6 mm thick) with paler colour, slightly expanded; apertural lip curved when observed from lateral view. Apertural lip with a furrow between inner and outer peristomes, with inner peristome thickened and cord-like. Parietal callus sharply defined and thickened with paler colour. Peristome interrupted by two canals; posterior canal ca. 0.8–0.9 mm long, 0.5 mm at its widest, curved outward and bulging at outer margin; anterior canal slit-like, as long as apertural lip width. Parietal tooth indistinct to thick; columellar tooth curved downward like an earlobe (ca. 1.5 mm long, 0.9 mm wide and 0.5 mm thick), covering anterior canal. Umbilicus closed. Operculum round, yellowish, transparent corneous with uneven edge.

Etymology. The Latin specific epithet *bilabiata* means "with double lip" representing the separation of the inner and outer peristomes by a furrow.

Distribution. Northeastern and southern Thailand.

Remarks. This new species has a disjunct distribution and shows varying degrees of thickness of the inner peristome within specimens from the same collecting localities.

Pupina godwinausteni Jirapatrasilp, sp. nov.

https://zoobank.org/EF5C2A8A-36DE-4C06-896A-CE55F9520C60
Figs 10C, 28Q, R, 32E, F, 33B, C

Type material. ***Holotype*** CUMZ 12090/1 (Figs 10C, 28Q, 33B), 5 June 2017, coll. C. Sutcharit, R. Srisonchai, A. Pholyotha. Measurement: shell height 8.8 mm, shell width 6.8 mm and 5 whorls. ***Paratypes*** CUMZ 12090/2−26 (24 shells and 1 specimen in ethanol; Figs 28R, 32E, 33C) and NHMUK 20210335 (3 shells), same data as holotype; CUMZ 12091 (20 shells and 24 specimens in ethanol; Fig. 32F) from the type locality, 5 Dec. 2020, coll. P. Jirapatrasilp, C. Sutcharit, A. Pholyotha.

Type locality. Khao Wong Cave, Ban Rai District, Uthai Thani Province, Thailand, 15°01'52.6"N, 99°27'23.3"E, 246 m amsl.

Other material examined. CUMZ 12092 (2 shells) from Tham Namthip Bureau of Monks, Lan Sak District, Uthai Thani Province, 28 July 2016. CUMZ 12093 (1 specimen in ethanol) from Hup Pa Tat, Lan Sak District, Uthai Thani Province, 1 Oct. 2018.

Diagnosis. Shell globose; last whorl ca. 80% of shell height. Apertural lip very thickened and slightly expanded; with a furrow between inner and outer peristomes; inner peristome thickened, cord-like; apertural lip angled when observed from lateral view. Columellar tooth curved downward like an earlobe.

Differential diagnosis. The globose shell shape of *P. godwinausteni* sp. nov. is most similar to *P. siamensis*, but *P. godwinausteni* sp. nov. differs from *P. siamensis* in having a larger shell, a more prominent parietal callus, a thicker apertural lip with a furrow between inner and outer peristomes, with an inner peristome thickened and cord-like, a longer posterior canal, a wider and more curved columellar tooth, and a more angled apertural lip when observed from lateral view.

Description. Shell height 7.7–9.5 mm; shell width 5.5–7.0 mm. Shell globose, solid, semi-transparent, brown, devoid of prominent sculpture on glazed smooth surface. Apex obtuse. Growth lines on shell surface inconspicuous. Whorls 5, last whorl large (ca. 80% of shell height) and bulging. Spire angle ca. 90°, somewhat extended. Sutures slightly impressed, but shallow. Aperture circular; lip highly thickened (ca. 0.4–0.5 mm wide and 0.5–0.6 mm thick) with darker colour, slightly expanded; apertural lip when observed from lateral view angled. Apertural lip with a furrow between inner and outer peristomes, with inner peristome thickened and cord-like. Parietal callus thickened with darker colour. Peristome interrupted by two canals; posterior canal ca. 1.0–1.2 mm long, 0.6 mm at its widest, curved outward and bulging at the outer margin; anterior canal slit-like, as long as apertural lip width. Parietal tooth thick; columellar tooth curved downward like an earlobe (ca. 2.2 mm long, 1.2 mm wide and 0.5 mm thick), covering anterior canal. Umbilicus closed. Operculum round, yellowish, and transparent corneous with uneven edge.

Etymology. The specific epithet is dedicated to H.H. Godwin-Austen, a British malacologist, who prominently contributed to malacological studies in South and Southeast Asia.

Distribution. This new species is found in Uthai Thani Province, Thailand.

Species of group II (*P. arula* species group) with uncertain record from Thailand

Pupina arula **Benson, 1856**

Figs 29A, B, 33D

Pupina arula Benson, 1856: 230. Type locality: ad Yunglaw, in valle Tenasserim [Tanintharyi Region, Myanmar]. Theobald 1858 [1857]: 247. Pfeiffer 1860: 141, pl. 37, figs 7–9. Hanley and Theobald 1870: 4, pl. 7, fig. 4. Reeve 1878: Pupinidae, pl. 1, sp. 5. Crosse 1879: 340 (part). de Morgan 1885: 413 (part). von Möllendorff 1887 [1886]: 314 (part). Godwin-Austen 1897: 37, 38, pl. 69, fig. 1, 1a. BEDO 2017: 88. Sutcharit et al. 2018: fig. 5–13e.
Pupina avula [sic]—Sowerby I 1866: Pupinidae, pl. 3 (pl. 265), *Pupina*, fig. 3.
Pupina (*Tylotoechus*) *arula*—Kobelt 1902: 307. Gude 1921: 193, 194 (part). Solem 1966: 12, Doi Sutep [Doi Suthep Mountain, Chiang Mai Province, Thailand]. Hemmen and Hemmen 2001: 39.
Pupina arula arula—Maassen 2001: 40.

Type material examined. ***Syntype*** UMZC I.103025 (1 shell; Figs 29A, 33D) from the R. McAndrew collection labelled "Bens. col., Ind".

Other material examined. Specimen NHMUK 1888.12.4.109 (1 shell; Fig. 29B) from Yunglaw, Myanmar, the W. Theobald collection.

Diagnosis. Shell ovate; last whorl ca. 80% of shell height. Shell surface matt. Apertural lip thickened but not expanded; apertural lip curved when observed from lateral view. Columellar tooth fin-shaped.

Differential diagnosis. *Pupina arula* can be distinguished from all other species in the *P. arula* species group from mainland Southeast Asia by a matt shell surface.

Distribution. Myanmar and an uncertain record from northern Thailand (Solem 1966).

Remarks. No material of this species was found during this survey. The specimen of *P. arula* mentioned in Davison (1995: 237) from Temengor dam, Perak, Malaysia possibly belongs to *P. perakensis*.

Pupina mouhoti Pfeiffer, 1861

Figs 29C, D, 33E

Pupina mouhoti Pfeiffer, 1861: 196. Type locality: Camboja [Cambodia]. Pfeiffer 1863b [1862]: 278, pl. 36, fig. 7. Sowerby I 1866: Pupinidae, pl. 3 (pl. 265), *Pupina*, fig. 16. von Martens 1867: 67, Siam (?). Reeve 1878: Pupinidae, pl. 2, sp. 13. Morlet 1889: 152, Montson Kreang [possibly refers to Phum Ang Sang Kream, Kampong Speu Province, Cambodia], Battambang [Battambang Province, Cambodia], forêt de Srakéo (Siam) [Srakeo Province, Thailand]. Fischer 1891: 108. Fischer and Dautzenberg 1904: 431, Mont Souten à l'Ouest de Xieng-Mai, Laos occidental [Chiang Mai Province, Thailand]; Luang-Prabang [Luang Prabang Province, Laos]. Saurin 1953: 113, Pa Hia, Tran Ninh Province, Laos [probably refers to Ban Namthong, Longchaeng District, Xaisomboun Province, Laos]. Fischer 1973: 48.

Pupina (*Tylotoechus*) *mouhoti*—Kobelt 1902: 317. Hemmen and Hemmen 2001: 39.

Type material examined. ***Possible syntypes*** NHMUK ex. Cuming coll. (3 shells; Figs 29C, D, 33E) from Cambodia.

Diagnosis. Shell ovate-fusiform; last whorl ca. 80% of shell height. Apertural lip slightly thickened and slightly expanded; apertural lip when observed from lateral view almost straight. Columellar tooth curved downward like an earlobe.

Differential diagnosis. *Pupina mouhoti* is most similar to *P. siamensis* and *P. vescoi*, but different from *P. siamensis* by a more ovate-fusiform shell shape and a smaller parietal tooth, and differs from *P. vescoi* by a smaller shell, a shorter spire, a more distinct parietal tooth, and having a columellar tooth curved downward like an earlobe.

Distribution. Cambodia, Laos, and an uncertain record from Thailand (Fischer 1891; Kobelt 1902).

Remarks. No material of this species was found during this survey. The specimens from Srakeo Province mentioned in Morlet (1889) possibly belong to *P. siamensis*. In addition, some specimens mentioned in Fischer and Dautzenberg (1904) and Saurin (1953) possibly belong to *P. peguensis*.

Species of group II (*P. arula* species group) from other parts of mainland Southeast Asia not recorded for Thailand

Pupina vescoi Morelet, 1862

Figs 29E, F, 33F, 34A

Pupina vescoi Morelet, 1862: 479. Type locality: Bien-Hoa Cochinchinae [Bien Hoa, Dong Nai Province, Vietnam]. Sowerby I 1866: Pupinidae, pl. 3 (pl. 265), *Pupina*, fig. 26. Morelet 1875: 287, 288, pl. 13, fig. 11. Nevill 1878: 299. Reeve 1878: Pupinidae, pl. 2, sp. 18. Fischer 1891: 107, Environs de Saigon [Ho Chi Minh City, Vietnam]; Fuyen-Moth [Phu Yen Province, Vietnam]. Fischer and Dautzenberg 1904: 432, Thudaumot [Thu Dau Mot, Binh Duong Province, Vietnam]. Raheem et al. 2017: 5 (plate figure).

Pupina (*Tylotoechus*) *vescoi*—Kobelt 1902: 325, Pulo-Condor [Con Dao Island, Ba Ria-Vung Tau Province, Vietnam].

Type material examined. ***Syntypes*** NHMUK 1893.2.4.767–769 (3 shells; Figs 29E, 33F) from Cochin China.

Other material examined. SMF 109956/1 (1 shell; Figs 29F, 34A) from Cochin China.

Diagnosis. Shell ovate-fusiform; last whorl ca. three quarters of shell height. Apertural lip slightly thickened and slightly expanded; apertural lip when observed from lateral view almost straight. Parietal tooth small, indistinct; columellar tooth fin-shaped, not covering slit-like anterior canal.

Differential diagnosis. *Pupina vescoi* is most similar to *P. mouhoti* and *P. siamensis*, but differs in having a larger shell with a higher spire, a smaller, indistinct parietal tooth, and a fin-shaped columellar tooth not covering a slit-like anterior canal.

Distribution. South Vietnam (Fischer and Dautzenberg 1904).

Pupina exclamationis Mabille, 1887

Figs 29I–K, 34B, C

Pupina exclamationis Mabille, 1887: 137, 138, pl. 4, figs 11, 12. Type locality: Tonkin. Fischer 1891: 108. Fischer and Dautzenberg 1904: 431, Bac-Kan, Tonkin; Monts Mauson, Tonkin [Mount Mau Son, Lang Son Province, Vietnam]. Do et al. 2015: 126, fig. 6a, Son La Province, Vietnam.

Pupina (*Tylotoechus*) *exclamationis*—Kobelt 1902: 312.

Type material examined. ***Syntypes*** MNHN-IM-2000-35840 (4 shells; Figs 29I, J, 34B) from Tonkin.

Other material examined. NHMUK 1901.12.23.205−210 “forma minor” ex. H. Fruhstorfer coll. (5 shells; Figs 29K, 34C) from Than-Moi, Tonkin.

Diagnosis. Shell ovate-fusiform to fusiform; last whorl ca. three quarters of shell height. Apertural lip somewhat thickened but not expanded; apertural lip slightly curved when observed from lateral view. Columellar tooth fin-shaped.

Differential diagnosis. *Pupina exclamationis* is most similar to *P. peguensis* in having a glossy surface and a curved apertural lip when observed from lateral view, but differs in having a more fusiform shell shape and a less distinct parietal callus.

Distribution. Northern Vietnam (Do et al. 2015).

Pupina perakensis Möllendorff, 1891

Figs 29G, 34D

Pupina arula var. *perakensis* Möllendorff, 1891: 345. Type locality: Bukit Pondong, Perak [Gunung Pondok, Perak State, Malaysia].

Pupina arula perakensis— van Benthem Jutting 1949: 58, Cameron Highlands, Pahang; Telom Valley, near Gunong Siku, Pahang; Kuala Legap, Plus Valley, Perak [Malaysia]. van Benthem Jutting 1960: 13, hill near the hot springs, ca. 400 m from the main road from Tandjong Rambutan to Ipoh, near Tambun, Perak. Maassen 2001: 40.
Pupina (*Tylotoechus*) *arula perakensis*—Laidlaw 1928: 34. Zilch 1957: 44, pl. 2, fig. 17.
Pupina lowi [non Morgan]—Foon et al. 2017: 40, 41, fig. 15d, Ipoh, Perak.
Pupina tchehelensis [non Morgan]—Foon et al. 2017: 41, fig. 16a, Ipoh, Perak.

Type material examined. ***Lectotype*** SMF 109969/1 (Figs 29G, 34D) from Bukit Pondong, Perak.

Diagnosis. Shell fusiform; last whorl ca. 70% of shell height. Apertural lip thickened but not expanded; apertural lip curved when observed from lateral view. Parietal callus and parietal tooth highly thickened; columellar tooth curved downward like an earlobe.

Differential diagnosis. *Pupina perakensis* is most similar to *P. crosseana*, but differs in parietal callus and parietal tooth very thickened, and a columellar tooth curved downward like an earlobe.

Distribution. Perak and Pahang States, Malaysia (Maassen 2001).

Remarks. This taxon has always been treated as a subspecies of *P. arula* (van Benthem Jutting 1949; Zilch 1957; Maassen 2001). However, it is different from *P. arula* in having a glossy shell surface, a more fusiform shape with a higher spire; and a less bulging last whorl; additionally, the occurrence of this taxon is ca. 1,800 km from that of *P. arula*. Thus, this taxon is herein elevated to the specific level.

By comparing with the type specimen, the specimen of *P. tchehelensis* figured in Foon et al. (2017: fig. 16a) from Gunung Tempurung Plot 2, Ipoh, Perak should belong to *P. perakensis* (Foon, pers. comm.). Although the *P. lowi* specimen figured in Foon et al. (2017: 15d) from Bat Cave Hill, Ipoh, Perak has a shorter spire, we preliminarily identify this specimen as *P. perakensis* as well due to an overall character in the *Pupina arula* species group, a similar glossy surface to the type specimen, and its nearby locality to the type locality.

Pupina excisa **Möllendorff, 1902**

Figs 29H, 34E

Pupina (*Tylotoechus*) *excisa* Möllendorff, 1902a: 143. Type locality: Kelantan [Malaysia]. Laidlaw 1928: 34. Zilch 1957: 45, pl. 2, fig. 18.
Pupina excisa—Chan 1998a: 4, Ipoh, Perak. Chan 1998b: 2. Maassen 2001: 41. BEDO 2017: 90.

Type material examined. ***Lectotype*** SMF 110778/1 (Figs 29H, 34E) from Kelantan.

Diagnosis. Shell ovate with higher spire; last whorl ca. three quarters of shell height. Apertural lip somewhat thickened but not expanded; apertural lip when observed from lateral view angled. Columellar tooth curved downward like an earlobe.

Differential diagnosis. *Pupina excisa* can be distinguished from all other species in the *P. arula* species group from mainland Southeast Asia by an ovate shell shape with a higher spire, and an angled apertural lip when observed from lateral view. *Pupina excisa* is different from *P. mouhoti* in having a thicker, more prominent parietal tooth.

Distribution. Kelantan and Perak States, Malaysia (Maassen 2001).

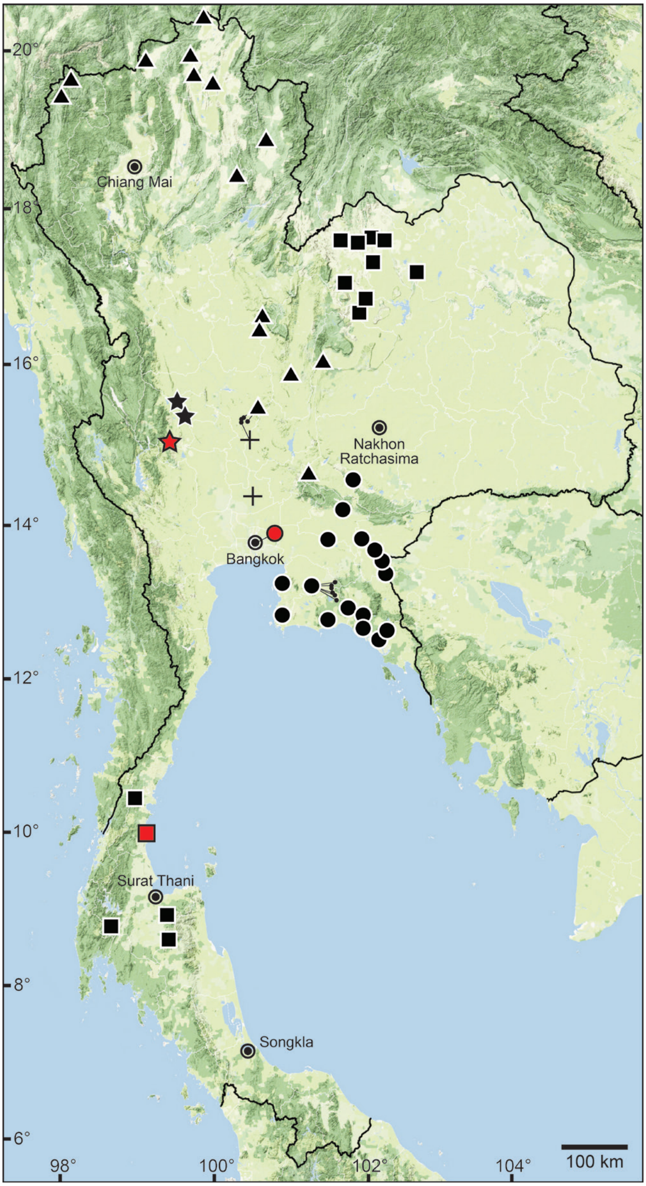

Figure 27. Distribution map of the *Pupina arula* species group: *Pupina peguensis* (triangle), *Pupina crosseana* (plus sign), *Pupina siamensis* (circle), *Pupina bilabiata* sp. nov. (square), and *Pupina godwinausteni* sp. nov. (star). Each red symbol indicates the type locality of its respective taxon. The occurrences of *Pupina arula* and *Pupina mouhoti* in northern Thailand are uncertain, thus their distributions are not mapped.

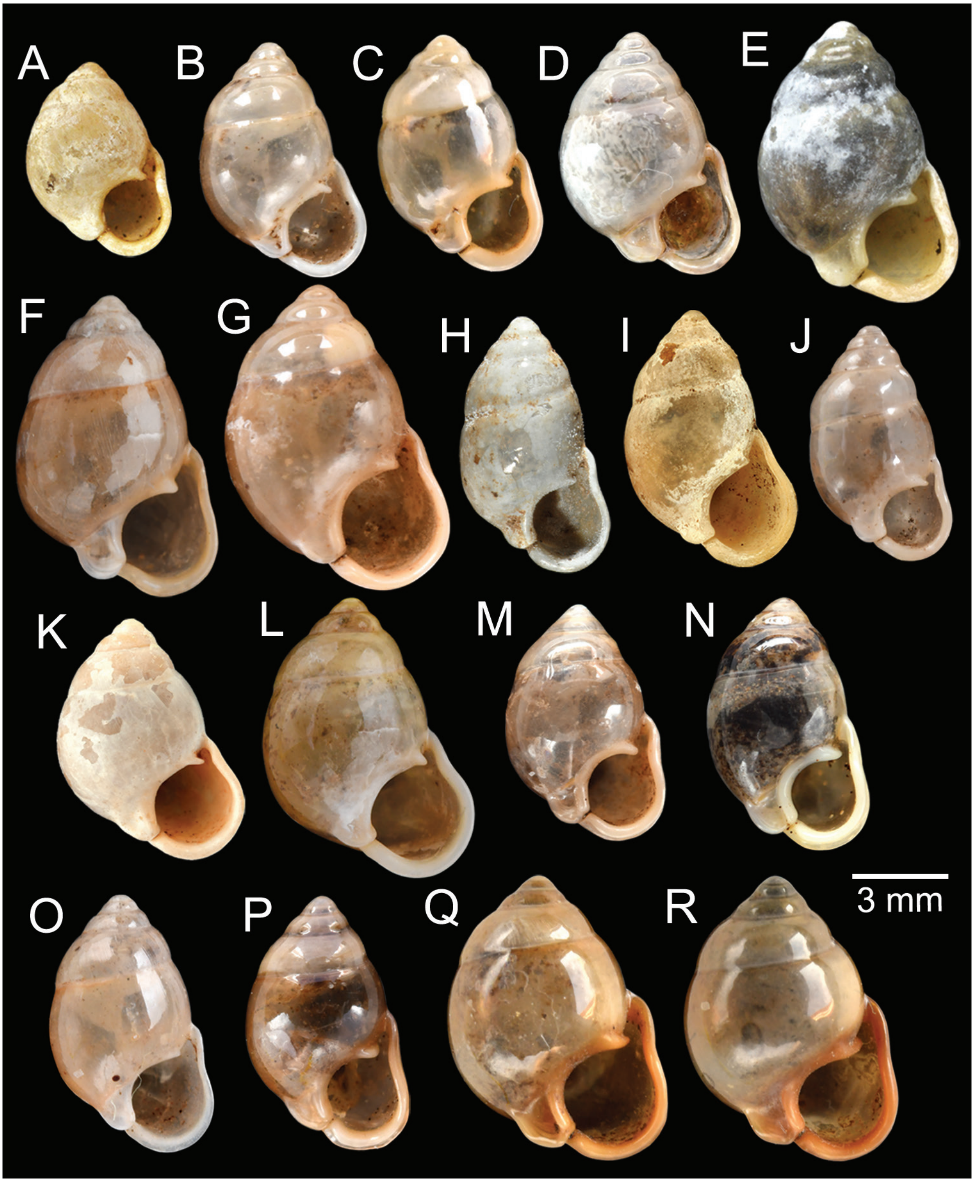

Figure 28. Shells of *Pupina arula* species group from mainland Southeast Asia **A–G** *Pupina peguensis* **A** syntype of *Pupina blanfordi* NHMUK 1888.12.4.100 and specimens **B** CUMZ 12105 **C** CUMZ 12050 **D** CUMZ 12103 **E** NHMUK ex. Cuming coll. **F** CUMZ 12094, and **G** CUMZ 12108 **H–J** *Pupina crosseana* **H** lectotype MNHN-IM-2000-35834 **I** paralectotype RBINS MT966/10591, and **J** specimen CUMZ 12049 **K, L** *Pupina siamensis* **K** lectotype SMF 109948 and **L** specimen CUMZ 12052 **M–P** *Pupina bilabiata* sp. nov. **M** holotype CUMZ 12073/1 and specimens **N** CUMZ 12079 **O** CUMZ 12081, and **P** CUMZ 12086 **Q, R** *Pupina godwinausteni* sp. nov. **Q** holotype CUMZ 12090/1 and **R** paratype CUMZ 12090/2. Photo: P. Maestrati, MNHN (**H**), F. Trus, RBINS (**I**).

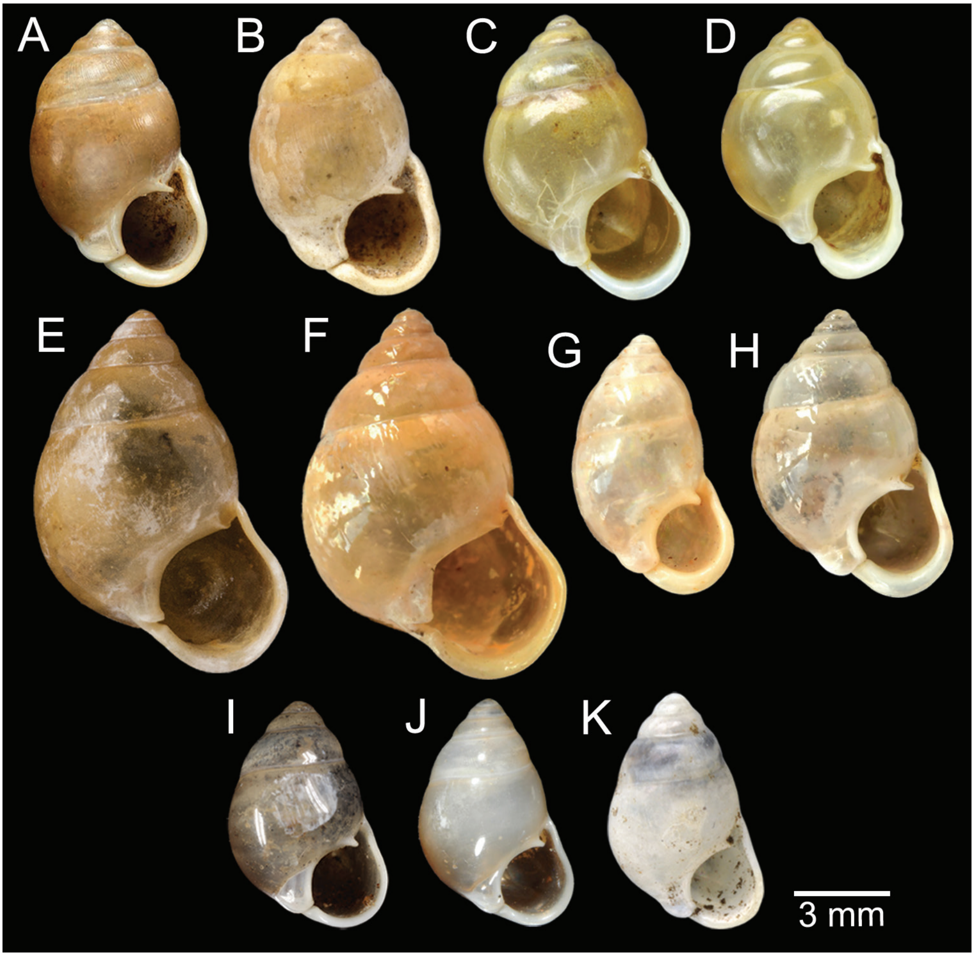

Figure 29. Shells of *Pupina arula* species group from mainland Southeast Asia **A, B** *Pupina arula* **A** syntype UMZC I.103025 and **B** specimen NHMUK 1888.12.4.109. **C, D** *Pupina mouhoti*, possible syntypes NHMUK ex. Cuming coll. **E, F** *Pupina vescoi* **E** syntype NHMUK 1893.2.4.767 and **F** specimen SMF 109956/1 **G** *Pupina perakensis*, lectotype SMF 109969/1 **H** *Pupina excisa*, lectotype SMF 110778/1 **I–K** *Pupina exclamationis* **I, J** syntypes MNHN-IM-2000-35840 and **K** specimen NHMUK 1901.12.23.205 "forma minor". Photo: J. Ablett, H. Taylor, NHM (**A**), A. Lardeur, P. Maestrati, MNHN (**I, J**).

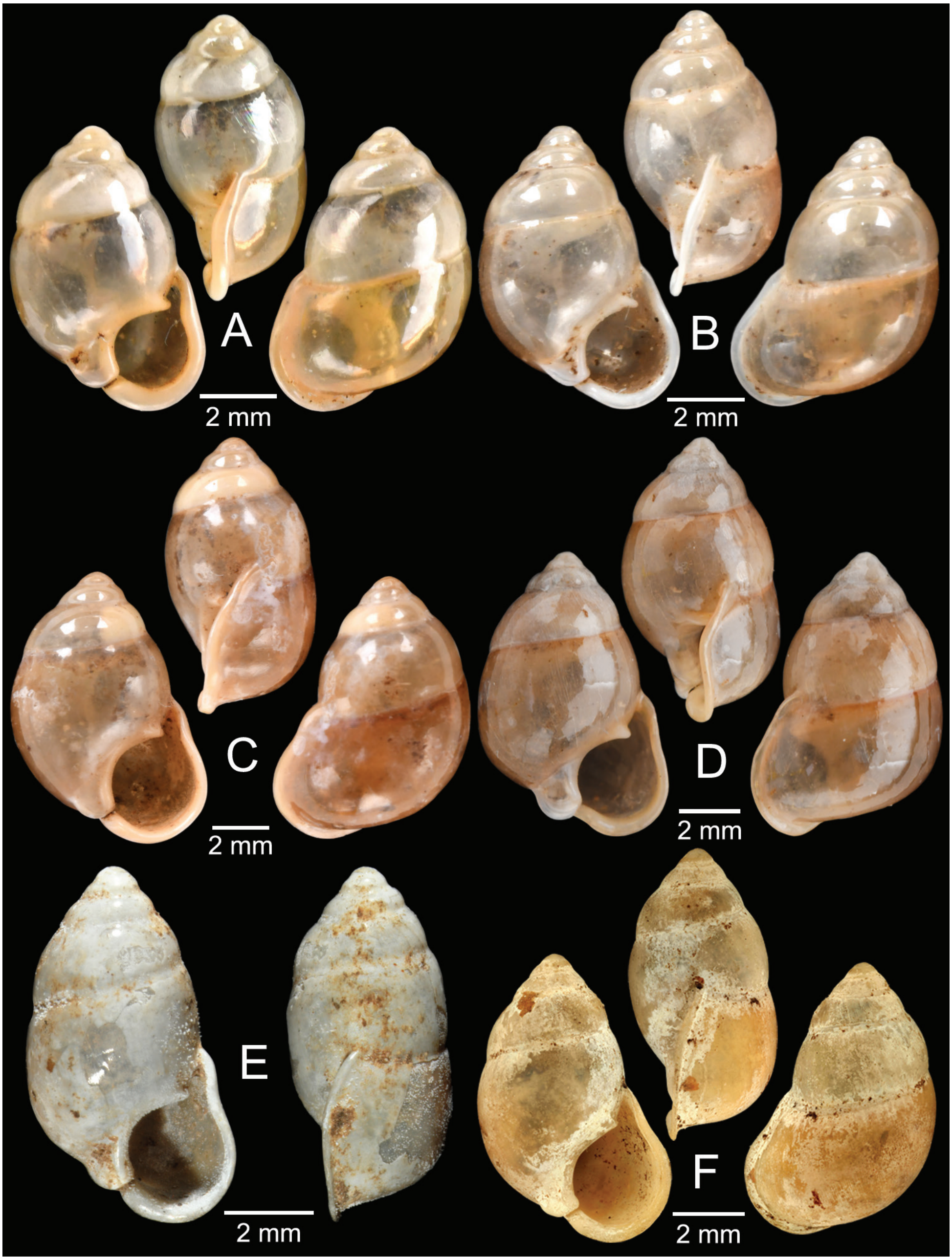

Figure 30. A–D *Pupina peguensis*: specimens **A** CUMZ 12050 from Chai Thong Wararam Temple, Nakhon Sawan **B** CUMZ 12105 from Thep Phithak Punnaram Temple, Nakhon Ratchasima **C** CUMZ 12108 from Tham Thep Bandan Temple, Phetchabun, and **D** CUMZ 12094 from Khao Tham Phra Temple, Chiang Rai **E, F** *Pupina crosseana* **E** lectotype MNHN-IM-2000-35834 from Cambodge and **F** paralectotype RBINS MT966/10591 from Phnom-Rohan, Cambodge. Photo: P. Maestrati, MNHN (**E**), F. Trus, RBINS (**F**).

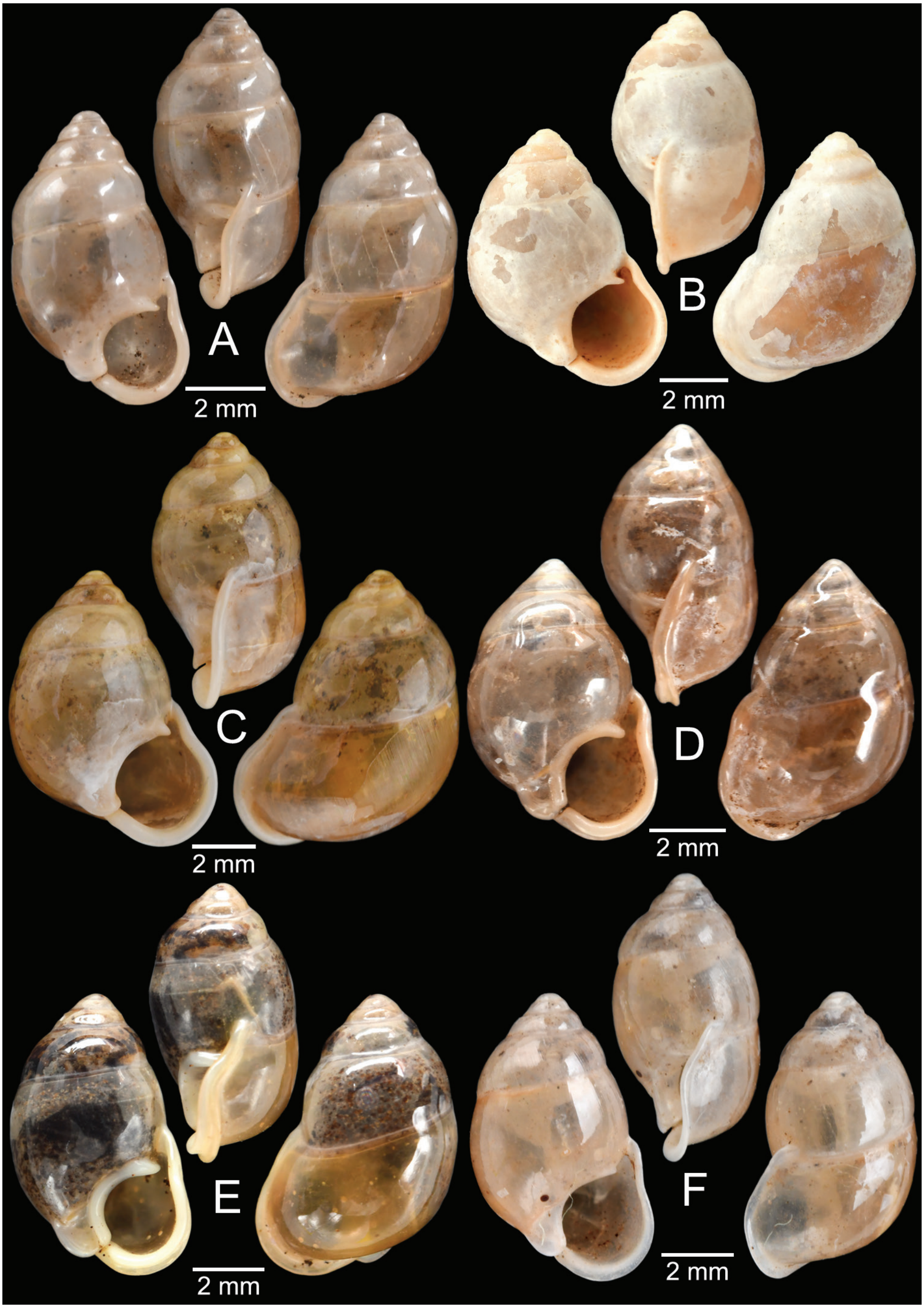

Figure 31. A *Pupina crosseana*, specimen CUMZ 12049 from Khao Jedee Temple, Nakhon Sawan **B, C** *Pupina siamensis*: **B** lectotype SMF 109948 and **C** specimen CUMZ 12052 from Sri Thong Cave, Sra Keo **D–F** *Pupina bilabiata* sp. nov. **D** holotype CUMZ 12073/1, and specimens **E** CUMZ 12079 from Tham Pha Ya Temple, Loei and **F** CUMZ 12081 from Pha Jor Cave, Nong Bua Lam Phu.

