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A review of the land snail genus *Alycaeus* (Gastropoda, Alycaeidae) in Peninsular Malaysia

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Abstract

A total of 11 species and 1 subspecies of *Alycaeus* were recognised in Peninsular Malaysia prior to this study. However, these taxonomic descriptions of *Alycaeus* taxa were based on limited numbers of examined materials, where a whole spectrum of morphological variations were not accounted for and diagnoses were often provided without sufficient comparison between congeners from across the peninsula. We reviewed Peninsular Malaysian *Alycaeus* through the examination of 5137 specimens in 522 collection lots from all major museum collections and literature sources. Based on these examined materials, we utilised a more comprehensive revised set of 39 shell and operculum characters, as well as living animal colour to describe all *Alycaeus* species in this paper. We also noted their habitat and ecology, as well as updated the distribution of each species. Of the 12 previously described taxa, 10 are reconfirmed as present on Peninsular Malaysia (*Alycaeus balingensis*, *Alycaeus carinata*, *Alycaeus conformis*, *Alycaeus gibbosulus*, *Alycaeus kapayanensis*, *Alycaeus kelantanensis*, *Alycaeus liratulus*, *Alycaeus perakensis perakensis*, *Alycaeus perakensis altispirus* and *Alycaeus thieroti*) and 2 are confirmed as absent from the peninsula (*Alycaeus jagori* and *Alycaeus pyramidalis*). A new record of *Alycaeus robeleni* is reported for Peninsular Malaysia. One species, *Chamalycaeus jousseaumei* is confirmed as present on the peninsula and is reassigned to *Alycaeus*. The subspecies *Alycaeus perakensis altispirus* Möllendorff, 1902, is elevated to species. Examined Peninsular Malaysian materials that do not fit previously recognised species are described as new species. A total of 11 new species are proposed (*Alycaeus selangoriensis* **sp. n.**, *Alycaeus costacrassa* **sp. n.**, *Alycaeus ikanensis* **sp. n.**, *Alycaeus alticola* **sp. n.**, *Alycaeus charasensis* **sp. n.**, *Alycaeus kurauensis* **sp. n.**, *Alycaeus regalis* **sp. n.**, *Alycaeus virgogravida* **sp. n.**, *Alycaeus senyumensis* **sp. n.**, *Alycaeus expansus* **sp. n.**, *Alycaeus clementsi* **sp. n.**). Overall, 23 species of *Alycaeus* are now recognised in Peninsular Malaysia.

Keywords
land snail, shell morphology, operculum, Alycaeinae, limestone karsts, Southeast Asia

Introduction

The family Alycaeidae Blanford, 1864, is a distinct group of operculated land snails defined by their globular, conical or discoid shell, whorl constriction prior to the aperture and a conspicuous tube at the suture ('breathing tube') which runs from the constriction to whorls prior to the constriction (Godwin-Austen 1889, Kobelt 1902, Egorov 2013). Within Alycaeidae, the genus *Alycaeus* Baird, 1850, is separated into three subgenera – *Alycaeus* Baird, 1850, *Pincerna* Preston, 1907, and *Stomacosmethis* Bollinger, 1918 (Egorov 2013). However, all of these subgenera [including *Pincerna* (see Páll-Gergely 2017)] remain inadequately diagnosed and will require extensive revision, a task that is beyond the scope of this study. As such, this review will solely focus on species in Peninsular Malaysia that are placed under the genus *Alycaeus* including two species recently reassigned under *Pincerna* (Páll-Gergely 2017) – *Alycaeus liratulus* Preston, 1907, and *Alycaeus thieroti* Morgan, 1885b, and one species formerly assigned under *Chamalycaeus* (Kobelt & Möllendorff, 1897) – *Alycaeus jousseaumei* Morgan, 1885a.

In Peninsular Malaysia, 11 species and 1 subspecies of *Alycaeus* were recognised prior to this study (Maassen 2001, Maassen 2006), namely *Alycaeus balingensis* Tomlin, 1948, *Alycaeus carinata* Maassen, 2006, *Alycaeus conformis* Fulton, 1902, *Alycaeus gibbosulus* Stoliczka, 1872, *Alycaeus jagori* Martens, 1859, *Alycaeus kapayanensis* Morgan, 1885b, *Alycaeus kelantanensis* Sykes, 1902, *Alycaeus liratulus* Preston, 1907, *Alycaeus perakensis perakensis* Crosse, 1879a, *Alycaeus perakensis altispirus* Möllendorff, 1902, *Alycaeus pyramidalis* Benson, 1856 (as *Dioryx pyramidalis*, see Habe 1965) and *Alycaeus thieroti* Morgan, 1885b.

Most past studies of *Alycaeus* in Peninsular Malaysia are either single species descriptions or checklists. There are only two studies that focused on the anatomy and radula of *Alycaeus* (Tielecke 1940, Venmans 1956) and three that focused on conservation biogeography of karst land snails (Davison and Kiew 1990, Clements et al. 2008, Foon et al. 2017). Besides these five non-conchological studies, all other *Alycaeus* taxonomic treatments to date were based on inconsistent and subjective diagnoses of few shell and operculum characters which have never been properly reviewed since their description or in the revisions by Kobelt (1902) and Egorov (2013). Even when detailed decriptions were given for a species (e.g. *Alycaeus perakensis* Crosse, 1879a, *Alycaeus carinata* Maassen, 2006), no comprehensive comparisons with other Peninsular Malaysian *Alycaeus* species were effected until now.

In view of this, we reviewed all *Alycaeus* species in Peninsular Malaysia using a revised set of 39 shell and operculum characters, as well as living animal colour. We consulted major museum collections in Europe, the United States of America, Singapore and Malaysia that house *Alycaeus* materials from Peninsular Malaysia, including

types. A large collection of recently sampled *Alycaeus* from across Peninsular Malaysia housed in the *BORNEENSIS* collection, Universiti Malaysia Sabah, were also studied.

Based on this review, we reconfirmed the presence of 10 previously recognised species on the peninsula (*A. balingensis*, *A. carinata*, *A. conformis*, *A. gibbosulus*, *A. kapayanensis*, *A. kelantanensis*, *A. liratulus*, *A. perakensis perakensis*, *A. perakensis altispirus* and *A. thieroti*) while 2 species are confirmed as absent on the peninsula (*A. jagori* and *A. pyramidalis*). For *Alycaeus jagori*, records of the species in Perak, Peninsular Malaysia were reported without further elaboration by some workers (Kobelt 1902, Laidlaw 1928, Schilthuizen et al. 1999, Maassen 2001, parts of BOR/MOL collection lots). Benthem Jutting (1948) expressed reservations about the validity of these Peninsular Malaysian records. We examined the syntype of *Alycaeus jagori* (SMF 109304/1) and concluded that it is indeed distinguished from any Peninsular Malaysian congeners in spire shape, whorl convexity, whorl sculpture and shell size. As such, *Alycaeus jagori* is herein confirmed as non-existent on Peninsular Malaysia. The source of this mislocation most likely originated from Kobelt and Möllendorff (1897) whereby past workers may have confused the locality of *A. jagori* (Java) with *A. kapayanensis* (Perak), both of which were listed next to each other in the text. For *Alycaeus pyramidalis*, the mislocation is traced back to a mistake by Habe (1965) in which specimens of *A. gibbosulus* from northern Malay Peninsula were misidentified as *A. pyramidalis*. Also, a new record of *Alycaeus robeleni* is reported for Peninsular Malaysia. One species, *Chamalycaeus jousseaumei* is confirmed as present on the peninsula and is reassigned to *Alycaeus*. The subspecies *Alycaeus perakensis altispirus* Möllendorff, 1902, is elevated to species. Overall, we redescribed all 12 previously known species of *Alycaeus* on Peninsular Malaysia.

Finally, we proposed and described 11 new species based on examined *Alycaeus* materials from Peninsular Malaysia that do not fit into previously recognised species: *Alycaeus selangoriensis* sp. n.*, Alycaeus costacrassa* sp. n., *Alycaeus ikanensis* sp. n., *Alycaeus alticola* sp. n., *Alycaeus charasensis* sp. n., *Alycaeus kurauensis* sp. n., *Alycaeus regalis* sp. n., *Alycaeus virgogravida* sp. n., *Alycaeus senyumensis* sp. n., *Alycaeus expansus* sp. n., *Alycaeus clementsi* sp. n. Overall, 23 species of *Alycaeus* are now recognised in Peninsular Malaysia.

Materials and methods

Study site

This study focuses solely on Peninsular Malaysia, with emphasis on limestone karsts where the majority of study materials were obtained. Peninsular Malaysia is situated at the lower end of the Malay Peninsula, which is also politically divided into Thailand and Myanmar in the north. Peninsular Malaysia is at the centre of the Tropical East Asian region and hence shares similar fauna with South and East Asia (Corlett 2014), including the genus *Alycaeus* (Kobelt 1902, Egorov 2013). Peninsular Malaysia is characterised by parallel, old (circa 200 million years old) and tall (circa 1000–2000 m

high) non-limestone mountain ranges aligned at a north-south axis, separating flat alluvial and knolled valleys (Paton 1961, Metcalfe 2013). Within these valleys, limestone bedrocks of various ages are occasionally exposed as disjunct or continous limestone tower karsts (Paton 1961). These tower karsts have been exposed for millions of years and have gradually become isolated from each other through weathering and erosion (Benthem Jutting 1960b, Paton 1961, Twidale 2006). As such, ecosystems on limestone karsts are well known to be analogous to island ecosystems and have high species endemism including land snails (Clements et al. 2006, Liew et al. 2014).

Literature, fieldwork and collection data management

For literature review, the term "*Alycaeus*" was used to obtain publications from the Zoological Record, Google Scholar and Biodiversity Heritage Library (on 15 March 2016 and 30 May 2017). All publications mentioning *Alycaeus* species from Peninsular Malaysia were studied and reviewed.

The management of data for examined materials follows Liew et al. (2014). Materials from BOR/MOL and ZRC were personally examined by the first author. Materials elsewhere and their associated measurements and photographs were obtained either through existing digitised museum collections or with help from curators (MNHN – Manuel Caballer and Virginie Héros, NHM – Jonathan Ablett) and visiting scientists (SMF – Páll-Gergely Barna, MNHN – Gopalasamy Reuben Clements, ANSP – Siong Kiat Tan, RMNH/ZMA – Thor-Seng Liew). The number of shells for each collection lot examined were indicated after the virgule that follows after the accession number.

The locality for each collection lot was identified and linked to its current name whenever possible. For limestone karst localities, we followed the standard format of code and name (e.g. PRK 18 Gunung Lanno) used in the limestone hill register by Liew et al. (2016). Place names in this paper contain Malay words, namely: Batu = rock; Bukit/Buket = hill; Gua = cave; Gunung/Gunong = mountain; Kota = large tower karsts or fortress; Kuala/Kwala = estuary or river confluence; Pulau = island; Sungai/Sungei = river; Tasik = lake; Wang = large doline or valley surrounded on all sides by tower karsts. Geographical coordinates for the type locality of each species was provided except when the stated type locality was not exact i.e. only state-level or island names were given as the type locality. The locality records for each species based on materials examined are shown in Figures 2, 3, 4, 5 and 6.

In addition to the previously collected museum materials, a systematic sampling of *Alycaeus* at 80 localities across Peninsular Malaysia was conducted in 2016 (for full list of localities, see Suppl. material 1). During the sampling, about 45 to 60 minutes were spent at each locality to search for living and dead *Alycaeus* individuals on all habitats (in the leaf litter, under rotten logs, on vegetation and on rocky substrates). Up to 20 individuals per species were observed and collected whenever possible. Animal colouration, habitat and other ecological observations were noted.