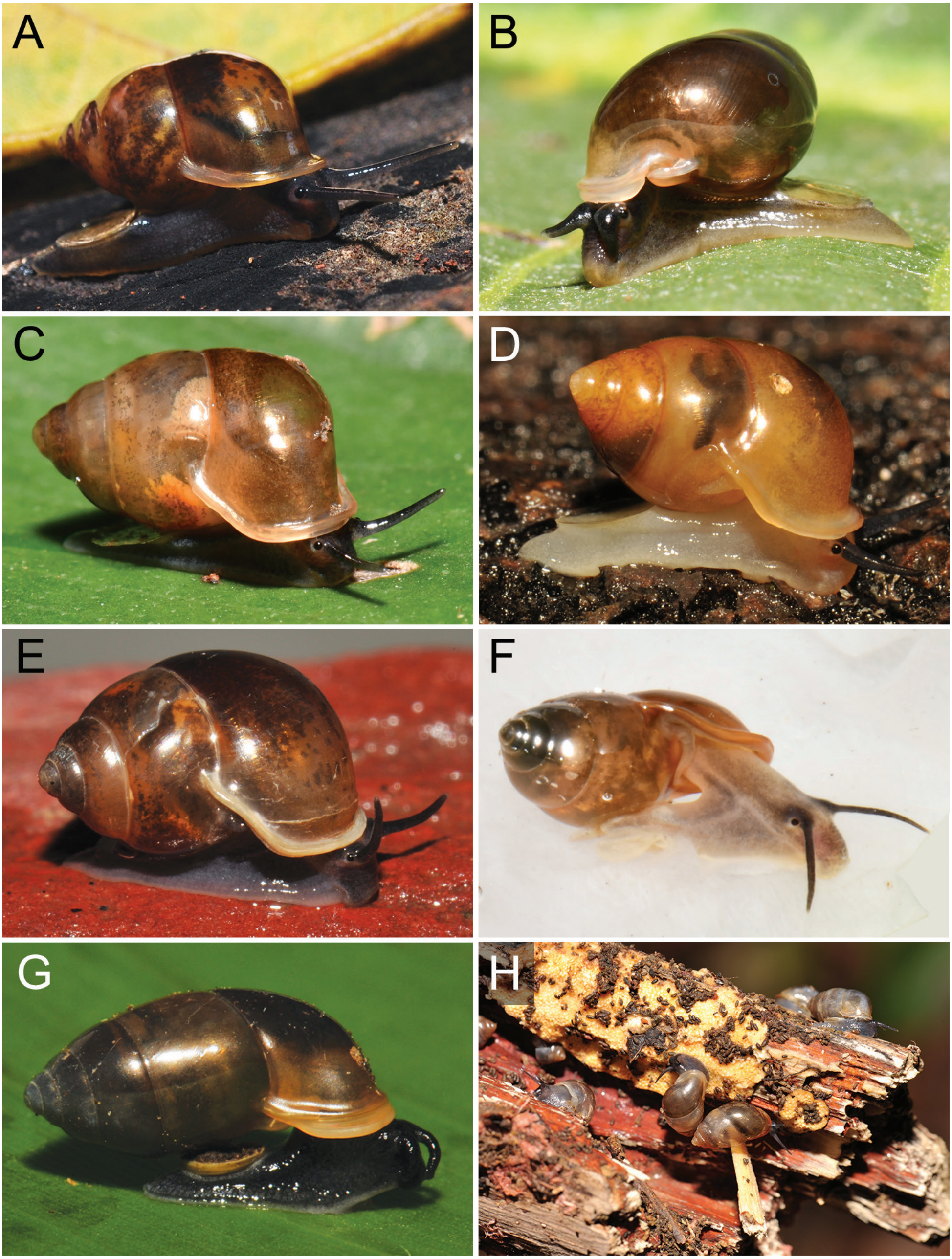

Figure 32. Live specimens of **A** *Pupina siamensis*, specimen CUMZ 12071 from Tham Khao Loi Temple, Rayong **B–D** *Pupina bilabiata* sp. nov. **B** paratype CUMZ 12073/2 from Banpot Pisai Temple, Chumphon and specimens **C** CUMZ 12082 from Pha Jor Cave, Nong Bua Lam Phu and **D** CUMZ 12087 from Ban Yai, Surat Thani **E, F** *Pupina godwinausteni* sp. nov.: paratypes **E** CUMZ 12090/26 and **F** CUMZ 12091 from Khao Wong Cave, Uthai Thani **G, H** *Pupina aureola*: specimens **G** CUMZ 12117 from Lod Cave, Nakhon Sri Thammarat and **H** CUMZ 12121 from Tham Thong Panara Temple, Nakhon Sri Thammarat, showing its microhabitat in rotten log. All not to scale.

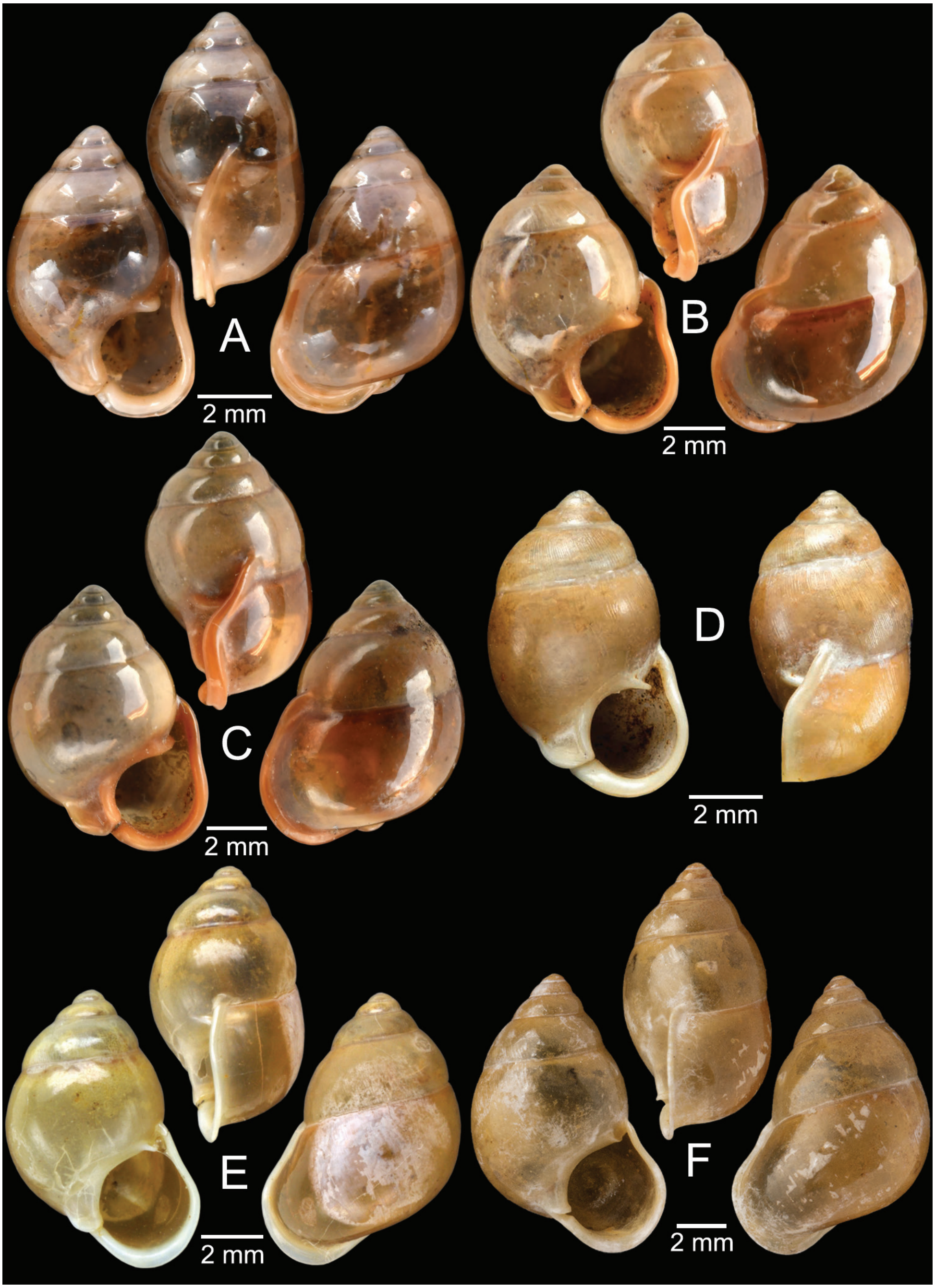

Figure 33. A *Pupina bilabiata* sp. nov., specimen CUMZ 12086 from Na San Temple, Surat Thani **B, C** *Pupina godwinausteni* sp. nov. **B** holotype CUMZ 12090/1 and **C** paratype CUMZ 12090/2 from Khao Wong Cave, Uthai Thani **D** *Pupina arula*, syntype UMZC I.103025 "Ind" **E** *Pupina mouhoti*, possible syntype NHMUK ex. Cuming coll. from Camboja **F** *Pupina vescoi*, syntype NHMUK 1893.2.4.767 from Cochin China. Photo: J. Ablett, H. Taylor, NHM (**D**).

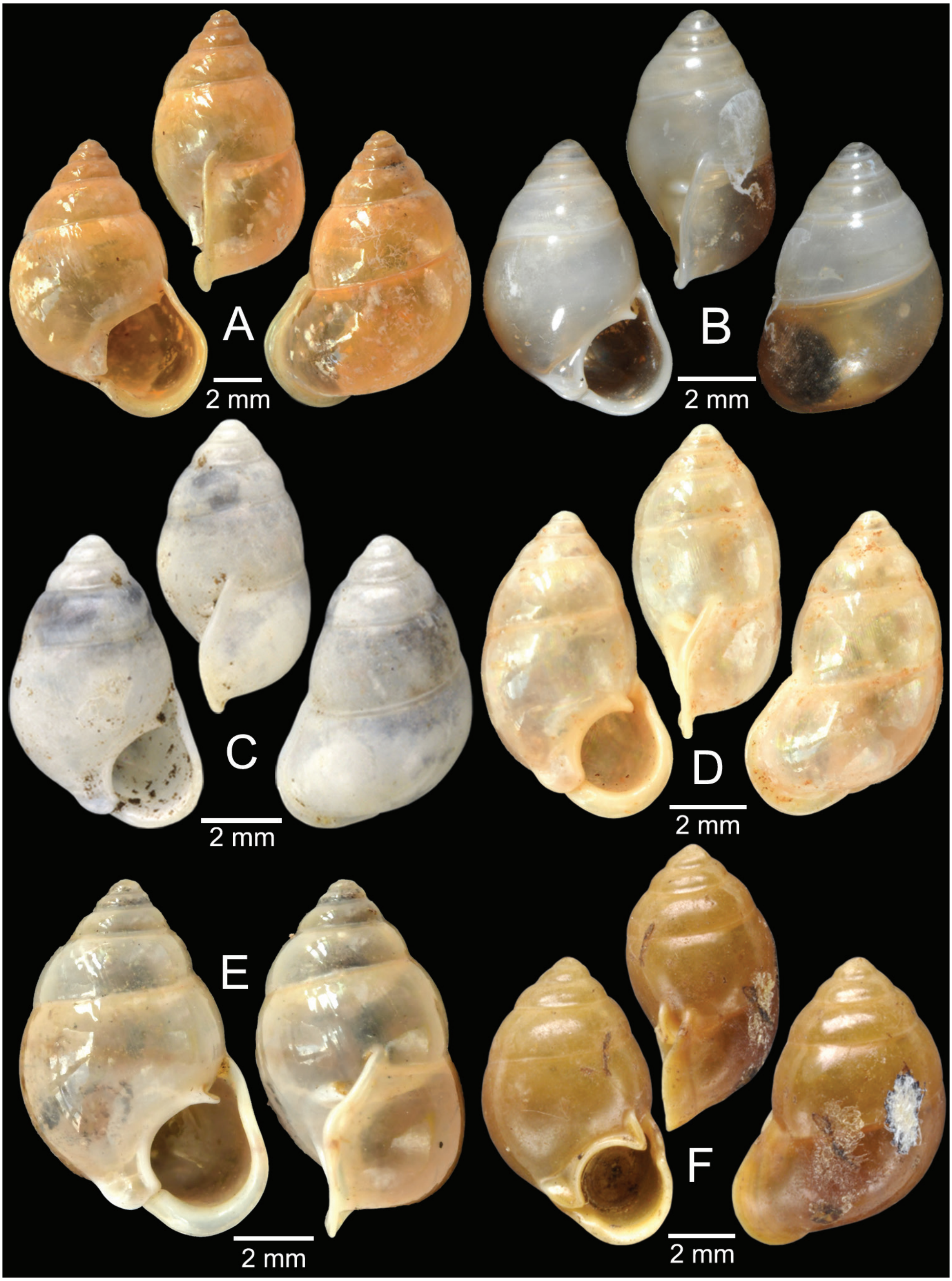

Figure 34. **A** *Pupina vescoi*, specimen SMF 109956/1 from Cochin China **B, C** *Pupina exclamationis* **B** syntype MNHN-IM-2000-35840 from Tonkin and **C** specimen NHMUK 1901.12.23.205 "forma minor" from Than-Moi, Tonkin **D** *Pupina perakensis*, lectotype SMF 109969/1 from Bukit Pondong, Perak **E** *Pupina excisa*, lectotype SMF 110778/1 from Kelantan **F** *Pupina aureola*, possible syntype NHMUK 1988.12.4.101 from Pinang. Photo: P. Maestrati, MNHN (**B**).

Group III. *Pupina aureola* species group

Figs 10D, 18D, 19C

This species group is characterised by an indistinct to thickened triangular or fin-shaped parietal tooth located next to a posterior canal. A columellar tooth is less thickened, never ear shaped and mostly fin-shaped, located next to an anterior canal. Both the anterior and posterior canals are either slit-like or widening toward the outer margin when observed from apertural view. An outer apertural lip is straight or slightly curved when observed from lateral view. An operculum is round, thick, flat to concave, multispiral, whitish to pale yellow, opaque corneous with smooth edge.

This species group from mainland Southeast Asia contains 13 species and one subspecies, including three nominal species, two new species (*P. latisulci* sp. nov. and *P. stoliczkai* sp. nov.), and one new subspecies (*P. dorri isanensis* ssp. nov.) from Thailand. The distribution of the *P. aureola* species group in Thailand is provided in Fig. 35. A synoptic view of all species within the *P. aureola* species group from mainland Southeast Asia is given in Figs 36, 37 to provide the comparative size.

Pupina aureola Stoliczka, 1872

Figs 10D, 19C, 32G, H, 34F, 36A–F, 38A–E

Pupina aureola Stoliczka, 1872: 267, pl. 10, figs 11, 12. Type locality: Penang [Penang State, Malaysia]. Nevill 1878: 299. de Morgan 1885: 414, Poulo Pinang, mont Tchora, près d'Ipoh (Kinta), [Perak State, Malaysia]. von Möllendorff 1891: 345. Sykes 1903: 197, Jalor [Yala Province, Thailand]. van Benthem Jutting 1949: 57, Gunong Pulai, Johore [Johor State, Malaysia]. van Benthem Jutting 1960: 13, limestone hill near kampong Tebing Tinggi, N. of Kangar, Perlis [Malaysia]. Chan 1998a: 4, Ipoh, Perak. Maassen 2001: 40, 41. BEDO 2017: 88. Sutcharit et al. 2018: fig. 5–13f.

Pupina (*Tylotoechus*) *aureola*—Kobelt 1902: 307. Laidlaw 1928: 34. Hemmen and Hemmen 2001: 39.

Pupina arula perakensis [non Möllendorff]—Foon et al. 2017: 40, fig. 15c, Ipoh, Perak.

Pupina sp.—Sutcharit et al. 2018: fig. 5–11b.

Type material examined. ***Possible syntype*** NHMUK 1988.12.4.101 (Figs 34F, 36A) from Pinang.

Other material examined. CUMZ 12112 (2 shells and 6 specimens in ethanol) from Phra Kayang Cave, Kra Buri District, Ranong Province, 4 Apr. 1998. CUMZ 12113 (3 specimens in ethanol) from Na Mueang Waterfall, Ko Samui District, Surat Thani Province, 4 Mar. 2007. CUMZ 12114 (5 specimens in ethanol) from Na Mueang Waterfall, Ko Samui District, Surat Thani Province, 3 Dec. 2015. CUMZ 12115 (4 specimens in ethanol) from Pra Puttabhat Sri Suratth Temple, Kanchanadit District, Surat Thani Province, 6 Dec. 2016. CUMZ 12116 (7 specimens in ethanol; Fig. 19C) from Khiri Rat Phatthana Temple, Wiang Sa District, Surat Thani Province, 4 July

2017. CUMZ 12117 (4 shells and 42 specimens in ethanol; Fig. 32G) from Lod Cave, Nopphitam District, Nakhon Si Thammarat District, 11 Mar. 2017. CUMZ 12118 (1 shell) from Kaeo Surakan Cave, Lan Saka District, Nakhon Si Thammarat Province, 11 Mar. 2017. CUMZ 12119 (6 specimens in ethanol) from Tham Thong Panara Temple, Tham Phannara District, Nakhon Sri Thammarat Province, 4 Apr. 2003. CUMZ 12120 (36 shells and 1 specimen in ethanol) from Tham Thong Panara Temple, Tham Phannara District, Nakhon Sri Thammarat Province, 11 Oct. 2006. CUMZ 12121 (> 100 specimens in ethanol; Figs 32H, 36F, 38A) from Tham Thong Panara Temple, Tham Phannara District, Nakhon Sri Thammarat Province, 11 June 2012. CUMZ 12122 (15 specimens in ethanol) from Tham Thong Panara Temple, Tham Phannara District, Nakhon Sri Thammarat Province, 15 Jan. 2014. CUMZ 12123 (12 shells) from Tham Thong Panara Temple, Tham Phannara District, Nakhon Sri Thammarat Province, 4 July 2017. CUMZ 12124 (3 shells and 1 specimen in ethanol; Figs 36B, 38B) from Talot Cave, Thung Song District, Nakhon Sri Thammarat Province, Thailand, 5 July 2017. CUMZ 12125 (1 shell and 1 specimen in ethanol) from Nam Phut Cave, Mueang Phang Nga District, Phang Nga Province, 6 Aug. 2015. CUMZ 12126 (9 shells; Figs 36C, 38C) from Khao Huai Haeng Temple, Huai Yot District, Trang Province, 6 Oct. 2006. CUMZ 12127 (5 specimens in ethanol) from Ban Khao Poon, Huai Yot District, Trang Province, 6 Oct. 2006. CUMZ 12128 (1 shell) from Trang Botanical Garden, Yan Ta Khao District, Trang Province, 6 Aug. 1999. CUMZ 12129 (4 specimens in ethanol) from Khao Pu Chao Bureau of Monks, Na Yong District, Trang Province, 8 July 2017. CUMZ 12130 (8 shells; Figs 10D, 36D, 38D) from Sra Morakot, Khlong Thom District, Krabi Province, 15 Jan. 2009. CUMZ 12131 (2 specimens in ethanol) from Sra Morakot, Khlong Thom District, Krabi Province, 17 May 2012. CUMZ 12132 (15 specimens in ethanol) from Toe Bu Cliff Viewpoint, Mueang Satun District, Satun Province, 7 Apr. 2008. CUMZ 12133 (7 shells; Figs 36E, 38E) from Khantiphol Cave, Thung Wa District, Satun Province, 13 Jan. 2009.

Diagnosis. Shell ovate to fusiform; last whorl ca. 70–75% of shell height. Apertural lip thickened to highly thickened but not expanded. Parietal tooth thickened, fin-shaped or tooth-like, always located next to but not covering posterior canal; columellar tooth fin-shaped, thickened, located next to anterior canal. Posterior canal slightly bulging outward.

Differential diagnosis. *P. aureola* is most similar to *P. stoliczkai* sp. nov. in shell shape and having both fin-shaped and highly thickened parietal and columellar teeth located next to their respective canals; the posterior canal slightly bulges outward. However, *P. aureola* does not have a furrow between inner and outer peristomes.

Distribution. Malaysia and southern Thailand (Maassen 2001).

Remarks. This species has high variation in shell shape from ovate to fusiform, and the parietal tooth varies from fin-shaped to tooth-like. Despite those shell variations, we assign these shell morphs to *P. aureola* due to the uniform position of a parietal tooth that is always located next to the posterior canal, and a columellar tooth that is always fin-shaped and not extending over the apertural lip.

By comparing with the possible type specimen, the specimen of *P. arula perakensis* figured in Foon et al. (2017: fig. 15c) from Gunung Datok Plot, Ipoh, Perak should belong to *P. aureola* (Foon, pers. comm.).

Pupina paviei **Morlet, 1883**

Figs 37F–I, 38F, G, 39A, B

Pupina paviei Morlet, 1883: 107, 108, pl. 4, fig. 4. Type locality: La chaîne de l'Éléphant et les forêts non inondées qui la bordent, particulièrement, près des rapides de Kamchay et aux environs de Kampot [The Elephant Range and the non-flooded forests that border it, particularly near the Kamchay rapids and around Kampot; currently Preah Monivong Bokor National Park, Kampot Province, Cambodia]. Morlet 1889: 152. Fischer 1891: 107. Fischer and Dautzenberg 1904: 431. Morlet 1904: 370, 371, pl. 20, fig. 13, 13a. Fischer-Piette 1950: 153. Fischer 1973: 48. BEDO 2017: 92.

Pupina (*Tylotoechus*) *paviei*—Kobelt 1902: 319.

Type material examined. Paralectotypes MNHN-IM-2000-35837 (4 shells; Figs 37F, 38F) from Chaîne de l'Eléphant, Kampot, Cambodge. Paralectotypes RBINS 525404 (76 shells; Figs 37G, 38G) from Kampot et forêts de la chaîne de l'Eléphant, Cambodge et Kamchay.

Material examined. NHMUK ex. Dautzenberg coll. (1 shell; Figs 37I, 39A) from Kampot, Cambodge. CUMZ 12134 (129 shells; Figs 37H, 39B) from Lalu, Ta Phraya District, Sa Kaeo Province, 24 Nov. 2006.

Diagnosis. Shell globose to ovate; last whorl ca. three quarters of shell height. Apertural lip slightly thickened but not expanded. Parietal tooth triangular, not thickened to slightly thickened, covering posterior canal but not extending beyond apertural lip; columellar tooth fin-shaped, slightly thickened, located next to slit-like anterior canal.

Differential diagnosis. *Pupina paviei* is similar to *P. tongupensis* in a globose shell shape, but differs in having a triangular parietal tooth that is either not thickened or slightly thickened, and a fin-shaped, slightly thickened columellar tooth that is located next to a slit-like anterior canal.

Distribution. Cambodia (Morlet 1883) and Sa Kaeo Province, eastern Thailand.

Remarks. As the original description did not explicitly state that the description of this species was based on a single specimen (nor could this be inferred), the designation of a holotype by Fischer-Piette (1950) in fact constitutes a lectotype designation (ICZN 1999: Art. 74.6).

Pupina tchehelensis **Morgan, 1885**

Figs 18D, 37A–C, 39C, D

Pupina tchehelensis Morgan, 1885: 414, 415, pl. 7, fig. 4. Type locality: mont Tchéhèl [possibly the hill in the vicinity of Ipoh, Perak, Malaysia]. von Möllendorff 1891: 346, Bukit Pondong. Maassen 2001: 41. BEDO 2017: 94.

Pupina artata [non Benson]— von Möllendorff 1887 [1886]: 314. von Möllendorff 1891: 345, 346.

Pupina (*Tylotoechus*) *tchehelensis*—Kobelt 1902: 323. Laidlaw 1928: 34.
Pupina tchechelensis [sic]— van Benthem Jutting 1949: 57, Sungei Siput, Perak.

Material examined. SMF 109947/6 (6 shells; Figs 37A, 39C) from Bukit Pondong, Perak. CUMZ 12135 (1 shell; Fig. 37B) from Tham Suea Temple, Mueang Krabi District, Krabi Province, 6 Oct. 2006. CUMZ 12136 (7 shells; Figs 18D, 37C, 39D) from limestone mountain, Phang Nga Province, 1 May 1999.

Diagnosis. Shell ovate; last whorl ca. 70–75% of shell height. Apertural lip slightly thickened but not expanded. Parietal tooth sharp, tooth-like, thickened; columellar tooth fin-shaped, slightly thickened, located next to slit-like anterior canal. Posterior canal gradually widening like a keyhole.

Differential diagnosis. *Pupina tchehelensis* is most similar to *P. lowi* and *P. brachysoma* in having a sharp, tooth-like, thickened parietal tooth, a fin-shaped, thickened, columellar tooth that is located next to a slit-like anterior canal, and a posterior canal that is gradually widening. However, *P. tchehelensis* is different from *P. lowi* by having a more ovate shell shape, and differs from *P. brachysoma* in that the apertural lip is not expanded.

Distribution. Malaysia (Maassen 2001) and southern Thailand.

Remarks. Both similar species *P. tchehelensis* and *P. lowi* were originally described by de Morgan (1885) from the same vicinity within Perak, peninsular Malaysia: de Morgan (1885) stated that *P. lowi* is "much larger than *P. tchehelensis*, and this species is distinguished by the shape of its whorls which are much more flattened." As the type materials of *P. tchehelensis* have not yet been discovered, and *P. tchehelensis* specimens have a slightly higher shell than *P. lowi*, we do not synonymise *P. tchehelensis* with *P. lowi*. Specimens from Thailand have a larger shell than those from Perak, Malaysia (Fig. 37A–C).

Pupina dorri isanensis Jirapatrasilp, ssp. nov.

Figs 36K, L, 39E, F

Type material. ***Holotype*** CUMZ 12140/1 (Figs 36K, 39E), 31 Aug. 2020, coll. C. Sutcharit, P. Jirapatrasilp, A. Pholyotha. Measurement: shell height 6.6 mm, shell width 4.6 mm and 5½ whorls. ***Paratypes*** CUMZ 12140/2 (22 shells) and NHMUK 20210337 (3 shells), same data as holotype.

Type locality. Pa Pha Ya Temple, Suwannakhuha District, Nong Bua Lam Phu Province, Thailand, 17°37'38.8"N, 102°10'13.7"E, 250 m amsl.

Other material examined. CUMZ 12137 (1 shell; Figs 36L, 39F) from Khao Wang Pha, Na Wang District, Nong Bua Lam Phu Province, 15 Oct. 2007. CUMZ 12138 (1 shell) from Pa Jor Cave, Na Wang District, Nong Bua Lam Phu Province, 15 Oct. 2007. CUMZ 12139 (9 shells) from Tham Suwannakhuha Temple, Suwannakhuha District, Nong Bua Lam Phu Province, 31 Aug. 2020. CUMZ 12141 (2 shells) from Namtok Thao To Forest Park, Mueang Nong Bua Lam Phu District, Nong Bua Lam Phu Province, 31 Aug. 2020. CUMZ 12142 (3 shells and 1 specimen in ethanol) from Phu Pha Lom, Mueang Loei District, Loei Province, 1 Sept. 2020. CUMZ 12143 (1 specimen in ethanol) from Hin Pha Ngam Park, Nong Hin District, Loei Province, 2 Sept. 2020. CUMZ 12144 (1 shell) from Phraya Nakharaj Cave, Phu Pha Man District, Khon Kaen Province, 21 July 2020. CUMZ 12145 (1 specimen in ethanol) from Phu Thong Thep Nimit Temple, Nong Saeng District, Udon Thani Province, 30 Aug. 2020. CUMZ 12170 (1 shell) from Khao Wong Cave, Kaeng Hang Maeo District, Chanthaburi Province, 15 Sept. 2009.

Diagnosis. Shell ovate-fusiform; last whorl ca. 70% of shell height. Apertural lip thickened but not expanded. Parietal tooth triangular, thickened, covering posterior canal, approaching but not extending beyond the outer margin of apertural lip; columellar tooth fin-shaped, thickened, located next to slit-like anterior canal.

Differential diagnosis. This new subspecies is slightly different from the nominotypical subspecies in having the apertural lip, and parietal and columellar teeth more thickened.

Description. Shell height 6.0–6.6 mm; shell width 4.2–4.6 mm. Shell ovate-fusiform, solid, semi-transparent, grey to pale brown, devoid of prominent sculpture on glazed smooth surface. Apex obtuse. Growth lines on shell surface inconspicuous. Whorls 5½, last whorl large (ca. 70% of shell height). Spire angle ca. 75–80°, slightly extended. Sutures slightly impressed, but shallow. Aperture circular; lip thickened (ca. 0.2 mm wide and 0.3–0.4 mm thick) with paler colour, not expanded. Parietal callus not sharply defined and somewhat thickened with paler colour. Peristome interrupted by two canals; posterior canal slit-like ca. 0.7 mm long; anterior canal slit-like continuing horizontally ca. 0.8–0.9 mm. Parietal tooth triangular, thickened (ca. 0.7 mm long, 0.5 mm at its widest and 0.3 mm thick), covering posterior canal, approaching but not extending beyond the outer margin of apertural lip. Columellar tooth thickened (ca. 1.0 mm long, 0.3 mm at its widest and 0.3 mm thick), fin-shaped. Umbilicus closed. Operculum round, thin, flat, multispiral, whitish to pale yellow, opaque corneous with smooth edge.

Etymology. The specific epithet refers to the Thai name "Isan" for the northeastern region of Thailand, where this new subspecies is mainly distributed.

Distribution. Northeastern and eastern Thailand.

Remarks. Although the collecting localities of this new subspecies are ca. 600 km from the known occurrence of the nominotypical subspecies, DNA data and morphometric analyses are required to demonstrate whether these Thai specimens are distinct from the Vietnamese specimens and should be elevated to specific status.

Pupina latisulci **Jirapatrasilp, sp. nov.**

https://zoobank.org/F59DBFAB-6DD5-4E44-A06F-5C18EB83C03A

Figs 37D, E, 40A, B

Type material. ***Holotype*** CUMZ 12146/1 (Figs 37D, 40A), 9 Apr. 2000, coll. C. Sutcharit, P. Tongkerd, S. Panha. Measurement: shell height 6.0 mm, shell width 4.6 mm and 5¾ whorls. ***Paratypes*** CUMZ 12146/2–8 (7 shells; Figs 37E, 40B) and NHMUK 20210338 (2 shells), same data as holotype.

Type locality. Khao Ok Talu, Mueang Phatthalung District, Phatthalung Province, Thailand, 7°37'32.2"N, 100°05'28.5"E, 120 m amsl.

Diagnosis. Shell ovate; last whorl ca. three quarters of shell height. Apertural lip thickened but not expanded. Parietal tooth sharp, tooth-like; columellar tooth sharp, triangular shaped. Both anterior and posterior canals widening like keyholes bordered by its respective tooth and a small bulge of the outer lip.

Differential diagnosis. *Pupina latisulci* sp. nov. can be distinguished from all other species in the *P. aureola* species group from mainland Southeast Asia by having both anterior and posterior canals widening like keyholes that are bordered by its respective tooth and a small bulge of the outer lip.

Description. Shell height 4.0–4.5 mm; shell width 5.9–6.3 mm. Shell ovate, solid, semi-transparent, whitish to pale brown, devoid of prominent sculpture on glazed smooth surface. Apex obtuse. Growth lines on shell surface inconspicuous. Whorls 5¾, last whorl large (ca. three quarters of shell height). Spire angle ca. 90°, slightly extended. Sutures slightly impressed, but shallow. Aperture circular; lip thickened (ca. 0.1–0.2 mm wide and 0.1–0.2 mm thick) with paler colour, not expanded. Parietal callus not sharply defined and somewhat thickened with paler colour. Peristome interrupted by two canals; posterior canal ca. 0.6 mm long, 0.4 mm at its widest, continuing obliquely to form a narrow groove that widens upward like a keyhole; bordered by parietal tooth and more thickened lip appearing as a small bulge. Anterior canal slit-like continuing horizontally ca. 0.7–0.8 mm, widening towards outer margin like a keyhole, bordered by columellar tooth and more thickened lip. Parietal tooth sharp, thickened (ca. 0.6 mm long, 0.4 mm at its widest and 0.2 mm thick), tooth-like. Columellar tooth thickened (ca. 0.6 mm long, 0.9 mm at its widest and 0.2 mm thick), sharp, triangular shaped. Umbilicus closed. Operculum unknown.

Etymology. The specific epithet *latisulci* is derived from the Latin word *latus* meaning wide and *sulci* [plural form of *sulcus*] meaning furrow or groove, which describes the widening of both anterior and posterior canals in the new species.

Distribution. This new species is found from Phatthalung Province, southern Thailand.

Pupina stoliczkai Jirapatrasilp, sp. nov.

https://zoobank.org/80A5D354-B516-4F67-9F08-817A29FBBEFB
Figs 36G, H, 40C, D

Type material. ***Holotype*** CUMZ 12147/1 (Figs 36G, 40C), 10 Sept. 2016, coll. R. Srisonchai, A. Pholyotha, T. Seesamut. Measurement: shell height 9.4 mm, shell width 6.3 mm and 6½ whorls. ***Paratypes*** CUMZ 12147/2 (1 specimen in ethanol) and NHMUK 20210336 (1 shell; Figs 36H, 40D), same data as holotype.

Type locality. Wat Ratburana School, Lang Suan District, Chumpon Province, Thailand, 9°56'18.0"N, 99°02'25.5"E, 20 m amsl.

Diagnosis. Shell ovate-fusiform; last whorl ca. 70% of shell height. Apertural lip highly thickened and slightly expanded; with a furrow between inner and outer peristomes; inner peristome thickened, cord-like. Both parietal and columellar teeth fin-shaped, very thickened, always located next to and not covering its respective canal. Posterior canal slightly bulging outward.

Differential diagnosis. *P. stoliczkai* sp. nov. is most similar to *P. aureola* in shell shape in having both fin-shaped and highly thickened parietal and columellar teeth located next to their respective canals, and the posterior canal slightly bulging outward. However, *P. stoliczkai* sp. nov. has a furrow between inner and outer peristomes, with inner peristome thickened and cord-like.

Description. Shell height 6.3–6.4 mm; shell width 9.0–9.5 mm. Shell ovate-fusiform, solid, semi-transparent, reddish brown, devoid of prominent sculpture on glazed smooth surface. Apex obtuse. Growth lines on shell surface inconspicuous. Whorls 6–6½, last whorl large (ca. 70% of shell height). Spire angle ca. 80–90°; slightly extended. Sutures slightly impressed, but shallow. Aperture circular; lip highly thickened (ca. 0.4–0.5 mm wide and 0.6–0.7 mm thick) with paler colour, slightly expanded. Aperture with a furrow between inner and outer peristomes, with inner peristome thickened, cord-like. Parietal callus sharply defined and thickened with paler colour. Peristome interrupted by two canals; posterior canal ca. 1.4 mm long and 0.7 mm at its widest, slightly bulging outward, continuing obliquely and widening vertically upward when observed from lateral view. Anterior canal curved and continuing obliquely upward ca. 2.0 mm. Parietal tooth fin-shaped, highly thickened (ca. 1.5 mm long, 0.5 mm at its widest and 0.3 mm thick), always located next to and not covering posterior canal. Columellar tooth fin-shaped, highly thickened (ca. 1.9 mm long, 0.5 mm at its widest and 0.3 mm thick), located next to anterior canal. Umbilicus closed. Operculum round, thick, flat, multispiral, whitish to pale yellow, opaque corneous with smooth edge.

Etymology. The specific epithet is dedicated to F. Stoliczka, a Czech palaeontologist and zoologist, who described *P. aureola*, to which this new species is associated with.

Distribution. This new species is found only from the type locality.

Species of group III (*P. aureola* species group) from other parts of mainland Southeast Asia not recorded for Thailand

Pupina lowi Morgan, 1885

Figs 37K, 40E

Pupina lowi Morgan, 1885: 414, pl. 7, fig. 3a–d. Type locality: Lahat, Kinta [Perak State, Malaysia]. von Möllendorff 1891: 345. Sykes 1903: 197, Gunong Inas, Perak. van Benthem Jutting 1949: 57, Larut Mills, Perak. van Benthem Jutting 1960: 13, limestone hill Kaki Bukit, near kampong Wang Tangga, Perlis [Malaysia]. Maassen 2001: 41.

Pupina (*Tylotoechus*) *lowi*—Kobelt 1902: 317. Laidlaw 1928: 34.

Pupina artata [non Benson]—Berry 1963: pl. 6, fig. 36. Foon et al. 2017: 40, fig. 15b, Ipoh, Perak.

Type material examined. ***Syntype*** MNHN-IM-2000-35846 (1 shell; Figs 37K, 40E) from Lahat, Perak.

Diagnosis. Shell globose; last whorl ca. three quarters of shell height. Apertural lip slightly thickened but not expanded. Parietal tooth sharp, tooth-like, thickened; columellar tooth fin-shaped, thickened, located next to slit-like anterior canal. Posterior canal gradually widening like keyhole.

Differential diagnosis. *Pupina lowi* is most similar to *P. tchehelensis* and *P. brachysoma* in having a sharp, tooth-like, thickened parietal tooth, a fin-shaped, thickened columellar tooth that is located next to a slit-like anterior canal, and a posterior canal that is gradually widening. However, *P. lowi* is different from *P. tchehelensis* by having a more globose shell shape, and different from *P. brachysoma* in that an apertural lip is not expanded.

Distribution. Perak and Perlis States, Malaysia (Maassen 2001).

Remarks. By comparing with the type specimen, the specimens of *P. artata* figured in Berry (1963: pl. 6, fig. 36) and Foon et al. (2017: fig. 15b) from Bat Cave Hill Plot 2, Ipoh, Perak should belong to *P. lowi* (Foon, pers. comm.). The specimen of *P. lowi* figured in BEDO (2017: 91) should constitute a different species as it is different from the syntype figured here in having a smaller, sharper parietal tooth revealing a wide posterior canal and an earlobe-shaped columellar tooth covering the anterior canal. Thus, that specimen should belong to the *P. arula* species group instead (see above).

Pupina dorri dorri **Dautzenberg, 1894**

Figs 36I, J, 40F, 41A

Pupina flava [non Möllendorff]—Morlet 1887: 261. Fischer 1891: 107.

Pupina dorri Dautzenberg, 1894 [1893]: 164, 165, pl. 8, fig. 3, 3a–c. Type locality: montagnes des environs d'Haïphong [Haiphong, Vietnam]. Fischer 1898: 333. Fischer and Dautzenberg 1904: 431, iles du golfe du Tonkin. Dautzenberg and Fischer 1905: 171. Fischer-Piette 1950: 160. Fischer 1963: 33. Do et al. 2015: 126, fig. 5f, Son La Province, Vietnam.

Pupina (*Tylotoechus*) *dorri*—Kobelt 1902: 311.

Type material examined. ***Lectotype*** MNHN-IM-2000-35835 from Haiphong. Paralectotypes MNHN-IM-2000-35836 (7 shells; Figs 36I, 40F) from Haiphong, Vietnam.

Other material examined. NHMUK ex. A.J. Piele Colln. Acc. No. 2242 (3 shells; Figs 36J, 41A) from Haiphong, Vietnam.