Collection repositories

ANSP Academy of Natural Sciences of Drexel University, Philadelphia, United States of America.
BOR/MOL BORNEENSIS Malacology Collection, Institute for Tropical Biology and Conservation, Universiti Malaysia Sabah, Kota Kinabalu, Malaysia.
CUIZM Chulalongkorn University Zoological Museum, Bangkok, Thailand.
HUJ National Mollusc Collection of the Hebrew University of Jerusalem, Jerusalem, Israel.
HW Private collection of Jens and Christa Hemmen, Wiesbaden, Germany.
MNHN Museum National d'Histoire Naturelle, Paris, France.
NHM The Natural History Museum, London, United Kingdom.
NHMUK When citing NHM registered specimens.
RMNH Naturalis Biodiversity Center (formerly Rijksmuseum van Natuurlijke Historie), Leiden, the Netherlands.
SMF Forschungsinstitut und Naturmuseum Senckenberg, Frankfurt am Main, Germany.
ZMA Naturalis Biodiversity Center (formerly Zoological Museum of Amsterdam), Leiden, the Netherlands.
ZRC Zoological Reference Collection, Lee Kong Chian Natural History Museum, National University of Singapore, Singapore.

Species description and delimitation

To date, most of the *Alycaeus* species in Peninsular Malaysia have been described and diagnosed using inconsistent, subjective, and descriptive conchological and opercular characters with little or no comparison with other congeners. No more than 7 characters were used in previous studies including (1) breathing tube shape and size, (2) aperture and peristome shape, (3) constriction shape, (4) whorl shape, (5) radial and spiral sculpture, (6) operculum characters and (7) shell shape (Godwin-Austen 1889, Kobelt 1902). These characters have not been reviewed since Kobelt (1902) and thus, their usefulness as diagnostic characters for species is unverified. Furthermore, phenotypic plasticity in *Alycaeus* shell features has not been studied although it is known in other terrestrial Caenogastropoda (Berry 1962, Liew et al. 2014). Thus, we employed a revised comprehensive assessment of 39 shell and operculum characters with empirical data, including living animal colour (Table 1, Figure 1). Living animal colour has been shown to be useful for distinguishing species in some caenogastropod genera (Reid 2007, 2014). However, in studies of the terrestrial caenogastropod genus *Plectostoma* Adam, 1865, intraspecific shell colour differences have been linked to sexual dimorphism (Schilthuizen et al. 2003). Given that no sexual dimorphism study has been done on *Alycaeus* to date and sex was not determined for the materials examined in this study, shell colour differences in *Alycaeus* will be described but not used for species diagnosis in this study.

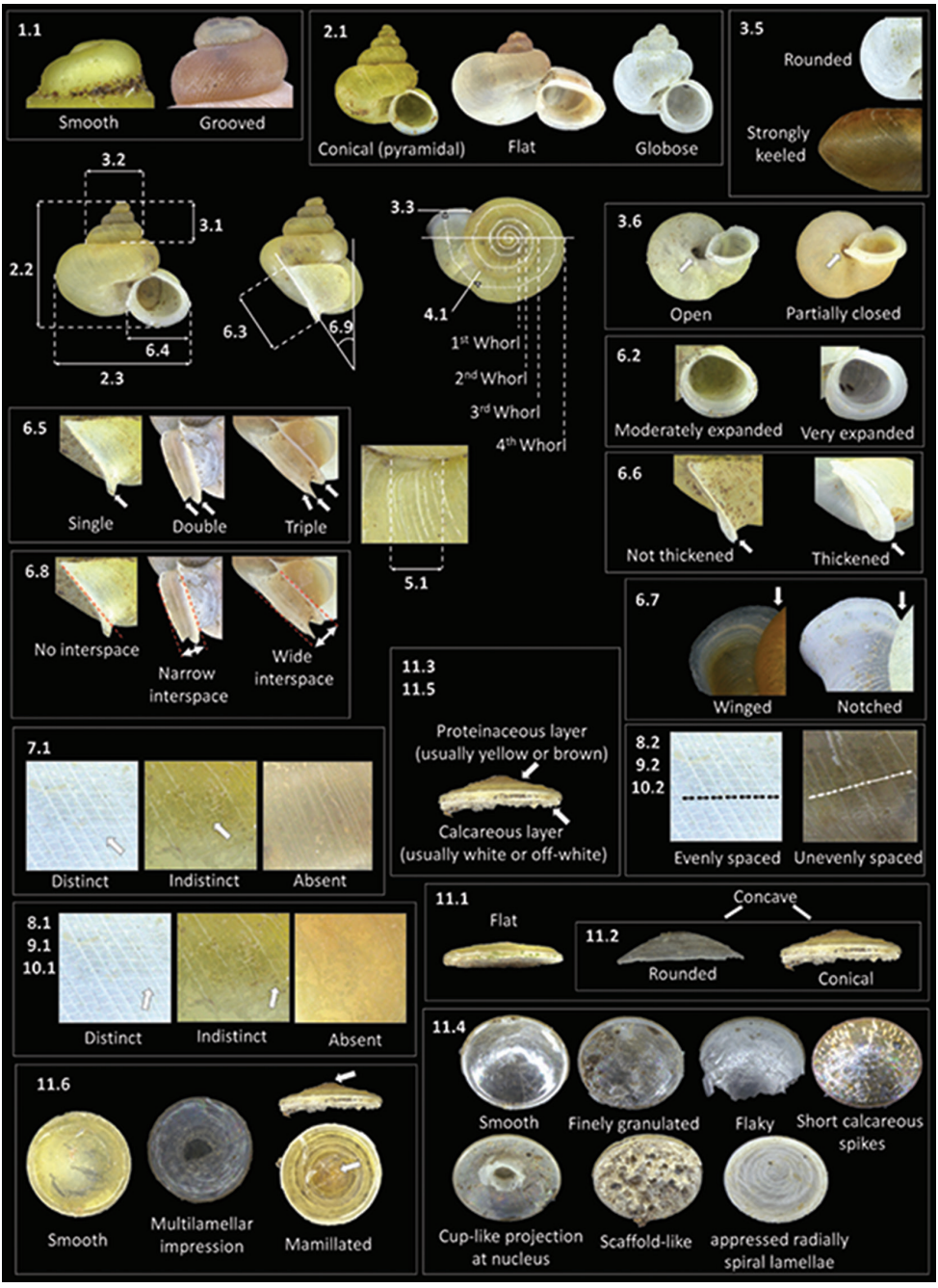

Figure 1. An illustrated synopsis of the framework for species description based on 39 shell and operculum features (excluding shell colour and living animal colour). Number codes ascribed to each character are linked to descriptions and measurement methods outlined in Table 1.

Table 1. Framework for species description based on 39 shell and operculum features, as well as living animal colour. Number codes are ascribed to each character and linked to illustrations in Figure 1 for visualisation of character descriptions and measurements, except shell colour and living animal colour.

Morphological section	Character	Descriptions and measurements
1. Protoconch	1.1 Sculpture seen at 5.0 × magnification	Smooth or grooved.
2. Shell shape and size	2.1 Shell shape	Conical (pyramidal), flat or globose.
	2.2 Shell height	Measured from apex to base of ultimate whorl parallel to coiling axis (in millimetres to the nearest 0.01 mm).
	2.3 Shell width	Measured at outermost edges of shell including aperture, perpendicular to coiling axis (in millimetres to the nearest 0.01 mm).
3. Spire	3.1 Spire height	Measured from apex to base of penultimate whorl at suture (in millimetres to the nearest 0.01 mm) (after Liew et al. 2014).
	3.2 Spire width	Measured at outermost edges of penultimate whorl perpendicular to coiling axis (in millimetres to the nearest 0.01 mm) (after Liew et al. 2014).
	3.3 Number of whorls	Maximum number of whorls posterior of protoconch (after Vermeulen and Whitten 1998). Non-integers are represented as fractions of 8 (⅛ to ⅞) for easier understanding (modified from Vermeulen and Whitten 1998).
	3.4 Spire shape	Oblong conical (width > height) (after Liew et al. 2014).
	3.5 Whorl periphery	Strongly keeled or rounded.
	3.6 Umbilicus	Open or partially closed (i.e. partially blocked by penultimate whorl and/or peristome extension at columella).
4. Whorl constriction	4.1 Position in whorl	Approximate position based on number of whorls posterior of protoconch. Non-integers are represented as fractions of 8 (⅛ to ⅞) for easier understanding (modified from Vermeulen and Whitten 1998).
5. Breathing tube	5.1 Length	Length from posterior end to anterior end (in millimetres to the nearest 0.01 mm).
6. Aperture and peristome	6.1 Aperture shape	Circular.
	6.2 Aperture margin	Margins moderately expanded or very expanded.
	6.3 Aperture height	Measured at outermost edges of aperture from the palatal to the basal side (in millimetres to the nearest 0.01 mm). Measurement made with aperture tilted parallel to the observer (after Liew et al. 2014)
	6.4 Aperture width	Measured at outermost edges of aperture from columella to palatal side (in millimetres to the nearest 0.01 mm). Measurement made perpendicular to coiling axis.
	6.5 Peristome types	Single, double or triple.
	6.6 Peristome thickness	Thickened or not thickened.
	6.7 Peristome shape	Notched or winged at suture. Upper palatal section sometimes folded posteriorly.
	6.8 Peristome spacing	No interspace (inner peristome impressed flatly on outer peristome), narrow interspace (inner peristome slightly protruded posteriorly beyond outer peristome), wide interspace (inner peristome protruded posteriorly far from outer peristome, creating a new section of whorl) (after Yamazaki et al. 2013).

Morphological section	Character	Descriptions and measurements
6. Aperture and peristome	6.9 Peristome orientation	Degrees of obliquity with respect to the coiling axis of the spire.
7. Spiral lines	7.1 Spiral line seen at 10.0 × magnification	Distinct (protruded from shell surface), indistinct (less protruded from shell surface) or absent.
	7.2 When present, spiral lines' spacing	Spacing between lines regular or irregular. Number of spiral lines per 1 millimetre.
8. Radial ribs running anterior of breathing tube	8.1 Radial ribs seen at 4.0 × magnification	Pronounced (i.e. protruded from shell surface), indistinct (i.e. less protruded from shell surface), or absent (i.e. replaced with radial growth lines).
	8.2 When present, radial ribs' spacing	Evenly or unevenly spaced. Number of radial ribs per 1 milimetre.
9. Radial ribs running perpendicular to breathing tube	9.1 Radial ribs seen at 4.0 × magnification	Pronounced (i.e. protruded from shell surface), indistinct (i.e. less protruded from shell surface), or absent (i.e. replaced with radial growth lines). Thick or not thick.
	9.2 When present, radial ribs' spacing	Evenly or unevenly spaced. Number of radial ribs per 1 milimetre.
10. Radial ribs running posterior of breathing tube	10.1 Radial ribs seen at 4.0 × magnification	Pronounced (i.e. protruded from shell surface), indistinct (i.e. less protruded from shell surface), or absent (i.e. replaced with radial growth lines). Thick or not thick.
	10.2 When present, radial ribs' spacing	Evenly or unevenly spaced. Number of radial ribs per 1 milimetre.
11. Operculum	11.1 Concavity	Concave (exterior cave-in) or flat.
	11.2 Shape	Rounded or conical.
	11.3 Exterior composition	Proteinaceous or calcareous layered.
	11.4 Exterior sculpture	Smooth, finely granulated, flaky, short calcareous spikes, cup-like projection at nucleus, scaffold-like calcareous deposits or appressed radially spiral lamellae.
	11.5 Interior composition	Proteinaceous or calcareous layered.
	11.6 Interior sculpture	Smooth, multilamellar impression, mamillate.
12. Shell colour	12.1 Shell colour	White, pinkish-white, pink, yellow, orange, red, brownish-red. brown, purple.
13. Living animal	13.1 Body colour	Cream-white, yellow, cream-yellow, light brown, brown, maroon, greenish-black, light grey, grey.
	13.2 Head colour	Orange, pink, pinkish-brown, brown, maroon, greenish-black, grey, dark grey.
	13.3 Tentacles colour	Uni-coloured (yellow, red, brown, reddish-brown, light grey, dark grey, black), or bi-coloured (green with brown tips, cream-white with pink tips, yellow with red tips).

To assist with visualising the descriptions, we provided photographs of five standard shell views (apertural, lateral, apical, umbilical and dorsal/oblique dorsal), three close-up shell views (breathing tube, apical whorls, radial rib and spiral line sculpture) and four standard operculum views (exterior, interior, side and oblique exterior) for each species. More than one specimen is illustrated for each species to represent the intraspecific variability if required. A synoptic plate of shells at apertural view representing the 23 *Alycaeus* taxa in Peninsular Malaysia (Figure 31) is provided to compare shell size and shape.

We measured up to 28 shells representing the whole spectrum of variation in shell height, shell width, spire height, spire width, aperture height and aperture width for

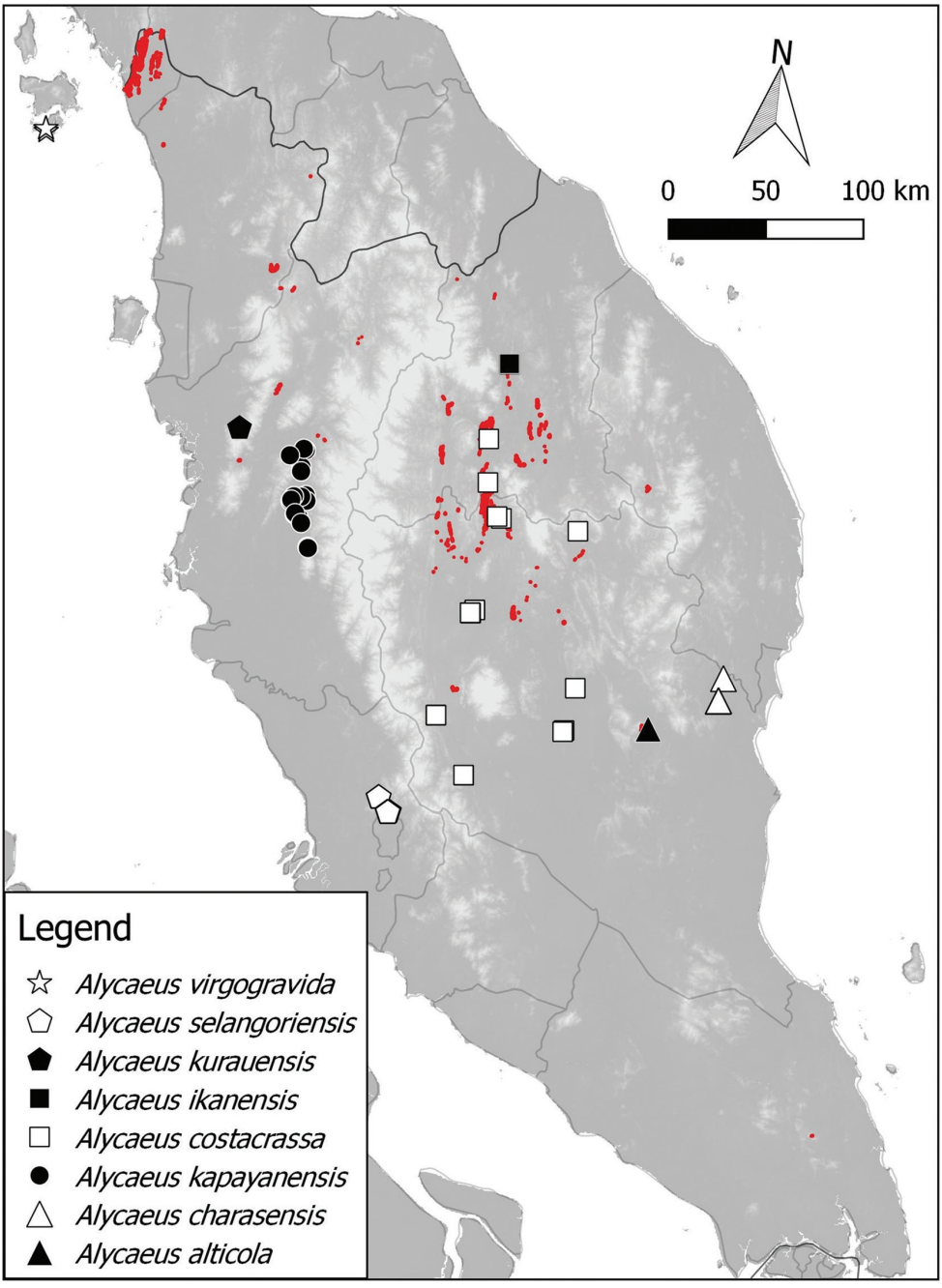

Figure 2. Distribution of 8 *Alycaeus* species in Peninsular Malaysia based on materials examined. *Alycaeus altispirus* is not included in the maps because no specific locality was given for the materials examined (see Discussion section under the species). Note the red areas are limestone karsts (derived from Liew et al. 2016).

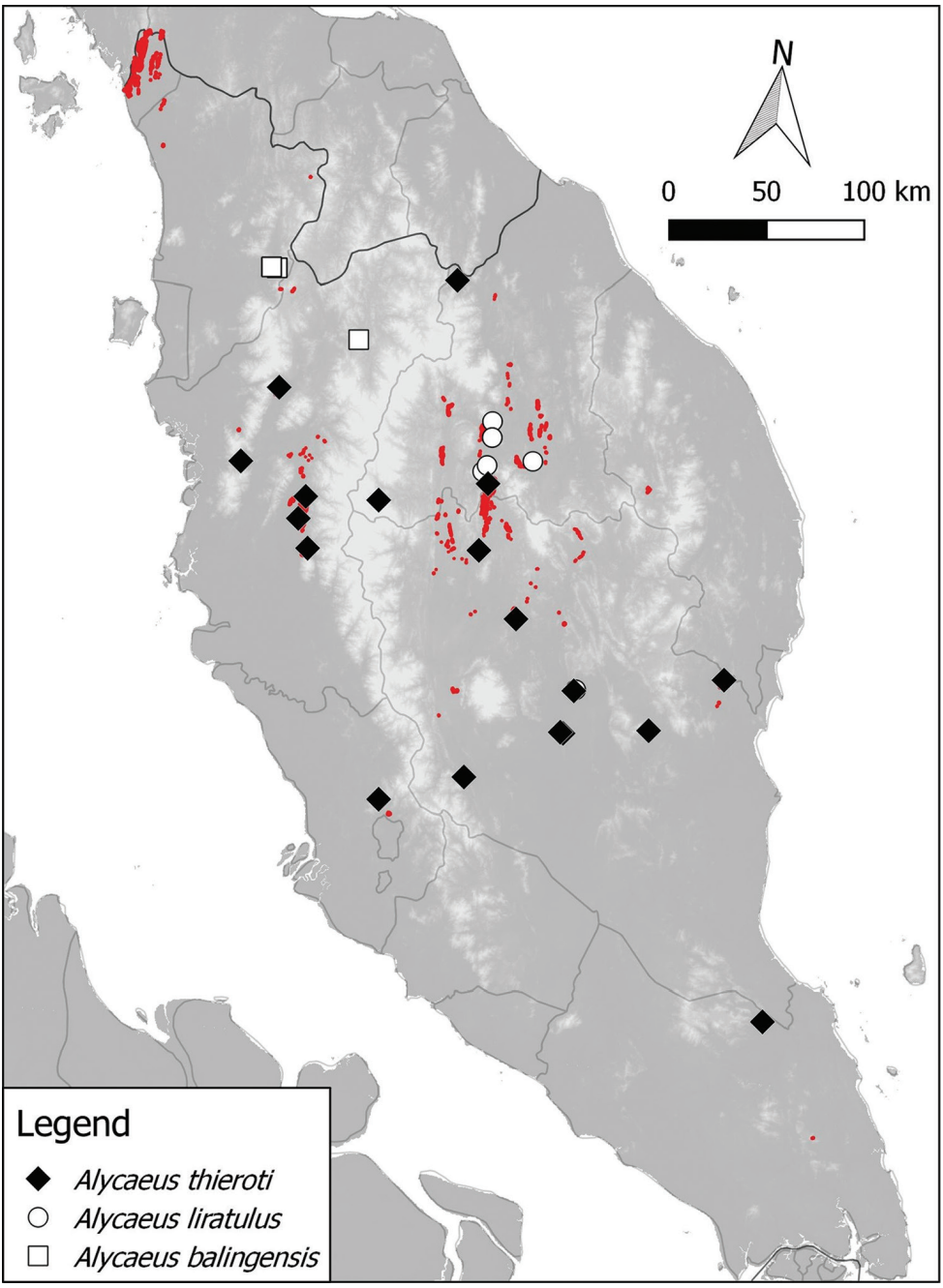

Figure 3. Distribution of 3 *Alycaeus* species in Peninsular Malaysia based on materials examined. Note the red areas are limestone karsts (derived from Liew et al. 2016).

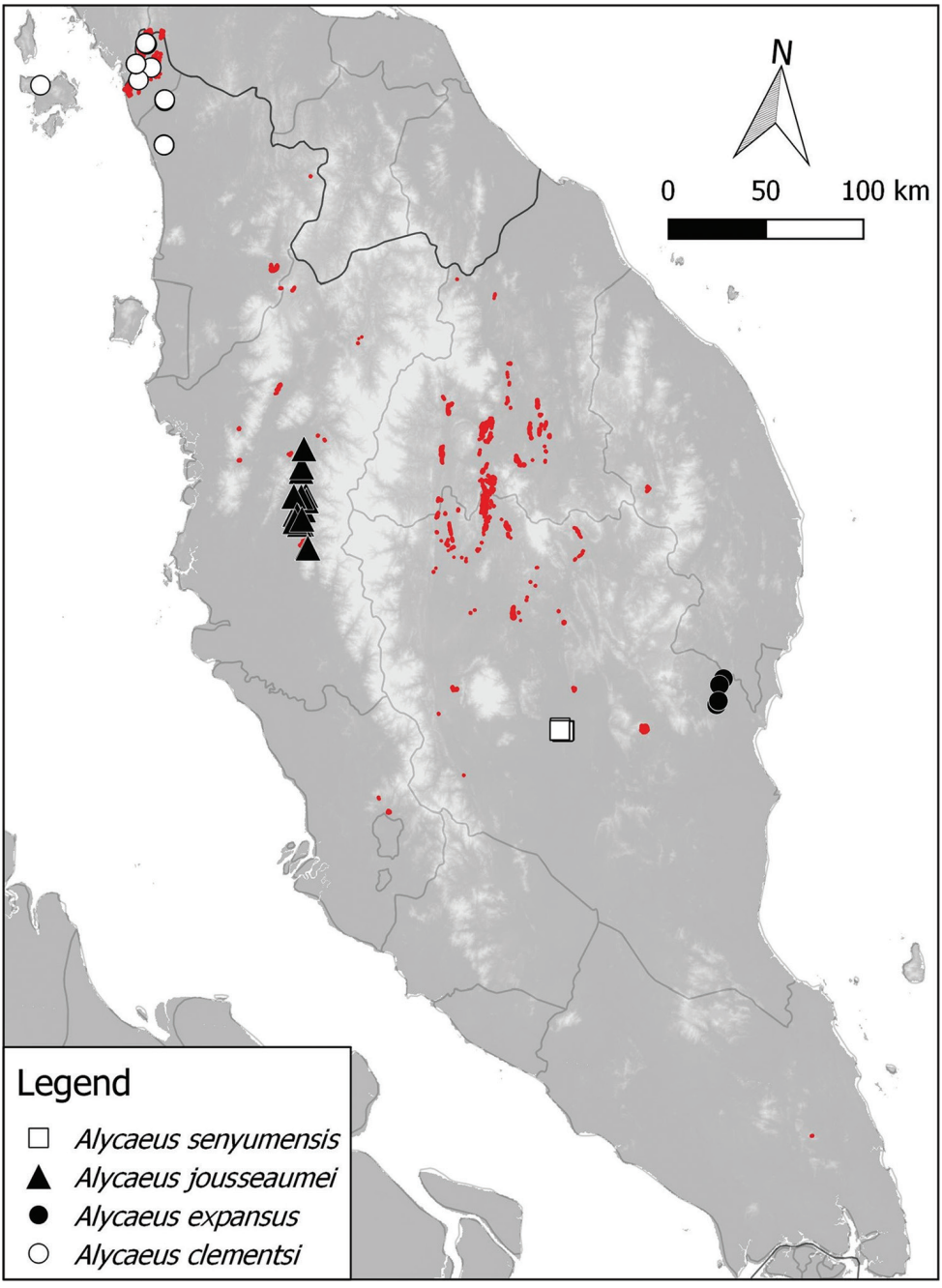

Figure 4. Distribution of 4 *Alycaeus* species in Peninsular Malaysia based on materials examined. Note the red areas are limestone karsts (derived from Liew et al. 2016).