Diagnosis. Shell ovate-fusiform; last whorl ca. 70–75% of shell height. Apertural lip slightly thickened but not expanded. Parietal tooth triangular, slightly thickened, covering posterior canal, approaching but not extending beyond the outer margin of apertural lip; columellar tooth fin-shaped, slightly thickened, located next to slit-like anterior canal.

Differential diagnosis. *Pupina dorri* can be distinguished from all other species in the *P. aureola* species group from mainland Southeast Asia by having a triangular, slightly thickened parietal tooth that is covering a posterior canal, and the parietal tooth approaching but not extending beyond the outer margin of apertural lip.

Distribution. Northern Vietnam (Do et al. 2015).

Remarks. As the original description did not explicitly state that the description of this species was based on a single specimen (nor could this be inferred), the designation of a holotype by Fischer-Piette (1950) in fact constitutes a lectotype designation (ICZN 1999: Art. 74.6).

***Pupina tongupensis* Godwin-Austen, 1897**

Figs 37J, 41B

Pupina tongupensis Godwin-Austen, 1897: 41, pl. 69, fig. 5, 5a. Type locality: Tongoop Pass, Arakan Hills, east side [probably refers to Toungup Road and the area on Arakan Hills, the path which connects Toungup, Rakhine State to Padaung, Pyay District, Bago Region, Myanmar].

Pupina (*Tylotoechus*) *tongupensis*—Kobelt 1902: 323. Gude 1921: 197, 198.

Type material examined. ***Syntypes*** NHMUK 1906.4.4.38 (2 shells; Figs 37J, 41B) from Tongoop Pass, Arakan Hills, east side.

Diagnosis. Shell globose; last whorl ca. three quarters of shell height. Apertural lip very slightly thickened, not expanded. Both parietal and columellar teeth thin, sharp, tooth-like; columellar tooth next to slit-like but widening anterior canal.

Differential diagnosis. *Pupina tongupensis* is similar to *P. paviei* in a globose shell shape, but differs in having thin, sharp, tooth-like parietal and columellar teeth, and a slit-like but widening anterior canal

Distribution. Known only from the type locality (Gude 1921).

***Pupina anceyi* Bavay & Dautzenberg, 1899**

Figs 37L, 41C

Pupina anceyi Bavay & Dautzenberg, 1899: 53, 54, pl. 3, fig. 5, 5a. Type locality: Entre Lang-Son [Lang Son Province, Vietnam] et That-Khé [That Khe, Lang Son Province, Vietnam]. Fischer and Dautzenberg 1904: 431. Fischer-Piette 1950: 167. Do et al. 2015: 126, fig. 5e, Son La Province, Vietnam.

Pupina (*Tylotoechus*) *anceyi*—Kobelt 1902: 306.

Eupupina anceyi—Dautzenberg and Fischer 1908: 207, Mo-Xat [west of Quang Uyen, Cao Bang Province, Vietnam].

Type material examined. ***Lectotype*** MNHN-IM-2000-35833 (Figs 37L, 41C) from Lang-Son and That-Khé.

Diagnosis. Shell fusiform; last whorl ca. 65% of shell height. Suture very shallow. Apertural lip highly thickened but not expanded. Parietal tooth triangular, thickened, covering posterior canal, approaching but not extending beyond the outer margin of apertural lip; columellar tooth fin-shaped, thickened, located next to slit-like anterior canal.

Differential diagnosis. *Pupina anceyi* is similar to *P. laffonti* in having a fusiform shell shape with very shallow suture and a fin-shaped, thickened, columellar tooth that is located next to a slit-like anterior canal, but differs in having a triangular, thickened, parietal tooth covering a posterior canal, and the parietal tooth approaching but not extending beyond the outer margin of apertural lip.

Distribution. Northern Vietnam (Do et al. 2015).

Remarks. As the original description did not explicitly state that the description of this species was based on a single specimen (nor could this be inferred), the designation of a holotype by Fischer-Piette (1950) in fact constitutes a lectotype designation (ICZN 1999: Art. 74.6).

Pupina laffonti **Ancey, 1899**

Figs 37M, 41D

Pupina laffonti Ancey in Bavay & Dautzenberg, 1899: 51–53, pl. 3, fig. 4, 4a. Type locality: Ile de Poulo Condor [Con Dao Island, Vietnam]. Fischer and Dautzenberg 1904: 431. Fischer-Piette 1950: 167. Wood and Gallichan 2008: 57, pl. 25, figs 4, v.

Type material examined. ***Lectotype*** MNHN-IM-2000-9656 (Figs 37M, 41D) from Poulo-Condor. Paralectotypes NMW.1955.158.24152 figured in Wood and Gallichan (2008: pl. 25, figs 4, v).

Diagnosis. Shell fusiform; last whorl ca. 70% of shell height. Suture very shallow. Apertural lip highly thickened but not expanded. Parietal tooth sharp, tooth-like, thickened; columellar tooth fin-shaped, thickened, located next to slit-like anterior canal. Posterior canal gradually widening like keyhole.

Differential diagnosis. *Pupina laffonti* is similar to *P. anceyi* in having a fusiform shell shape with very shallow suture, and a fin-shaped, thickened columellar tooth, located next to slit-like anterior canal, but differs in having a sharp, tooth-like, thickened parietal tooth, and a posterior canal that is gradually widening like keyhole.

Distribution. Known only from the type locality (Fischer and Dautzenberg 1904).

Remarks. As the original description did not explicitly state that the description of this species was based on a single specimen (nor could this be inferred), the designation of a holotype by Fischer-Piette (1950) in fact constitutes a lectotype designation (ICZN 1999: Art. 74.6).

***Pupina solidula* Möllendorff, 1901**

Figs 37N, 41E

Pupina (*Tylotechus*) *solidula* Möllendorff, 1901: 81. Type locality: Lang-son [Lang Son Province, Vietnam], Mansongebirge [Mou Son Mountain, northern Vietnam]. Zilch 1957: 45, pl. 2, fig. 14.

Pupina solidula—Fischer and Dautzenberg 1904: 432, Lang-Son; Monts Mauson, Tonkin; ile Ba-Moun, golfe du Tonkin [Bah Mun Island].

Type material examined. ***Lectotype*** SMF 109915/1 (Figs 37N, 41E) from Lang Son, Tonkin.

Diagnosis. Shell yellow, ovate-fusiform; last whorl ca. three quarters of shell height. Suture very shallow. Apertural lip highly thickened but not expanded. Parietal tooth fin-shaped, thickened, not covering posterior canal; columellar tooth fin-shaped, thickened, located next to slit-like anterior canal.

Differential diagnosis. *Pupina solidula* can be distinguished from all other species in the *P. aureola* species group from mainland Southeast Asia by having a glossy, yellow shell with very shallow suture.

Distribution. Northeast Vietnam (Fischer and Dautzenberg 1904).

***Pupina brachysoma* Ancey, 1904**

Figs 36M, 41F

Pupina brachysoma Ancey in Bavay & Dautzenberg, 1904 [1903]: 230, 231, pl. 10, figs 15, 16. Type locality: Haut-Tonkin [northern Vietnam]. Fischer-Piette 1950: 171. Wood and Gallichan 2008: 31, pl. 25, figs 5, vi.

Type material examined. ***Lectotype*** MNHN-IM-2000-9652 (Figs 36M, 41F) from Haut Tonkin. Paralectotypes NMW.1955.158.24153 figured in Wood and Gallichan (2008: pl. 25, figs 5, vi).

Diagnosis. Shell ovate-fusiform; last whorl ca. three quarters of shell height. Apertural lip somewhat thickened, slightly expanded. Parietal tooth sharp, tooth-like, thickened; columellar tooth fin-shaped, slightly thickened, located next to slit-like anterior canal. Posterior canal widened.

Differential diagnosis. *Pupina brachysoma* is most similar to *P. tchehelensis* and *P. lowi* in having a sharp, tooth-like, thickened parietal tooth, a fin-shaped, thickened columellar tooth that is located next to a slit-like anterior canal, and a posterior canal that is gradually widening. However, *P. brachysoma* is different from both *P. tchehelensis* and *P. lowi* by a more ovate-fusiform shell shape, and a less thickened but slightly expanded apertural lip. *Pupina brachysoma* is also similar to *P. dorri dorri* in shell shape, but differs in having a gradually widening posterior canal.

Distribution. Known only from the type locality (Bavay and Dautzenberg 1904).

Remarks. As the original description did not explicitly state that the description of this species was based on a single specimen (nor could this be inferred), the designation of a holotype by Fischer-Piette (1950) in fact constitutes a lectotype designation (ICZN 1999: Art. 74.6).

Pupina douvillei Dautzenberg & Fischer, 1906

Fig. 37O

Pupina douvillei Dautzenberg & Fischer, 1906 [1905]: 440, pl. 10, figs 10–12. Type locality: Ha-Giang, Tonkin [Vietnam]. Fischer 1963: 33.

Type material examined. ***Holotype*** MNHN-IM-2000-35532 (Fig. 37O) from Ha-Giang, Tonkin.

Diagnosis. Shell ovate-fusiform; last whorl ca. three quarters of shell height. Apertural lip thickened but not expanded. Parietal tooth fin-shaped, thickened, located next to wide posterior canal; columellar tooth fin-shaped, thickened, located next to slit-like anterior canal.

Differential diagnosis. *Pupina douvillei* can be distinguished from all other species in the *P. aureola* species group from mainland Southeast Asia by having a high spired shell and a fin-shaped, thickened parietal tooth that is located next to a wide posterior canal.

Distribution. Known only from the type locality (Fischer 1963).

Remarks. As *P. douvillei* was described based on a single specimen as explicitly stated in the original description, that specimen is the holotype fixed by monotypy (ICZN 1999: Art. 73.1.2).

Species from other parts of mainland Southeast Asia with uncertain affiliation

Pupina porcellana Rochebrune, 1881

Pupina porcellana Rochebrune, 1881: 62. Type locality: Montagnes de Chaudoe, Cambodge [Chau Doc, An Giang Province, Vietnam]. Fischer 1891: 108. Fischer and Dautzenberg 1904: 431. BEDO 2017: 93.

Remarks. This species has an uncertain affiliation as there is no figure in the original description or in other later works. The type series were searched for in March 2022 and could not be located in the MNHN by B. Páll-Gergely or P. Bouchet, and were deemed presumably lost (B. Páll-Gergely and P. Bouchet, pers. comm.).

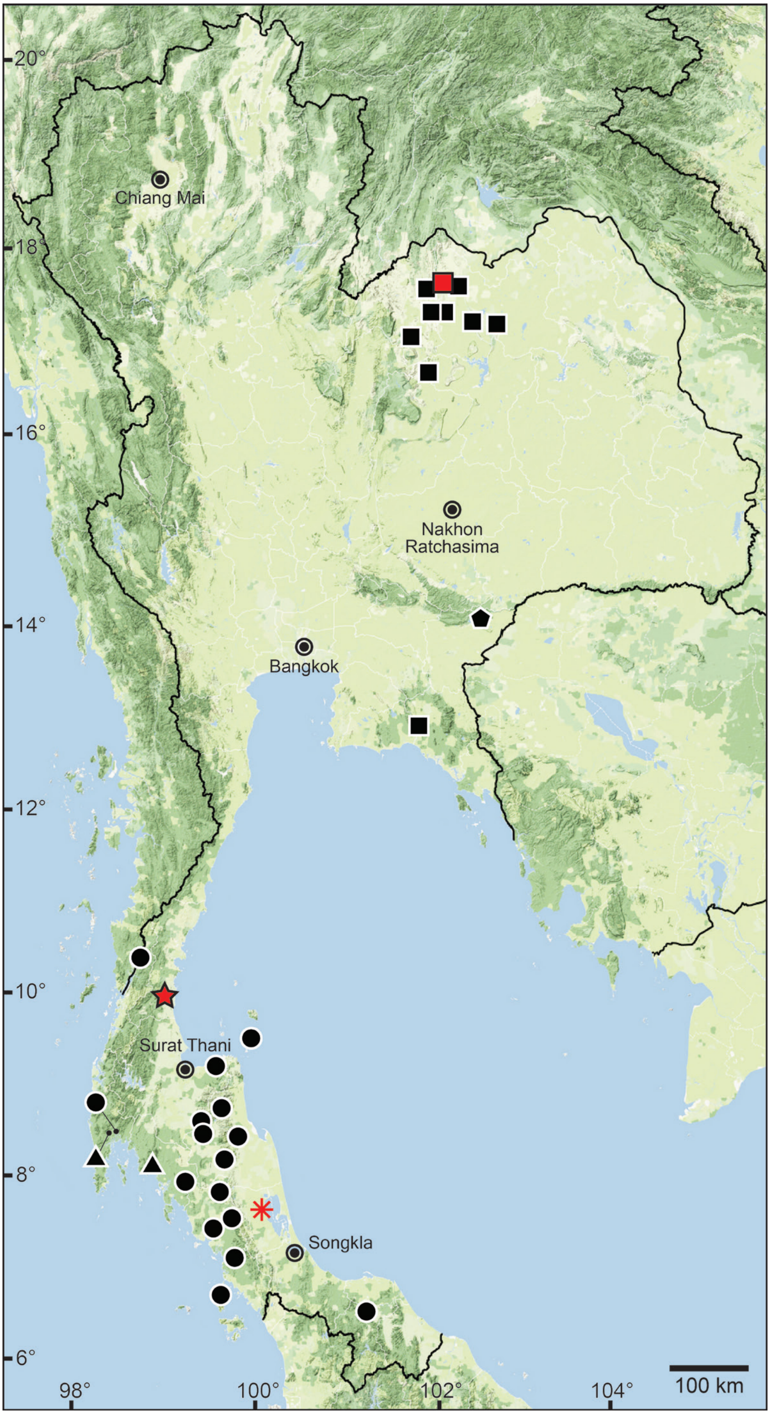

Figure 35. Distribution map of the *Pupina aureola* species group: *Pupina aureola* (circle), *Pupina paviei* (pentagon), *Pupina tchehelensis* (triangle), *Pupina dorri isanensis* ssp. nov. (square), *Pupina latisulci* sp. nov. (asterisk), and *Pupina stoliczkai* sp. nov. (star). Each red symbol indicates the type locality of its respective taxon.

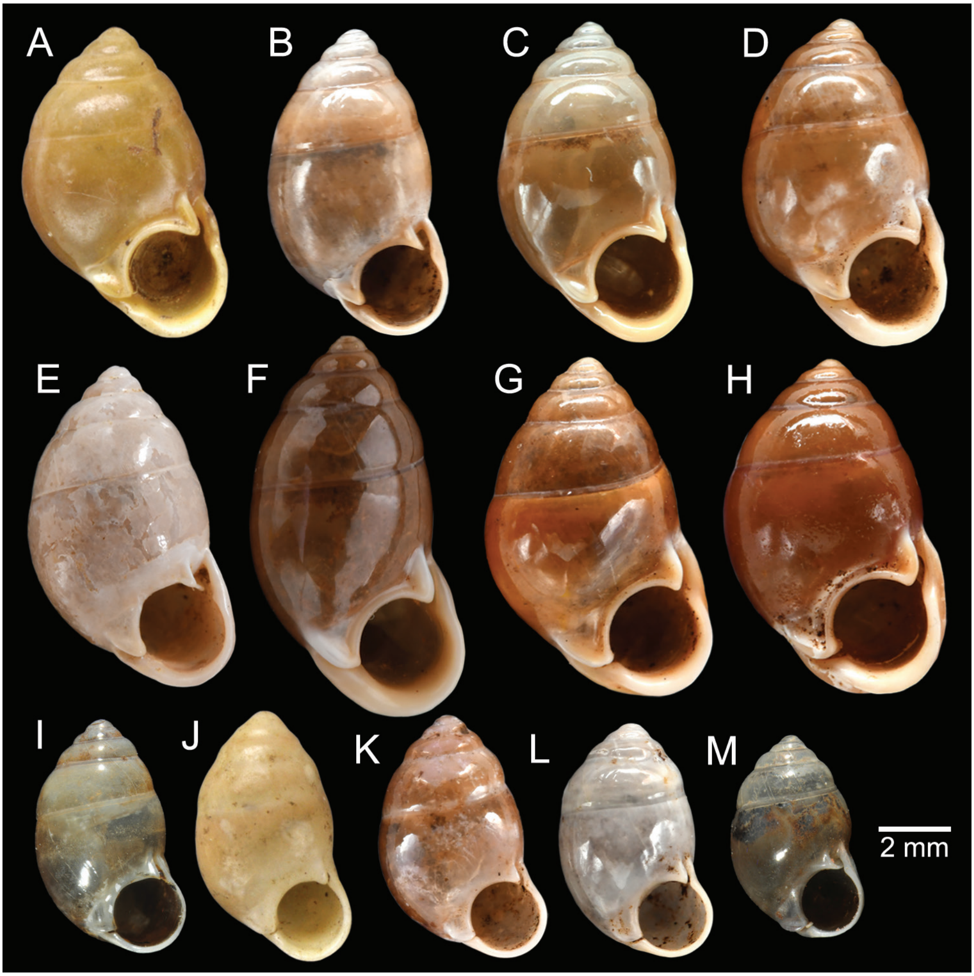

Figure 36. Shells of *Pupina aureola* species group from mainland Southeast Asia **A–F** *Pupina aureola* **A** possible syntype NHMUK 1988.12.4.101 and specimens **B** CUMZ 12124 **C** CUMZ 12126 **D** CUMZ 12130 **E** CUMZ 12133, and **F** CUMZ 12121 **G, H** *Pupina stoliczkai* sp. nov. **G** holotype CUMZ 12147/1 and **H** paratype NHMUK 20210336 **I, J** *Pupina dorri dorri* **I** paralectotype MNHN-IM-2000-35836 and **J** specimen NHMUK ex. A.J. Piele Colln. Acc. No. 2242 **K, L** *Pupina dorri isanensis* spp. nov. **K** holotype CUMZ 12140/1 and **L** specimen CUMZ 12137 **M** *Pupina brachysoma*, lectotype MNHN-IM-2000-9652. Photo: P. Maestrati, MNHN (**I, M**)

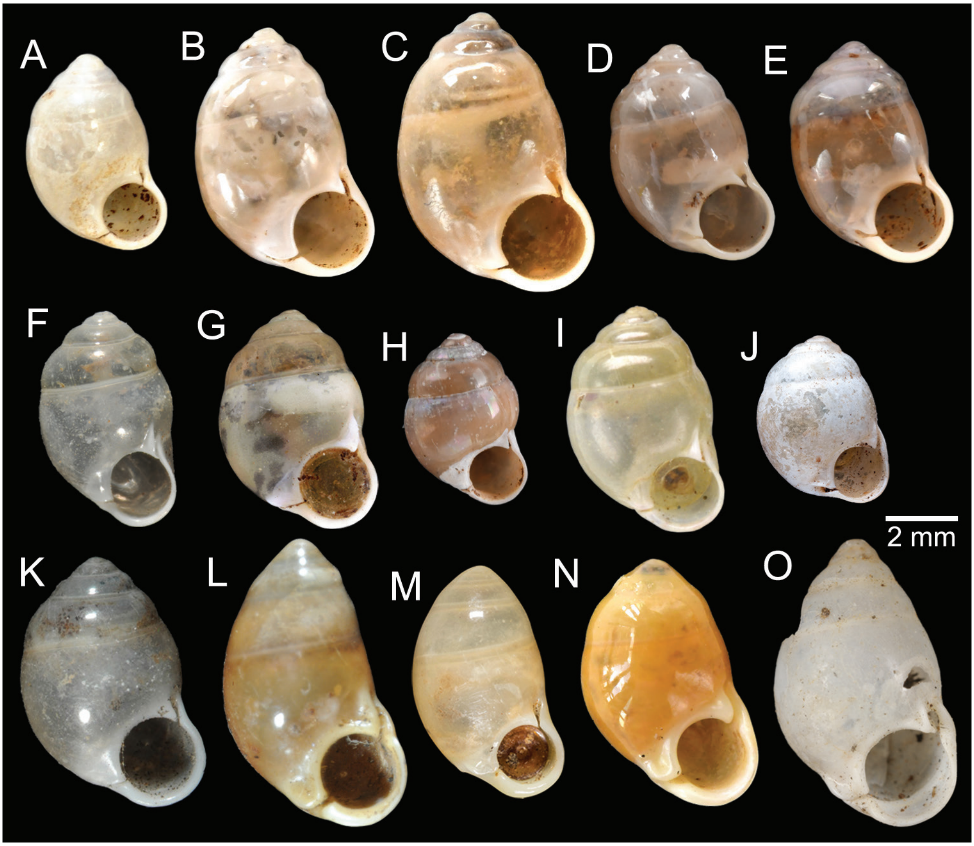

Figure 37. Shells of *Pupina aureola* species group from mainland Southeast Asia. **A–C** *Pupina tchehelensis*: specimens **A** SMF 109947/6 **B** CUMZ 12135, and **C** CUMZ 12136 **D, E** *Pupina latisulci* sp. nov. **D** holotype CUMZ 12146/1 and **E** paratype CUMZ 12146/2 **F–I** *Pupina paviei* **F** paralectotype MNHN-IM-2000-35837 **G** paralectotype RBINS 525404, and specimens **H** CUMZ 12134 and **I** NHMUK ex. Dautzenberg coll. **J** *Pupina tongupensis*, syntype NHMUK 1906.4.4.38 **K** *Pupina lowi*, syntype MNHN-IM-2000-35846 **L** *Pupina anceyi*, syntype MNHN-IM-2000-35833 **M** *Pupina laffonti*, syntype MNHN-IM-2000-9656 **N** *Pupina solidula*, lectotype SMF 109915/1 **O** *Pupina douvillei*, holotype MNHN-IM-2000-35532. Photo: M. Caballer, P. Maestrati, MNHN (**F, K–O**), F. Trus, RBINS (**G**), J. Ablett, H. Taylor, NHM (**J**).

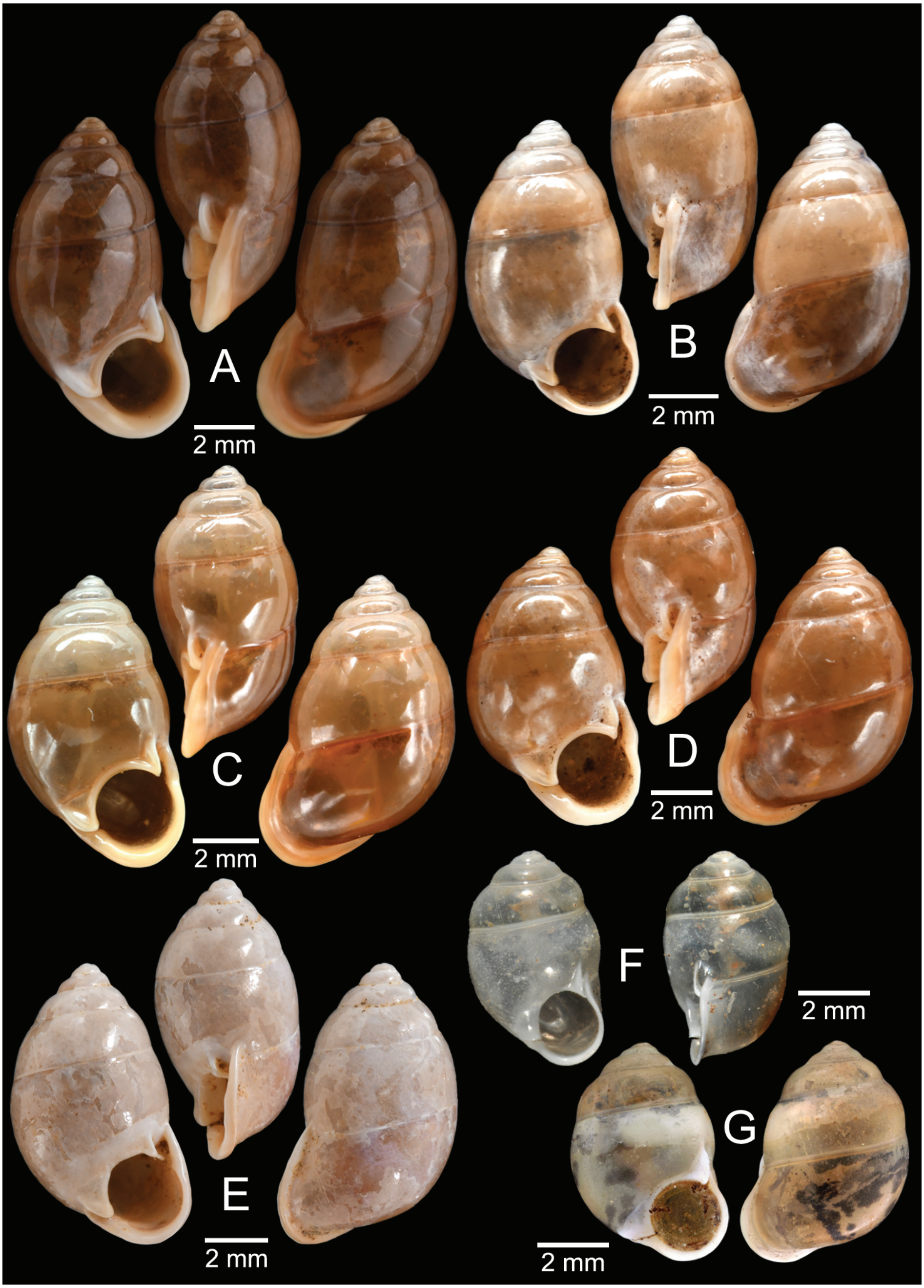

Figure 38. A–E *Pupina aureola*: specimens **A** CUMZ 12121 from Tham Thong Panara Temple, Nakhon Sri Thammarat **B** CUMZ 12124 from Talot Cave, Nakhon Sri Thammarat **C** CUMZ 12126 from Khao Huai Haeng Temple, Trang **D** CUMZ 12130 from Sra Morakot, Krabi, and **E** CUMZ 12133 from Khantiphol Cave, Satun **F, G** *Pupina paviei*: paralectotypes **F** MNHN-IM-2000-35837 from Chaîne de l'Eléphant, Kampot, Cambodge and **G** RBINS 525404 from Kampot et forêts de la chaîne de l'Eléphant, Cambodge et Kamchay. Photo: P. Maestrati, MNHN (**F**), F. Trus, RBINS (**G**).

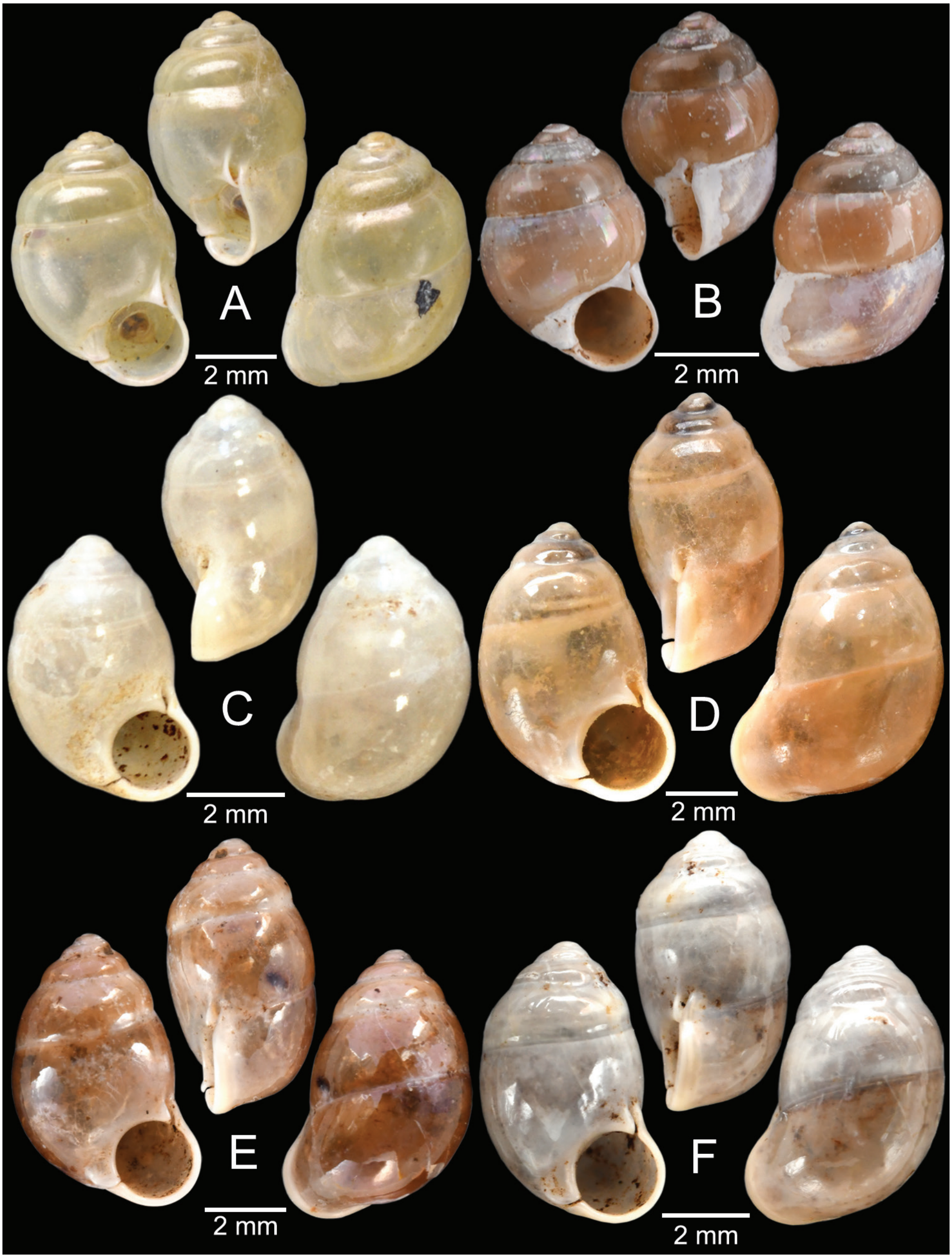

Figure 39. A, B *Pupina paviei*: specimens **A** NHMUK ex. Dautzenberg coll. from Kampot, Cambodge and **B** CUMZ 12134 from Lalu, Sa Kaeo **C, D** *Pupina tchehelensis*: specimens **C** SMF 109947/6 from Bukit Pondong, Perak and **D** CUMZ 12136 from limestone mountain, Phang Nga **E, F** *Pupina dorri isanensis* ssp. nov. **E** holotype CUMZ 12140/1 and **F** specimen CUMZ 12137 from Khao Wang Pha, Nong Bua Lam Phu.

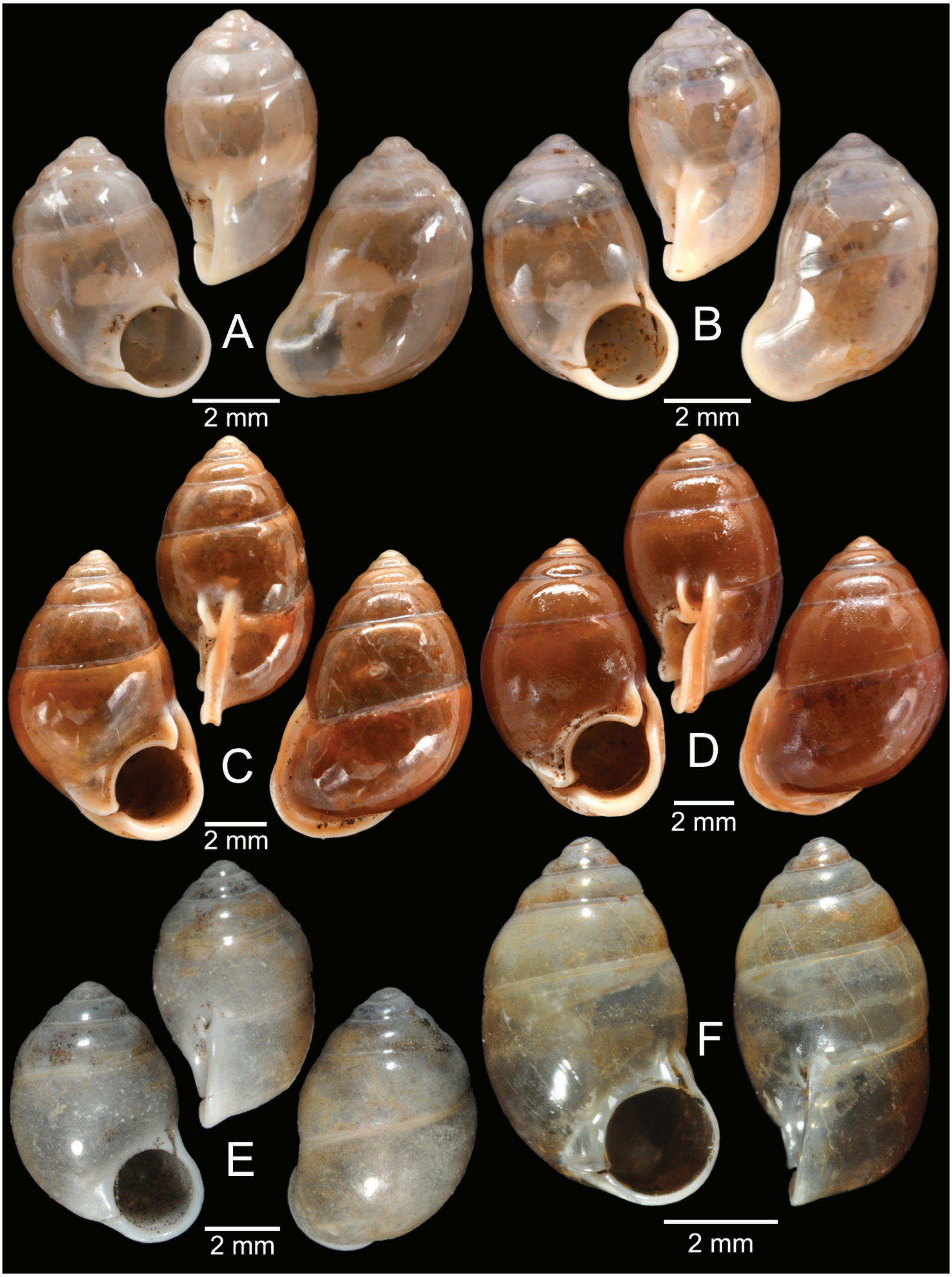

Figure 40. A, B *Pupina latisulci* sp. nov. **A** holotype CUMZ 12146/1 and **B** paratype CUMZ 12146/2 from Khao Ok Talu, Phatthalung **C, D** *Pupina stoliczkai* sp. nov. **C** holotype CUMZ 12147/1 and **D** paratype NHMUK 20210336 from Wat Ratburana School, Chumpon **E** *Pupina lowi*, syntype MNHN-IM-2000-35846 from Lahat, Perak **F** *Pupina dorri dorri*, paralectotype MNHN-IM-2000-35836 from Haiphong, Vietnam. Photo: P. Maestrati, MNHN (**E, F**).

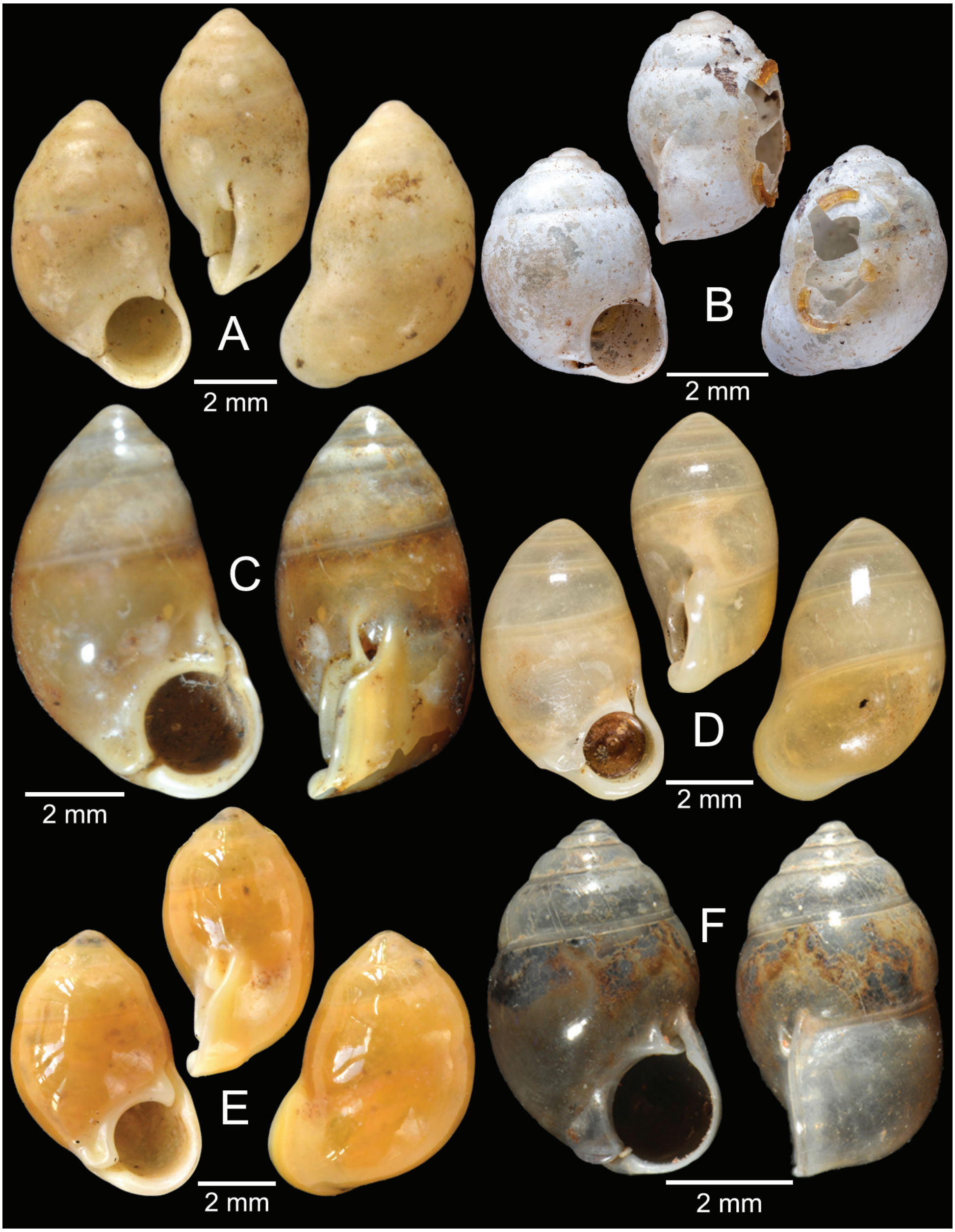

Figure 41. A *Pupina dorri dorri*, specimen NHMUK ex. A.J. Piele Colln. Acc. No. 2242 from Haiphong, Vietnam **B** *Pupina tongupensis*, syntype NHMUK 1906.4.4.38 from Tongoop Pass, Arakan Hills, east side **C** *Pupina anceyi*, syntype MNHN-IM-2000-35833 from Lang-Son and That-Khé **D** *Pupina laffonti*, syntype MNHN-IM-2000-9656 from Poulo-Condor **E** *Pupina solidula*, lectotype SMF 109915/1 from Lang Son, Tonkin **F** *Pupina brachysoma*, syntype MNHN-IM-2000-9652 from Haut Tonkin. Photo: J. Ablett, H. Taylor, NHM (**B**), P. Maestrati, M. Caballer, MNHN (**C–F**).