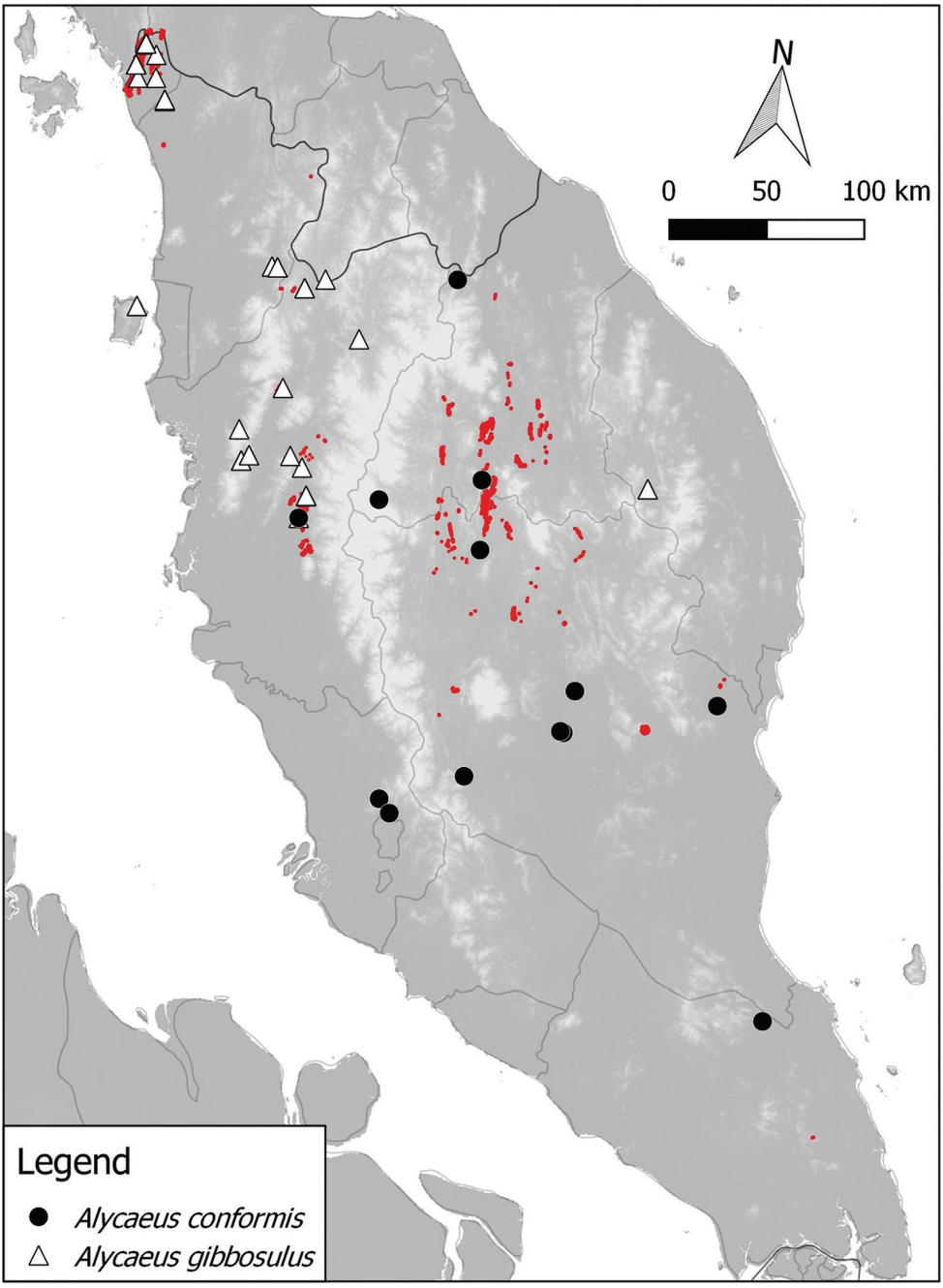

Figure 5. Distribution of 2 *Alycaeus* species in Peninsular Malaysia based on materials examined. Note the red areas are limestone karsts (derived from Liew et al. 2016).

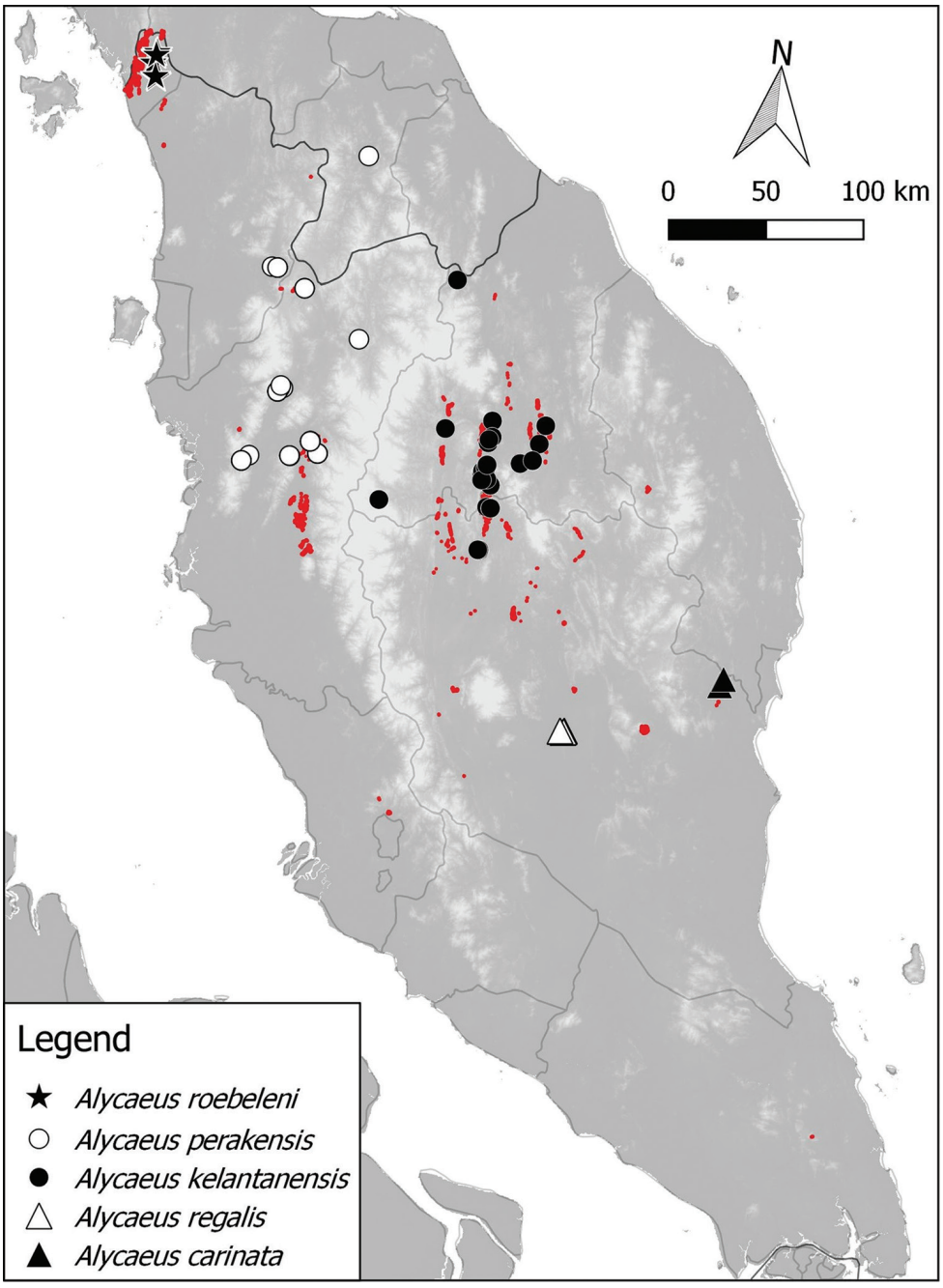

Figure 6. Distribution of 5 *Alycaeus* species in Peninsular Malaysia based on materials examined. Note that two records of *Alycaeus roebeleni* in Thailand, north of Peninsular Malaysia are not shown in the map. The red areas are limestone karsts (derived from Liew et al. 2016).

each species to gauge intraspecific variation of shell dimensions against interspecific variation (Table 1, Figure 1). In addition to this, up to 9 shells representing the whole spectrum of shell shape and sizes for each species were measured for the number of whorls, position of whorl constriction, length of breathing tube, spiral line spacing, radial ribs spacing and peristome orientation (Table 1, Figure 1). The variations are summarised in the species description (for raw data of individual shell measurements, see Suppl. material 2). Type materials available to us were also measured. They were then assigned to respective species based on the assessment framework in Table 1. Overall, materials examined totalled 5137 specimens from 522 collection lots which is comprised of: ANSP – 9 collection lots (including 1 type lot), 22 specimens in total; BOR/MOL – 411 collection lots (including 48 type lots), 3031 specimens in total; MNHN – 6 collection lots (including 6 type lots), 10 specimens in total; NHM – 3 collection lots (including 3 type lots), 5 specimens in total; RMNH – 13 collection lots (including 2 type lots), 137 specimens in total; SMF – 2 collection lots (including 2 type lots), 2 specimens in total; ZMA – 5 collection lots, 7 specimens in total; ZRC – 73 collection lots, 1923 specimens in total.

Overall, we employed the morphological species concept in this study as our comprehensive 39 characters assessment on a large sample size enables us to understand intraspecific variation of shell dimensions against interspecific variation. In addition to this, we also follow previous studies in recognising the major role of limestone hill isolation and biogeography in vicariance and speciation of karst restricted taxa especially land snails in Peninsular Malaysia (Clements et al. 2008, Hoekstra and Schilthuizen 2011, Liew et al. 2014). Notably, a study of another limestone restricted genus *Plectostoma* inhabiting limestone hills that are near each other but separated by biogeographic barriers may only differ a little in morphology but is sufficiently genetically distinct to be considered as different species (Liew et al. 2014). Given that many of the *Plectostoma* species in Liew et al. (2014) were sampled from the same localities as *Alycaeus* in this study and that most *Alycaeus* species are also restricted to limestone areas, it is very likely that *Alycaeus* in this study will show the same trend of morphological variation and speciation as *Plectostoma*. To conclude, this study represents the first attempt at a systematic taxonomic review of *Alycaeus* species in Peninsular Malaysia and has used a large quantity of materials and characters to arrive at an empirically supported species hypothesis. The emergence of additional evidences such as genetics and anatomy in the future will be useful to further assess these species hypotheses.

Shell and operculum characters

The description of shell and operculum characters partially follows the terminology established by Godwin-Austen (1889) and Kobelt (1902). However, a revised set of 39 shell and opercular characters are introduced in this study to provide a comparative morphological framework with objective empirical data for all *Alycaeus* specimens that were examined in this study (Table 1, Figure 1). All measurements are in millimetres and are

rounded up to the nearest 0.01 mm. Most of the characters can be observed by stereomicroscope at 2.0 × magnification except protoconch sculpture, spiral lines and radial ribs (some species) which can only be seen with at least 4.0 × magnification. Two archaic terms have also been replaced based on latest findings: (1) "horny operculum" (Godwin-Austen 1889) to proteinaceous operculum (see Checa and Jiménez-Jiménez 1998), (2) "sutural tube" (Godwin-Austen 1889) to breathing tube (see Páll-Gergely et al. 2016).

Systematic part

Class Gastropoda Cuvier, 1797
Family Alycaeidae Blanford, 1864

Genus *Alycaeus* Baird, 1850

Alycaeus Baird, 1850: 27–28.