Discussion

This is the first comprehensive study focusing on the family Pupinidae in Thailand since the checklists of Thai land snails by Hemmen and Hemmen (2001) and BEDO (2017). This study reports a total of 30 Thai nominal species with two subspecies from seven pupinid genera, an increase from 12 species from four genera in Hemmen and Hemmen (2001), and from 25 species with one subspecies from five genera in BEDO (2017). The updated information in this study includes the recent discovery of *Pseudopomatias caligosus* from northern Thailand (Páll-Gergely and Hunyadi 2018b) with the discovery of two new *Pseudopomatias* species and three new records (*Coptocheilus sumatranus*, *Pupinella mansuyi*, and *Rhaphaulus tonkinensis*). Five species and one subspecies of *Pupina* are newly described herein after the discovery of new *Pupina* species from Thailand more than a century ago. BEDO (2017) reported three *Pupina* species, *P. excisa*, *P. lowi*, and *P. porcellana*, which were not discovered in our survey. Comparing our faunal list to the record of land snails from West Malaysia, Maassen (2001) reported a total of 15 species from five pupinid genera, wherein *Pseudopomatias* and *Pupinella* were not reported. Other related pupinid genera, i.e., *Streptaulus* (which is related to *Rhaphaulus*) and *Vargapupa* (related to *Pseudopomatias*), were not discovered from Thailand in this study, suggesting that these genera are rare and restricted to limited geographic ranges (Páll-Gergely et al. 2014, 2015, 2017; Páll-Gergely and Grego 2019). More thorough investigations, especially along the country's border, combined with other sampling methods (e.g., litter sieving) may uncover more species or even genera in the family Pupinidae.

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REVIEW ARTICLE

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Available names for *Rangifer* (Mammalia, Artiodactyla, Cervidae) species and subspecies

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Abstract

Advancements in molecular and phylogenetic analysis have revealed the need for greater taxonomic resolution since *Rangifer* (Reindeer and caribou: Cervidae) was last revised in 1961. Recent literature shows that many of the subspecies and several species synonymised out of existence are, in fact, valid, some names have been misapplied, and new subspecies-level clades are in need of description. This paper reviews available names for recently defined ecotypes of reindeer and caribou in compliance with ICZN rules for zoological nomenclature.

Keywords

caribou, Reindeer, systematics, taxonomy

Introduction

Eighteen *Rangifer* species or subspecies have been named in North America; 31 in Europe and Asia (Fig. 1; see Suppl. material 1: Synonymy). The Mammal Diversity Database, a digital, publicly accessible, and regularly updated list of all mammalian species (Burgin et al. 2018), lists 51 synonyms of *Rangifer tarandus* L., 1758. Although many were unjustified by evolving standards and definitions of species (e.g., Mayr 1963; Masters and Spencer 1989; Nixon and Wheeler 1990), the DNA revolution has revealed diversity at the species and subspecies levels that is not reflected in current classifications.

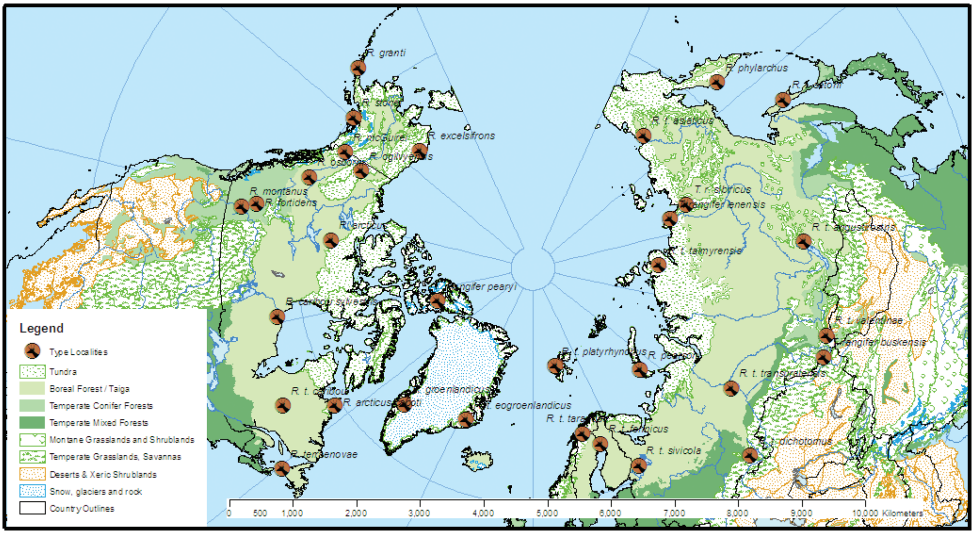

Figure 1. All *Rangifer* type localities overlaid on WWF terrestrial biomes (Olson et al. 2001).

Rangifer species and subspecies are called reindeer in Eurasia and caribou in North America. As species concepts evolved, Ellerman and Morrison-Scott (1951) lumped all of the Eurasian species into one and implied the same for North America by giving the distribution of *Rangifer tarandus* as "Arctic regions of Old and New Worlds … Arctic regions of North America, Greenland included." Banfield (1961) accepted this for the species and further lumped subspecies, leaving just four in Canada or six, counting the extinct Dawson caribou of Haida Gwai and the introduced Eurasian reindeer. Banfield reduced the caribou of Alaska and Yukon, which formerly had six species or subspecies (Fig. 2), to one subspecies, *R. t. granti*. Now even *granti* is gone, subsumed into *groenlandicus*.

McTaggert Cowan (1962) objected immediately, finding that Banfield (1961), having lumped valid subspecies into one another but still needing to distinguish obviously different kinds of caribou, created a sub-subspecific category, "demes", a concept not applicable in this context; had used inappropriate statistical methods to summarise and compare morphological data to define subspecies and "demes"; did not provide quantitative characteristics differentiating between adjoining subspecies or demes; failed to show how the "graphs and tables … support …the conclusions drawn"; and even "exceeded his quota" on spelling and grammar mistakes.

Many ungulate taxonomists (e.g., Corbet 1978; Gauthier and Farnell 1986; Groves and Grubb 1987, 2011; Geist 1998, 2007; Mallory and Hillis 1998; Couturier et al. 2010) agreed that Banfield's (1961) scheme did not reflect subspecies diversity based on morphological measurements.

Despite clear morphological distinctions and profound ecological and behavioural differences, Canadian biologists have felt taxonomically bound by Banfield's (1961)

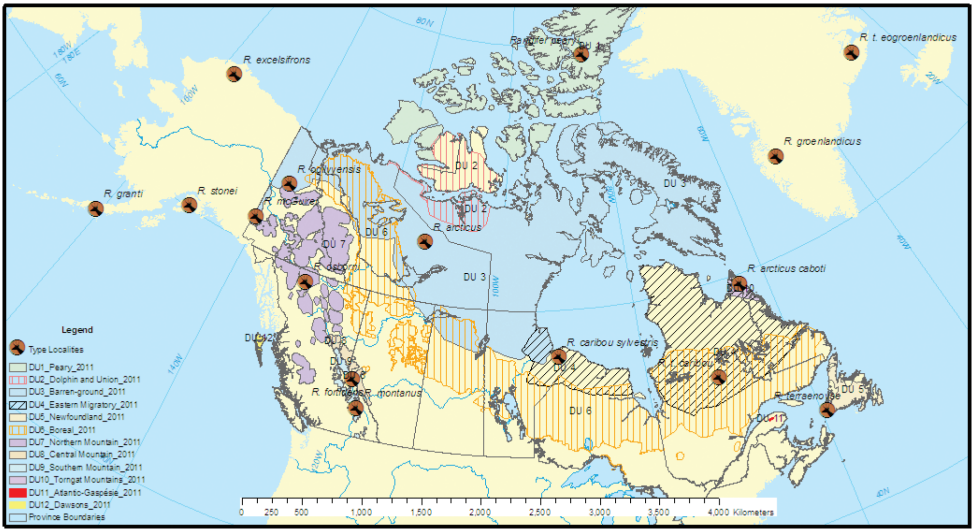

Figure 2. COSEWIC designated units of caribou overlain with *Rangifer* type localities in North America.

inadequate and obsolete classification, perhaps in part because he entrenched it further in 'Mammals of Canada' (Banfield 1974). Needing, for management and conservation, to continue distinguishing these different caribou, Canadian biologists began referring to distinctive populations as "ecotypes" (e.g., Nagorsen 1990). Since ecotypes are not phylogenetically based, however, they cannot substitute for taxonomy.

Not so elsewhere: in their seminal works, 'Mammalian Species of the World', Wilson and Reeder (2005) followed by Wilson and Mittermeier (2011), revised the subspecies under the circumpolar *Rangifer tarandus*, citing Markov et al. (1994) and Geist (2007), to validate three subspecies in North America and eight in Eurasia that Banfield (1961) had synonymised.

Molecular analyses are showing how discrete, diagnosable caribou populations differ from Banfield's (1961) taxonomy. COSEWIC (2011), noting that Banfield (1961) "is out-of-date with respect to current science and does not capture the variability of caribou across their range in Canada," defined 12 "designatable units" (DU: Fig. 2) for conservation and management. This designation, an adaptation of "evolutionary significant units" (cf. Waples 1995), makes each a "wildlife species" within the meaning of the Species at Risk Act, which provides for recognition of intraspecific populations (cf. Harding 2020). DUs were based on biological, morphological, ecological and, importantly, genetic data; their ranges largely paralleled those of currently accepted or previously named subspecies (or species), without naming them as such, and with new English names.

The purpose of this paper is to review available Latin and English names for distinct reindeer and caribou populations identified by molecular data.

Materials and methods

This review is based on both historic and recent literature. Maps were made using ArcMAP GIS layers (ESRI 2004) including the World Wildlife Fund terrestrial biomes (Olson et al. 2001). There was no research on live animals.

Results

Caribou evolution

Rangifer originated in the early Pleistocene, a 2+ million-year period of multiple glacier advances and retreats. Several named *Rangifer* fossils in Eurasia and North America predate the evolution of *Rangifer tarandus* sensu lato (Croitor 2018). *Rangifer constantini* Flerov, 1934, for example, was described from late Pleistocene deposits throughout central Eurasia. Despite its adaptations for open-landscape grazing, it was not adapted to very cold Arctic conditions. Archaeologists distinguish modern tundra reindeer from their ancestors, in part, on the basis of the shape of their nasal bones:

> *"Unlike modern reindeer, the volume of nasal cavity of* R. tarandus constantini *is rather small indicating that the Paleolithic reindeer did not evolve yet adaptations to cold air breathing (Flerov 1952). The function of increased nasal cavity is air warming and moistening before its entrance to the trachea and lungs. Nasal cavity is correlated with muzzle breadth and the maximal volume of nasal cavity is recorded in modern arctic reindeer (Croitor 2018)."*

The oldest North American *Rangifer* fossil is from Yukon, 1.6 million years before present (BP) (Harington 2011). A fossil skull fragment from Süßenborn, Germany, *R. arcticus stadelmanni* Kahlke, 1963, with "rather thin and cylinder-shaped" (Kahlke 1963) antlers (this refers to a fundamental difference between "arcticus-type" and woodland caribou antlers, which are flattened in cross-section), dated to the middle Pleistocene (Günz) period, 680,000 to 620,000 BP (Croitor 2010). *Rangifer* fossils become increasingly frequent in circumpolar deposits beginning with the Riss glaciations (Banfield 1961), the second youngest of the Pleistocene epoch, roughly 300,000–130,000 BP. By the 4-Würm period (110,000–70,000 to 12,000–10,000 BP) its European range was extensive (Kurtén 1968), supplying a major food source for prehistoric Europeans.

Geist (1998) notes that European prehistoric cave paintings represent both tundra and forest forms, the latter either *R. t. fennicus* or *R. t. angustirostris*, an eastern Siberian forest form (Fig. 3). DNA analysis showed that people independently domesticated reindeer at least twice, both from tundra forms after the last glacial maximum (LGM), in Fennoscandia and western Russia, and possibly also eastern Russia (Røed et al. 2008; Weldenegodguad et al. 2020).

North American fossils outside of Beringia that predate the LGM are of Rancholabrean age (240,000–11,000 years BP) and occur along the fringes of the Rocky Mountain and Laurentide ice sheets as far south as northern Alabama; and in Sangamonian deposits (~ 100,000 years BP) from western Canada (Geist 1998 and references therein).

Subspecies and ecotypes

Rangifer tarandus subspecies accepted by the American Society of Mammologists and referenced to Wilson and Mittermeier (2011) are: Eurasia (Fig. 3): *tarandus*, *buskensis*, *fennicus*, *pearsoni*, *phylarchus*, *platyrhynchus* and *sibiricus*; and North America (Fig. 2): *caboti*, *caribou*, *dawsoni*, *groenlandicus*, *osborni*, *pearyi*, and *terraenovae*. Authorities of all taxa cited in the text are given in Suppl. material 1: Synonymy.

Europe

Russian scholars (e.g., Kharzinova et al. 2018; Mizin et al. 2018; Rozhkov et al. 2020; Vasilchenko et al. 2020) recognise 4–8 subspecies within Russia (Fig. 3): those mentioned above plus *angustirostris*. Of these, *fennicus*, *valentinae*, *angustrostris*, and *phylarchus* are forest reindeer and are larger, longer-legged, and darker and have shorter, heavier, and more branched antlers than tundra reindeer (Baskin 1986; Rozhkov et al. 2020). Although Wilson and Reeder (2005), followed by Wilson and Mittermeier (2011), chose *R. t. buskensis* Millais, 1915, as a senior synonym for *R. t. valentinae*, Millais (1915a) is not a valid taxonomic authority (see Discussion).

Eurasian Tundra reindeer

Because of Banfield's (1961) lumping, Western scholars have often not distinguished between true *R. t. tarandus* of the western European mountains, and the far more widespread *R. t. sibiricus*. For this reason, papers on genetic diversity must be read carefully to determine the provenance of the specimens.

Although Eurasian tundra reindeer and North American barren-ground caribou are distinguishable by different allele frequencies at several loci, they have low genetic differentiation (Cronin et al. 2005). They have diagnostically different pelage patterns and other morphological differences (see Geist 1998 for descriptions).

The "mountain reindeer" of Norway (and formerly Sweden and Finland) are tundra reindeer (*R. t. tarandus*) that have adapted to high-elevation alpine tundra with snow characteristics similar to Arctic tundra: hard-packed, shallow snow that they can paw through to reach terrestrial lichens. The haplotype composition of reindeer from southern Norway is similar to, but "substantially genetically different from" that of the tundra reindeer from western Russia, *R. t. sibiricus* (von Schreber, 1784) (Baranova et al. 2012).

Figure 3. *Rangifer* type localities in Eurasia overlaid on WWF terrestrial biomes (Olson et al. 2001).

Rangifer t. sibiricus includes 19 herds, named for their calving grounds, from Arkhangelsk in European Russia to Chukotka, Siberia (Mizin 2018; Rozhkov et al. 2020). Although domestic reindeer descended from tundra types, there is a "clear genetic differentiation between domestic and wild reindeer populations" with ~ 6% introgression by wild reindeer into domestic clades and none the other way (Kharzinova et al. 2018; Rozhkov et al. 2020). There is little genetic difference among wild tundra populations of *R. t. sibiricus* in Taymyr, northern Yakutia, and Chukotka (Kharzinova et al. 2018).

Based on mtDNA, wild reindeer in Genhe, north of the Greater Khingan Mountains in Heiliongjiang, China (Temperate Coniferous Forest zone, Fig. 3), are of Beringian-Eurasian lineage semi-domesticated by the Ewenki people that lost their migratory habits, not forest reindeer as previously supposed (Wang et al. 2019; Ju et al. 2020).

Svalbard reindeer

Despite Lydekker's (1915) attempt to bring it under *R. tarandus*, Sokolov (1937, 1963) insisted that its skull shape, especially the rostrum, and the dentition, were different enough to maintain *R. platyrhynchus* Lönnberg, 1909 as a species. Svalbard (and the extinct east Greenland and Peary's) caribou derived from ancient Beringian-Eurasian pre-glacial populations, based on shared mtDNA haplotypes, but evolved in separate refugia during the LGM (Flagstad and Røed 2003; Kvie et al. 2016). Svalbard reindeer (with West Greenland caribou; see below) are the most genetically distinct of all *Rangifer* subspecies (average genetic differentiation [Fixation Index, F_{ST}] 41% to all other reindeer and caribou); they are not, however, closely related to each other, with a 69% genetic differentiation between them (Yannic et al. 2013). The large genetic differentiation qualifies Svalbard reindeer as *R. platyrhynchus* Lönnberg, 1909 (Miller 1912a).

Russian Arctic archipelago

Based on mtDNA control region sequences, reindeer of the High Arctic archipelagos of Franz Josef Land and Novaya Zemlya, *R. t. pearsoni* Lydekker, 1902, descended from wild tundra reindeer from the Eurasian mainland after the LGM, but before humans could have brought domesticated reindeer (Kvie et al. 2016). Reindeer occupied Franz Josef Land briefly, having migrated there after the Holocene climatic optimum (~ 6,000–4,500 years ago) when the climate again became colder and the sea-ice more persistent, and became extinct historically (Mizin et al. 2018). Novaya Zemlya reindeer occupied the island only 7,000–5,000 years ago and were described by their distinctive phenotypical appearance (Lydekker 1902); however, today's population is mostly feral domestic reindeer, the endemic *R. t. pearsoni* having either not survived or the few remaining individuals mixed with domestic reindeer (Mizin et al. 2018 and references therein).

Kamchatka reindeer

The Okhotsk or Kamchatka reindeer, *R. t. phylarchus* Hollister, 1912, has pelage patterns and antler formation more like Canadian barren-ground caribou than other Eurasian subspecies, prompting Geist (1998) to conclude that, "This is no reindeer, but a caribou." It probably dispersed from Beringia in the late Pleistocene in a "second radiation into Siberia", after Canadian and Eurasian forms had evolved distinctive patterns and adaptations (Geist 1998). Rozhkov et al. (2020) showed that wild reindeer from Kamchatka cluster separately from those living west of the Sea of Okhotsk, which are indistinguishable genetically from the Jano-Indigirka, East-Siberian taiga, and Chukotka populations of *R. t. sibiricus* (von Schreber, 1784). The range of Kamchatka reindeer therefore should be restricted to the Kamchatka Peninsula.

Forest reindeer

Finnish or European forest reindeer, *R. t. fennicus* Lönnberg, 1909, was described from Finnish Lapland (Fig. 3). Ellerman and Morrison-Scott (1951) synonymised it with the Kerelian forest reindeer *R. t. silvicola* Hilzheimer, 1936 and Siberian forest forms *R. t. transuralensis* Hilzheimer, 1936, *R. t. dichotomus* Hilzheimer 1936, and *R. t. angustirostris* Flerov, 1932 as junior synonyms. That it is considerably larger than *R. t. tarandus* "can hardly be due to nutritional factors alone"; it also has:

> *"significantly longer legs…[that] are an important adaptation to taiga conditions, where the snow cover is usually deep and soft. The mountain types [*R. t. tarandus *in Norway] have evolved in areas with hard-packed tundra snow, and consequently the semi-domestic reindeer have difficulty surviving in coniferous forests, especially in winters with deep, soft snow (Nieminen and Helle 1980)."*

Rangifer t. fennicus has statistically significant cranial differences from tundra reindeer, particularly its arched nasal bones (flattened in tundra reindeer: Banfield 1961). Its antlers are "…reminiscent of barren-ground antlers, but with oval beams and a bez tine set well above the brow tine…shaped like tundra-type antlers but more massive and show some palmation" (Geist 1998). Its pelage pattern is similar (see Geist 1998 for descriptions).

Rangifer t. fennicus evolved in isolation from the tundra type in a separate western European refugium and adapted to forest environments; it shares no mtDNA haplotypes with any North American caribou (Flagstad and Røed 2003; Røed 2005).

Between wild tundra and taiga reindeer (subspecies not stated; presumably *R. t. fennicus* sensu lato) pairwise F_{ST} values, using a "genome-wide bovine SNP genotyping array", averaged 3.8%–9.4%, "consistent with their morphological and ecological differences" (Kharzinova et al. 2018). Weldenegodguad et al. (2020), based on microsatellites, also found that Finnish reindeer clustered separately from all other ecotypes (Eurasia tundra, Alaska, and Svalbard). Genetic distances (see Suppl. material 2: Genetic distance) and differences in morphology and ecology between *fennicus* and *tarandus* suggest that the former should be returned to full species status, with subspecies *R. fennicus fennicus*, *R. f. valentinae*, and possibly *R. f. angustirostris*.

Rangifer t. angustirostris, the East Siberian forest reindeer, currently numbers ~ 1,000 animals, distributed east of Lake Baikal (Mizin 2018). Its status, whether more allied to *fennicus* than to *sibiricus*, is best "left in doubt until data on its genetics become available" (Rozhkov et al. 2020).

Croitor (2010) hypothesised that *R. t. fennicus* evolved from *Cervus geuttardi* Desmarest, 1822, a reindeer that adapted to forest habitats in western Europe as forests expanded during an interglacial period before the LGM (the Würmian or Weichsel glaciation); *geuttardi* was later replaced by *R. constantini*, a more evolved tundra form (cf. Baranova et al. 2016), in a second immigration 19,000–20,000 years ago when the LGM turned its forest habitats into tundra, while *fennicus* survived in isolation in south-western Europe. If correct, *fennicus* does not share a common ancestor with *R. tarandus* and cannot be conspecific. Its name would be *Rangifer fennicus* Lönnberg (Miller 1912a).

Wild reindeer from Murmansk/Kola Peninsula are forest reindeer, *R. t. fennicus*, sharing a clade with those from Karelia and Arkhangelsk; these share two haplotypes with domestic reindeer from the same regions, but show only a low incidence of hybridisation, indicating ancient introgression (Baranova et al. 2016; Korolev et al. 2017; Vasilchenko et al. 2020).

The Altai-Sayan forest reindeer (*Rangifer tarandus valentinae* Flerov, 1933) is a montane form whose ecology parallels that of British Columbia's mountain caribou (see below). It migrates altitudinally in dense coniferous forests at elevations of 400–1,500 m, where snow cover is 130–250 cm, and forages arboreal lichens in winter (Baskin 1986). Its mating system also is similar to that of British Columbia mountain caribou: males guard 3–5 females during rutting season and calving is dispersed in alpine habitats (Shaposhnikov 1955, cited by Sobansky 1976). It has a unique mitochondrial genome and shows no signs of introgression of domestic reindeer mtDNA (Vasilchenko et al. 2020). Its genetic differentiation (using a genome-wide genotyping array to compare single nucleotide polymorphism, SNP, markers) from three populations of putative *R. t. sibiricus* is F_{ST} = 3.1%–3.5% (Kharzinova et al. 2018). See Geist (1998) for descriptions of pelage patterns.

Interestingly, the two forest forms, *fennicus* and *valentinae*, cluster together as sister clades, based on mtDNA haplotypes, even though separated by 3,800 km and with the East European Taiga population of *sibiricus* between them; and these two form a sister clade with a Siberian taiga population of *sibiricus* to the exclusion of *tarandus*, *pearsoni*, and *phylarchus* (Rozhkov et al. 2020). This qualifies them as *R. fennicus valentinae*. Davydov et al. (2007) also united *valentinae* with *fennicus* as closely-related subspecies that clustered apart from tundra and Arctic island forms in Eurasia and North America.

North America

Early genetic analyses showed two major lineages of caribou in North America: migratory barren-ground caribou, whose ancestors survived the LGM in Beringia, that calve on the tundra and migrate in winter to boreal forest; and a non-migratory, exclusively forest clade whose ancestors persisted south of the ice-sheets that covered northern North America and the western cordillera (Courtois et al. 2003; Flagstad and Røed 2003; Zittlau 2004; Cronin et al. 2005). COSEWIC (2011) and others refer to these as the BEL (Beringian-Eurasian) and NAL (North American) lineages, respectively.

Currently recognised Canadian BEL barren-ground caribou subspecies are *R. t. groenlandicus* sensu lato of the mainland tundra, *R. t. caboti* of Labrador, *R. t. osborni* of the northern cordillera, *R. t. pearyi* of the High Arctic, and the extinct insular *R. t. dawsoni* (Wilson and Mittermeier 2011). However, Banfield (1961) erred, both in failing to recognise the species-level separation of *R. tarandus* from *R. arcticus*, and in assigning the subspecies name *groenlandicus* to mainland barren-ground caribou, as discussed below. Its proper name is *R. arcticus* Richardson, 1829 (Allen 1942).

Western montane ecotypes

All three western montane ecotypes (Osborn's caribou, Rocky Mountain caribou and Selkirk caribou: Fig. 2) are of BEL ancestry, but are deeply divergent genetically and ecologically, having split from barren-ground caribou some 60,550 years ago in the Illinois-Wisconsin interglacial; each is a different combination of separate BEL lineages (Klütsch et al. 2012; Polfus et al. 2017; Taylor et al. 2021).

The "southern group of the Southern Mountain population of Woodland caribou", *R. tarandus caribou* (cf. COSEWIC 2014) was originally described as the Mountain or Selkirk caribou, *R. montanus* Seton-Thompson, 1899; the Central Mountain population was Rocky Mountain caribou, *R. fortidens* Hollister, 1912; and the Northern Mountain population was Osborn's caribou, *R. osborni* Allen, 1902. These scientists distinguished the three mountain types based on quantitative differences in dentition, skeletal and antler measurements, pelage colour and size, as well as ecology.

Anderson (1946) concurred with Jacobi (1931) in retaining the subspecies designations of all three western montane ecotypes under Arctic caribou: *R. arcticus osborni*, *R. arcticus montanus*, and *R. arcticus fortidens*.

When Ellerman and Morrison-Scott (1951) revised *Rangifer* into a single species, the Eurasian name, *R. tarandus* taking priority, Selkirk caribou became *R. t. montanus*, and Osborn's caribou, *R. t. osborni* (McTaggart Cowan and Guiguet 1956). Significantly, although Banfield (1961) acknowledged that his measurements showed Osborn's and Selkirk caribou as morphologically separate from each other and from barren-ground caribou and woodland caribou, he still lumped them with *R. t. caribou* Gmelin, 1788. Nagorsen (1990), then Curator of Mammals at the Royal British Columbia Museum, objected: "...these two morphs [Mountain and Osborn's] exhibit some differences in size, antler morphology and pelage colour… a modern study of geographic variation … is needed to resolve the systematics of woodland-mountain caribou".

Geist (1991) maintained the separation of *montanus* from *osborni* on the basis of size, pelage patters and colour, *montanus* being smaller and darker. Osborn's caribou, currently recognised as *R. t. osborni* (Wilson and Mittermeier 2011), therefore reverts to *R. a. osborni* Jacobi (1931).

Serrouya et al. (2012), Harding et al. (2020) and others called the Selkirk caribou "deep-snow mountain caribou", because, uniquely, they winter high on the mountains where they walk on top of a 2–5 m deep snowpack to forage arboreal lichens. The name, *Rangifer arcticus montanus* Seton-Thompson, 1899 (Jacobi 1931) is available; or *Rangifer montanus* Seton-Thompson, 1899, as Murie (1935) insisted and as its genetic distance from others (see above and Suppl. material 2: Genetic distance) suggests.

Rocky Mountain caribou, or the Central Mountain population DU8 per COSEWIC (2011), occupy the east slope of the Rocky Mountains (Fig. 2) where the continental climate results in light, shallow snow in which they forage terrestrial lichens in winter. They average 55 km horizontal migration to forested winter ranges, a little less than Osborn's caribou and far more than "sedentary" boreal woodland caribou (Theoret et al. 2022). They are mountain caribou that have hybridised in ancient times with woodland caribou, with which they share haplotypes (McDevitt et al. 2009; Taylor et al. 2021). The name *R. a. fortidens* Hollister, 1912 (Jacobi 1931) is available and appropriate.

Haida Gwai

A caribou antler from Haida Gwaii, British Columbia was dated to ~ 43,200 years BP in the mid-Wisconsin Olympia Interglacial (Mathewes et al. 2019). More recent (4,000–6,000 BP) bones of the extinct, insular Dawson caribou, originally *R. dawsoni* Seton-Thompson, 1900, were similar to barren-ground caribou but smaller, evidence of island dwarfism (Byun et al. 2002 and references therein). Evidently, they evolved in a coastal refugium after the LGM when rising sea levels isolated them. Byun et al. (2002), using molecular and ancient DNA techniques, were able to sequence a short fragment of the mtDNA from remains of Dawson caribou. Their results allied them phylogenetically with the caribou on the adjacent mainland (which at the time were thought to be *R. t. caribou*, but which are now known to be BEL lineage *R. a. osborni*) and a little less closely to Alaska barren-ground caribou (see Suppl. material 2: Genetic distance).

Alaska-Yukon

In Alaska, of 13–32 caribou herds that have been recognised, including four that overlap with Yukon (Hemming 1971; Valkenburg 1998), four (Porcupine, Central Arctic, Teshekpuk, and Western Arctic) are small, phenotypically barren-ground caribou with long migrations and aggregated, tundra calving grounds (Prichard et al. 2020), while a fifth (Steese-Fortymile) is intermediate in form and behaviour (Hemming 1971; Gauthier and Farnell 1986; Valkenburg 1998; Mager et al. 2014).

Allen (1902) described Grant's caribou, *R. granti* Allen, 1902, of the Alaska Peninsula and archipelago (Fig. 2), noting that it was "not closely related to *R. stonei* of the Kenai Peninsula, from which it differs not only in its very much smaller size, but in important cranial characters and in [pale] coloration." It remained a species or subspecies (see Suppl. material 1: Synonymy) until Banfield (1961) erroneously brought all other Alaska caribou under it as junior synonyms, thus expanding its range to the whole state and northern Yukon. Youngman (1975) began a trend to replace *granti* with *R. t. groenlandicus* sensu lato. Because Geist (1998) could find no morphological features to distinguish Alaskan from Canadian barren-ground caribou, *granti* was not accepted by Wilson and Reeder (2005) and Wilson and Mittermeier (2011). Caribou geneticists agree that they are barely distinguishable (e.g., Cronin et al. 2005; Yannic et al. 2018). As originally described, however, *granti* survives (see below).

Murie (1935) brought *Rangifer excelsifrons* Hollister, 1912, *Rangifer mcguirei* Figgins, 1919, and *Rangifer ogilviensis* Millais, 1915, under *R. stonei* Allen, 1901 (Fig. 2). Stone's caribou was said to range from the Kenai and Alaska Peninsulas to western Yukon "and more sparingly to the eastward" (Murie 1935): a large, dark caribou with a well-developed white fringe on the throat and "antlers large and rangy, of the *arcticus* type, but heavier". The former *R. ogilviensis* (Millais, 1915b) is the Porcupine Herd (named for a river that flows from Yukon into Alaska) of barren-ground caribou that winters mainly in the Ogilvie Mountains, Yukon, and calves on the Alaska-Yukon coastal plain. Their migratory, rutting and calving-aggregation behaviours and small size (consistently smaller than mountain caribou to the south and west: Gauthier and Farnell 1986) reveal their barren-ground identity.

In Alaska, some two dozen herds are genetically, morphologically (larger and darker than barren-ground caribou: Gauthier and Farnell 1986) and ecologically similar to the western Canada montane forms (Mager et al. 2014 sampled 20 of the 26 currently recognised herds). Nevertheless, they clustered clearly into two groups at $K = 2$, one of which encloses the Alaska Peninsula type locality of *R. granti* (Fig. 2). Colson et al. (2014) found a lack of dispersal or introgression from adjacent ecotypes, suggesting reproductive isolation of the Alaska Peninsula/archipelago cluster. Yannic et al. (2018) confirmed the genetic distinctiveness of this ecotype, which had been previously found to differ morphologically as well (cf. Murie 1935; see Suppl. material 1: Synonymy).

Thus, *R. a. granti* is rediscovered, its range restricted (as originally: Allen 1902) to the Alaska Peninsula and archipelago.

At $K = 4$, six "mainland" (i.e., not peninsula/island) herds, all geographically small, isolated mountain herds, "appeared relatively discrete with > 0.50 population assignment to one cluster, rather than several [and] had high pairwise differentiation" (Mager et al. 2014). One of these, the Chisana herd, which spans the Alaska-Yukon border, contains the type locality (Fig. 2) of *Rangifer mcguirei* Figgins, 1919. Figgins (1919) found differences, which he thought sufficient to name a new species, in the pelage, cranial and dental features, and antler formation of six specimens of Chisana caribou, compared to the same morphological characters in *osborni* and *stonei*. Murie (1935), followed by Anderson (1946), synonymised *mcguirei* with *stonei* because "No part of the original description would distinguish the type specimen from *R. arcticus stonei*. Furthermore, the type locality lies squarely in the path of migration of the large herd of *stonei*, the principal herd of Alaska-Yukon caribou, at a point where hundreds of thousands pass through each year during the rutting season."

This reasoning is flawed because none of these mountain herds migrate long distances: rather, each migrates altitudinally if at all (most winter in alpine tundra where wind clears snow from the terrestrial lichens) and maintains separate alpine rutting and calving areas. Murie (1935) no doubt had observed the Steese-Fortymile herd on migration. Nevertheless, Osgood (1909) and Murie (1935) were prescient in bringing all of these under *R. arcticus*.

Likewise, 16 southern Yukon and northern British Columbia herds, 15 of them currently identified as *R. t. osborni*, clustered into four groups based on microsatellite DNA analysis and three based on mtDNA (Kuhn et al. 2010). Haplotypes of the migratory Steese-Fortymile herd (the others are sedentary), were spread throughout the others, suggesting it as ancestral to all with perhaps occasional introgression.

The clustering pattern described above (Kuhn et al. 2010; Mager et al. 2014) argues for restoring the subspecies name, *R. a. stonei* Allen 1901 (Murie 1935), to Chisana and all other interior Alaska mountain caribou that cluster together and apart from *osborni*, *granti* sensu stricto, and Alaskan barren-ground caribou, including Steese-Fortymile, as subspecies of *R. arcticus*. This is another case of the pre-Banfield taxonomy being confirmed by genetic data.

Introductions of *R. t. tarandus* sensu lato and *R. t. sibiricus* into Alaska and thence to Nunavut were detailed by Anderson (1946). Some interbreeding between reindeer and wild caribou in Alaska has been documented, but with very little introgression in either direction, probably because of low fitness of hybrid animals in the wild; relatively little crossbreeding has been observed when the two have been in captivity together (Cronin et al. 2006).

Barren-ground Caribou

Banfield (1961) unjustifiably renamed *R. arcticus* as *R. t. groenlandicus* (see below). It has seven recognised herds on mainland Canada, defined by calving grounds, and extends into Alaska. Barren-ground caribou are smaller and paler than woodland caribou, but have longer, thinner antlers that, in males, sweep back, up and forward, main beams reaching > 135 cm with multiple tines at the top, often palmated (see Geist 1998 for diagnostic features). Its beams are round in cross-section vs. flattened in woodland caribou.

Anderson (1913) described the migration of the Dolphin and Union herd, DU2 (Fig. 2), across Dolphin and Union Straits from Victoria Island to the mainland and back. He also briefly described its diagnostic pelage pattern and cranial morphology (e.g., "...The heads of these Caribou appeared to be much shorter than those of the Great Bear Lake Caribou, with a noticeable fullness or convexity between forehead and nose"). He intended to name a new form of caribou and to select a type specimen from among the 84 he collected in 1911 and sent to the American Museum of Natural History; any of mature males AMNH 34431, 34432, and 34435 would be a suitable holotype. He also sent 24 to what is now the Canadian Museum of Nature, but never completed a formal report of his second (1913–1916) expedition (Anderson 1917). Thomas and Everson (1982) later confirmed its unique skeletal features quantitatively. It was long thought to be either a race of Peary caribou or a hybrid between Peary and barren-ground caribou (e.g., Manning 1960) until genetic and other data showed it to be a distinct race of barren-ground caribou (Zittlau 2003; COSEWIC 2004, 2017). Since it was never formally described, there is no available subspecies name for this ecotype.