Description for Peninsular Malaysian species. Protoconch. Smooth. In some species, second whorl grooved.

Shell shape and size. Conical (pyramidal), flat or globose. Shell height: 3.03–10.91 mm. Shell width: 3.36–15.04 mm.

Spire. Spire height: 0.93–3.21 mm. Spire width: 1.40–4.00 mm. Number of whorls: up to 3–5 ½. Spire shape always oblong conical. Whorl periphery strongly keeled or rounded. Always umbilicated. Umbilicus open or partially closed.

Whorl constriction. Position of constriction about 2 ¼–5 ¼ whorls posterior of protoconch.

Breathing tube. Always present, varies in length: 0.29–6.52 mm.

Aperture and peristome. Aperture always circular. Apertural margin moderately expanded or very expanded. Aperture height: 1.59–7.30 mm. Aperture width: 1.60–6.59 mm. Peristome single, double or triple. Peristome thickened or not thickened. Peristome notched or winged at suture. Interspace between peristome none, narrow or wide. Peristome orientation varies 4°–55° oblique to the coiling axis.

Spiral lines. Absent or present. When present, distinction varies (distinct or indistinct), spacing always regular to irregular. Number of spiral lines: 11–60 lines per 1 mm.

Radial ribs running anterior of breathing tube. Pronounced, indistinct or absent. Even or unevenly spaced. 6–21 radial ribs per 1 mm.

Radial ribs running perpendicular to breathing tube. Pronounced, indistinct or absent. Radial ribs sometimes are thicker and whiter compared to radial ribs anterior of breathing tube. Even or unevenly spaced. 6–29 ribs per 1 mm.

Radial ribs running posterior of breathing tube. Pronounced, indistinct or absent. Usually unevenly spaced. 2–25 ribs per 1 mm.

Operculum. Concave or flat. Rounded or conical. Exterior usually calcareous layered of variable thickness. Exterior texture varies (smooth, finely granulated, flaky,

short calcareous spikes, cup-like projection at nucleus, scaffold-like calcareous deposits or appressed radially spiral lamellae). Interior usually proteinaceous layered. Interior sculpture smooth, with multilamellar impression or mamillated.

Shell colour. Varies between and within species (white, pinkish-white, pink, yellow, orange, red, brownish-red. brown, purple). Apical whorls either in white or non-white colours, always fading to white in subsequent whorls.

Living animal. Body colour variable but lighter than head and tentacle (cream-white, yellow, cream-yellow, light brown, brown, maroon, greenish-black, light grey, grey). Head colour variable (orange, pink, pinkish-brown, brown, maroon, greenish-black, grey, dark grey). Tentacle either uni-coloured (yellow, red, brown, reddish-brown, light grey, dark grey, black), or bi-coloured (green with brown tips, cream-white with pink tips, yellow with red tips). Head and tentacle often darker coloured relative to the body.

Habitat and ecology. Three distinct habitats: rock (crevices, rock walls, solution holes, moss and lichen covered rocks), vegetation (low shrubs, tree trunks) or forest floor (rotten logs, leaf litter). Usually in moist areas but ocassionally found in drier areas. Always in forested habitats.

Remarks. The genus *Alycaeus* Baird, 1850, is separated into three subgenera – *Alycaeus* Baird, 1850, *Pincerna* Preston, 1907, and *Stomacosmethis* Bollinger, 1918 (Egorov 2013). However, all of these subgenera (including *Pincerna* (see Páll-Gergely 2017)) remain inadequately defined as no clear diagnostic characters have ever been identified (Godwin-Austen 1889) and hence will require extensive revision, a task that is beyond the scope of this study and will instead be treated in later studies (B. Páll-Gergely, pers. comm.). Thus, we do not provide a diagnosis for the genus *Alycaeus* here pending a revision of the Alycaeidae and resolution of diagnostic characters useful for supraspecific groups. Instead, consistent with our study scope, we will only provide a description of characters relevant to Peninsular Malaysian *Alycaeus* species.

Alycaeus alticola sp. n.

http://zoobank.org/E88B3EDB-0DEE-417F-BDEA-613A67ADA99B
Figures 7J, 8, 31G

Type locality. PHG 77 Bukit Mengapur, Pahang (3°44'42"N, 102°50'16"E).

Type material. *Holotype.* PHG 77 Bukit Mengapur, Pahang: BOR/MOL 12977. *Paratypes.* PHG 77 Bukit Mengapur, Pahang: BOR/MOL 6888/1, BOR/MOL 8398/26.

Other examined materials. PHG 77 Bukit Mengapur, Pahang: BOR/MOL 8397(11).

Etymology. Latin for "dweller at heights". Named after the species' apparent ecological preference for habitats at higher and drier parts of limestone hills.

Description. Protoconch. Smooth.

Shell shape. Conical. Shell height: 5.08–6.04 mm. Shell width: 5.04–5.87 mm.

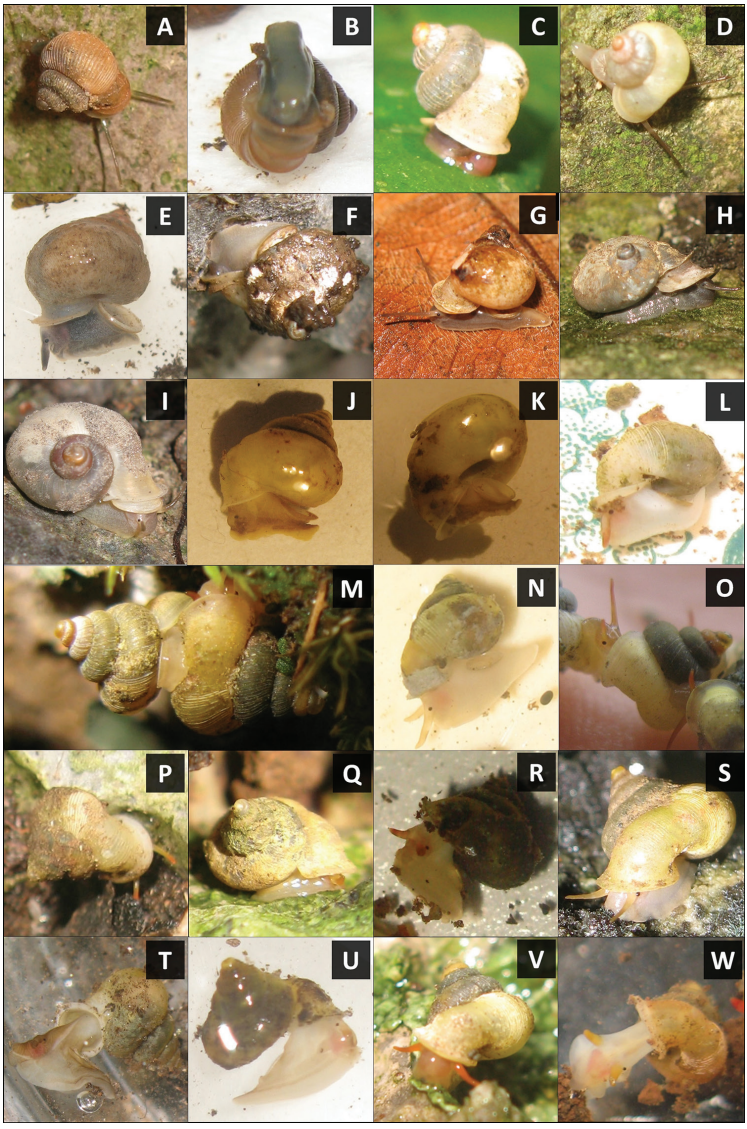

Figure 7. Photographs of 18 living *Alycaeus* species. **A–B** *Alycaeus balingensis* Tomlin, 1948, BOR/MOL 8356 **C** *Alycaeus liratulus* (Preston, 1907), BOR/MOL 8334 **D** *Alycaeus thieroti* Morgan, 1885b, BOR/MOL 6835 **E** *Alycaeus conformis* Fulton, 1902, BOR/MOL 6809 **F** *Alycaeus gibbosulus* Stoliczka, 1872, BOR/MOL 6850 **G** *Alycaeus gibbosulus* Stoliczka, 1872, BOR/MOL 8526 **H** *Alycaeus jousseaumei* Morgan, 1885a, BOR/MOL 8341 **I** *Alycaeus jousseaumei* Morgan, 1885a, BOR/MOL 8336 **J** *Alycaeus alticola* sp. n., BOR/MOL 8398 **K** *Alycaeus charasensis* sp. n., BOR/MOL 8399 **L** *Alycaeus clementsi* sp. n., BOR/MOL 8364 **M** *Alycaeus costacrassa* sp. n., BOR/MOL 6811 **N** *Alycaeus expansus* sp. n., BOR/MOL 6367 **O** *Alycaeus kapayanensis* Morgan, 1885b, BOR/MOL 13005 **P** *Alycaeus kelantanensis* Sykes, 1902, BOR/MOL 8325 **Q** *Alycaeus kelantanensis* Sykes, 1902, BOR/MOL 6200 **R** *Alycaeus kurauensis* sp. n., BOR/MOL 6851 **S** *Alycaeus perakensis* Crosse, 1879a, BOR/MOL 6852 **T** *Alycaeus regalis* sp. n., BOR/MOL 6881 **U** *Alycaeus selangoriensis* sp. n., BOR/MOL 6371 **V–W** *Alycaeus senyumensis* sp. n., BOR/MOL 6249. All photographs by Junn Kitt Foon.

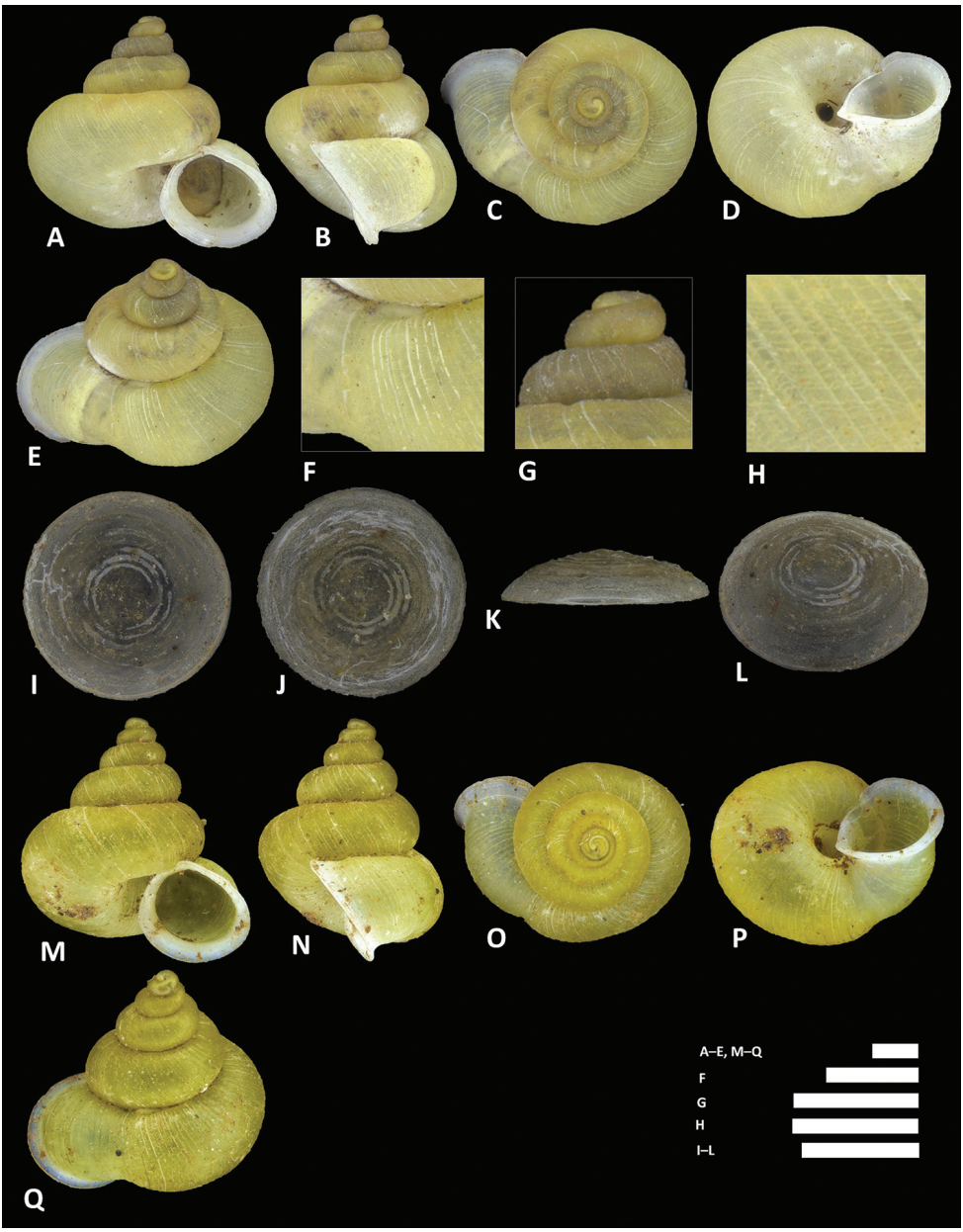

Figure 8. *Alycaeus alticola* sp. n. **A–E** Shell of holotype, BOR/MOL 8398 **F–H** Close up of shell of holotype, BOR/MOL 8398 **I–L** Operculum of paratype, BOR/MOL 8398 **M–Q** Shell of paratype, BOR/MOL 8398. Scale bars: **A–G, I–Q** 1 mm; H 0.5 mm. All photographs by Junn Kitt Foon.