The High Arctic

Peary's caribou, *R. t. pearyi*, of the Arctic Archipelago except for Baffin Island (Fig. 2), is "clearly most genetically similar to the Canadian barren-ground caribou (*R. t. groenlandicus*) from North West Territories … suggesting common origin of the ancestors of these populations" (Røed 2005). Peary caribou diverged from barren-ground caribou 96,000–185,000 BP and evolved in isolation through two glacial cycles (Klütsch et al. 2017). COSEWIC (2004) restricted its distribution to the High Arctic islands and the Boothia Peninsula, except for most of Victoria Island, based on Harding (2003) and Zittlau (2003). A BEL lineage, it is DU1 (COSEWIC 2011).

Baffin Island

Baffin Island caribou comprise insular populations that are geographically and genetically disjunct from both mainland barren-ground and Peary caribou (Fig. 2). It differs from the mainland barren-ground caribou in lacking large-scale migrations and with calving being dispersed rather than aggregated (Jenkins et al. 2012). Its genetic differentiation (pairwise F_{ST} based on 16 microsatellite loci) "is evidence of evolutionary significance and points to Baffin Island caribou as a candidate for consideration as a DU" (Jenkins et al. 2018).The most common allele in Baffin Island caribou is absent or occurs in very low frequencies in other barren-ground caribou populations including the nearby Beverly herd on the adjacent mainland; likewise, the Beverly herd has eight alleles that are absent from the Baffin Island samples, indicating "a large genetic distance" between them (gel electrophoresis: Røed et al. 1991). Baffin Island caribou share one haplotype (C10) with those in Labrador and two each with Dolphin and Union and Bluenose herds of barren-ground caribou (Cronin et al. 2005). The genetic distances (see Suppl. material 2: Genetic distance) and other data suggest at least a subspecies. There is no available name for a Baffin subspecies.

Greenland

Small, *pearyi*-sized caribou occupied the ice-free parts of Greenland in the Illinoian-Wisconsin interglacial and through the LGM and early Holocene (Meldgaard 1986). Degerbøl (1957) described *R. t. eogroenlandicus*, which became extinct ~ 1900, from a relict enclave in north-eastern Greenland (Fig. 2). However, Bennike (1988), comparing bones and noting that Peary caribou have been documented crossing Nares Strait to Greenland, doubted that *pearyi* and *eogroenlandicus* were subspecifically distinct. That Peary caribou shared certain mtDNA haplotypes and morphological similarities with it (Kvie et al. 2016) casts further doubt on the validity of *R. t. eogroenlandicus*.

The larger West Greenland caribou is problematic. It is darker than typical *arcticus* and much darker than *pearyi*, resembling woodland caribou in its dark-brown body, with neck and ventral area much lighter (Allen 1908). Allen (1908) gives Greenland caribou average condylobasal length and upper maxillary tooth row metrics, both greater than in mainland *arcticus* and considerably more than in the “little *pearyi*”. He also notes that antlers of Greenland caribou adult males, although within the range of *arcticus* in total length, are “slenderer, less palmated, and more recurved”. Historic and archaeological records show that barren-ground-sized caribou immigrated to West Greenland, possibly from Baffin Island via the Davis Strait, in the middle Holocene (Meldgaard 1986). However, a reconstruction of glacial retreat and caribou advance (Yannic et al. 2013) shows colonisation by NAL lineage caribou more likely.

Greenland caribou, with Svalbard caribou, are the most geographically and genetically isolated ecotypes among all extant caribou (average fixation index 41%: Yannic et al. 2013) based on 16 microsatellite loci. They share low relatedness values with all Canadian caribou (Solmundson et al. in press).

The (West) Greenland caribou is neither of the BEL lineage, from which descend all Eurasian and Canadian tundra reindeer and caribou, nor the NAL lineage of woodland caribou: it clusters outside of the BEL cluster, as do Svalbard reindeer (Yannic et al. 2013). Yannic et al. (2018) were unable to include it in their hierarchical analysis “because of their high genetic differentiation”. It is best left as Linnaeus (1767) originally classified it: *Rangifer groenlandicus* L., 1767 (Miller 1924).

Mackenzie River Valley

Polfus et al. (2017), using nuclear and mtDNA, discovered another distinct “woodland” clade in the Northwest Territories between the Mackenzie River and Great Bear Lake that descends, not from the NAL lineage as other woodland caribou, but from the BEL lineage. They quoted Geist (2007), who, using pelage and antler characteristics and taxonomic inferences, suggested that the mountain and boreal "woodland" caribou north of 60° latitude were more likely "splinter populations of barren ground caribou, which have adapted to a more sessile life-style, increased in body size, and assumed some 'woodland mannerisms'". Since the best-supported model of Polfus et al. (2017) shows descent from *R. a. osborni*, it should be considered an ecotype of Osborn's caribou.

Woodland caribou

Gmelin (1788), editing the 13th edition of Linnaeus' 'Systema Naturæ', carried forward Brisson's (1756) "Le Karibou" as a subspecies, *Cervus tarandus γ caribou*. Gmelin (1788) did not name a type locality. Miller (1912b) and Lydekker (1915) both gave it as "Eastern Canada" without attribution. Banfield (1963) later designated a neotype and neotype locality at Quebec (City), Province of Quebec, Canada. In Fig. 2, I placed the type locality symbol in the middle of the Province of Quebec.

Historically, most *Rangifer* taxonomists (e.g., Baird 1859; Ross 1861; Allen 1896; Lydekker 1898; Miller 1912b) thought the differences from barren-ground caribou warranted species status, *R. caribou*, based on the larger size, darker colour, different antlers, and sedentary habits (see Suppl. material 1: Synonymy). Lydekker (1915) described woodland caribou antlers as "…stout, flattened, much palmated, and not of excessive length, one of the brow-tines being much expanded, while the other is simple; the bez-tine is also more palmated than in the Scandinavian reindeer."

Genetic and morphological analyses (e.g., Klütsch et al. 2012; Horn et al. 2018; Yannic et al. 2018) have confirmed the woodland caribou's distinctiveness and divergence from other ecotypes ~ 357,000 BP (Horn et al. 2018). These differences and its genetic distance from other ecotypes (see Suppl. material 2: Genetic distance) warrant restoration of *Rangifer caribou* Gmelin, 1788 (Baird 1859).

Three haplogroups of woodland caribou are evidence of isolation in three refugia (in the Rocky Mountains, east of the Mississippi, and the Appalachian Mountains) during the LGM, giving rise to two clades of boreal woodland caribou east and west of a "suture zone" in Manitoba (Klütsch et al. 2012). A fourth, coastal refuge was later identified (Wilkerson et al. 2018). Mid-continent clades have a few barren-ground haplotypes, arising after the LGM when the latter rutted far enough south to encounter the former; however, barren-ground caribou do not have woodland caribou haplotypes (McQuade Smith 2009; Yannic et al. 2018).

COSEWIC (2011), based mainly on molecular data, divided Banfield's (1961) woodland caribou, *R. t. caribou*, into five Designated Units (Fig. 2): Eastern Migratory DU4, Newfoundland DU5, Boreal DU6, Torngat DU10, and Atlantic-Gaspésie DU11, in addition to the three western montane ecotypes discussed above.

Richardson (1829), without specifying a type locality, had described the "western woodland caribou", *R. t. sylvestris* (Richardson, 1829). He gave its range as west of Hudson's Bay and James Bay in rocky (Precambrian Shield) habitat, west to Lake Superior and Lake Athabasca. In Fig. 2, I placed the type locality symbol approximately in the middle of the range given by Richardson (1829). He said:

> *"Contrary to the practice of the Barren-Ground Caribou, the Woodland variety travels to the southward in the spring. They cross the Nelson and Severn Rivers [in Manitoba and Ontario, respectively] in immense herds in the month of May, pass the summer on the low, marshy shores of James' Bay, and return to the northward, and … retire more inland in the month of September."*

Richardson (1829), although one of the greatest Arctic explorers of his era, had little experience with caribou south of the Barrenlands. He did not mention having examined museum specimens back in London, did not figure the animal or give metrics supporting its being "much larger than the Barren-Ground Caribou [and] has smaller horns" and most of his account of *R. t. sylvestris* is hearsay. His description of "immense herds" in migration precludes its application to woodland caribou.

Serrouya et al. (2012), using microsatellite markers, confirmed earlier conclusions (McLoughlin et al. 2004) that the caribou of the woodland ecotype DU6, sampled in Alberta north and south of the Peace River, clustered separately and were genetically distant from each other (average F_{ST} = 5.9% between pairs). Could those north of the Peace River be the newly discovered BEL clade of boreal "woodland" caribou in the Mackenzie Valley (cf. Polfus et al. 2017)?

Atlantic-Gaspésie caribou

The Atlantic-Gaspésie caribou (Fig. 2), DU11 (COSEWIC 2011), is an isolated montane ecotype (Pelletier et al. 2019). It is significantly differentiated from Labrador and boreal woodland caribou in Québec, F_{ST} 10.3%–17.2%, based on microsatellite loci (Courtois et al. 2003). Yannic et al. (2018), also based on microsatellite loci, gave its average F_{ST} from all other Canadian populations as 19%. This and its unique ecology (Pelletier et al. 2019; Frenette et al. 2020), warrant at least subspecific distinction. It remains unnamed.

Labrador or Ungava caribou

Allen (1914) described the "Barren-ground Caribou of Labrador" from the Ungava Peninsula (Fig. 2) as *Rangifer arcticus caboti* Allen, 1914. Jacobi (1931) and Anderson (1946) thought it morphologically distinct enough for species status, *R. caboti*. Geist (1998) considered it a diagnostically "distinct form of barren-ground caribou" with antlers of "classical barren-ground form, but with short tines; brow and bez tines very close together; antlers usually widely spread". Loughrey and Kelsall (1970) called it a migratory form of woodland caribou, *R. c. caboti*, and Cronin et al. (2005) confirmed that Labrador caribou share mtDNA haplotypes and have similar microsatellite allele frequencies to woodland caribou with ancient admixture from barren-ground caribou. There has been little recent introgression (Boulet et al. 2007; Klütsch et al. 2016; Taylor et al. 2021). It shares only one haplotype with barren-ground caribou and that is from the Baffin Island population (Cronin et al. 2005), itself unique as noted above.

Even though it is a currently accepted subspecies (Wilson and Mittermeier 2011), COSEWIC (2011) renamed it the Eastern Migratory ecotype, DU4 (Fig. 2). COSEWIC (2011) also extended its range to the west of Hudson's Bay and James Bay, based on small migratory/aggregated calving populations at the south end of James Bay in Ontario and Quebec (Abraham and Thompson 1998; Brown et al. 2003) and west into Manitoba (Pond et al. 2016). Genetic evidence supports this extension (Klütsch et al. 2016).

COSEWIC (2011) further designated a montane ecotype in the Torngat Mountains as DU12, based on ecological differences from the migratory ecotype (Bergerud 2000; Boulet et al. 2007; Couturier et al. 2010). Using satellite tracking and microsatellite markers, Boulet et al. (2007) found no significant genetic differentiation (pairwise F_{ST} all ≤ 0.5%) between migratory and montane herds, whereas woodland caribou of southern Quebec were significantly differentiated (F_{ST} = 1.8%–4.8%). Yannic et al. (2016) confirmed the lack of genetic distinction between Torngat and migratory Labrador caribou. Labrador caribou are also smaller than Quebec woodland caribou (Couturier et al. 2010). Since the Torngat Mountain montane ecotype DU12 is not genetically distinct at the subspecies level from other Labrador caribou, it needs no formal description as a subspecies and Allen's type specimen designation from the Torngat Mountains (Fig. 2) remains valid for Labrador caribou, *R. c. caboti* Allen, 1914.

Newfoundland caribou

By contrast, the "totally different" (Geist 2007) Newfoundland caribou, *R. t. terraenovae* Allen, 1896, currently a valid subspecies (Wilson and Mittermeier 2011; Wilkerson et al. 2018), has distinctive pelage and antlers of the "classical 'woodland form' but of large dimensions and spreading" (Geist 1991). Analysis of mtDNA haplotypes confirmed that they are NAL woodland caribou that likely diverged during the LGM in a coastal refugium (Cronin et al. 2005; Wilkerson et al. 2018; Yannic et al. 2018). The name *R. caribou terraenovae* Allen, 1896 (Jacobi 1931; Anderson 1946) is available and appropriate, given its genetic proximity and phylogenetic descent from other woodland caribou.

Discussion

Invalid taxonomies

Some of the writers credited for caribou ecotypes' first descriptions and names should not have been. Although Millais (1915b; 1915a), writing about trophy big game hunting in 'The Gun at Home and Abroad', produced a great travelogue for hunters, it is of little use to the taxonomist. He collected no type specimens, designated no type localities, and gave little or no description of anything except the horns and antlers. Outram Bangs, a member of a Boston nature club, named a couple dozen mammal species in club newsletters and pamphlets, including a two-page leaflet purporting to describe *R. terrænovæ* (Bangs 1896); he did not designate a type locality and his leaflet does not qualify as "published". John J. Audubon was a great artist and an icon of American natural history, but he never saw a caribou, painted wildlife named by others, designated no type localities, and sent no specimens to any museum. His and John Bachman's 'The Quadrupeds of North America' (Audubon and Bachman 1849), while a wonderful resource for artists and natural historians, does not quality as a taxonomic reference. I omit these from the synonymy (Suppl. material 1: Synonymy). Because Jacobi (1931) gave the same names to wild and domesticated reindeer from the same places, his descriptions of Eurasian *Rangifer* taxa are unreliable.

What is a subspecies?

Traditional taxonomy, based on measurable morphological differences, usually in dental, cranial and skeletal characters, advanced greatly with the advent of phylogeny, or evolutionary history, with its emphasis on derived characters, especially those with functional significance. This is still the default paradigm for classifying fossils, except in rare cases where ancient DNA can be extracted. Geist (2007) said that Banfield's (1961) principal error was using only skeletal (mainly cranial) metrics that, although seemingly objective, vary by age, gender, and condition of the specimens; he advocated using "nuptial" characteristics such as pelage colour patterns and antler shape, which are sexually selected and vary with mating systems, to diagnose subspecies: "These characteristics vary with the age of the males, are minimally affected by environment and are best expressed in old males at breeding time… selection for nuptial characteristics is done through female sexual selection" (Geist 2007).

The visual stimuli of pelage markings that differ by named subspecies (Geist 1998, 2007) are the "mate recognition system," a central component of the "recognition concept" of the biological species definition (Patterson 1980). The pelage features that Geist (1998) asserts are sexually selected, highly conserved and variable among (but not within) subspecies are (1) the patterns of white and dark in the mane, (2) a light neck field that in some ecotypes extends onto the withers, (3) white socks or black hooves set off by a white band, (4) a light or dark rostrum, (5) a dark and/or a light lateral stripe, (6) a white belly that in some forms extents up the flanks and sides, (7) a secondary white rump patch, (8) white inside of the hind legs (and in some forms, the front legs) contrasting with brown or black frontal leg markings and (9) presence or absence of a light eye-ring.

Mating systems include, besides mate choice, male "fighting behaviour arising from a fundamental difference in mate-holding strategies", female calving strategies, and anti-predator strategies (Geist 1991). They contrast markedly among the sedentary, dispersed forest types that use harem-holding or harem defence (cf. Hirotani 1989) and hide their calves in bogs, to the montane types with vertical migrations that also use harem-herding but disperse to calve on mountain ridges; and the tundra types that form tending bonds within large mating herds, synchronise calving, and form calf aggregations to minimise wolf predation (e.g., Bergerud 1974; Bergerud and Page 1987; Barrette and Vandal 1990; Mallory and Hillis 1998; Brown et al. 2003; Wittmer et al.

2006; Holand et al. 2007; Heatta 2009; Hegel et al. 2012; Flasko 2014; MacNearney et al. 2016; Weladji et al. 2017).

Butler (1986) showed that the social requirements of caribou females during the rut determines the mating strategies of males and, consequently, the form of male antlers.

Although sexually selected features are highly conserved, environment also drives both antlers (smaller to avoid entanglement in trees; shape and position of brow tines, "ice tines" in European parlance, to facilitate cratering in snow) and pelage (cryptic colouration: darker in forest, lighter on tundra). Forest reindeer and woodland caribou tend to have darker pelage, although the Altai reindeer (see above; Fig. 3), is sand- to red-coloured and not as dark as woodland caribou (Geist 1998). Woodland caribou are uniformly darker than barren-ground caribou, besides being up to twice their size. Geist (1991, 1998) illustrated the pelage patterns and antler types of mature males of most recognised subspecies: woodland, Newfoundland, Peary, barren-ground, Osborn's, Labrador caribou, European tundra, and Svalbard reindeer; and he described diagnostic nuptial pelage and antler shapes of those that he did not illustrate: European forest, Novaya Zemlya, Siberian tundra, Altai, and Kamchatka reindeer. In considering how genetic data confirms or rejects traditional taxonomy, we should not overlook morphological features that have always guided diagnosis and that, in any case, remain essential for fossil forms (cf. Croitor 2018).

Genetic distances

There are no generally accepted thresholds of genetic distance to distinguish species within a genus or subspecies within a species. Genetic distances comparing mtDNA sequences among cervid genera are generally 12%–18% (see Suppl. material 2: Genetic distance). Within cervid genera (i.e., between species), genetic distances in mtDNA sequences are generally around 3%–6% (e.g., Cronin 2003; Cai et al. 2016; Gutiérrez et al. 2017) and between subspecies around 1%–3% (e.g., Avise et al. 1998; Cai et al. 2016).

Nuclear microsatellite data give higher genetic distances, e.g., 16%–20% between pairs of white-tailed deer (*Odocoileus virginianus*) subspecies (Rosa-Reyna et al. 2012). For comparison, genetic distance (Cavalli-Sforza and Edwards 1967) of microsatellite allele frequencies between pairs of Eurasian and North American tundra reindeer and caribou (that is, excluding Svalbard and Fennoscandian reindeer and Greenland and woodland caribou) ranged from 27.6% to 32.1% (see Suppl. material 2: Genetic distance).

Genetic differentiation, F_{ST}, measures the variance in allele frequency among populations and describes the degree of genetic similarity among individuals within populations. F_{ST} and genetic distance measures are often highly correlated for a set of population or species pairs, the former usually being a little higher.

Genetic distances and F_{ST} data mentioned herein, and other data given in Suppl. material 2: Genetic distance, show that (1) within *Rangifer* exist populations currently identified as subspecies or below (e.g., ecotypes, populations) that are at least as distinct as species in other taxa, and (2) many previously named subspecies and some previously unidentified ecotypes are distinct enough to be recognised as subspecies, or even as full species.

Taxonomic conclusions

The following names are available and should be used for ecotypes and phylogenetic clades of *Rangifer*:

Rangifer groenlandicus

At a microsatellite genetic difference of F_{ST} = 44% from all other caribou (Yannic et al. 2013), the original name, *Rangifer groenlandicus* Gmelin, 1788 (Baird 1859) as Greenland caribou, type locality "Greenland", distribution Greenland, is the appropriate name.

Rangifer platyrhynchus

The Svalbard Reindeer, as different from other Eurasian reindeer as Greenland caribou are from other North American caribou, should retain its original name, *Rangifer platyrhynchus* Vrolik, 1829 (Sokolov 1932, 1963).

Rangifer caribou

The genetic difference estimates between woodland caribou and barren-ground caribou, based on mtDNA, range from F_{ST} = 33% to > 50% (see Suppl. material 2: Genetic distance); this and lack of shared haplotypes except for minor, ancient introgression in some populations, is easily enough to separate them at the species level. Divergence time estimates of the split between forest (NAL) and barren-ground (BEL) clades range from 135,600 years ago during the penultimate (Illinoian) interstadial (Taylor et al. 2021) to a pre-Illinoian glacial period 300,000 years ago (Yannic et al. 2013). Moreover, woodland caribou may descend from extinct species of *Rangifer* in southern North America that never had contact with barren-ground caribou. This would not show up in genetic data except that they have unique haplotypes. In addition, they have a fundamentally different morphology (body size, antler size and formation including flattened vs. round tines, pelage, differences in dentition and in rostral structure), ecology, and behaviour. This clearly supports that the woodland caribou should be restored to species level, *Rangifer caribou* Gmelin, 1788 (Baird 1859).

Among *R. caribou* ecotypes and clades, the pattern of high differentiation of microsatellite allele frequencies and mtDNA haplotypes (relative to the barren-ground clade) results from isolation in at least four glacial refugia south of the ice sheets (Flagstad and Røed 2003; Cronin et al. 2005; Wilkerson et al. 2018). This justifies several subspecies. The following NAL lineage ecotypes, designated as distinct evolutionary units (DU—COSEWIC 2011) have available names:

- *R. c. caribou* Gmelin, 1788. Boreal woodland caribou DU6. Range restricted to mostly south of Labrador caribou with some overlap. Currently recognised (Wilson and Mittermeier 2011).

- *R. c. caboti* Allen, 1914 (Loughrey and Kelsall 1970), Labrador or Ungava caribou, Eastern Migratory caribou DU4, is currently recognised (Wilson and Mittermeier 2011).
    - The Torngat Mountains montane caribou clade remains a valid ecotype.
- *R. c. terraenovae* Allen, 1896 (Jacobi 1931), Newfoundland caribou DU5. Currently recognised (Wilson and Mittermeier 2011).

The Atlantic-Gaspésie ecotype, DU11, is significantly differentiated genetically from other populations in Québec and throughout Canada. There is no available name.

Other woodland caribou clades across the boreal forest have considerable genetic distinction and may warrant subspecific designation but need more investigation.

Rangifer arcticus

Mainland barren-ground caribou, currently recognised as *R. t. groenlandicus* (Wilson and Mittermeier 2011) is genetically and morphologically distinct from European tundra caribou and from woodland caribou. It clusters separately from Eurasian tundra reindeer and has pairwise genetic distances (microsatellite variation: Nei) of 20% to wild *R. t. tarandus* from Norway, but only 5% to Alaskan barren-ground caribou (Røed 2005). Cronin et al. (2006), using the Cavalli-Sforza and Edwards formula with microsatellite allele frequencies, put the genetic distance between Russian tundra reindeer and Canadian barren-ground caribou at 0.310. A microsatellite genetic distance of 20% to > 30% suggests specific differences between Eurasian tundra reindeer and North American barren-ground caribou.

However, *groenlandicus* cannot be applied to Canadian barren-ground caribou as a species name, as discussed above. *Rangifer arcticus* Richardson 1829, the first name applied to North American mainland barren-ground caribou (Ross 1861; Murray 1866) is the appropriate name.

Currently-accepted subspecies of *Rangifer arcticus*:

- *R. a. arcticus* Richardson, 1829, barren-ground caribou, DU3. Currently recognised as *R. t. groenlandicus* (Wilson and Mittermeier 2011) but restricted to tundra (summer) and boreal forests (winter) of mainland Canada and Alaska.
- *R. a. pearyi* Allen, 1908, Peary caribou, DU1. Currently recognised (Wilson and Mittermeier 2011).
- † *R. a. dawsoni* Seton-Thompson, 1899 (Jacobi 1931), the Queen Charlotte Islands caribou, DU12, currently recognised (Wilson and Mittermeier 2011), an *arcticus* subspecies of BEL lineage, as noted above (and see Suppl. material 2: Genetic distance).[*]
- *R. a. osborni* Allen, 1902 (Murie 1935), Osborn's caribou, DU7. Currently recognised (Wilson and Mittermeier 2011).
    - The unnamed "woodland ecotype" of BEL lineage in the Mackenzie Valley (Polfus et al. 2017) warrants recognition as a unique ecotype of *R. a. osborni*.

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[*] † Extinct

Formerly recognised subspecies of *R. arcticus* that should be reinstated:

- *R. a. granti* Allen, 1902, Grant's caribou. Restricted to Alaska Peninsula and archipelago, Alaska (Colson et al. 2014; Mager et al. 2014).
- *R. a. stonei* Allen, 1901 (Osgood 1909), Stone's caribou, is available for interior Alaskan mountain caribou as a group that is coherently separable at the subspecies level from *granti*, *osborni*, and *arcticus*.
    - *R. a. mcguirei* Figgins, 1919, Chisana mountain caribou. Original range provisionally designated as "the vicinity of the Alaska-Yukon boundary from the base of Mt. St. Elias northward" (Figgins 1919), restricted to that mapped by Mager et al. (2014). However, Murie (1935) gave good reasons for relegating *mcguirei* to a junior synonym of *R. a. stonei.*
- *R. a. fortidens* Hollister, 1912 (Jacobi 1931), DU8, Rocky Mountains caribou.
- *R. a. montanus* Seton-Thompson, 1899 (Jacobi 1931), Selkirk or mountain caribou, DU9, was formerly assigned to *R. arcticus* (Jacobi 1931; Anderson 1946), which its BEL lineage (see above) shows to have been correct.

Molecular analyses (see above) have revealed distinct subspecific clades of *R. arcticus* that have yet to be described:

- Dolphin and Union barren-ground caribou, DU2. Anderson's (1913) brief, informal description of pelage and cranial differences from other barren-ground caribou, in view of later quantitative confirmation (e.g., Thomas and Everson 1982), would seem to warrant the new name of *R. arcticus andersoni* 1913. AMNH M-34433 would be a suitable neotype specimen, type locality "south side of Coronation Gulf".
- Unnamed Baffin subspecies. Manseau et al. (2019) found it subspecifically distinct and Jenkins et al. (2018) recommended a DU designation. There is no available name.

Eurasian Tundra reindeer

Eurasian reindeer diversity is clouded in the English literature because many geneticists labelled their samples as "*Rangifer tarandus*" whether they were from domestic or wild types, or *R. t. tarandus*, *R. t. sibiricus* or *R. t. fennicus* (Western scholars seem not to have included *R. t. phylarchus*, *R. t. angustirostris*, and *R. t. valentinae* in their samples).

Domestic reindeer, a large, multi-faceted industry throughout Russia and Siberia, show little genetic exchange with wild reindeer and their population identities are mutually exclusive (e.g., Røed et al. 2008; Korolev et al. 2017).

- *R. t. tarandus* Trouessart, 1898, mountain reindeer, is restricted to Norway, Sweden, Finland and Russia (Murmansk).

- *R. t. sibiricus* von Schreber, 1784. Siberian reindeer, ranges from Arkhangelsk eastwards.
    - If the Taymyr reindeer were to be separated from other Siberian reindeer on the basis of its migratory behaviour (Krivoshapkin 2016), as some have recommended (e.g., Michurin 1965; Pavlov et al. 1989), its name would be *R. t. taimyrensis* Michurin, 1965. However, its genetic separation (single-nucleotide polymorphisms, SNP) from the Yakutsk population of *R. t. sibiricus*, > 1,000 km to the east, is only F_{ST} = 0.5% (Kharzinova et al. 2020).

Forest reindeer

Within Eurasian reindeer (Fig. 3), the most different in size and ecology from *R. t. tarandus* is the Finnish forest reindeer *R. t. fennicus.* Forest reindeer were probably isolated the longest of other forms and their apparent descent from the fossil reindeer *Cervus guettardi* Desmarest, 1820, precludes assignment to *R. tarandus*. Morphological, ecological, and genetic differences suggest *R. fennicus* Lönnberg, 1909 (Miller 1912a) as the appropriate name, with junior synonyms *silvicola*, *transuralensis*, and *dichotomus* (Fig. 3).

Subspecies are:

- the Finnish or western European forest reindeer *R. fennicus fennicus* Lönnberg, 1909. Range: forested parts of Finland and Murmansk/Kola Peninsula, Karelia, and Arkhangelsk in Russia.
- the Altai Mountains forest reindeer *R. f. valentinae* Flerov, 1933 (Sokolov 1937), its range restricted to the Altai Mountains.
- *R. t.* (*f.*?) *angustirostris* awaits genetic sampling and phylogenetic analysis.

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Supplementary material 1

Synonymy

Authors: Lee E. Harding

Data type: docx file

Explanation note: Synonymy as it would have been before Ellerman and Morrison-Scott (1951) for Eurasia and before Banfield (1961) for North America.

Link: https://doi.org/10.3897/zookeys.1119.80233.suppl1

Supplementary material 2

Genetic distance

Authors: Lee E. Harding

Data type: docx file

Explanation note: Literature review on glacial periods and genetic distance relevant to *Rangifer*.

Link: https://doi.org/10.3897/zookeys.1119.80233.suppl2

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REVIEW ARTICLE

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A review of the *sinica* species group within the genus *Lilioceris* (Coleoptera, Chrysomelidae, Criocerinae)

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Abstract

A new species group of the genus *Lilioceris* Reitter, 1913 is proposed and reviewed, the *sinica* group. It includes six species: *L. gressitti* Medvedev, 1958; *L. rugata* (Baly, 1865); *L. sieversi* (Heyden, 1887); *L. sinica* (Heyden, 1887); *L. theana* (Reitter, 1898) **stat. nov.**; and *L. thibetana* (Pic, 1916). Among them, *L. theana* is resurrected as a valid species from synonymy with *L. rugata*, and is newly reported from China. Redescriptions, an identification key, figures of habitus and male and female genitalia, geographic distributions, host plants, and habitats (if known) are provided for these species.

Keywords

Distribution, genitalia, key, shining leaf beetle, taxonomy

Introduction

Lilioceris Reitter, 1913 is the second largest genus of Criocerinae, includes approximately 150 species to date (Monrós 1960; Heinze and Pinsdorf 1962; Gressitt 1965; Warchałowski 2011; Bezděk and Schmitt 2017). The genus is widely distributed in tropical and subtropical parts of the world, with the highest species diversity in the Oriental Region. Species of *Lilioceris* are characterized by a more or less elongate body shape, of medium or small size (5–12 mm); the thorax is subcylindrical or subquadrate, without lateral margins, and the lateral sides constricted in middle; the tibiae has two spurs. Species of *Lilioceris* usually live in margins of forest or farmland habitats, and all life stages are associated with the host plant. Most of their host plants are from the families Smilacaceae, Dioscoreaceae, and Liliaceae (Jolivet 1988; Schmitt 1988), and a few *Lilioceris* species are economically important. *Lilioceris* is unquestionably monophyletic group within Criocerinae as shown by recent phylogenetic studies (Schmitt 1985; Matsumura et al. 2014). There are many taxonomic works focusing on regional species of the genus (e.g., Jacoby 1904, 1908; Gressitt and Kimoto 1961; Heinze and Pinsdorf 1962, 1963, 1964; Kimoto and Gressitt 1979; Tishechkin et al. 2011; Warchałowski 2011; Xu et al. 2021), but still many species are difficult to identify based on existing keys, and therefore more revisionary work is needed.

Tishechkin et al. (2011) proposed the *impressa* species group in the genus based on adults with a glabrous scutellum, flattened and short antennomeres 6–10 (wider than long), and strongly punctate elytral striae. Recently, when examining specimens of *Lilioceris* in the National Zoological Museum, Chinese Academy of Sciences, we found that some species were similar to members of the *impressa* species group, but differed in having cylindrical and longer antennomeres 6–10 (longer than wide). These species include *L. gressitti* Medvedev, 1958, *L. rugata* (Baly, 1865), *L. sieversi* (Heyden, 1887), *L. sinica* (Heyden, 1887), and *L. theana* (Reitter, 1898). We also found *L. thibetana* (Pic, 1916) to be very similar to *L. gressitti* Medvedev, and is not a member of the *impressa* group.

The primary purpose of this paper is to propose the *Lilioceris sinica* species group, and properly document the species included in this new group.

Materials and methods

The specimens from several museums and collections were examined. Collections cited in this article are indicated by the following abbreviations:

HNHM	Hungarian Natural History Museum, Budapest, Hungary;
IZCAS	National Zoological Museum, Institute of Zoology, Chinese Academy of Sciences, Beijing, China;
MBSU	The Museum of Biology, Sun Yat-Sen University, Guangzhou, China;
MCAU	The Museum of China Agricultural University, Beijing, China;
MHU	The Museum of Hebei University, Baoding, China;
MNHN	Museum National d'Histoire Naturelle, Paris, France;
NHMB	Naturhistorisches Museum (Museum Frey, Tutzing), Basel, Switzerland;
NHML	The Natural History Museum, London, UK;
NIBR	National Institute of Biological Resources, Incheon, Korea;
SDEI	Senckenberg Deutsches Entomologisches Institut, Germany.

Except as noted, all specimens examined are deposited in IZCAS.

Dry specimens were soaked in hot water for 1–2 h to soften the body. The abdomen was opened at its latero-apical margin and genitalia were pulled out using forceps.

Genitalia were soaked in warm 10% KOH for 1 h, and dyed in Chlorazol Black E. The basal orifice of the aedeagus was injected with 100% ethanol with a micro-injector until the internal sac was fully everted. The aedeagus with its everted internal sac was photographed using a large depth-of-field 3D digital microscope (Keyence VHX–1000C), and finally edited in Photoshop. A microvial with genitalia was pinned to the specimen from which the genitalia were removed for storage.

Body length (**BL**) was measured from the anterior margin of the labrum to the apex of the elytra; body width (**BW**) was measured along the greatest elytral width (**EW**); head length (**HL**) was measured along the anterior margin of the labrum to the posterior margin of tumid gena; head width (**HW**) was measured along the widest part of the head including eyes; pronotum length (**PL**) was measured along the median line of the pronotum; pronotum width (**PW**) was measured across the widest part of the pronotum; elytra length (**EL**) was measured along the suture from the base of the scutellum to the elytral apex.

Other methods of specimen observation and preparation follow previous publications (Tishechkin et al. 2011; Li et al. 2013). Morphological terminology follows Chou et al. (1993) and Matsumura et al. (2013).

Taxonomy of the *Lilioceris sinica* species group

Diagnosis. Small size, length less than 9.5 mm. Head, antennae, and ventral surface black, legs black or with femora bicolored; pronotum yellow, brown, or dark brown, without metallic luster; elytra unicolored, red, brown, black, or blue, without bands or patches, without metallic luster. Antennae short, nearly 1/3 as long as body length, antennomeres 5–10 cylindrical, longer than wide, densely pubescent and punctate. Pronotum disc with punctures distinct, scattered, not aligned into rows in the middle. Scutellum lingulate, glabrous, at most pubescent along basolateral margins. Elytra with ten rows of completely punctate striae, punctures large, present at apex; intervals flat or convex at apex, without punctures. Mesosternal process short, perpendicularly connected with metasternite. Male genitalia with tegmen Y-shaped and slender, combined with second connecting membrane. Internal sac membranous, with dorsal, median, and ventral sclerites moderately sclerotized. Female genitalia with tergites 8 and 9 and sternites 8 and 9 sclerotized, posterior areas of tergite 8 and sternite 8 with dense setae, without apodemes.

Species of the *Lilioceris sinica* group are similar to those of *Lilioceris impressa* group in having glabrous scutellum, completely punctate elytral striae, and three moderately sclerotized sclerites in aedeagus. However, the most significant difference between the two groups is that antennomeres 6–10 are distinctly flattened and quadrate or even transverse (Figs 36–41) in the *impressa* group (Tishechkin et al. 2011), while obviously cylindrical (Figs 30–35) in the *sinica* group. Generally, body size in the *impressa* group (length 7.5–11.8 mm; mean 9.18 ± 0.20) is greater than that in the *sinica* group (length 6.0–9.0 mm; mean 7.13 ± 0.22).

We recognize six species belonging to *sinica* group based on examination of the type specimens and / or descriptions. As to the African *Lilioceris* treated by Heinze and Pinsdorf (1962), several species with a pronotum irregularly punctate, the elytra unicolored and strongly punctate, and the antennomeres 6–10 slightly longer than wide, probably fall into this group (e.g., *L. cafra* (Lacordaire, 1845), *L. consobrina* (Clark, 1866), *L. latipennis* (Clark, 1866), *L. lumbwensis* (Weise, 1926) *L. puncticollis* (Lacordaire, 1845), and *L livida* (Dalman, 1823)). These species will be treated when types are available to us in the future. Known host plants of the group are *Dioscorea* spp. (Dioscoreaceae).

Key to species of the *Lilioceris sinica* species group

1 Lateral side of metasternite nearly glabrous, with only little pubescence occasionally near the border (Figs 13C, 14C, 17C) **2**
– Lateral side of metasternite with a wide or narrow strip of pubescence, extending from anterior to posterior margin (Figs 12C, 15C, 16C) **4**
2 Pronotal disc with strong and deep punctures (Fig. 13A); punctures of elytra large and deep, intervals convex at apical 1/4 (Fig. 13D)................ ***L. rugata***
– Pronotal disc with fine and shallow punctures (Figs 14A, 17A); punctures of elytra small and shallow, intervals flat at apex (Figs 14D, 17D).................. **3**
3 Elytra black or blackish blue (Fig. 17D).. ***L. sieversi***
– Elytra red or yellow (Fig. 14D) .... ***L. thibetana***
4 Lateral side of metasternite with a narrow strip of pubescence (Fig. 12B); punctures of elytra large on basal half, diminishing posteriorly, intervals flat (Fig. 12D).. ***L. gressitti***
– Lateral side of metasternite with a wide strip of pubescence (Figs 15B, 16B); punctures of elytra large, not diminishing posteriorly, intervals convex at apical 1/4 (Figs 15D, 16D).. **5**
5 Lateral 1/4 of metasternite glabrous (Fig. 15B); lateral transverse impressions on abdominal sternites 2–5 distinct, glabrous, other area of sternite pubescent (Fig. 15C) .... ***L. sinica***
– Lateral 1/4 of metasternite sparsely pubescent (Fig. 16B); lateral transverse impressions on abdominal sternites 2–5 absent, sternite wholly pubescent (Fig. 16C)... ***L. theana***

Lilioceris gressitti **Medvedev, 1958**

Figs 1, 12, 18, 24, 30, 42–44

gressitti Medvedev 1958: 111 (China, Prov. Yunnan, holotype, gender ?).