Spire. Spire height: 1.64–2.23 mm. Spire width: 2.32–2.71 mm. Number of whorls: up to 5. Spire shape: oblong conical. Whorl periphery rounded. Umbilicus open.

Whorl constriction. At about 4 ¾ whorls posterior of protoconch.

Breathing tube. Length: 0.42–0.58 mm.

Aperture and peristome. Aperture circular, moderately expanded. Aperture height: 2.40–2.70 mm. Aperture width: 2.32–2.72 mm. Peristome double, not thickened, slightly notched at suture. Peristome orientation 35–38° oblique with respect to the coiling axis.

Spiral lines. Indistinct, regularly spaced. Approximately 22–44 lines per 1 mm.

Radial ribs running anterior of breathing tube. Radial ribs pronounced, evenly spaced. Approximately 10–14 ribs per 1 mm.

Radial ribs running perpendicular to breathing tube. Radial ribs pronounced, white and thicker than those anterior of breathing tube, evenly spaced. Approximately 9–15 ribs per 1 mm.

Radial ribs running posterior of breathing tube. Radial ribs absent immediately posterior of constriction, becoming pronounced and regularly spaced at the middle until prior to aperture. Approximately 7–15 ribs per 1 mm.

Operculum. Concave, rounded. Exterior covered with very thin calcareous layer, with indistinct appressed multilamellae. Interior covered with proteinaceous coating, smooth, with indistinct appressed multilamellae and indistinct mamilla.

Shell colour. Whorls yellow, fading to white posterior of constriction. Peristome white.

Living animal. Body cream-white with fine brown blotches. Head brown. Tentacles brown.

Habitat and ecology. Lives on rock surfaces covered with powdery lichen at higher and drier areas of the limestone hills, often at open places exposed to ambient sunlight. They never appear on wet and mossy sections of limestone rocks and are rarely seen in lower parts of limestone hills that are shaded by forest cover.

Distribution range. Restricted to Bukit Mengapur, Pahang.

Differential diagnosis. *Alycaeus alticola* sp. n. varies in the degree of ultimate whorl expansion within population but has a consistently more expanded and globose whorl compared to *A. costacrassa* sp. n., *A. selangoriensis* sp. n. and *A. kapayanensis*. *Alycaeus alticola* sp. n. shares similar shell shape with *Alycaeus charasensis* sp. n. but differs in the presence of pronounced radial ribs and spiral lines, as well as less expanded ultimate whorl.

Discussion. *A. alticola* sp. n. is among the larger yellow, conical shelled *Alycaeus* in Peninsular Malaysia.

Alycaeus altispirus Möllendorff, 1902

Figures 9, 31U

Alycaeus perakensis altispirus Möllendorff, 1902: 144–145; Maassen 2001: 23; Tarruella and Domènech 2011: 72.

Alycaeus (*Alycaeus*) *perakensis altispirus*: Zilch 1957: 147, plate 6, figure 32.

Type locality. Kelantan.

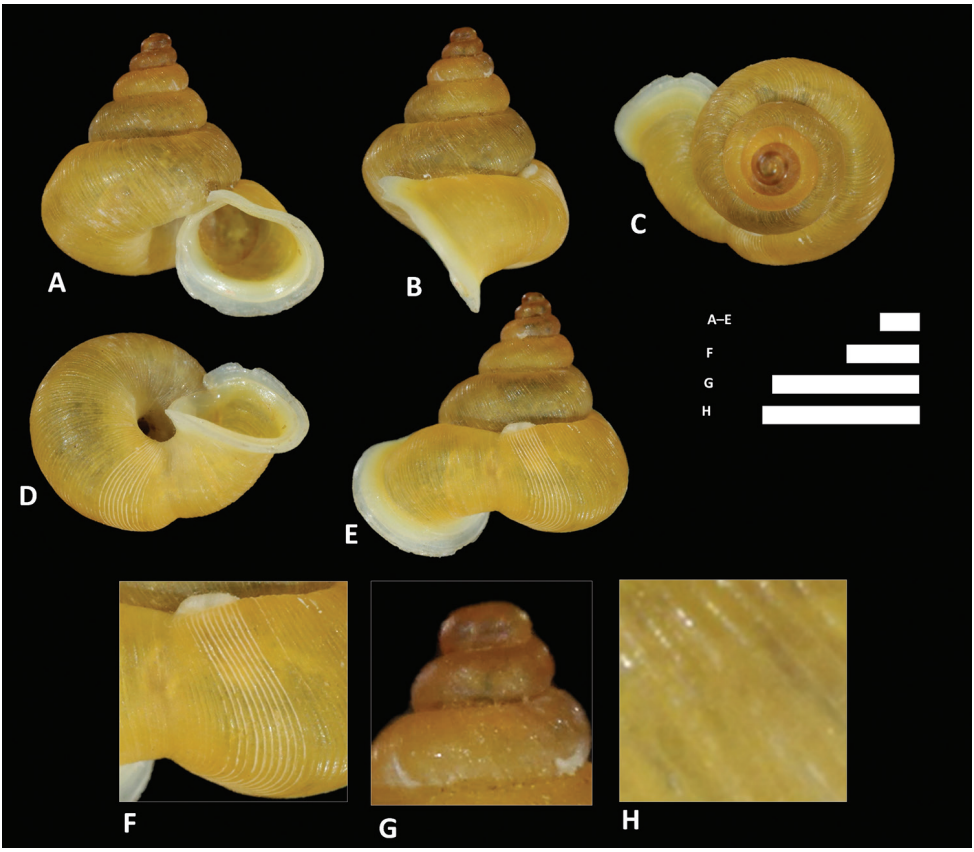

Figure 9. *Alycaeus altispirus* (Möllendorff, 1902) **A–E** Shell of lectotype, SMF 109738 **F–H** Close up of shell of lectotype, SMF 109738. Scale bars: **A–G** 1 mm; **H** 0.5 mm. All photographs by Páll-Gergely Barna, courtesy of R. Janssen, SMF.

Type material. *Lectotype*. Kelantan: SMF 109738 (Seen). *Paralectotypes*. Kelantan: SMF 109739/3(Not seen).

Description. Protoconch. Smooth.

Shell shape. Conical. Shell height: 6.40 mm. Shell width: 6.30 mm.

Spire. Spire height: 2.37 mm. Spire width: 2.68 mm. Number of whorls: up to 5 ½. Spire shape: oblong conical. Whorl periphery rounded. Umbilicus open.

Whorl constriction. At about 5 ¼ whorls posterior of protoconch.

Breathing tube. Length: 0.77 mm.

Aperture and peristome. Aperture circular, moderately expanded. Aperture height: 2.87 mm. Aperture width: 3.36 mm. Peristome double, not thickened, notched at suture, upper palatal section folded posteriorly into a wing-like structure. Peristome orientation 36° oblique with respect to the coiling axis.

Spiral lines. Absent.

Radial ribs running anterior of breathing tube. Radial ribs pronounced, evenly spaced. Approximately 8 ribs per 1 mm.

Radial ribs running perpendicular to breathing tube. Radial ribs pronounced, white and thicker than those anterior of breathing tube, evenly spaced. Approximately 16 ribs per 1 mm.

Radial ribs running posterior of breathing tube. Radial ribs absent immediately posterior of constriction, becoming pronounced and evenly spaced from the middle section until prior to aperture. Approximately 10 ribs per 1 mm.

Operculum. Unknown.

Shell colour. Whorls yellow. Peristome white.

Living animal. Unknown.

Habitat and ecology. Unknown.

Distribution range. Unknown. Appears to be restricted to Kelantan.

Differential diagnosis. *Alycaeus altispirus* is most similar to *Alycaeus regalis* sp. n. in having a large shell (shell height: 6.40–7.18 mm, shell width: 5.86–6.87 mm) and tall spire (spire height: 2.32–2.90 mm) but differs in the ultimate whorl being more keeled-like, upper palatal section folded posteriorly into a wing-like structure and peristome orientated oblique to the coiling axis. Unlike *Alycaeus perakensis*, *Alycaeus altispirus* is smaller (smaller by about 0.23 mm in shell height, 0.25 mm in shell width) and has a much less expanded ultimate whorl.

Discussion. To date, this species is only known from the four type specimens collected by John Waterstradt (Möllendorff 1902, Zilch 1957) presumably from the same locality as *A. kelantanensis*, on Pulai Princess Cave hill (4°47'38"N, 101°56'31"E), Kelantan (see Discussion under *A. kelantanensis*; Waterstradt 1902, Liew et al. 2014). Yet no recent shells have been found on surveyed limestone hills near the locality (about 5 km from Pulai Princess Cave hill) or elsewhere in Kelantan. At the time of its description, Möllendorff (1902) considered *A. altispirus* a subspecies of *A. perakensis* but did not elaborate why. We disagree with this decision because the two taxa differ markedly from each other in shell shape especially the degree of expansion and shape of the ultimate whorl as well as their very disjunct distribution range. As such, we consider *A. altispirus* a species on its own.

Alycaeus balingensis Tomlin, 1948

Figures 7A–B, 10, 31A

Alycaeus balingensis Tomlin, 1948: 224–226, plate 11, figure, 3; Maassen 2001: 21; Clements et al. 2008: 2760; Tarruella and Domènech 2011: 72.

Type locality. KDH 01 Bukit Baling, Kedah (5°40'50"N, 100°54'25"E).

Type material. *Syntype.* Bukit Baling, Kedah: NHMUK 1948.10.2.4/1 (1 specimen seen).