Type material examined. 1 holotype (NHMB, photo), China, Prov. Yunnan, Vallis flumin Soling-ho / Lilioceris gressitti m, L. N. Medvedev det. 1957, holotype / Type.

Other material examined. Total 24 specimens. **China: Yunnan:** 1♂, Kunming, 1941.V.23 / Lilioceris gressitti Medvedev, Peiyu Yu Det.; 1♂, Kunming, 1942.VI.27; 1♂1♀, Kunming, Zhujie Temple / 1958.IX.10; 1♂1♀, Yongsheng, Liude, 2400 m / 1984.VII.18, Shuyong Wang coll.; 1♂, Tengchong, Dahaoping, Hao Huang, 2005. VI; 1♂, Xishuangbanna, Mengzhe, 1750 m / 1958.VI.25, Fuji Pu coll.; 1♂, Xishuangbanna, Menghai, 1200–1600 m / 1958.VII.22, Fuji Pu coll.; 1♀, Kunming, Anning / 1980.VIII.6, 1900 m / Lilioceris gressitti Medvedev, Peiyu Yu Det.; 2♀, Xishuangbanna, Mengsong, 1600 m / 1958.VII.25, Leyi Zheng coll.; 1♀, Xishuangbanna, Menghai, 1200–1600 m / 1958.VII.22, Shuyong Wang coll.; 1♀, Lancang, 1100 m / 1957.VIII.8, Shuyong Wang coll.; Kunming, suburb, 1900 m, 1956.II.16, Panfilov coll.; 3♂5♀, Wuding, Chadian, Changji Road, 25.74144°N, 102.30336°E / 2296 m, 2020.VII.11 D1, Yuan Xu & Neng Zhang coll.; 1♂2♀ (MHU), Puer, Laiyang River, 2007.VII.28, Guodong Ren, Wenjun Hou & Yachai Li coll.; 1♂ (MHU), Lvchun, 2004.VII.27, Jing Li & Caixia Yuan coll.; 1♂ (MCAU), Kunming, 1946.V; 1♂ (MCAU), Kunming, Xi Shan, V.16; 1♂ (MCAU), Kunming, 1947; **Sichuan**: 1♀, Xiangcheng, 2900–3200 m / 1982.VI.28, Shuyong Wang coll.; **Guizhou**: 1♂ (MHU), Yinjiang, Fanjing Shan, 2010.VIII.19–21, Yiping Niu & Yong Zhou coll.

Diagnosis. Femora bicolored, black with brownish red middle; pronotum disc with fine punctures; elytral punctures large on basal half, diminishing posteriorly; lateral side of metasternite with a narrow strip of pubescence; abdominal sternites with a row pubescence, interrupted in the middle, lateral transverse impressions present on sternites 2–5, with sparse pubescence outside the impressions.

Redescription. BL = 6.0–7.0 mm, BW = 3.0–3.5 mm. The front part of the head, antennae, ventral surface black; occiput, pronotum, scutellum and elytra brownish red, femora bicolored, brownish red with apex black.

Head (Fig. 1). HL/HW = 1.2–1.5; vertex with a shallow groove in the middle, punctate and setose laterally; frontoclypeal area triangular, disc with fine punctures and sparse setae; labrum transverse, with sparse setae; antennomeres 5–10 slightly longer than wide (Fig. 30).

Pronotum (Figs 1, 12A). PW / HW = 1.1–1.3, PL / PW = 1.1–1.2; anterior angle slightly protruding; posterior angle not protruding; sides distinctly constricted in the middle; middle of disc with fine and scattered punctures; anterior and posterior transverse impression indistinct, basal transverse groove shallow.

Elytra (Figs 1, 12D). EL/EW = 1.2–1.4; sutural angle rounded; humeri protruding, humeral groove distinct, basal transverse impression indistinct; scutellary striole composed of 3–5 punctures; strial punctures large at base, diminishing posteriorly; intervals flat, at most convex at extremity of intervals 9 and 10; epipleura raised, with a row of fine punctures.

Mesosternite pubescent. Lateral side of metasternite with narrow strip of pubescence, extending from anterior margin to lateroposterior corner (Fig. 12B); metepisternum densely pubescent.

Abdominal sternites with a row of pubescence, interrupted in the middle; lateral transverse impressions present on sternites 2–5, area outside the impression densely pubescent (Fig. 12C).

Legs slender; tibiae with dense punctures and pubescence; femora with dense pubescence on dorsal surface, with sparse pubescence on ventral surface.

Male genitalia (Fig. 18A–D). Median foramen occupying 1/5 length of median lobe (Fig. 18A); apex rounded (Fig. 18B); basal piece of the tegmen triangular, lateral lobes strongly sclerotized; posterior part of dorsal sclerite in dorsal view more or less parallel-sided, slightly narrowed at apex (Fig. 18C, D).

Female reproductive organs (Fig. 24A–C). Spiculum gastrale short, X-shaped, distal part strongly widened, apical margin straight; ovipositor with dense setae, distal part of the ovipositor cylindrical, short, with a small protuberance; spermatheca greatly convoluted.

Distribution. China (Yunnan, Sichuan, Guizhou).

Host plant and habitat. (Figs 43, 44) One collecting locality of *L. gressitti* in Wuding county of Yunnan province is situated in subtropical area. This species fed on *Dioscorea* sp. (Dioscoreaceae) according to observations of the first author (XY) in Yunnan (Fig. 44). The vegetation is subtropical evergreen forest. The climate is characterized by distinct rainy summer and dry winter, annual temperature generally ranges from 6 °C to 22 °C. The forests are composed of tall trees, woody vines, and epiphytes. The host plant *Dioscorea* sp. shares its habitat with other plants such as *Pinus yunnanensis* (Pinaceae), *Alnus* sp. (Betulaceae), *Eucalyptus* sp. (Myrtaceae), *Adiantum* sp. (Pteridaceae), *Abelia* sp. (Caprifoliaceae), *Ageratina* sp. (Asteraceae), *Artemisia* sp. (Asteraceae), and *Ficus* sp. (Moraceae). *Lilioceris fouana* are collected together with this species.

Remarks. Medvedev (1958) indicated that *L. gressitti* was similar to *L. rugata* (Baly, 1865), especially to *L. rugata sparsipunctata* Medvedev, 1958 (synonymized with *L. sinica* by Gressitt and Kimoto 1961), but differed by the smaller and narrower body, finer punctures on the pronotum, and less strong punctures on the elytra. In addition, it differs from *L. sinica* in the abdominal sternites having less pubescence.

Lilioceris rugata (Baly, 1865)

Figs 2, 13, 19, 25, 31, 42, 45

rugata Baly, 1865: 154 (Japan, syntype, gender ?). (*Crioceris*). Chûjô 1941: 453 (*Lilioceris*).

Type material examined. 1 type (NHML, photo), Type / Type / Japan / Crioceris rugata Baly, Japan / BMNH (E) 1342969.

Other material examined. Total 10 specimens. 1♂1♀, Museum Paris, Nippon Moyen, env de Tokyo et alpes de Nikko, J. Harmand, 1901; 1♀, Karisnmi, 1932. VII.23; 1♂, Mont Takao, Pr. Hachigji, Japon: 1911.V.28, Edme Gallois / Lilioceris Rugata (Baly), Peiyu Yu Det.; 1♂, Kyoto, 1931.I.18, K. Eki; 1♂, Kibune, Kyoto, 1931.VI.14, K. Eki / Crioceris rugata Baly, det by S. Yie; 1♂, Japan, G. Lewis, 1910–

320 / Crioceris rugata Baly, P. M. Hammond det. 1980; 1♂2♀, Karuizawa, 1907. IX.27 / Lilioceris rugata, det. Peiyu Yu.

Diagnosis. Femora black; pronotum disc with large punctures; elytral punctures strong and not diminishing posteriorly, intervals convex apically; lateral side of metasternite nearly glabrous, without strip of pubescence; abdominal sternites smooth.

Redescription. BL = 6.9–8.0 mm, BW = 3.2–3.8 mm. Head, legs, and ventral surfaces black, pronotum, scutellum, and elytra brownish red.

Head (Fig. 2). HL/HW = 1.3–1.4; vertex with groove and fovea in the middle, punctate and setose laterally; frontoclypeal area triangular, disc with fine punctures and sparse setae; labrum transverse, with long setae on both apical angles; antennomeres 5–7 nearly 1.5 times as long as wide, 8–10 slightly longer than width (Fig. 31).

Pronotum (Fig. 13A). PW / HW = 1.0–1.2, PL / PW = 1.0–1.3; anterior angle slightly protruding; posterior angle not protruding; sides slightly constricted in the middle; middle of disc with large and deep punctures; anterior and posterior transverse impressions indistinct, basal transverse groove shallow.

Elytra (Fig. 13D). EL/EW = 1.5–1.7; sutural angle rounded; humeri protruding, humeral groove shallow, basal transverse impression indistinct; scutellary striole composed of 4–7 punctures; strial punctures large, not diminishing posteriorly, intervals convex at apical 1/4; epipleura raised, with row of fine punctures.

***Mesosternite pubescent*.** Lateral side of metasternite nearly glabrous, with little pubescence along anterior and posterior margins (Fig. 13B); metepisternum densely pubescent.

Abdominal sternites nearly smooth (Fig. 13C).

Legs slender; tibiae with dense punctures and pubescence; femora with dense pubescence on the dorsal surface, with sparse pubescence on the ventral surface.

Male genitalia (Fig. 19A–D). Median foramen occupying 1/5 length of median lobe (Fig. 19A); apex rounded (Fig. 19B); basal piece of the tegmen triangular, lateral lobes weakly sclerotized; posterior part of dorsal sclerite in dorsal view widely rounded, directed laterally (Fig. 19C, D).

Female reproductive organs (Fig. 25A–C). Spiculum gastrale short, X-shaped, distal part strongly widened, apical margin straight; ovipositor with dense setae, distal part of ovipositor cylindrical and short, with a small protuberance; spermatheca small and greatly convoluted.

Host plant and habitat. This species feeds on *Dioscorea japonica* and *D. tokoro* (Kimoto, 1964). The habitat is unknown.

Distribution. Japan.

Remarks. This species is similar to *L. sinica*, but differs from the latter by having its pronotal disc with strong and deep punctures, metasternite and abdominal sternites nearly smooth (in *L. sinica*, pronotal disc with fine and shallow punctures, lateral side of metasternite with a wide strip of pubescence, and abdominal sternites densely pubescent except the glabrous abdominal transverse impressions). In addition, the genitalia of *L. rugata* differ from those of *L. sinica* by posterior part of dorsal sclerite in dorsal view widely rounded, directed laterally (in *L. sinica*, posterior part of dorsal sclerite in dorsal view slightly narrowed at apex, more or less parallel-sided). Chûjô (1941) synonymized *L. sinica* with *L. rugata*, which is not justified in the light of the present study.

Lilioceris rugata is widely distributed in Japan, obviously isolated geographically from other species in China, Russian and Korea. The records of this species from Russia and Korea are questionable. We found some photographs identified as *L. rugata* on websites from Russia (https://www.zin.ru/animalia/coleoptera/eng/lilrugkm.htm) and Korea (https://blog.naver.com/onegunah/110021296278) that are actually *L. theana*. Cho and An (2020) recorded nine specimens of *L. rugata* collected from South Korea. They are probably also *L. theana* (see Cho and An 2020: 7, fig. 13). The materials of *L. rugata* from Russia and Korea need more study.

Lilioceris sieversi (Heyden, 1887a)

Figs 3, 14, 20, 26, 32, 42, 46

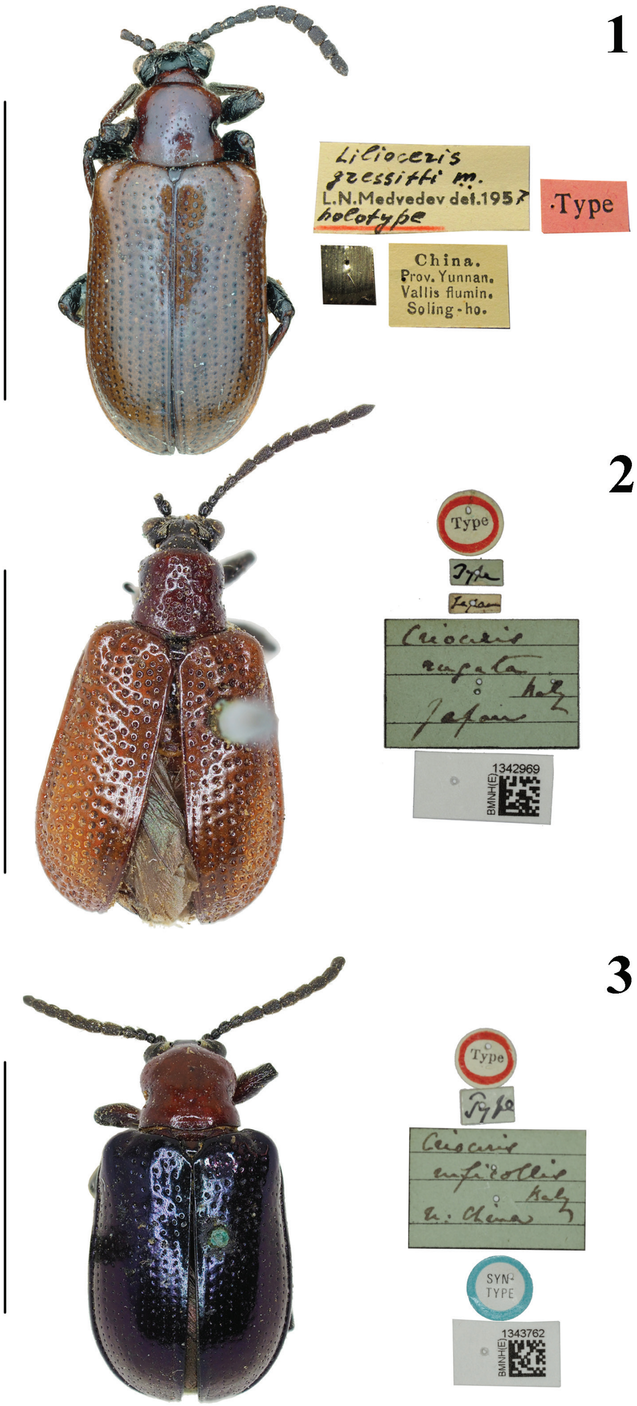
sieversi Heyden, 1887: 271 (China, Mun. Pecking). (*Crioceris*). Medvedev 1958: 108 (*Lilioceris*).

ruficollis Baly, 1865: 155 (N. China, syntype, gender ?) (*Crioceris*). [homonym of *Crioceris ruficollis* Fabricius, 1787].

rubricollis White, 1981: 41 [replacement name of *Crioceris ruficollis* Baly, 1865].

Type material examined. 1 syntype of *Crioceris ruficollis* (NHML, photo), Crioceris ruficollis Baly, N China / SYN-TYPE / BMNH (E) 1343762.

Other material examined. Total 64 specimens. **China:** Heilongjiang: 2♂3♀, Harbin, Ertsentientze, Manchuria, 1941.VI.15; **Jilin**: 1♂1♀, Ma-an Shan / Lilioceris ruficollis Baly, Peiyu Yu Det.; **Beijing**: 1♀, Badaling, 700 m / 1962.VI.30, Chunguang Wang coll. / Lilioceris ruficollis (Baly), Peiyu Yu Det.; 1♀1♂, Badaling, 570 m / 1962.VIII.23, Shuyong Wang coll.; 2♀1♂, Badaling, 570 m / 1962.VIII.23, Shengqiao Jiang coll.; 1♀1♂, Badaling, 570 m / 1962.IX.6, Shuyong Wang coll.; 1♀, Shangfang Shan, 400 m / 1961.VII.18, Xuezhong Zhang coll.; 2♀, Sanpu / 1974.VII.18, Shengqiao Jiang coll.; 3♂, Sanpu / 1973.VIII.23, Shengqiao Jiang coll.; 1♂, Sanpu / 1980.VI.12, Jiang coll. / Lilioceris ruficollis (Baly); 1♂, Sanpu / 1973.VIII.23, Shengqiao Jiang coll. / Dioscorea nipponica Makino; 1♂, Badaling, 700 m / 1962.VI.29, Chunguang Wang coll.; 1♂, Shangfang Shan, 400 m / 1961.VII.14, Shuyong Wang coll.; 1♂, Mentougou, Yanchi, 301 m, 40.00237°N, 115.80577°E, 2021.VII.8, Yuan Xu, Yuyao Qin & Hongbin Liang coll.; 1♂, Changping, Baiyanggou, 301 m, 40.23828°N, 115.96238°E, 2021.VII.8, Yuan Xu, Yuyao Qin & Hongbin Liang coll.; 1♀, Shangfang Shan, Shengshuiyu, Yunxia Shanzhuang, 566 m, 39.65727°N, 115.78220°E, 2021.07.16, Yuan Xu, Yuyao Qin & Hongbin Liang coll.; 1♀1♂, Mentougou, Yanchi, 301 m, 40.00237°N, 115.80577°E, 2021.08.26, Hongbin Liang coll.; 3♀1♂, Mentougou, Zhaitang, Malan forest farm, 2021.VI.14, Meiying Lin coll.; 3♀3♂, Mentougou, Zhaitang, Cenfu, 2021.06.12, Meiying Lin



Figures 1–3. Habitus of *Lilioceris* spp. **1** *L. gressitti*, type, China (Yunnan), photographed by Christoph Germann **2** *L. rugata*, type, Japan, photographed by Hongbin Liang **3** *L. ruficollis*, type, north of China, photographed by Hongbin Liang. Scale bars: 5.0 mm.

coll.; 1♀, Mentougou, Wangping, Guacaodi Scenic Area, 2021.VIII.12, Yong Wang coll.; **Hebei**: 1♀, Chahar / Chahar, Yangkiaping / 1937.VII.6, O. Piel coll. / Lilioceris ruficollis (Baly), Peiyu Yu det.; 2♀, Chahar / Chahar Yangkiaping / 1937.VII.3, O. Piel coll.; 1♀, Chahar / Chahar, Yangkiaping / 1937.VII.5, O. Piel coll.; 1♂, Chahar / Chahar, Yangkiaping / 1937.VII.6, O. Piel coll.; 1♂, Xinglong, Taqian, 700 m / 1963.VII.3, Shengqiao Jiang coll.; **Hubei**: 2♂, Shennongjia, Zongluo, 900 m, 1981.VI.18, Yinheng Han coll.; **Shaanxi**: 1♀, 1936.6.9; **Zhejiang**: 2♂, Tianmu Shan, 1931.5.30; **Guizhou**: 1♂, 1910; **Jiangxi**: 1♂, Tonggu, 500 m / 1973.IV.24 / Lilioceris ruficollis (Baly), Peiyu Yu det.; **Fujian**: 1♀, Wuyi Shan, 1982.6.26, Fan Jiang coll. / Lilioceris ruficollis (Baly), Peiyu Yu det.; 1♀, Fuzhou / 1955.IV.21; 1♀, Fuzhou / 1955.IV.23; 1♀, Fujian; 1♀, Fuzhou, 1955.VIII.10; 1♀1♂, Fu-an, Shizitou, 1946.V.9; 1♀, Fu-an, Baisha, 1946.V.3–25; 1♂, Fuding, 1946.V; 1♂, Fuzhou / 1955.IV.23.

Diagnosis. Pronotum brownish red, elytra black or dark blue, femora black; pronotum disc with fine punctures; elytral punctures large on basal half, diminishing posteriorly; metasternite almost glabrous; abdominal sternites have a row pubescence and the rest of area nearly smooth, transverse impressions present on sternites 2–5, area outside the impression with sparse pubescence.

Redescription. BL = 6.5–8.5 mm, BW = 3.5–4.5 mm. Front part of head, antennae, legs, ventral surface black; occiput, pronotum brownish red, elytra dark blue or black; scutellum black slightly with brownish red.

Head (Fig. 3). HL/HW = 1.3–1.5; vertex without or with an indistinct groove in the middle, finely punctate and setose laterally; frontoclypeal area triangular, disc with dense punctures and setae; labrum transverse, with sparse setae; antennomeres 5–10 slightly longer than wide (Fig. 32).

Pronotum (Fig. 14A). PW / HW = 1.0–1.1, PL / PW = 1.2–1.3; anterior and posterior angle not protruding; sides constricted in the middle; middle of disc with fine and scattered punctures; anterior and posterior transverse impression indistinct, basal transverse groove shallow.

Elytra (Fig. 14D). EL/EW = 1.5–1.8; sutural angle rounded; humeri protruding, humeral groove distinct, basal transverse impression indistinct; scutellary striole composed of 5–8 punctures; strial punctures large at base, diminishing posteriorly; intervals flat; epipleura raised, with row of fine punctures.

Mesosternite pubescent. metasternite almost glabrous, only with sparse pubescence (Fig. 14B); metepisternum densely pubescent.

Abdominal sternites with a distinct row of pubescence, sparse in the middle; lateral transverse impressions present on sternites 2–5, area outside the impression sparsely pubescent (Fig. 14C).

Legs slender; tibiae with dense punctures and pubescence; femora with dense pubescence on the dorsal surface, with sparse pubescence on the ventral surface.

Male genitalia (Fig. 20A–D). Median foramen occupying 1/4 length of median lobe (Fig. 20A); apex triangular (Fig. 20B); basal piece of tegmen triangular, lateral lobes weakly sclerotized; posterior part of dorsal sclerite in lateral view curved, directed ventrally, narrowed at apex in dorsal view (Fig. 20C, D).

Female reproductive organs (Fig. 26A–C). Spiculum gastrale short, Y-shaped, distal part widened; ovipositor with dense setae, distal part of ovipositor cylindrical, short, with small protuberance; spermatheca slightly convoluted.

Distribution. China (Heilongjiang, Jilin, Beijing, Hebei, Shaanxi, Hubei, Zhejiang, Guizhou, Jiangxi, Fujian); Korea (Park et al. 2012; Cho and An 2020).

Host plant and habitat. This species feeds on *Dioscorea nipponica* and *D. polystachya* in Beijing according to our observations; in addition, *D. septemioba*, *D. batatas*, and *D. japonica* are also its hosts (Park et al. 2012).

One collecting locality of it in Beijing (Fig. 46) is situated at the north temperate zone. The climate is a temperate monsoon climate, with hot and rainy summers, and cold and dry winters with an average temperature below 0 °C. Affected by the climate, temperate deciduous broad-leaved forests grow here. The host plant *Dioscorea polystachya* shares a habitat with other plants such as *Koelreuteria paniculata* (Sapindaceae), *Menispermum dauricum* (Menispermaceae), *Vitex negundo* var. *heterophylla* (Lamiaceae), *Populus* sp. (Salicaceae), *Ulmus pumila* (Ulmaceae), *Humulus scandens* (Cannabaceae), *Persicaria* sp. (Polygonaceae) and others.

Remarks. This species is unique in *sinica* group for its dark blue or black elytra, aedeagus with an acute apex, and the dorsal sclerites curved in lateral view. The color of ventral side and the femora of this species is variable: specimens from northern China are completely black, while those from southern China are black with brownish red.

Lilioceris sinica **(Heyden, 1887b)**

Figs 6, 7, 15, 21, 27, 33, 42, 47–50

sinica Heyden, 1887: 270 (China, Mun. Pecking, syntype, gender ?) (*Crioceris*). Medvedev 1958: 112 (*Lilioceris*).

chinensis Jacoby, 1888: 340 (China, Pref. Kiukiang, syntype, gender ?) (*Crioceris*) [synonymized by Gressitt and Kimoto 1961: 58].

rugata sparsipunctata Medvedev, 1958: 111 (China, Mount. Tienmuschan, holotype, gender ?) [synonymized by Gressitt and Kimoto 1961: 58].

Type material examined. 1 syntype of *Lilioceris sinica* (SDEI, photo), Pecking, Staudgr. 1885 / crioceris 2 / Syntypus / SDEI Coleoptera # 300896; 1 syntype of *Lilioceris of chinensis* (NHML, photo), Syntype / Kiukiang / Jacoby coll. 1909-28a / BMNH (E) 1343930; Holotype of *Lilioceris rugata sparsipunctata* (NHML, photo), Tienmuschan, N.W. China Rtt. / Lilioceris rugata sbsp. sparsipunctata m. L N. Medvedev det. 1957 holotype / Type.

Other material examined. Total 208 specimens (gender undetermined). **Beijing**: 2, Fangshan, 400 m, 1961.VI.17–18 / Shuyong Wang coll.; 4, Haidian, Xiang Shan, Yingtaogou, 40.01027°N, 116.19609°E / 131 m, 2021.VII.16, Yuan Xu, Yuyao Qin & Hongbin Liang coll.; 3, Fangshan, Shengshuiyu, Yunxia Shanzhuang, 565 m, 39.65727°N, 115.78220°E, 2021.VII.16, Yuan Xu, Yuyao Qin & Hongbin Liang coll.;

1, Miyun, Shicheng, Wangzhuang, 2020.VIII.9, Pengchang Yan coll.; 1 (MCAU), Xiang Shan, 1962.VII.12, Zhenping Zhu coll.; 1 (MCAU), Ming Tombs, 1956.VII.24, Jikun Yang coll.; **Shaanxi**: 1, 1936.V.3; 1, Liuba, Miaotaizi, 1470 m / 1999.VII.1, Chaodong Zhu coll.; 1 (MCAU), Zhongnan Shan, Taiyigong, 1956.VI.26, Jikun Yang coll.; **Shandong**: 6, Jinan; **Jiangsu**: 1, Nanjing Tangshan, 1935.V.8; 5, cemetery of Chen, 1935.IV.7–V.27; 1, Nanjing, 1923.V.16; **Henan**: 1, Xinyang, Shangcheng, Huangbai Shan, 31.3816°N, 115.3017°E / 850 m, 2020.VII.13, Pingzhou Zhu coll.; 1, Xinyang, Xinxian, Jinlan Shan, 31.6213°N, 114.7980°E / 657 m, 2020.VII.9, Lihao Zheng coll.; 1, Tongbai, Tongbai Shan, 32.3560°N, 113.3428°E / 416 m, 2020.VII.25, Lihao Zheng coll.; 5, Xinyang, Tanjiahe, 31.8683°N, 113.9382°E / 285 m, 2020.VII.7, Pingzhou Zhu coll.; 2, Xinyang, Jigong Shan, 31.8011°N, 114.0745°E / 730 m, 2020.VII.4, Pingzhou Zhu coll.; **Hubei**: 1, Shennongjia Songbai Town, 900–1200 m / 1981.V.23, Yinheng Han coll.; **Hunan**: 1, Chengbu, Dankou, 2018.05.07, Kaiqin Li coll.; **Zhejiang**: 7, Tianmu Shan, 1936.VI.9–VII.23; 1, Tianmu Shan, 1937.V.11; 1, Tianmu Shan, 1937.VIII.14; 1, Tianmu Shan, 1932.V.8; 7, Mogan Shan, 1936.IV.30–V.29; 3, Mogan Shan, 1935.V.21–VI.7; 1, Mogan Shan, 1937.VI.9; 11, Zhoushan, 1931.V.3–VI.3; 1, Zhoushan, 1923.VII.7; 4, Zhoushan, 1935.VI.12–19; 2, Zhoushan, 1934.VI.28; 2, Hangzhou, 1933.V.18–19; 1, Hangzhou, 1925; 1, Hangzhou, 1954.VI.12; 1, Taizhou, 1924.IV.30; 1, Gushan, 1933.V.23; 1, Hangzhou, West Lake, 1931.V.3; 1 (MCAU), Tianmu Shan, Chanyuan Temple, 1957.VII.1, Fasheng Li coll.; **Jiangxi**: 2, Tonggu, Taiyangling, 1974.XI.25; **Fujian**: 45, Chongan, Xingcun, Sangang, 740–900 m / 1960.V.14–VIII.24, Yiran Zhang, Chenglin Ma, Fuji Pu & Shengqiao Jiang coll.; 1, Chongan, Xingcun, San-gang, 720 m / 1973.VI.9, Peiyu Yu coll.; 8, Chongan, Xingcun, Qili Bridge, 840–870 m / 1960.V.25–VI.25, Shengqiao Jiang, Fuji Pu coll.; 14, Chongan, Xingcun, Tongmuguan, 800–1150 m / 1960.V.15–VII.10, Shengqiao Jiang, Yiran Zhang & Chenglin Ma coll.; 12, Jianyang, Dazhulan, Xianfengling, 950–1170 m / 1960.V.2–VII.5, Chenglin Ma, Yiran Zhang, Fuji Pu; 9, Jianyang, Huangkeng, Aotou, 680–950 m / 1960.IV.26–VIII.8, Fuji Pu & Yiran Zhang coll.; 4, Chongan, Xingcun, Tongmuguan, Guanping, 800–1000 m / 1960.V.30–VIII.13, Shengqiao Jiang & Fuji Pu coll.; 4, Chongan, Xingcun, Longdu, 580–800 m / 1960.V.19–VI.5, Shengqiao Jiang & Yong Zuo coll.; 1, Jianyang, Huangkeng, Dazhulan, 900–1170 m, 1960.VII.24, Jiang Shengqiao; 1, Jianyang, Huangkeng, Dazhulan, 900 m / 1973.VI.6, Peiyu Yu coll.; 1, Chongan, Chengguan, 240 m / 1960.IX.19, Yiran Zhang coll.; 1, Chongan, Wuyishan Sanatorium, 175–300 m / 1960.VII.3, Fuji Pu coll.; 2, Jianyang, Huangkeng, Guilin, 270 m / 1960.IV.11, Yiran Zhang coll.; 1, Dazhulan, 1948.VL.20; 2, Fujian; Chongan, Xingcun, Shili Factory, 840 m / 1960.V.25, Shengqiao Jiang coll.;1, Chongan, Xingcun, Guadun, 900–1160 m / 1960.VI.8, Chenglin Ma coll.; 1, Chongan, Xingcun, Sangang, 700 m / 1982.VI.8, Juanjie Tan coll.; **Guangxi**: 1, Ziyuan, 1976.VII.14, Baolin Zhang coll.; 3, Guilin, 1952.IV.19–XII.8; 2, Guilin, Yan Shan, 1953.IV.24–V.12; 1, Yan Shan, 1952.XI.24; 1, Yangshuo; 1, Yao Shan, 1938.V.6; 1, Baishou, 1952.VI.28; **Sichuan**: 4, Luding, Moxi, 1500 m / 1983.VL.17–20, Shuyong Wang; 1, Xiangcheng, 2900–3200 m, 1982.VI.28, Shuyong Wang coll.; **Guizhou**: 7, Huaxi, 2000.VI.8; 1, Bazhai, 1930.VII.22;3, Guizhou; 1 (MBSU), Kweichow. SW. China, Kweiyang, alt. 1000 meters. 1940.VII.11, J. L. Gressitt / chinensis / Crioceris chinensis Jac., J. L. Gressitt det. 1940 / Lilioceris sinica (Heyden), det. Jianguo Long / En–077357; **Yunnan:** 1, Yongsheng, Liude, 2100 m / 1984.VII.18, Shuyong Wang coll.; 1 (MCAU), Kunming, 1946.V.

Diagnosis. Femora bicolored, black with brownish red middle; pronotum disc with fine punctures; elytral punctures strong, not diminishing posteriorly, intervals convex at apical 1/4; lateral side of metasternite with a wide strip of pubescence; abdominal transverse impressions present on lateral area of sternites 2–5, glabrous, other area of sternite pubescent.

Redescription. BL = 6.2–9.0 mm, BW = 3.0–4.5 mm. The front part of the head, antennae, ventral surface black; occiput, pronotum, scutellum and elytra brownish red, femora bicolored, brownish red with apex black.

Head (Fig. 6). HL/HW = 1.1–1.2; vertex with a shallow groove in the middle, punctate and setose laterally; frontoclypeal area triangular, disc with dense punctures and setae; labrum transverse, with long setae on both apical angles; antennomeres 5–10 slightly longer than their widths (Fig. 33).

Pronotum (Fig. 15B). PW / HW = 0.9–1.1, PL / PW = 1.0–1.1; anterior angle slightly protruding; posterior angle not protruding; sides distinctly constricted in the middle; middle of disc with fine punctures; anterior and posterior transverse impression indistinct, basal transverse groove shallow.

Elytra (Fig. 15D). EL/EW = 1.4–1.6; sutural angle rounded; humeri protruding, humeral groove shallow, basal transverse impression indistinct; scutellary striole composed of 4–7 punctures; strial punctures large, not diminishing posteriorly, intervals convex at apical 1/4; epipleura raised, with a row of fine punctures.

Mesosternite pubescent; lateral side of metasternite with wide strip of pubescence, extending from anterior to posterior margin, lateral 1/4 near metepisternum glabrous (Fig. 15B); metepisternum densely pubescent.

Lateral transverse impressions present on abdominal sternites 2–5, other area of sternite densely pubescent (Fig. 15C).

Legs slender; tibiae with dense punctures pubescence; femora with dense pubescence on the dorsal surface, with sparse pubescence on the ventral surface.

Male genitalia (Fig. 21A–D). Median foramen occupying 1/5 length of median lobe (Fig. 21A); apex rounded (Fig. 21B); basal piece of the tegmen triangular, relatively broad, lateral lobes weakly sclerotized; posterior part of dorsal sclerite in dorsal view more or less parallel-sided, slightly narrowed at apex (Fig. 21C, D).

Female reproductive organs (Fig. 27A–C). Spiculum gastrale long, Y-shaped, distal part slightly widened, apical margin rounded; ovipositor with dense setae, distal part of the ovipositor cylindrical, short, with a small protuberance; spermatheca simply convoluted.

Distribution. Beijing, Shandong, Shaanxi, Henan, Jiangsu, Hubei, Hunan, Zhejiang, Jiangxi, Fujian, Guangxi, Yunnan, Sichuan, Guizhou; Korea (Cho and An 2020).

Host plant and habitat. (Figs 47–50) This species feeds on *Dioscorea polystachya* according to our field observation in Beijing (Fig. 49).

This species lives on elevations from 131 to 3200 m. One collecting locality of *L. sinica* in Beijing (Fig. 50) is situated at the north temperate zone. The climate here is a temperate monsoon climate, with hot and rainy summers, and cold and dry winters with an average temperature below 0 °C. Affected by the climate, temperate deciduous broad-leaved forests grow here. The host plant *Dioscorea polystachya* shares habitat with other plants such as *Metasequoia glyptostroboides* (Cupressaceae), *Juniperus chinensis* (Cupressaceae), Pinus tabuliformis (Pinaceae), *Syringa oblata* (Oleaceae), *Morus alba* (Moraceae), *Vitex negundo* var. *heterophylla* (Lamiaceae), *Inula japonica* (Asteraceae), *Polygonum aviculare* (Polygonaceae), *Potentilla chinensis* (Rosaceae) and *Oxalis corniculate* (Oxalidaceae).

Remarks. *Lilioceris rugata sparsipunctata* Medvedev, 1958 was described from Zhejiang and *Lilioceris chinensis* (Jacoby 1888) was described from Jiangxi. Gressitt and Kimoto (1961: 58) synonymized them with *L. sinica*. We compared the types (Figs 4, 5) and agree with their treatment.

Lilioceris jakobi (White 1981) was originally described as *Lilioceris minima* by Jakob (1961) from Zhejiang and Fujian (White 1981). This species is similar to *L. chinensis* according to original literature (Jakob 1961), but it has a smooth pronotum, so should not belong to the *sinica* group. Unfortunately, the status of this species is unclear because we could not locate the type depository.

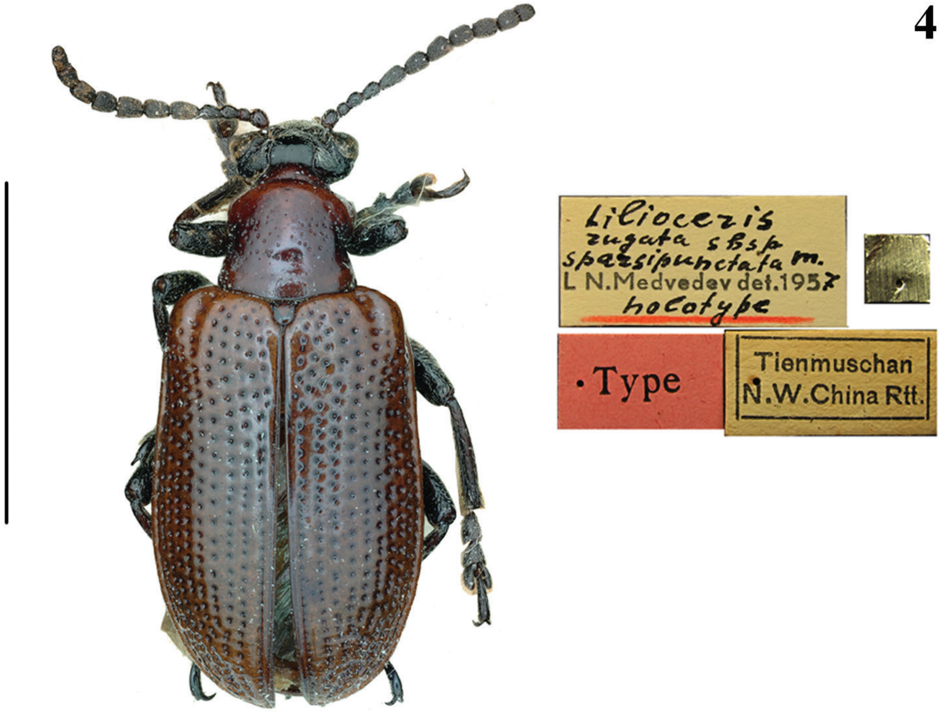
Lilioceris theana (Reitter, 1898)

Figs 8, 9, 16, 22, 28, 34, 42, 51–54

theana Reitter, 1898: 22 (Russia, Sibiria, holotype, gender ?). (*Crioceris*). Chûjô 1941: 453 (*Lilioceris*).

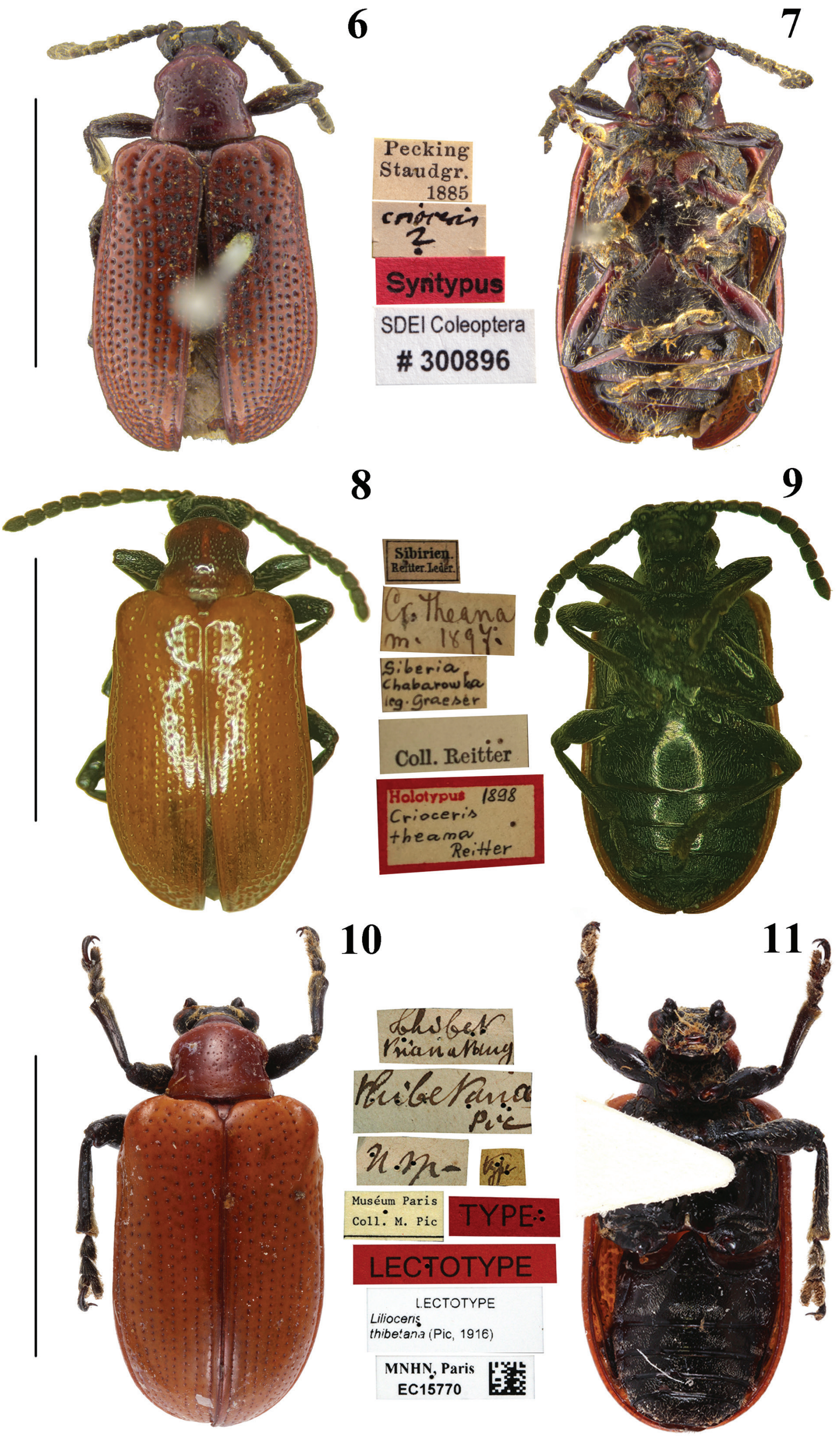
Type material examined. ***Holotype*** (HNHM, photo), Sibirien, Reitter Leder / Siberia Chabarowba, leg. Graeser / Cr. theana m. 1897 / Holotypus, 1898, Crioceris theama [mis-spelling of theana], Reitter / Coll. Reitter.

Other material examined. Total 92 specimens. China: **Heilongjiang**: 1♀ Harbin / 1931.IX.30; 1♀ Mao'er Shan / 1962, Comprehensive Investigation Department, Ministry of Forestry coll.; 1♀ Dailing / 1971.V.22; **Liaoning**: 2♀ Qian Shan / 1987.VI.2, Jinke Li coll.; 1♀ Qingyuan / 1934.5.12; 2♂2♀, Shenyang, Qipan Shan, 2020.VII.11, Haicheng Shan coll.; 1♀, Shenyang, Qipan Shan, 2020.VII.13, Haicheng Shan coll.; 2♂, Shenyang, Qipan Shan, 2020.VII.23, Haicheng Shan coll.; 1♂1♀, Shenyang, Qipan Shan, 2020.VIII.2, Haicheng Shan coll.; 60 (♂, ♀), Shenyang, Qipan Shan, 2021.V.10–VI.13, Haicheng Shan coll.; **Hebei**: 1♂ Wuling Shan, 800 m, 1981.VI.1, Peiyu Yu coll.; 5♀ Wuling Shan, Liushuigou, 1400 m, 1981.VI.4, Peiyu Yu coll.; **Beijing**: 1♀ Xiaolongmen, Forestry Farm, elevation 1140 m, 2003.V.18, Dakang Zhou coll.; 1♀ Yanqing, Song Shan, elevation 800 m, 2003.VI.4–7, Dakang Zhou coll.; 1♀ Wuling Shan, Western Gate, host unknown / 2006.V.4, Ye Liu coll.; **Zhejiang**: 1♀ Tianmu Shan, 1936.VI.9; 2♂ Tianmu Shan, 1936.VII.23; **Fujian**: 2♀ Wuyi Shan, Nature Reserve, 4



5

Figures 4, 5. Habitus of *Lilioceris* spp. **4** *L. rugata sparsipunctata*, type, China (Tienmuschan = Tianmu Shan), photographed by Christoph Germann **5** *L. chinensis*, syntype, China (Kiukiang = Jiujiang), photographed by Hongbin Liang. Scale bars: 5.0 mm.



Figures 6–11. Habitus of *Lilioceris* spp. **6, 7** *L. sinica*, type, China (Pecking = Beijing), photographed by Mandy Schröter **8, 9** *L. theana*, holotype, Siberia, photographed by Raorao Mo **10, 11** *L. thibetana*, type, China (Tibet), photographed by Antoine Mantilleri. Scale bars: 5.0 mm.

670–1420 m, 2004.IV.24–5.13, Dakang Zhou coll. **Russia**: 1♂, Primorsky Krai 12 km. Chernigovka, Gribnoe / Punza / 1974.V.16 Ler. **South Korea**: 1 (NIBR), Korea (GB) Bonghwa-gun, Chunyang- myeon, Seobyeok-ri. Joong Youb Kim, 2018.V.23 / Lilioceris sinica (Heyden, 1887b), Det: Jong Eun Lee, 2018.IX.19 / NIBR 0000921396.

Diagnosis. Femora bicolored, black with brownish red middle; pronotum disc with fine punctures; elytral punctures strong, not diminishing posteriorly, intervals convex at apical 1/4; lateral side of metasternite with a wide strip of pubescence; abdominal transverse impressions absent on sternites 2–5, sternite wholly pubescent.

Redescription. BL = 7.2–8.0 mm, BW = 3.5–3.8 mm. The front part of the head, antennae, ventral surface black; occiput, pronotum, scutellum and elytra brownish red, femora bicolored, brownish red with apex black.

Head (Fig. 8). HL/HW = 1.1–1.3; vertex with a deep groove in the middle, punctate and setose laterally; frontoclypeal area triangular, disc with dense punctures and setae; labrum transverse, with sparse setae; antennomeres 5–10 slightly longer than wide (Fig. 34).

Pronotum (Fig. 16A). PW / HW = 0.9–1.1, PL / PW = 1.0–1.2; anterior angle slightly protruding; posterior angle not protruding; sides slightly constricted in the middle; middle of disc with fine and scattered punctures; anterior and posterior transverse impression indistinct, basal transverse groove shallow.

Elytra (Fig. 16D). EL/EW = 1.4–1.5; sutural angle rounded; humeri protruding, humeral groove shallow, basal transverse impression indistinct; scutellary striole composed of 6–8 punctures; strial punctures large, not diminishing posteriorly, intervals convex at apical 1/4; epipleura raised, with a row of fine punctures laterally.

Mesosternite pubescent. Lateral side of metasternite with wide strip of pubescence, extending from anterior to posterior margin, 1/4 near metepisternum sparsely pubescent (Fig. 16B); metepisternum densely pubescent.

Lateral transverse impressions absent on abdominal sternites 2–5, all sternites densely pubescent (Fig. 16C).

Legs slender; tibiae with dense punctures pubescence; femora with dense pubescence on dorsal surface, with sparse pubescence on ventral surface.

Male genitalia (Fig. 22A–D). Median foramen occupying 1/4 length of median lobe (Fig. 22A); apex rounded (Fig. 22B); basal piece of tegmen triangular, relatively broad, lateral lobes strongly sclerotized; posterior part of dorsal sclerite in dorsal view in dorsal view widely rounded, directed laterally (Fig. 22C, D).

Female reproductive organs (Fig. 28A–C). Spiculum gastrale long, Y-shaped, distal part slightly widened, apical margin rounded; ovipositor with dense setae, distal part of the ovipositor cylindrical, long, with small protuberance; spermatheca simply convoluted.

Host plant. This species feeds on *Dioscorea nipponica* in Liaoning Province (Fig. 54). Adults appeared on host plants from May to September.

Distribution. China (Heilongjiang, Liaoning, Jilin, Hebei, Beijing, Zhejiang, Fujian); Russia; Korea.

Remarks. *Lilioceris theana* was described by Reitter (1898) from Siberia, Russia. Chûjô (1941: 453) synonymized it with *L. rugata*, and Gressitt and Kimoto (1961: 58) synonymized it with *L. sinica*. Subsequent researchers have followed Chûjô's treatment (e.g., Warchałowski 2011; Bezděk and Schmitt 2017). According to our study of the types (Figs 8, 9), *L. theana* is a distinct species, and it clearly differs from *L. rugata* by having a wide strip of pubescence on the lateral side of the metasternite and abdominal sternites with dense pubescence (sides of metasternite and abdominal sternites nearly smooth in *L. rugata*). *Lilioceris theana* differs from *L. sinica* in the transverse impressions on abdominal sternites 2–5 absent (having clear transverse impressions on abdominal sternites 2–5 in *L. sinica*). In addition, the spiculum gastrale and spermatheca of the three species are distinctly different (Figs 25A–C, 27A–C, 28A–C).

Lilioceris thibetana **(Pic, 1916)**

Figs 10, 11, 17, 23, 29, 35, 42

thibetana Pic, 1916: 18 (China, Prov. Thibet, Type / Lectotype, male). (*Crioceris*). Gressitt and Kimoto 1961: 59 (*Lilioceris*).

Type material examined. 1♂, type [MNHN, photo], Thibet, Trianatang / thibetana Pic / n. sp / Type / Museum Paris Coll. M. Pic / TYPE / LECTOTYPE / LECTOTYPE Lilioceris thibetana (Pic, 1916) / MNHN, Paris EC15770.

Other material examined. Total 3 specimens. **China: Yunnan:** 1♂, Xishuangbanna, Meng-a, 1050–1080 m / 1958.VI.9, Shuyong Wang coll.; 1♀, Xishuangbanna, Menghai, 1200–1600 m / 1958.VII.22, Fuji Pu coll.; 1♂, Lushui, Pianma, 1750 m / 1981.V.27, Xuezhong Zhang coll. / ? Lilioceris gressitti Medvedev, Peiyu Yu det.

Diagnosis. Femora black. Pronotum disc with fine punctures; elytral punctures small, slightly diminishing or not diminishing posteriorly; metasternite almost glabrous; abdominal sternites with sparse pubescence, transverse impressions present on sternites 2–5.

Redescription. BL = 6.0–7.0 mm, BW = 3.0–3.5 mm. Front part of head, antennae, ventral surface, and legs black; occiput, pronotum, scutellum, and elytra brownish red.

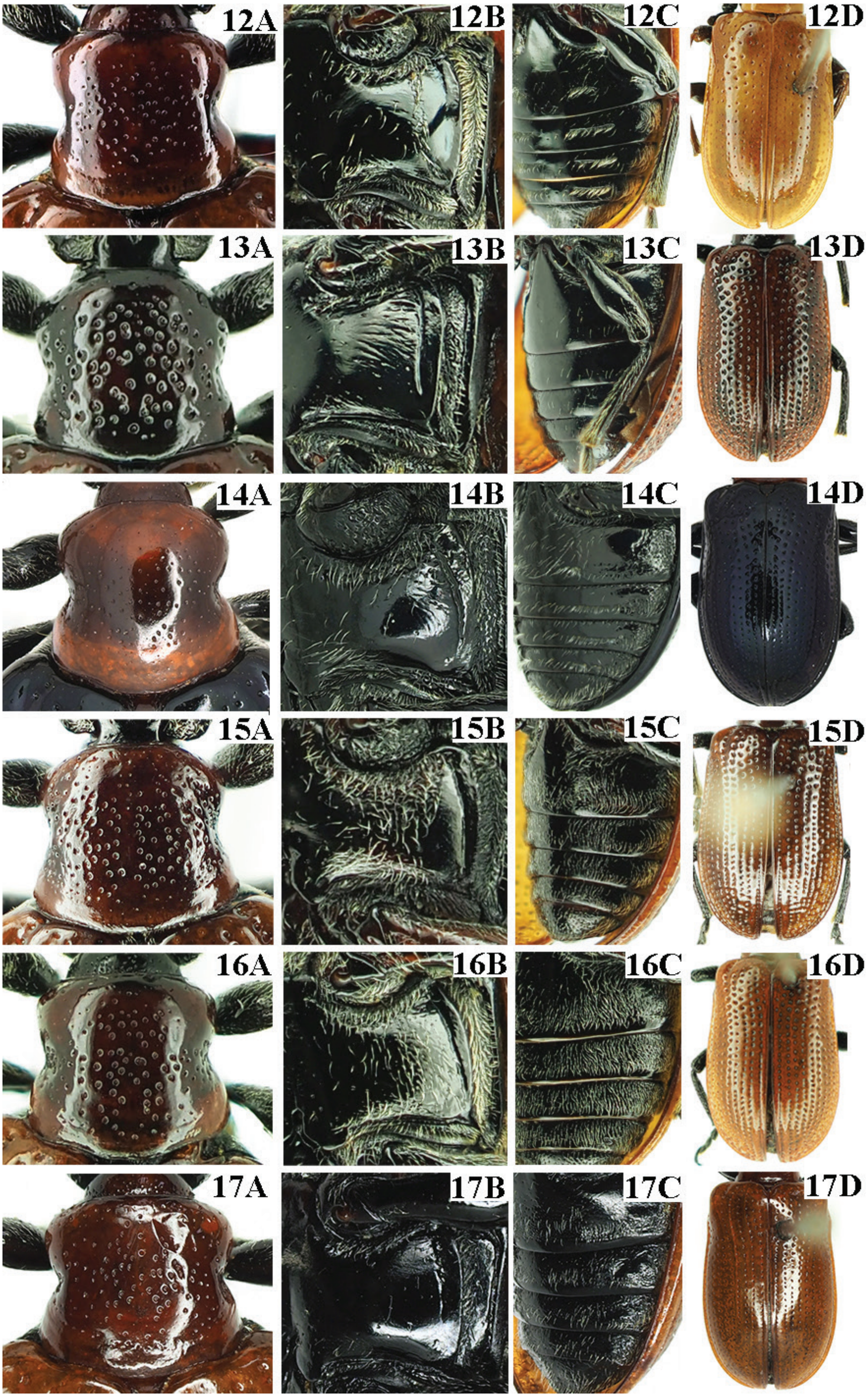
Head (Fig. 10). HL/HW = 1.1–1.2; vertex without groove in the middle, finely punctate and setose laterally; frontoclypeal area triangular, disc with sparse punctures and setae; labrum transverse, with sparse setae; antennomeres 5–10 each slightly longer than wide (Fig. 35).

Pronotum (Fig. 17A). PW / HW = 1.0–1.1, PL / PW = 0.9–1.0; anterior and posterior angle not protruding; sides distinctly constricted in the middle; middle of disc with fine and scattered punctures; anterior and posterior transverse impression indistinct, basal transverse groove shallow.

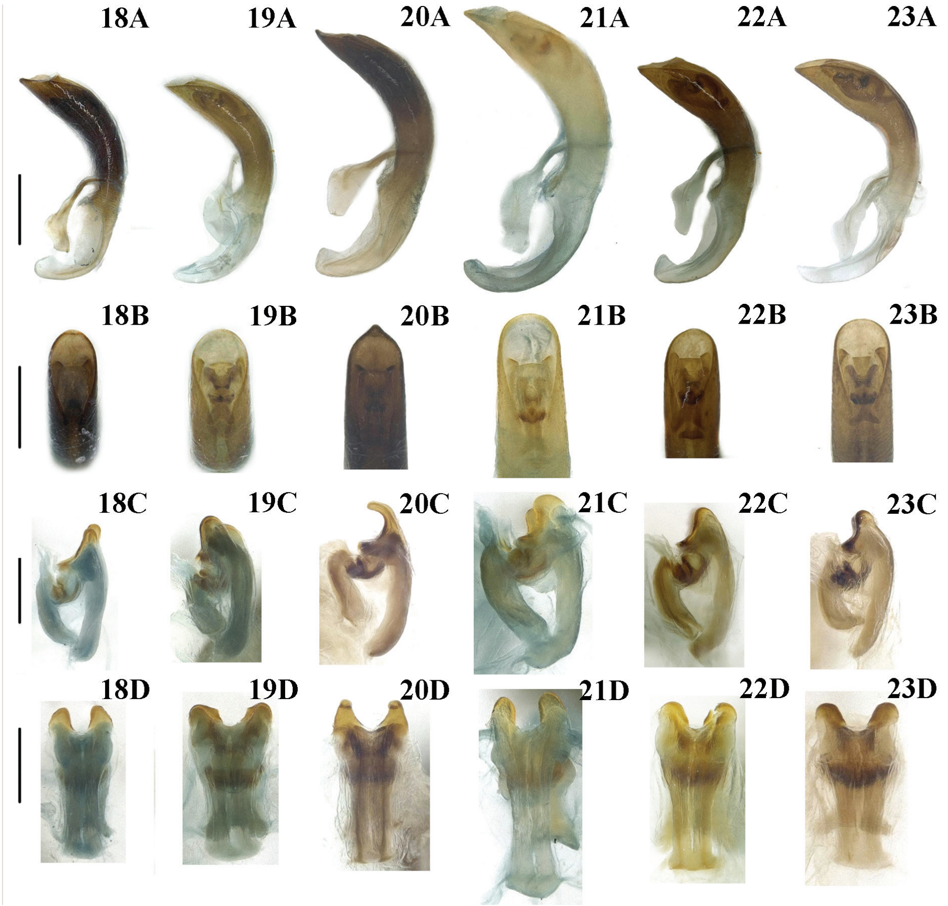
Elytra (Fig. 17D). EL/EW = 1.3–1.5; sutural angle rounded; humeri protruding, humeral groove distinct, basal transverse impression indistinct; scutellary striole composed of 5–8 punctures; strial punctures small, slightly diminishing or not diminishing posteriorly; intervals flat; epipleura raised, with row of fine punctures.

Mesosternite pubescent. Lateral side of the metasternite nearly smooth (Fig. 17B); metepisternum densely pubescent.

Abdominal sternites with sparse pubescence; lateral transverse impressions present on sternites 2–5, area outside the impression densely pubescent (Fig. 17C).



Figures 12–17. Pronotum, mesoventral disc, abdominal sternites and elytra of *Lilioceris* spp. **12** *L. gressitti*, ♂, China (Yunnan: Kunming) **13** *L. rugata*, ♂, Japan (Mont Takao) **14** *L. sieversi*, ♂, China (Beijing) **15** *L. sinica*, ♂, China (Beijing) **16** *L. theana*, ♀, China (Liaoning: Shenyang) **17** *L. thibetana*, ♀, China (Yunnan: Xishuangbanna) **A** pronotum **B** mesoventral disc **C** abdominal sternite **D** elytra.



Figures 18–23. Male genitalia of *Lilioceris* spp. **18** *L. gressitti*, China (Yunnan: Wuding) **19** *L. rugata*, Japan **20** *L. sieversi*, China (Beijing) **21** *L. sinica*, China (Beijing) **22** *L. theana*, China (Liaoning: Shenyang) **23** *L. thibetana*, China (Yunnan: Xishuangbanna **A** aedeagus, lateral view **B** aedeagus, dorsal view **C** sclerites in internal sac, lateral view **D** dorsal sclerite, dorsal view. Scale bars: 0.5 mm (**A, B**); 0.2 mm (**C, D**).

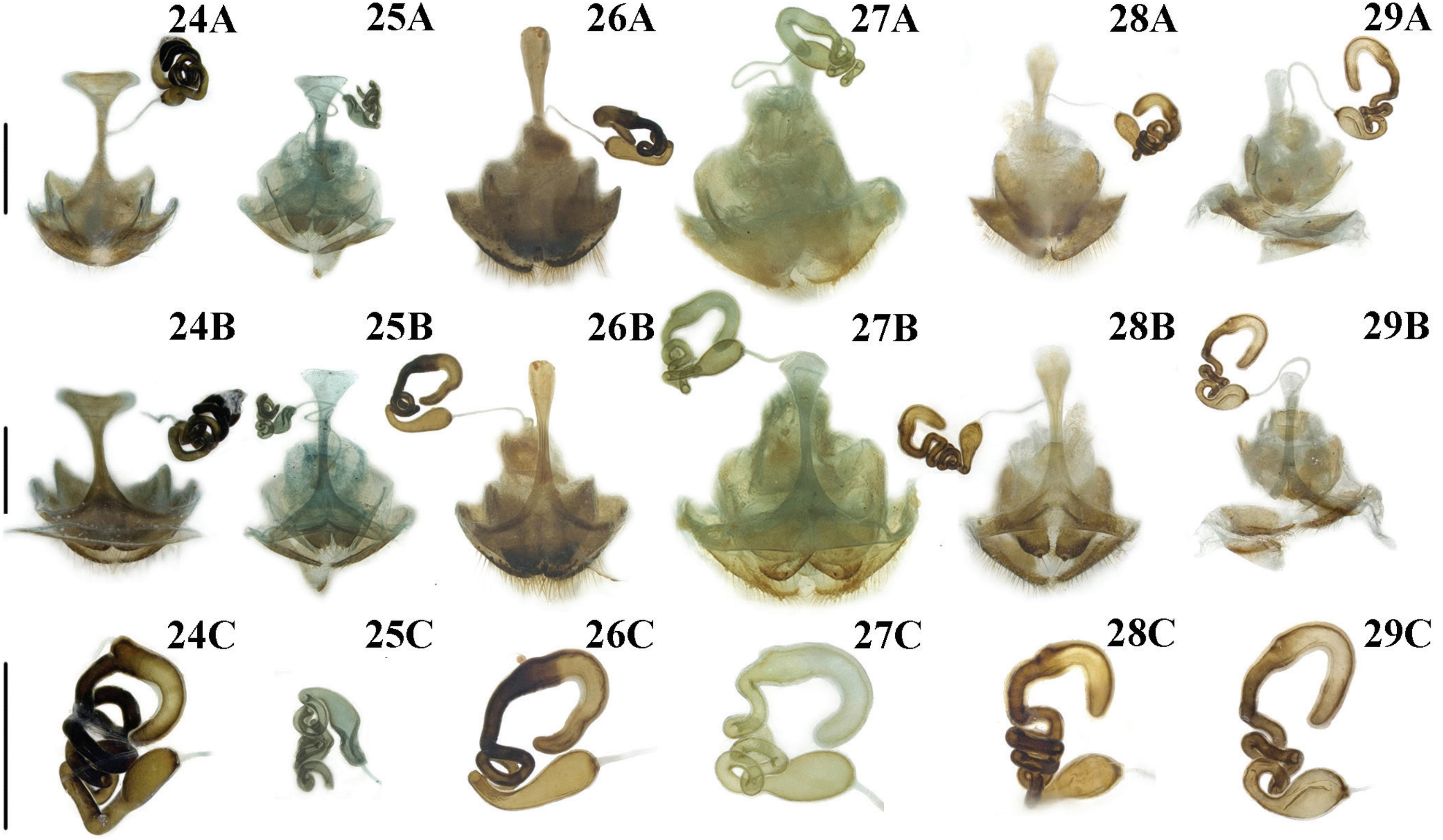
Legs slender; tibiae with dense punctures and pubescence; femora with dense pubescence on dorsal surface, with sparse pubescence on ventral surface.

Male genitalia (Fig. 23A–D). Median foramen occupying 1/5 length of median lobe (Fig. 23A); apex rounded (Fig. 23B); basal piece of tegmen triangular, lateral lobes slightly sclerotized; posterior part of dorsal sclerite in dorsal view in dorsal view widely rounded, directed laterally (Fig. 23C, D).

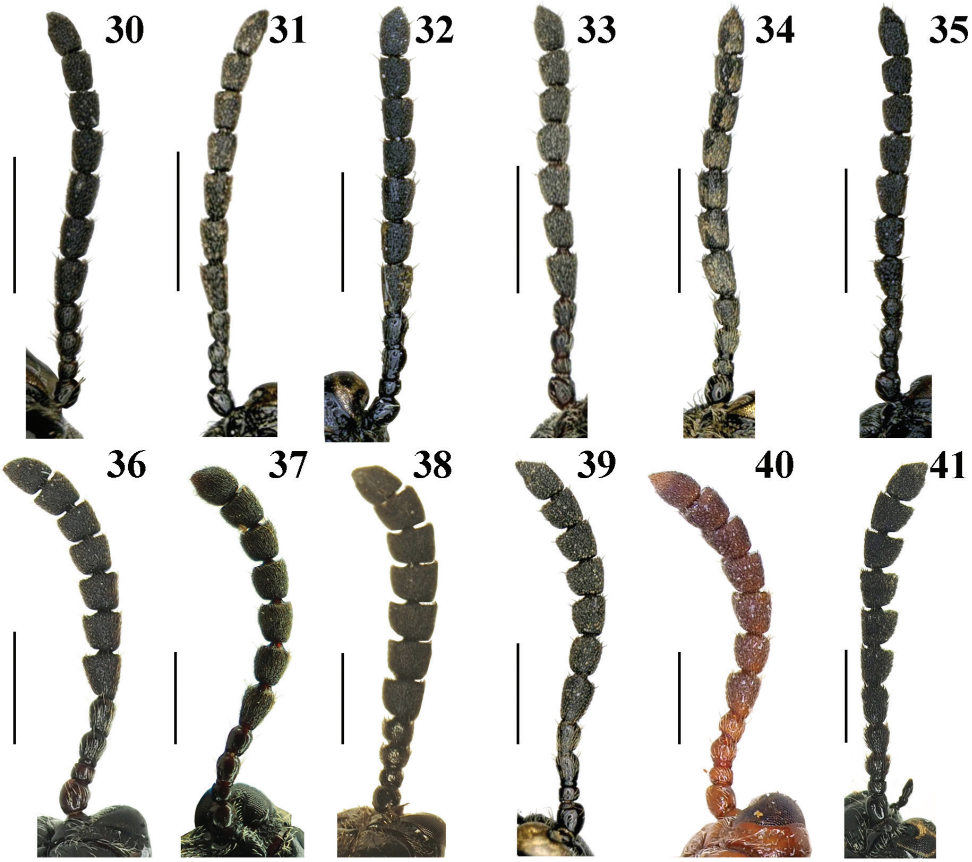
Female reproductive organs (Fig. 29A–C). Spiculum gastrale short, Y-shaped, distal part slightly widened, apical margin rounded (it was broken during dissection, Fig. 29A, B); ovipositor with dense setae, distal part of the ovipositor cylindrical, short, with small protuberance; spermatheca greatly convoluted.

Distribution. China (Tibet, Yunnan).

Host plant and habitat. Unknown.



Figures 24–29. Female reproductive organs of *Lilioceris* spp. **24** *L. gressitti*, China (Yunnan: Wuding) **25** *L. rugata*, Japan (Tokyo) **26** *L. sieversi*, China (Beijing) **27** *L. sinica*, China (Beijing) **28** *L. theana*, China (Liaoning: Shenyang) **29** *L. thibetana*, China (Yunnan: Xishuangbanna) **A** dorsal view **B** ventral view **C** spermatheca. Scale bars: 0.5 mm.



Figures 30–41. Antennae of *Lilioceris* spp. **30** *L. gressitti*, ♂, China (Yunnan: Tengchong) **31** *L. rugata*, ♂, Japan (Kibune: Kyoto) **32** *L. sieversi*, ♀, China (Beijing) **33** *L. sinica*, ♂, China (Anhui: Yuexi) **34** *L. theana*, ♀, China (Liaoning: Shenyang) **35** *L. thibetana*, ♂, China (Yunnan: Lushui) **36** *L. cheni*, ♂, China (Guangdong: Shixing) **37** *L. egena*, ♂, China (Tibet: Mêdog) **38** *L. impressa*, ♂, China (Yunnan: Gongshan) **39** *L. laosensis*, ♂, China (Tibet: Mêdog) **40** *L. malabarica*, ♂, India (Mahe: Malabar) **41** *L. yunnana*, ♂, China (Yunnan: Tengchong). Scale bars: 1.0 mm.

Remarks. In original labels, the type locality is 'Thibet, Trianatang'. There are at least three villages with similar pronunciation to Trianatang, first village 'Qiunatong' is in Gongshan county, northwestern Yunnan (28.09655°N, 98.57368°E, 1816 m), very close to Tibet; the second village 'Qunatang' is in Zayü county, Tibet (28.33884°N, 98.58602°E, 2460 m), and the third village 'Qunatang' is in Mêdog county, Tibet (29.46423°N, 95.74406°E, 2084 m). They are not far from each other, and all are possibilities to be the type locality of 'Trianatang'.

Lilioceris thibetana was formerly placed in the *impressa* group (Tishechkin et al. 2011), probably due to its similarity with *Lilioceris malabarica* as stated in original description by Pic (1916). In the holotype, the antennae are missing, so it is difficult to determine whether it belongs to the *impressa* group or the *sinica* group based on the antennae. Fortunately, we have three specimens from Yunnan which fit well with

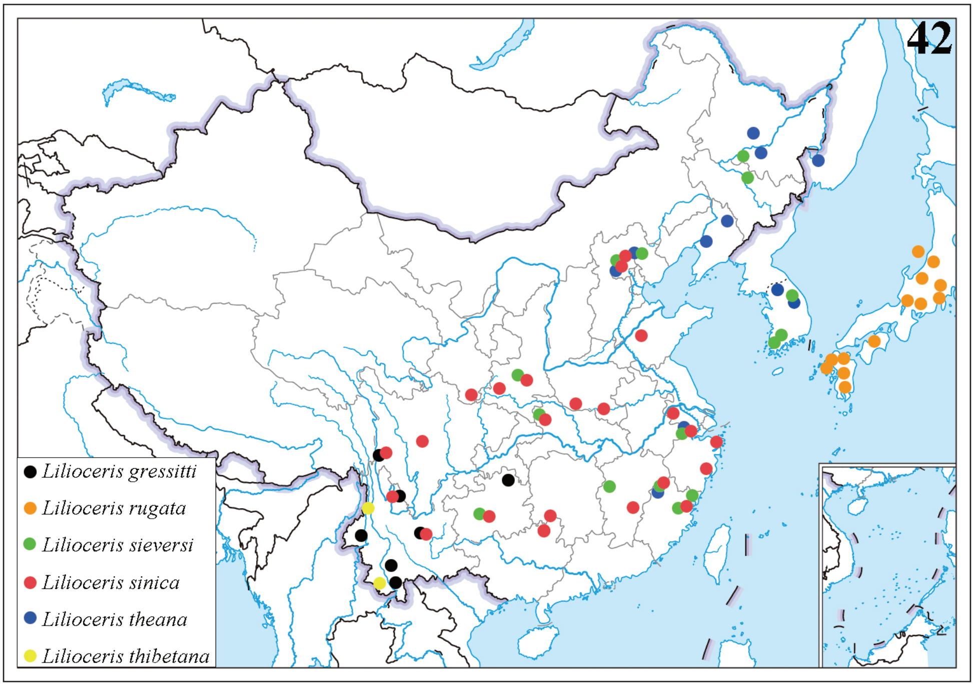
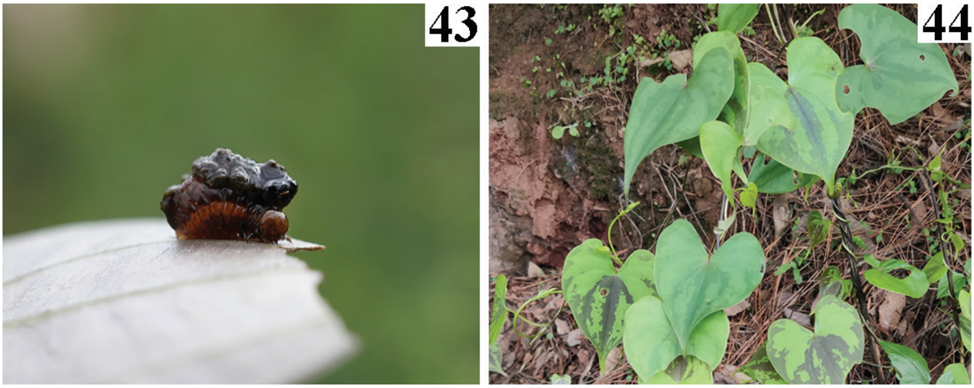


Figure 42. Distribution map of *Lilioceris* spp. (*L. sinica* in Korea and *L. thibetana* in Tibet are not marked because of lack of precise locality data).



Figures 43, 44. *Lilioceris gressitti* in China (Yunnan: Wuding), 2021.VII.11, photographed by YX **43** larva **44** host plant, *Dioscorea* sp.

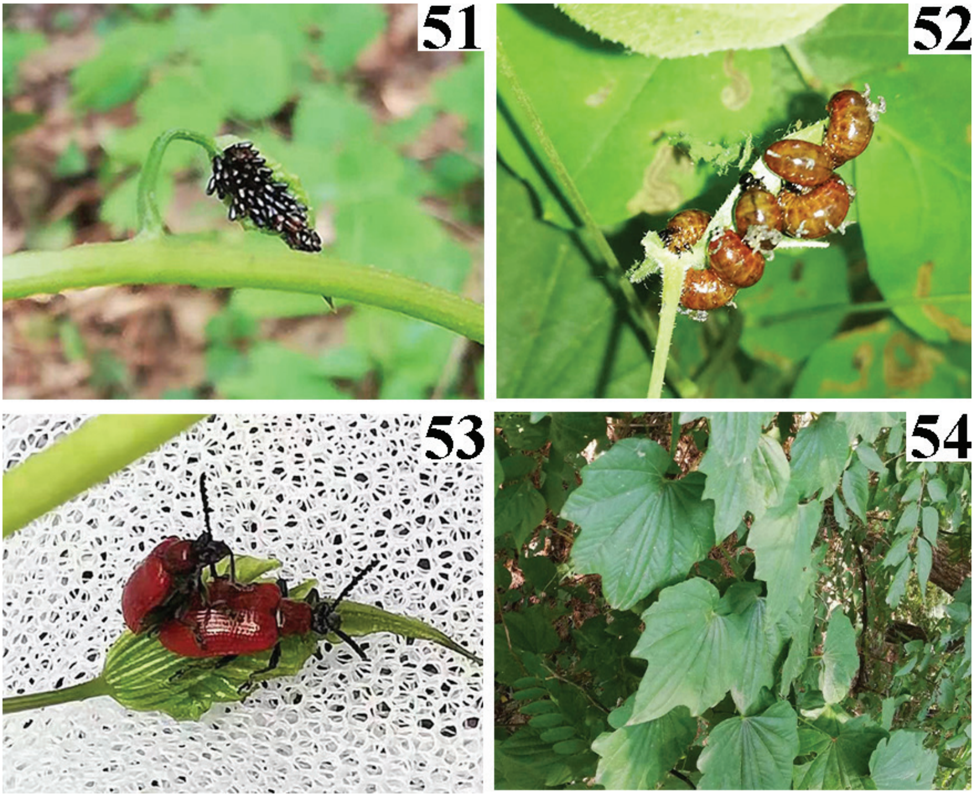
the type in body size, body color, punctures on pronotum and elytra, pubescence on metasternites and abdominal sternites, and in the shape of the aedeagus (compared with the illustration of Tishechkin et al. 2011: fig. 29). However, their antennomeres 5–10 are all cylindrical so we moved *L. thibetana* into the *sinica* group.