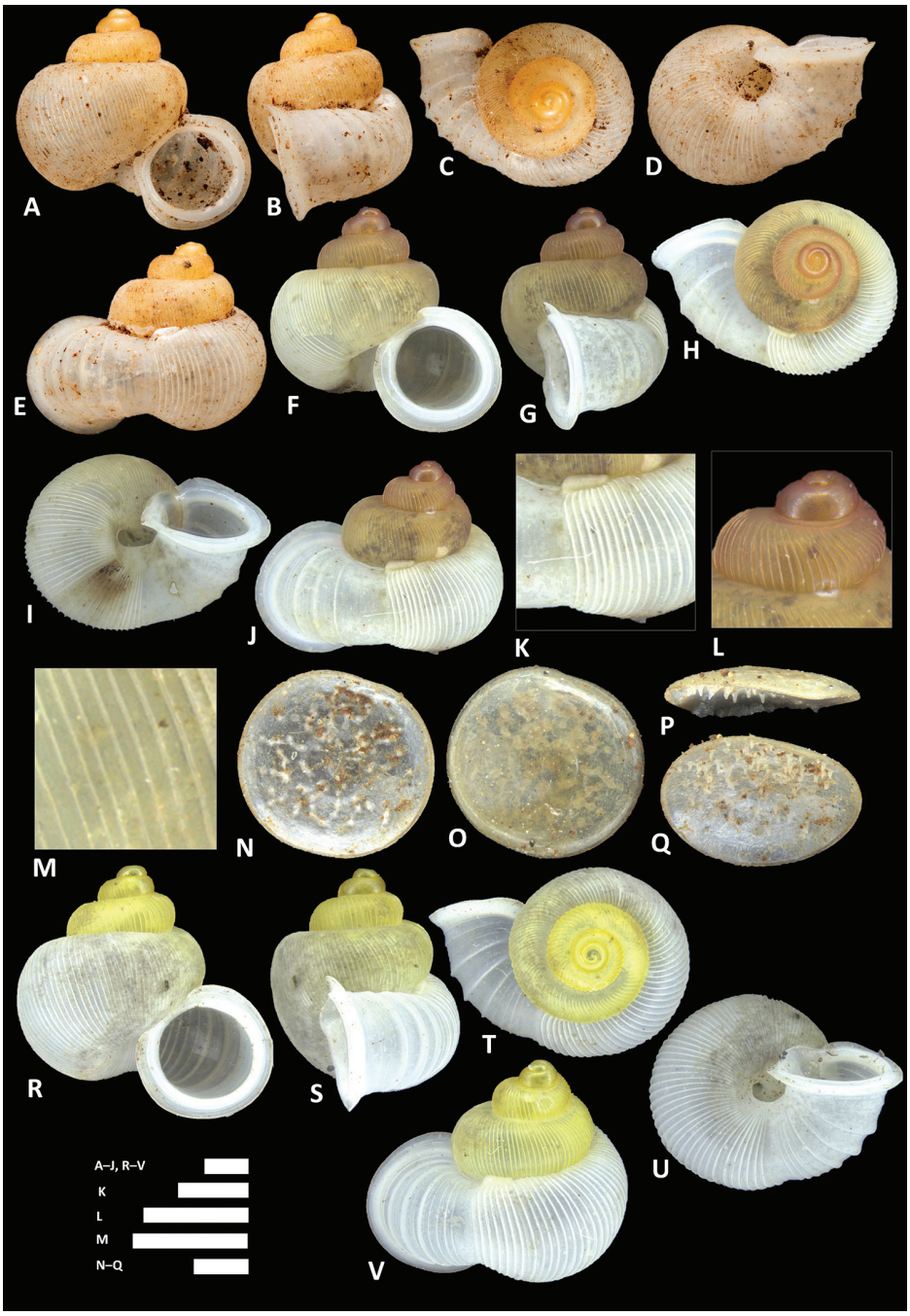

Figure 10. *Alycaeus balingensis* Tomlin, 1948. **A–E** Shell of syntype, NHMUK 1948.10.2.4 **F–J** Shell of BOR/MOL 8357 **K–M** Close up of shell of BOR/MOL 8357 **N–Q** Operculum of BOR/MOL 8357 **R–V** Shell of BOR/MOL 8361. Scale bars: **A–J, R–V, K, L** 1 mm; **M, N–Q** 0.5 mm. Photographs **A–E** by NHM staff (copyright of NHM, reproduced with permission). Photographs **F–V** by Junn Kitt Foon.

Other examined materials. KDH 01 Bukit Baling, Kedah: BOR/MOL 6524/1, BOR/MOL 6853/1, BOR/MOL 8356/13, BOR/MOL 8357/27, ZRC 1997/4, ZRC 1975.2.21.1-85/85. KDH 02 Gunung Pulai, Kedah: BOR/MOL 6856/1, BOR/MOL 8360/18, BOR/MOL 8361/26. Mykarst-171 'Tasik Temenggor Hill S2', Perak: BOR/MOL 6245/1.

Description. Protoconch. Smooth.

Shell shape and size. Globose. Shell height: 4.75–5.87 mm. Shell width: 5.11–6.00 mm.

Spire. Spire height: 1.23–2.16 mm. Spire width: 2.09–2.54 mm. Number of whorls: up to 4 ⅛. Spire shape: oblong conical. Whorl periphery rounded. Umbilicus open.

Whorl constriction. At about 3 ¾ whorls posterior of protoconch.

Breathing tube. Length: 0.70–0.82 mm.

Aperture and peristome. Aperture circular, moderately expanded. Aperture height: 2.60–3.13 mm. Aperture width: 2.69–3.22 mm. Peristome double, not thickened, slightly notched at suture. No interspace. Peristome orientation 4–8° oblique with respect to the coiling axis.

Spiral lines. Absent.

Radial ribs running anterior of breathing tube. Radial ribs pronounced, evenly spaced. Approximately 9–16 ribs per 1 mm.

Radial ribs running perpendicular to breathing tube. Radial ribs pronounced, evenly spaced. Approximately 7–10 ribs per 1 mm.

Radial ribs running posterior of breathing tube. Radial ribs initially indistinct and dense, but increasingly becomes pronounced and evenly-spaced towards the aperture. Approximately 2–4 ribs per 1 mm.

Operculum. Concave, rounded. Exterior covered by calcareous layer, with short calcareous spikes. Interior covered by proteinaceous layer, smooth.

Shell colour. Red, yellow or white at apical whorls. All colours fade to white towards ultimate whorl.

Living animal. Body greenish-black. Head greenish-black. Tentacle green with brown tips.

Habitat and ecology. Lives in crevices on wet limestone boulders and shrubs close to the ground. In forested areas of limestone hills.

Distribution. Restricted to northern Perak (mykarst-171) and northeastern Kedah (Bukit Baling and Gunung Pulai).

Differential diagnosis. *Alycaeus balingensis* shares similar shell shape (globose whorls) with *Alycaeus liratulus* and *Alycaeus thieroti* but differs in having whorls with denser and more pronounced radial ribs, absence of spiral lines, operculum exterior with short spikes and greenish-black body.

Discussion. *Alycaeus balingensis* is listed as Critically Endangered in the IUCN Red List as it was known only from the actively quarried Bukit Baling at the time of assessment (Clements 2009). Given that new populations have now been discovered in two other localities in Kedah and Perak, the conservation status of *A. balingensis* should be revised.

***Alycaeus carinata* Maassen, 2006**
Figures 11, 31Q

Alycaeus carinata Maassen, 2006: 137–138, figures 10–13; Tarruella and Domènech 2011: 72.

Type locality. PHG 74 Bukit Sagu, Pahang (3°58'54"N, 103°08'39"E).

Type material. *Holotype.* PHG 74 Bukit Sagu, Pahang: RMNH 104428 (Not seen). *Paratypes.* PHG 74 Bukit Sagu, Pahang: RMNH 104427/2 (1 specimen seen), HW /58 (Not seen), CUIZM /2 (Not seen), HW /200 (Not seen). PHG 75 Bukit Tenggek, Pahang: RMNH 104426/2 (Not seen), HW /37 (Not seen).

Description. Protoconch. Smooth.

Shell shape. Almost flat, conical. Shell height: 2.2–3.0 mm. Shell width: 4.0–4.6 mm. Shell measurements derived from Maassen (2006) and re-examination of one paratype (RMNH 104427).

Spire. Spire height: 3.0 mm. Spire width: 4.5 mm. Number of whorls: up to 4. Spire shape: oblong conical. Whorl periphery strongly keeled except posterior of the constriction, where it becomes rounded. Umbilicus open.

Whorl constriction. At about 3 ¾ whorls posterior of protoconch.

Breathing tube. Length: 0.3 mm.

Aperture and peristome. Aperture circular, moderately expanded. Aperture height: 2.2 mm. Aperture width: 2.0 mm. Peristome double, not thickened, winged at suture. Interspace narrow. Peristome orientation is 30–55° oblique with respect to the coiling axis.

Spiral lines. Indistinct. Regularly spaced. Approximately 25 lines per 1 mm.

Radial ribs running anterior of breathing tube. Radial ribs indistinct to absent, only unevenly spaced radial growth lines present.

Radial ribs running perpendicular to breathing tube. Radial ribs pronounced, evenly spaced. Approximately 13 ribs per 1 mm.

Radial ribs running posterior of breathing tube. Radial ribs indistinct to absent, only unevenly spaced radial growth lines present.

Operculum. Concave, rounded. Exterior and interior composition and sculpture not examined. Maassen (2006) considered the operculum entirely proteinaceous.

Shell colour. Whorls yellow to brown. Peristome white.

Living animal. Unknown.

Habitat and ecology. Lives on limestone walls in a large, collapsed cave (Maassen 2006). Probably prefers very moist environments only (Maassen 2006).

Distribution range. Restricted to Bukit Sagu and Bukit Tenggek, Pahang.

Differential diagnosis. *Alycaeus carinata* is distinguished from all other Peninsular Malaysian *Alycaeus* species by its strongly keeled periphery, relatively low spire, very expanded ultimate whorls and very oblique peristome orientation with respect to the coiling axis (Maassen 2006).

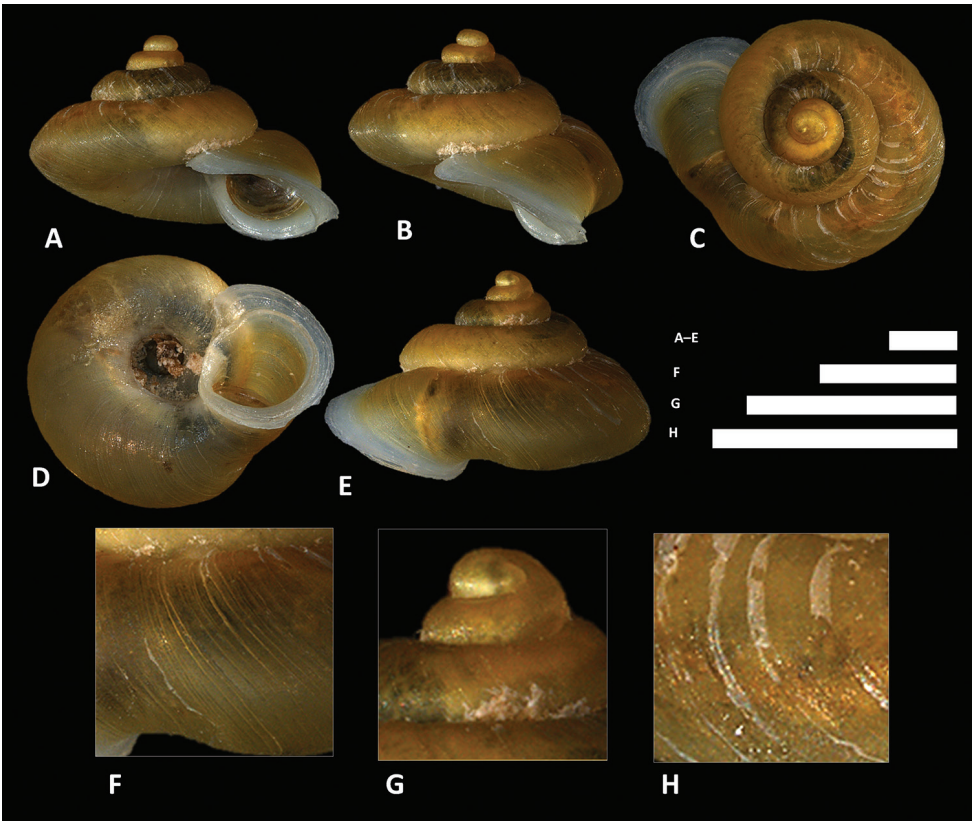

Figure 11. *Alycaeus carinata* Maassen, 2006 **A–E** Shell of paratype, RMNH 104427 **F–H** Close up of shell of paratype, RMNH 104427. Scale bars: **A–G** 1 mm; **H** 0.5 mm. All photographs by Thor Seng Liew.