This species is similar to *Lilioceris gressitti*, but differs by having the metaventral disc nearly smooth (in *L. gressitti*, the metaventral disc has a narrow pubescent strip).

Furthermore, in *L. thibetana*, the spiculum gastrale is Y-shaped, slightly wider in the distal part, and the apical margin is rounded, while in *L. gressitti*, the spiculum gastrale is X-shaped, strongly widened in the distal part, and the apical margin is straight.

Figures 45, 46. *Lilioceris* spp. **45** *Lilioceris rugata* in Japan, 2003.V.9, photographed by Masakazu Hayashi **46** *Lilioceris sieversi* in China (Beijing), 2021.VI.12, photographed by Meiying Lin.

Figures 47–50. *Lilioceris sinica* in China (Beijing), 2021.VII.16 **47** larva **48** adult **49** host plant, *Dioscorea* sp. **50** Habitat **47, 48** photographed by HBL. **49, 50** photographed by YX.



Figures 51–54. Biology of *Lilioceris theana*. China (Liaoning: Shenyang), 2021.V.23, Photographed by Haicheng Shan **51** eggs **52** larvae **53** adults **54** host plant, *Dioscorea nipponica*.

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RESEARCH ARTICLE

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Pinctada phuketensis sp. nov. (Bivalvia, Ostreida, Margaritidae), a new pearl oyster species from Phuket, western coast of Thailand

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Abstract

A new species of the genus *Pinctada* is described from samples collected from the east coast of Phuket Island, Thailand in the Andaman Sea. *Pinctada phuketensis* **sp. nov.** is distinguished from other species on both molecular and morphological data. Morphologically, the valves of *P. phuketensis* are characterized by a slightly developed to undeveloped posterior auricle, a small, narrow slit-like byssal notch, the absence of hinge teeth, and a pale to transparent non-nacreous border, with a few dark brown or red blotches. This new species resembles *P. fucata* but differs by its smaller size and the absence of hinge teeth. Phylogenetic analyses based on both mitochondrial (COI) and nuclear (18S rDNA, ITS1 and ITS2) genes and species delimitation using COI data strongly support that *P. phuketensis* is a distinct species, which is closely related to *Pinctada albina* and *Pinctada nigra*.

Keywords

Indian Ocean, mollusk, new species, phylogeny, taxonomy

Introduction

Pearl oysters in the genus *Pinctada* (Röding, 1798) (family Pteriidae) are widely distributed from shallow to deep waters of the tropical and subtropical regions between the Indo-Pacific and western Atlantic (Wada and Tëmkin 2008; Cunha et al. 2011). *Pinctada* contains approximately 20 species according to the latest taxonomic records of MolluscaBase (2022). Several *Pinctada* species are used widely in pearl aquaculture and in industry including the Akoya pearl oyster *Pinctada fucata* (Gould, 1850) in Japan (Matsuyama et al. 2021); the black-lip pearl oyster *Pinctada margaritifera* (Linnaeus, 1758) in the South Pacific and Indo-Pacific Islands (Aideed et al. 2014; Ky et al. 2019); and the silver-lipped pearl oyster, *Pinctada maxima* (Jameson, 1901) in western Australia (Steve et al. 2021).

While the pearl farming industry has expanded rapidly during recent decades, our understanding of biodiversity, evolution, and conservation of *Pinctada* species is still limited. Traditionally, systematics and taxonomy of *Pinctada* species have primarily focused on morphological parameters (Hynd 1955, 1960; Wada and Tëmkin 2008). The identification of *Pinctada* species is largely based on the soft tissues and shell characteristics; however, such morphological features vary greatly and are sometimes indistinguishable between species, particularly if the specimens are young (Ranson 1961; Wada and Tëmkin 2008). Accordingly, these studies are relatively complicated and challenging due either to their non-discrete differentiation or high levels of morphological variation (Cunha et al. 2011; Scuderi et al. 2019). In order to address these problems related to morphology-based taxonomy, molecular approaches, together with detailed comparative morphology have been increasingly applied to elucidate the classification, distribution pattern and evolutionary history of *Pinctada* species (Yu and Chu 2006; Tëmkin 2010; Cunha et al. 2011; Lal et al. 2018; Reisser et al. 2019). Additionally, a recent proposal to raise the infraspecific taxon *P. margaritifera persica* to specific rank as *P. persica* (Jameson) has been supported primarily by partial mitochondrial cytochrome oxidase subunit 1 (COI) sequences and two different species delimitation methods (general mixed Yule-coalescent: GMYC and Automatic Barcode Gap Discovery: ABGD) (Sharif Ranjbar et al. 2016). The aforementioned study clearly confirms the potential of DNA sequences to unveil hidden diversity, geographic origin, and phenotypic plasticity of pearl oyster *Pinctada* species.

In the Southeast Asian region, nine species of *Pinctada* are currently recognized: *P. albina* (Lamarck, 1819), *P. chemnitzii* (Phillipi, 1849), *P. fucata*, *P. imbricata* Röding, 1798, *P. maculata* (Gould, 1850), *P. margaritifera*, *P. maxima*, *P. nigra* (Gould, 1850) and *P. radiata* (Leach, 1814) (Cheah 2007; Sanpanich and Duangdee 2018; MolluscaBase 2022). All nine *Pinctada* species have been recorded in Thailand (Wells et al. 2021). However, diversity and taxonomic studies of Thai *Pinctada* species have relied heavily on morphological features, and the research is outdated when compared with studies from other areas, such as the Central Pacific Ocean (Yu et al. 2006; Miyake et al. 2016; Saruwatari et al. 2018) and Indo-West Pacific (Colgan and Ponder 2002; Cunha et al. 2011; Reisser et al. 2019). Considering this fact, we postulate that the diversity of *Pinctada* species has yet to be fully revealed in Thai waters and adjacent areas.

Among Thai species, *P. fucata* and *P. maxima* are the main species used for pearl culture in Phuket, the island province off the western coast of Thailand (Bussarawit 1995; Kanjanachatree et al. 2004). As a consequence of great abundance and high demand for these two *Pinctada* species, most previous studies focused on their life cycle, physiology and cultivation techniques (Kanjanachatree et al. 2004, 2006; Piyathamrongrut et al. 2009), whereas little is known about their biodiversity and genetic resources. We recently collected several *Pinctada* specimens from Phuket, and some of them were quite different in external appearance from other reported *Pinctada* species in this area. Accordingly, the present study aims to clarify the taxonomic status of these recently collected *Pinctada* specimens based on morphological and molecular analyses.

Materials and methods

A total of 15 pearl oyster specimens were collected around Dok Mai Island (7°47.84'N, 98°31.84'E), Phuket Province, western coast of Thailand by SCUBA diving. All specimens were allocated a registration code (NMR) to facilitate sample tracking. A small piece of adductor muscle from each oyster was preserved in 90% ethanol for DNA analyses. For morphological observation, we carefully examined both shell and soft body features (Wada and Tëmkin 2008), especially shell shape, hinge teeth pattern, posterior auricle and byssal notch. All characteristics were observed under the stereomicroscope. Voucher specimens were deposited at Kasetsart University Museum of Fisheries (Natural History Museum) mollusk collection (KUMF.MOLL.), Faculty of Fisheries, Kasetsart University, Thailand.

Genomic DNA extraction from mantle tissue was performed using NucleoSpin Tissue Kit (Macherey-Nagel, Germany). Mitochondrial cytochrome oxidase subunit 1 (COI) gene, nuclear 18S rDNA gene and nuclear ribosomal DNA internal transcribed spacer 1 and 2 (ITS1 and ITS2) regions were selected for molecular phylogenetic analysis according to previous studies (e.g., Yu and Chu 2006; Tëmkin 2010; Cunha et al. 2011; Sharif Ranjbar et al. 2016). Primer details, PCR amplification profile and procedure followed Folmer et al. (1994) for COI, Tëmkin (2010) for 18S rDNA and Yu and Chu (2006) for ITS1 and ITS2. PCR was carried out using PCR Master Mix solution (i-Taq^{TM}) (iNtRON Biotechnology DR, South Korea) in a total volume of 20 µl, consisting of 10 µl of i-Taq, 10 pmol of each primer and 2 µl of DNA (~ 10–20 ng). PCR products were purified with ExoSAP-IT (USB, Cleveland, Ohio USA) and then sequenced commercially (U2Bio Inc., Seoul, South Korea).

Newly generated sequences, including seven COI sequences, six 18S rDNA sequences and five ITS1 and ITS2 sequences, were deposited in NCBI. All sequences were edited, assembled, and aligned for individual and concatenated data sets using the Geneious Prime software package (Biomatters, available from http://www.geneious.com/) with the MAFFT sequence alignment algorithm, and were further manually refined. Additional sequences of *Pinctada* species were retrieved from NCBI and included in the alignment (Suppl. material 1). *Pteria* (Scopoli, 1777) species were selected as outgroups.

Phylogenetic trees were reconstructed for both individual (COI and 18S rDNA) and concatenated data sets (ITS1 + ITS2) using maximum likelihood (ML) implemented in IQ-TREE (Minh et al. 2020) and Bayesian inference (BI) implemented in MrBayes v.3.2 (Ronquist et al. 2012). ML analyses were carried out with the best-fit model selection implemented in ModelFinder (Kalyaanamoorthy et al. 2017). The nodal support values were estimated using the nonparametric bootstraps with 1000 replicates. For BI analyses, the nucleotide models of substitution were selected using Kakusan 4 (Tanabe 2011). BI analyses were conducted by two parallel runs of four Markov chains for a million generations with sampling every 1000 generations. The first 2500 trees (burn-in) were removed before determining a consensus tree and posterior probabilities. The best partition schemes (partitioned by codon position for COI dataset and by gene for ITS datasets) and substitution models of ML and BI methods for all datasets are listed in Suppl. material 2. Both ML and BI trees were edited and visualized with the program FigTree v.1.4.4 (Rambaut 2019).

Additionally, due to low variation of nuclear DNA sequences among species, we utilized only COI sequences for the three different species delimitation methods: the general mixed Yule-coalescent (GMYC) model (Pons et al. 2006), the Bayesian Poisson tree processes method (bPTP) (Zhang et al. 2013) and Assemble Species by Automatic Partitioning (ASAP) (Puillandre et al. 2021). The single-threshold GMYC analyses were performed via GMYC web server (http://species.h-its.org/gmyc/) using an ultrametric input tree. Ultrametric tree was constructed using BEAST v.2.5 (Bouckaert et al. 2019) with the uncorrelated lognormal relaxed clock, the GTR + I + R model and a coalescent tree prior. For the bPTP analyses, BI tree was used as input and implemented by web server (http://species.h-its.org/ptp/) with the setting of 100,000 MCMC generations and thinning value of 100. Additionally, the ASAP approach was applied using a web server (https://bioinfo.mnhn.fr/abi/public/asap/asapweb.html). The nucleotide substitution model K2P was selected, and other parameters were set to their default values.

Results

Systematics

Family Pteriidae Gray, 1847
Genus *Pinctada* Röding, 1798

***Pinctada phuketensis* Somrup, Sangsawang, Liu & Muangmai sp. nov.**
https://zoobank.org/7B7B55A0-F42A-4067-8966-54F5B2A4ECD4
Figs 1–3

Type locality. Dok Mai Island, Phuket Province, Thailand, 7°47.84'N, 98°31.84'E, at 5–10 m depth.

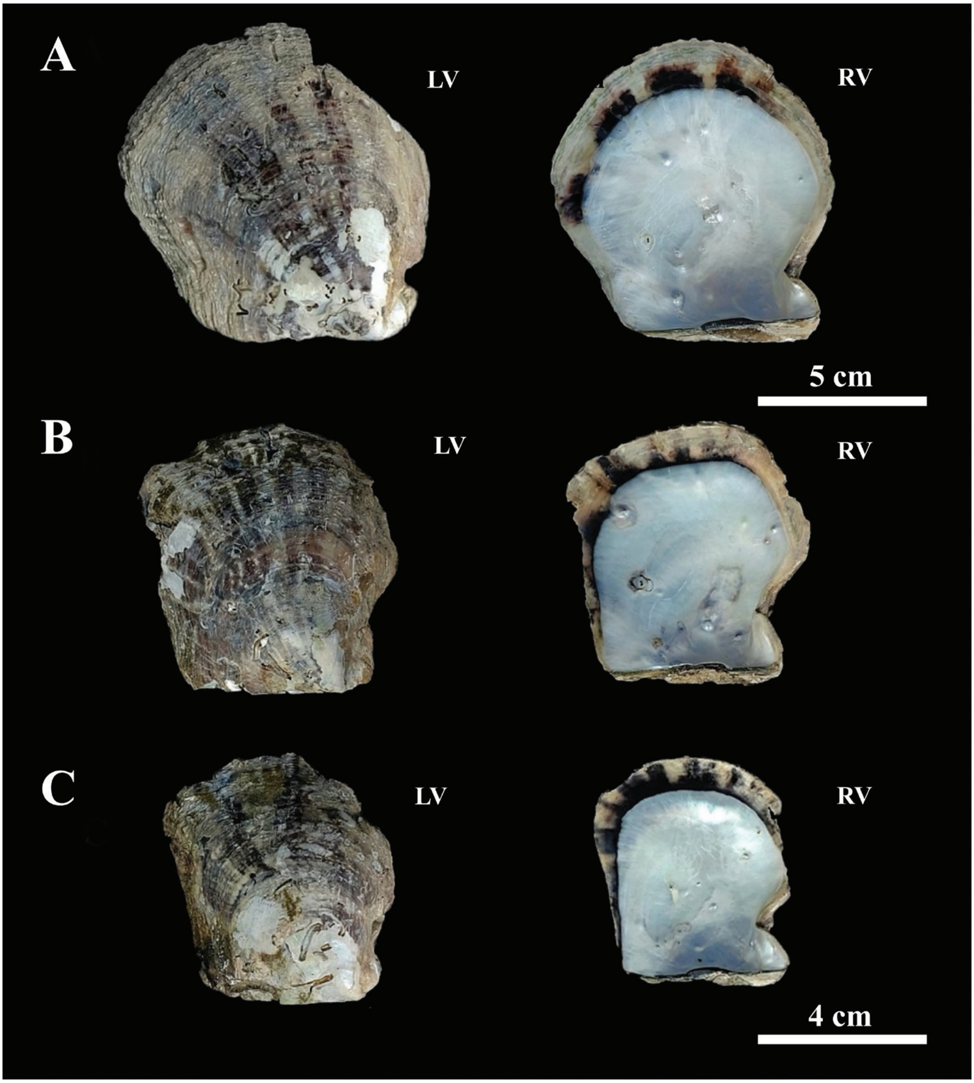

Figure 1. Shell of *Pinctada phuketensis* sp. nov. from Dok Mai Island, Phuket, Thailand. External and internal views of left and right valves **A** paratype, KUMF.MOLL.1204 (NMR077) (scale bar: 5 cm) **B** holotype, KUMF.MOLL.1206 (NMRA079) **C** paratype, KUMF.MOLL.1205 (NMR078) (scale bar: 4 cm). Abbreviations: LV, left valve; RV, right valve.

Material examined. ***Holotype*:** KUMF.MOLL.1206 (NMR079) (Figs 1B, 2), 10 August 2021, collected by SCUBA diving. ***Paratypes*:** two specimens, KUMF.MOLL.1204 (NMR077) (Fig. 1A) and KUMF.MOLL.1205 (NMR078) (Fig. 1C), 10 August 2021, collected by SCUBA diving. **Non-type material.** KUMF.MOLL.1201–KUMF.MOLL.1203, 5 February 2022, collected by SCUBA diving. All examined specimens were collected from the type locality by S. Somrup.

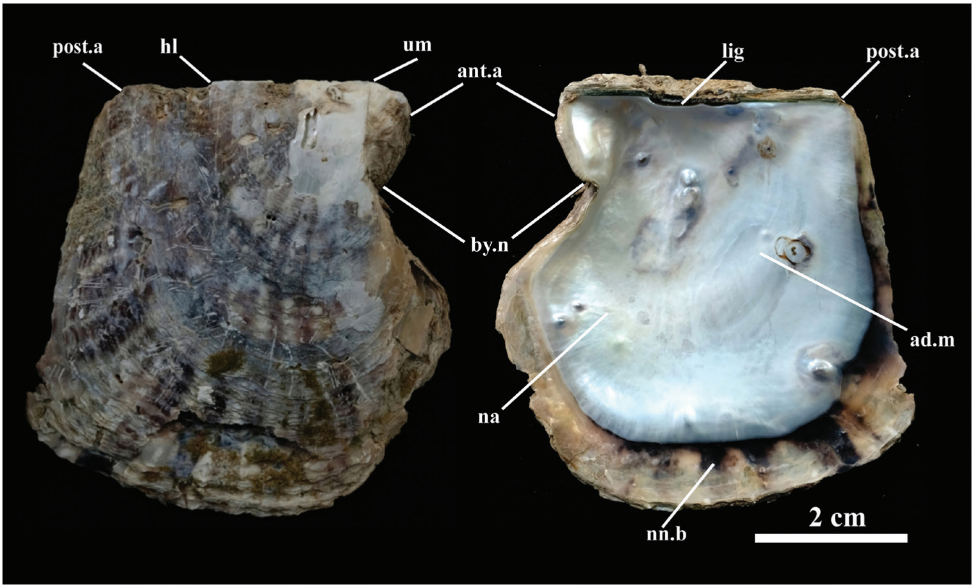

Figure 2. Right valve of holotype, KUMF.MOLL.1206 (NMR079), of *Pinctada phuketensis* sp. nov., showing shell shape and structures. Abbreviations: ad.m, adductor muscle scar; ant.a, anterior auricle; by.n, byssal notch; hl, hinge line; lig, ligament; na, nacreous; nn.b, non-nacreous border; post.a, posterior auricle; um, umbo.

Diagnosis. Shell is anteriorly oblique, inequilateral, laterally compressed, and subcircular to quadrate in outline. Byssal notch is small, narrow and slit-like. Hinge teeth are absent. Adductor muscle scar is kidney- or bean-shaped with the distal extremities of the posterior pedo-byssal retractor muscle scar inserted into the concavity on its anterior border. The non-nacreous border is relatively pale to transparent, with few dark brown or black blotches.

Description. Holotype, KUMF.MOLL.1206 (NMR079), specimen is approximately 60.4 mm height, 53.1 mm length, 23.1 mm depth, and 22.9 mm width (Figs 1B, 2). Paratypes, KUMF.MOLL.1204 (NMR077) and KUMF.MOLL.1205 (NMR078), 53 and 78 mm height, 46 and 75 length mm, 8.3 and 43.7 mm depth, and 38.5 and 54 mm width (Fig. 1A, C), respectively.

The shell is rather thin and small. The shell height, which does not exceed 80 mm, is slightly greater than the length (Figs 1, 2). The shell convexity is moderate, with the left valve more convex than the right valve. The exterior surface of the shell (both valves) is typically dark greyish brown or green, crossed radially by alternating brownish black and lighter colored stripes. The non-nacreous margin has white porcelaneous patches, generally alternating with irregular, dark brown or black blotches and corresponding to the external coloration pattern. Growth processes on the outer surface of valves are small, flattened and brittle imbricating concentric scales which bear slender spines projecting radially towards the edge of the shell (Fig. 2). The posterior border is either small or absent from the posterior auricle. The dorsal margin is slightly curved

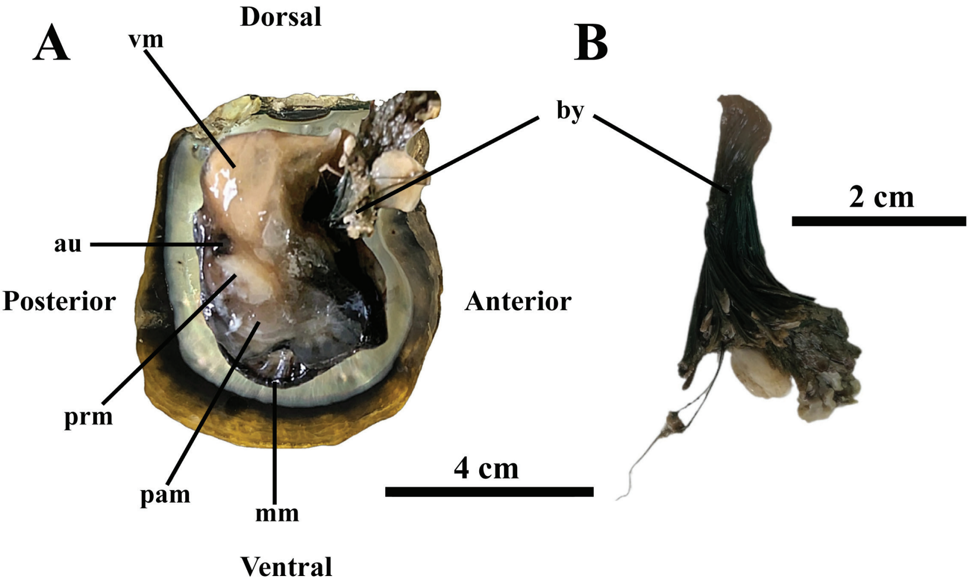

Figure 3. External view of the soft body parts of adult *Pinctada phuketensis* sp. nov. **A** and close-up view of overall of byssus **B**. Scale bars: 4 cm (**A**); 2 cm (**B**). Abbreviations: au, auricle; by, byssus; mm, mantle margin; pam, posterior adductor muscle; prm, posterior pedo-byssal retractor muscle; vm, visceral mass.

and the umbonal area is low. Ridges on the back are high and obtuse, running from the umbo to the back end, with two faint secondary ridges (Fig. 2). The dark ligament is strong on the hinge line. Ligament is narrow, about $^3/_4$ of hinge and elongation. The hinge line is straight, long and slightly shorter than the antero-posterior axis of the shell, with a ratio of 1:1.35 (Fig. 2). Hinge teeth are absent in the left valve and right valve (Fig. 2). The adductor muscle scar is kidney- or bean-shaped and clearly visible on the left valve. The right valve shows a larger attainment point scar on the shell. Scars on the back of the adductor muscle are very small. The anterior pedo-byssal retractor muscle scars are asymmetrical (Fig. 2). This structure is formed of individual byssal thread strands and extends ventrally and laterally from the base of the byssal groove to the short foot.

For the soft body, the foot is a tongue-shaped organ located in the dorsal-anterior region of body, between the mouth and the byssus (Fig. 3A). Byssus threads are dark green with thickened stalk (Fig. 3B). Visceral mass is yellow and roughly half the size of its shell. It is ventral to the hinge and connected to the posterior adductor. The visceral mass contains digestive glands and gonad tissue. The heart is located posterior to the visceral mass, and consists of ventricle and auricles. Mantle margin is translucent dark, occupying most of the area between valves and extending from the hinge line (Fig. 3A). The color of the mantle margin is dark, corresponding to the internal non-nacreous shell, which has blotches or streaks of dark pigment. The posterior adductor muscle is large, kidney- or bean-like in outline and located slightly posterior to the visceral mass and attached to each valve (Fig. 3A). The posterior pedo-byssal retractor muscles

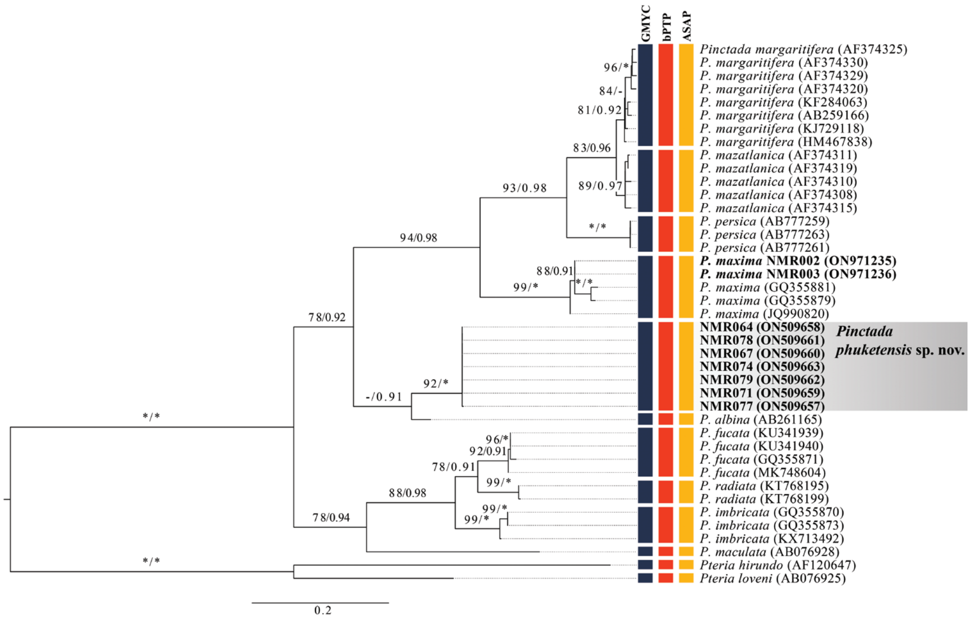

Figure 4. Maximum likelihood tree (-In L 4923.702) of partial COI sequences. Sequences of *Pinctada* specimens generated in this study are highlighted in bold. Support values are bootstrap/posterior probabilities. Asterisks indicate bootstrap (ML) value of 100% and posterior probability (BI) value of 1.00. Values < 50% ML bootstrap and < 0.90 posterior probability are not shown. GenBank accession numbers are given in parentheses. After the registration number or species name. Results of three species delimitation methods, namely GMYC model (blue column), bPTP (red column) and ASAP (yellow column), are indicated at the right edge of the tree.

are adjacent to the posterior adductor muscle and frequently inserted into its concave anterior border (Fig. 3A).

Etymology. The specific epithet refers to the locality of Phuket Island, where this species was found.

Phylogenetic analyses. Partial sequences of COI, 18S rDNA, ITS1, and ITS2 of recently collected *Pinctada* samples were successfully generated in this study. All sequences of *P. phuketensis* were identical for COI and 18S rDNA, and nearly identical for ITS1 (0.1–0.9% pairwise difference) and ITS2 (0.1–0.8% pairwise difference) but differed from sequences from other *Pinctada* species by at least 7% for COI, 0.2% for 18S rDNA, 2% for ITS1 and 1% for ITS2.

The COI-based phylogenetic trees obtained by ML and BI analyses were topologically similar, and only the ML tree is shown (Fig. 4). The ML analyses indicated that all COI sequences of *P. phuketensis* sp. nov. formed a monophyletic group. *Pinctada phuketensis* sp. nov. was clearly phylogenetically distinguished from other species with high support (ML = 96%, BI = 1.00), and was sister to *P. albina* from Japan (Fig. 4).

Additionally, phylogenetic analyses based on partial 18S rDNA sequences using ML and BI methods were highly congruent (Fig. 5). The ML tree supported the

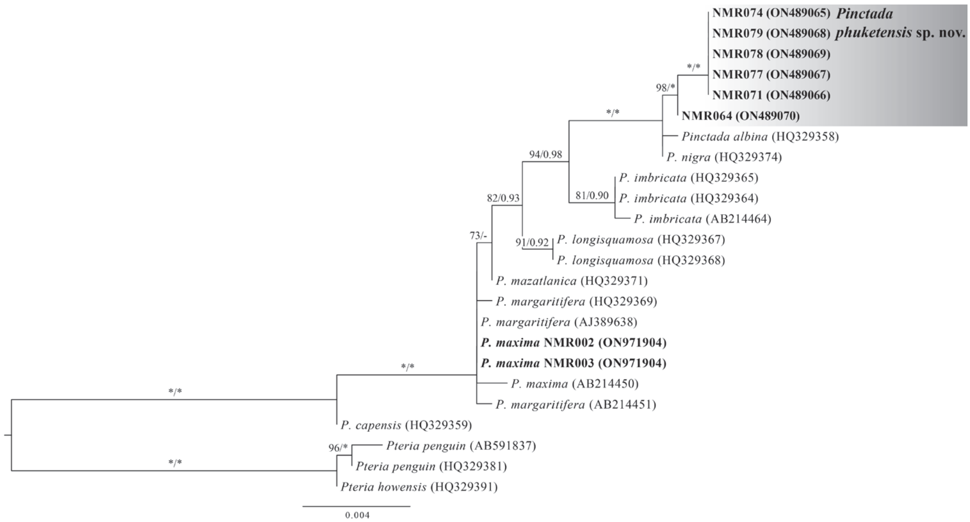

Figure 5. Maximum likelihood tree (-In L 3134.144) of 18S rDNA sequences. Sequences of *Pinctada* specimens generated in this study are highlighted in bold. Support values are bootstrap/posterior probabilities. Asterisks indicate bootstrap (ML) value of 100% and posterior probability (BI) value of 1.00. Values < 50% ML bootstrap and < 0.90 posterior probability are not shown. GenBank accession numbers are given in parentheses after the registration number or species name.

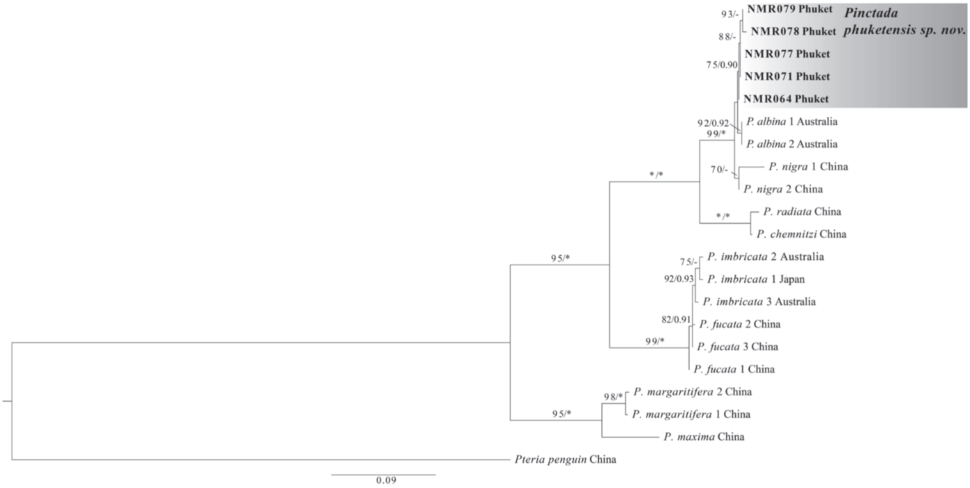

Figure 6. Maximum likelihood tree (-In L 4787.958) of combined ITS 1 and ITS 2 sequences. Sequences of *Pinctada* specimens generated in this study are highlighted in bold. Support values are bootstrap/posterior probabilities. Asterisks indicate bootstrap (ML) value of 100% and posterior probability (BI) value of 1.00. Values < 50% ML bootstrap and < 0.90 posterior probability are not shown.

monophyly of *P. phukentensis* sp. nov., and a close relationship between *P. phuketensis* sp. nov. and two other *Pinctada* species, namely *P. albina* and *P. nigra*, with high bootstrap value (ML = 100%, BI = 1.00) (Fig. 5).

Similarly, the phylogenetic relationships constructed by ML and BI methods based on the concatenated ITS1 and ITS 2 data set showed very similar topologies (Fig. 6). All sequences of *P. phukentensis* sp. nov. formed a well-supported clade, and this clade was grouped with *P. albina* from Australia and *P. nigra* from China with high support (ML = 99%, BI = 1.00) (Fig. 6).

Species delimitation

Three different methods used for species delineation yielded the same number of putative species within *Pinctada* (Fig. 4). All methods, namely GMYC ($L_{G\text{-}MYC} = 138.8684 > L_0 = 134.1486$, $P = 0.008$), bPTP (acceptance rate = 0.14530, merge = 49971, split = 50029) and ASAP ($P = 0.00004$), clearly showed *P. phukentensis* sp. nov. to be distinct from its congeners (Fig. 4).

Discussion

Our analyses using morphological and genetic data clearly distinguished the *Pinctada* samples recently collected from Dok Mai Island, Phuket Province, western coast of Thailand, from other *Pinctada* species in the region. Accordingly, these pearl oysters should be recognized as a new species, and we have named it as *Pinctada phuketensis* sp. nov. This new species can be distinguished from other members of the genus by its smaller size, a subquadrate shell with moderately long ligament, slightly developed to undeveloped posterior auricle, the absence of hinge teeth, a pale to transparent non-nacreous margin with dark brown or black blotches, and brownish stripes on the external surface. A morphological comparison of *P. phuketensis* and some closely related species is presented in Table 1.

Among the *Pinctada* species distributed in Southeast Asian waters, the new species of *P. phuketensis* morphologically resembles *P. fucata*, *P. nigra* and *P. albina*, but can be distinguished from these three species based on shell shape, hinge teeth and anterior/posterior auricles. Both *P. fucata* and *P. nigra* can be easily distinguished from *P. phuketensis* by having conspicuous hinge teeth. In addition, *P. fucata* can be separated from *P. phuketensis* by being larger in size and having a large and developed anterior auricle (Takemura and Okutani 1958; Colgan and Ponder 2002; Wada and Tëmkin 2008), while *P. nigra* clearly differs from our new species by exhibiting a large and developed posterior auricle and deep posterior sinus (Deng et al. 2019) (Table 1). On the other hand, *P albina* and *P. phuketensis* are similar in having no hinge teeth, but they can be differentiated by the characteristics of byssal notch and anterior border. *Pinctada albina* is distinguished from our new species by having a broad byssal notch and anterior border that projects well beyond the reference line (a line drawn at right angles to the hinge line through the byssal notch) (Hynd 1955) (Table 1).

Among the Indo-Pacific Ocean species, our new species, *P. phuketensis* closely resembles *P. sugillata* (Reeve, 1857) from Australia in having a weakly developed to

Table 1. Comparative morphology of *Pinctada phuketensis* sp. nov. with other morphologically similar *Pinctada* species.

Character	***P. phuketensis* sp. nov.**[1]	***P. albina***[2,3]	***P. sugillata***[2,3]	***P. chemnitzi***[2]	***P. fucata***[2,4,5]	***P. nigra***[6]
Size	Small	Small	Small	Small	Small	Small
Shell shape	Slightly oblique	Slightly to moderately oblique	Very oblique	Moderately oblique and markedly inequivalve	Slightly oblique	Obliquely elongate
Anterior auricle	Small	Small	Small	Moderately to well developed	Larger	Small
Posterior auricle	Short and broadly rounded or absent	Small	Small	Larger	Short and broadly rounded	Large
Byssal notch	Small, narrow, slit-like	Broad	Moderately wide slit	Slit-like	Narrow and slit-like	n/a
Hinge teeth	Absent	Absent	Present	Present	Present	Present
External color	Green, yellow, brown, or partially continuous white blotches	White, possibly sun-bleached	Rayed or dark and white pattern to an evenly dark monochrome	Dull brownish, indistinctly rayed with paler shades	Red, brown, green and bronze	Green and dark
Nacre	White luster, nacreous and narrow black band on the non-nacreous border	Pale yellow throughout the nacre	Narrow black band on the non-nacreous border	Yellow throughout the nacre	White metallic luster, yellow, silver, gold, or pink tint	n/a

[1]This study, [2]Hynd (1955), [3]Hynd (1960), [4]Takemura and Okutani (1958), [5]Wada and Tëmkin (2008), [6]Deng et al. (2019); n/a indicates information was not available.

undeveloped posterior ear and a nearly 1:1 ratio of the hinge line to the antero-posterior axis of the shell (Hynd 1955, 1960). However, these two species differ in shell shape (slightly oblique in *P. phuketensis* and very oblique in *P. sugillata*), hinge teeth (absent in *P. phuketensis* and present in *P. sugillata*) and byssal notch (narrow and slit-like in *P. phuketensis* and moderately wide and slit-like in *P. sugillata*) (Table 1; Hynd 1955, 1960). Unfortunately, genetic data for *P. sugillata* are not available. Further studies on *P. sugillata* will be useful for confirming that these two species are distinct.

Our phylogenetic analyses and species delimitation approach showed that *P. phuketensis* is genetically distinct from other described *Pinctada* species. While our observations indicated that our new species is morphologically similar to *P. fucata*, genetic analyses revealed the distant phylogenetic relationship between these two species, implying that morphological traits probably do not reflect their real evolutionary history. Additionally, our phylogenetic analyses showed that *P. phuketensis* is more closely related to *P. albina* and *P. nigra* than to *P. fucata*. We also found that phylogenetic relationships of some *Pinctada* species in this study had weak nodal support and were incompletely resolved. It is apparent that further work on *Pinctada* species based on combined data of different genetic markers and more expansive sampling from different geographic regions will uncover their diversity, phylogenetic relationships and evolutionary patterns.

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Supplementary material 1

Table S1

Authors: Supannee Somrup, Akkarasiri Sangsawang, Nichanun McMillan, Supanida Winitchai, Jitti Inthoncharoen, Shikai Liu, Narongrit Muangmai

Data type: Docx file.

Explanation note: List of additional GenBank accession numbers for ITS1 and ITS2 sequences used in the present study. New sequences produced for this study are indicated in bold type.

Link: https://doi.org/10.3897/zookeys.1119.87724.suppl1

Supplementary material 2

Table S2

Authors: Supannee Somrup, Akkarasiri Sangsawang, Nichanun McMillan, Supanida Winitchai, Jitti Inthoncharoen, Shikai Liu, Narongrit Muangmai

Data type: Docx file.

Explanation note: The best partitioning scheme and models of maximum likelihood (ML; IQ-TREE) and Bayesian inference (BI; MrBayes) methods for all datasets.

Link: https://doi.org/10.3897/zookeys.1119.87724.suppl2