Discussion. Interestingly, no *A. carinata* was found during the 1950s University of Malaya, Singapore expedition to the type locality although congeners *Alycaeus charasensis* sp. n. and *Alycaeus expansus* sp. n. were obtained (ZRC collection lots). This suggests *A. carinata* may be restricted to upper sections of limestone hills that became accessible only during quarrying in the 1990s. However, viable habitats at Bukit Sagu and Bukit Tenggek are now very likely lost to quarrying (Schilthuizen and Clements 2008, Liew et al. 2014).

***Alycaeus charasensis* sp. n.**
http://zoobank.org/05839D39-E09B-4635-9254-BBF285A60A90
Figures 7K, 12, 31H

Type locality. PHG 73 Bukit Charas, Pahang (3°54'35"N, 103°08'48"E).

Type material. *Holotype.* PHG 73 Bukit Charas, Pahang: BOR/MOL 12981. *Paratypes.* PHG 75 Bukit Tenggek, Pahang: BOR/MOL 264/2. PHG 73 Bukit Charas, Pahang: BOR/MOL 267/3, BOR/MOL 6891/1.

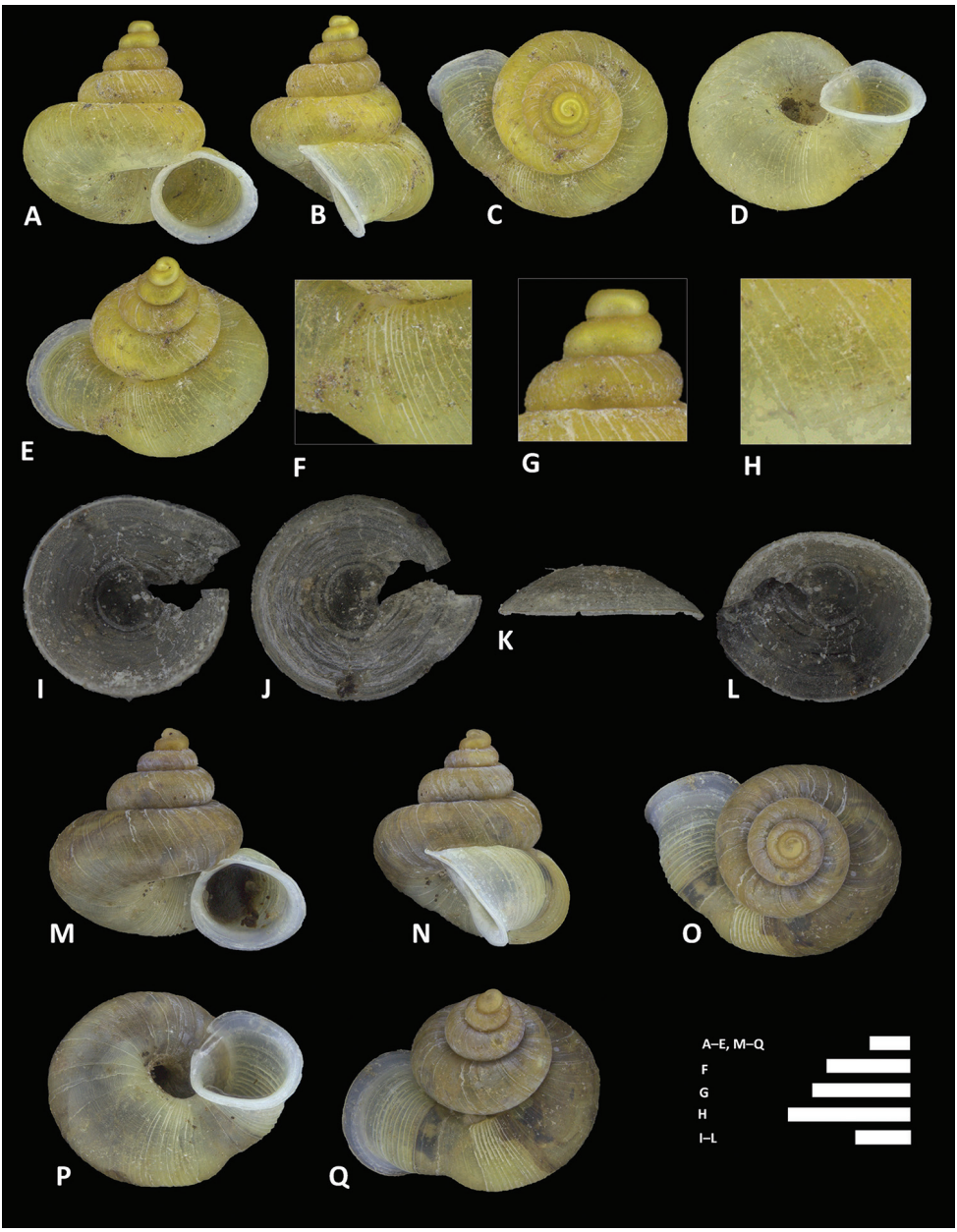

Figure 12. *Alycaeus charasensis* sp. n. **A–E** Shell of holotype, BOR/MOL 8400 **F–H** Close up of shell of holotype, BOR/MOL 8400 **I–L** Operculum of paratype, BOR/MOL 6891 **M–Q** Shell of paratype, BOR/MOL 267. Scale bars: **A–G, M–Q, H** 1 mm; **I–L** 0.5 mm. All photographs by Junn Kitt Foon.

Other examined materials. PHG 73 Bukit Charas, Pahang: BOR/MOL 8399/14, BOR/MOL 8401/26, BOR/MOL 8402/166, BOR/MOL 12982/120, ZRC 1975.2.21.431-434/4, ZRC 1975.2.22.444-677/234, ZRC 1975.2.24.132-

153/22, ZRC 1975.2.24.1-43/43, ZRC 1975.2.24.93-131/38, ZRC 1975.2.24.83-89/6. PHG 75 Bukit Tenggek, Pahang: ZRC 1975.2.24.44-/>1.

Etymology. Subspecific epithet named after the type locality, Bukit Charas.

Description. Protoconch. Smooth.

Shell shape. Conical. Shell height: 5.09–5.82 mm. Shell width: 5.23–6.62 mm.

Spire. Spire height: 1.57–2.11 mm. Spire width: 2.38–2.77 mm. Number of whorls: up to 5. Spire shape: oblong conical. Whorl periphery rounded. Umbilicus open.

Whorl constriction. At about 4 ⅞ whorls posterior of protoconch.

Breathing tube. Length: 0.46–0.57 mm.

Aperture and peristome. Aperture circular, moderately expanded. Aperture height: 2.58–2.90 mm. Aperture width: 2.47–2.84 mm. Peristome double, not thickened, slightly notched at suture. Peristome orientation 34–43° oblique with respect to the coiling axis.

Spiral lines. Indistinct, regularly spaced. Approximately 16–60 lines per 1 mm.

Radial ribs running anterior of breathing tube. Radial ribs indistinct, unevenly spaced. They are sometimes absent and are replaced by evenly spaced radial growth lines.

Radial ribs running perpendicular to breathing tube. Radial ribs pronounced, white and thick, evenly spaced. Approximately 8–15 ribs per 1 mm.

Radial ribs running posterior of breathing tube. Radial ribs absent immediately posterior of constriction, becoming pronounced and evenly spaced at the middle until prior to aperture. Approximately 7–19 ribs per 1 mm.

Operculum. Concave, rounded. Exterior covered with thin calcareous layer, with indistinct appressed multilamellae. Interior covered with proteinaceous coating, smooth, with indistinct appressed multilamellae.

Shell colour. Whorls yellow, fading to white posterior of constriction. Peristome white.

Living animal. Body cream-white with fine brown blotches. Head brown. Tentacles brown.

Habitat and ecology. Lives on rock surfaces covered with powdery lichen at higher and drier areas of the limestone hills, often at open places exposed to ambient sunlight. They never appear on wet and mossy sections of limestone rocks and are not found in lower parts of limestone hills that are shaded by forest cover.

Distribution range. Restricted to Bukit Charas and Bukit Tenggek, eastern Pahang.

Differential diagnosis. *Alycaeus charasensis* sp. n. shares similar variability in shell shape with *Alycaeus alticola* sp. n. but consistently differs in having a larger shell, wider ultimate whorl, widely spaced spiral lines and uneven, widely spaced radial growth lines in place of radial ribs. *Alycaeus charasensis* sp. n. is distinguished from other tall spired, conical yellow shelled *Alycaeus* in Peninsular Malaysia by its lack of distinct radial ribs.

Discussion. *A. charasensis* sp. n. is among the larger yellow, conical shelled *Alycaeus* in Peninsular Malaysia.

***Alycaeus clementsi* sp. n.**
http://zoobank.org/713345B0-4FB9-4AFF-9DD3-9A3AF78B19B1
Figures 7L, 13, 31J

Alycaeus perakensis: Benthem Jutting 1960a: 13. [not *Alycaeus perakensis* Crosse, 1879]

Type locality. Gua Kelam, PRS 64 Wang Ulu, Perlis (6°38'41"N, 100°12'09"E).

Type material. *Holotype.* Gua Kelam, PRS 64 Wang Ulu, Perlis: BOR/MOL 12970. *Paratypes.* Gua Kelam, PRS 64 Wang Ulu, Perlis: BOR/MOL 276/3, BOR/MOL 6865/1, BOR/MOL 8371/2. Bukit Ayer, PRS 64 Wang Ulu, Perlis: BOR/MOL 8365/2. Hill 9 km along the road from Kangar to Kaki Bukit, Perlis: BOR/MOL 270/1. KDH 10 Bukit Kodiang, Kedah: BOR/MOL 12969/1, BOR/MOL 8377/62. KDH 04 Gunung Keriang, Kedah: BOR/MOL 8407/7, BOR/MOL 12968/1. Limestone hill north of Sungai Ewa, Pulau Langkawi, Kedah: BOR/MOL 265/3.

Other examined materials. Gua Kelam, PRS 64 Wang Ulu, Perlis: BOR/MOL 6194/4, BOR/MOL 6867/1, BOR/MOL 8370/11, BOR/MOL 8373/3, ZRC 1997.21/2. Bukit Ayer, PRS 64 Wang Ulu, Perlis: BOR/MOL 6251/6, BOR/MOL 6861/1, BOR/MOL 8364/10. PRS 40 Bukit Merbok, Perlis: BOR/MOL 7071/1. KDH 04 Gunung Keriang, Kedah: BOR/MOL 6246/8, BOR/MOL 6252/20, BOR/MOL 6864/1, BOR/MOL 8369/40, BOR/MOL 8378/1, BOR/MOL 12971/1, BOR/MOL 6191/10, ZRC 1997.19/2. ZRC 1997.20/2, ZRC 1975.2.22.67-98/32. KDH 10 Bukit Kodiang, Kedah: BOR/MOL 6872/1.

Etymology. Named after Gopalasamy Reuben Clements, in recognition of his contribution to the study of land snail biogeography on Peninsular Malaysian karsts.

Description. Protoconch. Smooth.

Shell shape. Conical. Shell height: 5.65–6.98 mm. Shell width: 5.71–7.32 mm.

Spire. Spire height: 1.87–2.62 mm. Spire width: 2.39–3.32 mm. Number of whorls: up to 5 ⅛. Spire shape: oblong conical. Whorl periphery rounded. Umbilicus open.

Whorl constriction. At about 4 ¾whorls posterior of protoconch.

Breathing tube. Length: 0.59–0.90 mm.

Aperture and peristome. Aperture circular, moderately expanded. Aperture height: 2.95–3.88 mm. Aperture width: 2.83–3.49 mm. Peristome double, thickened, notched at suture. Peristome orientation 25–45° oblique with respect to the coiling axis.

Spiral lines. Distinct. Regularly spaced. Approximately 11–34 lines per 1 mm.

Radial ribs running anterior of breathing tube. Radial ribs pronounced, evenly spaced. Approximately 9–16 lines per 1 mm.

Radial ribs running perpendicular to breathing tube. Radial ribs pronounced, white and thicker than those anterior of breathing tube, evenly spaced. Approximately 11–16 radial ribs per 1 mm

Radial ribs running posterior of breathing tube. Radial ribs pronounced, unevenly spaced immediately posterior of constriction, becoming pronounced and evenly spaced from the middle section until prior to aperture. Approximately 11–16 ribs per 1 mm.

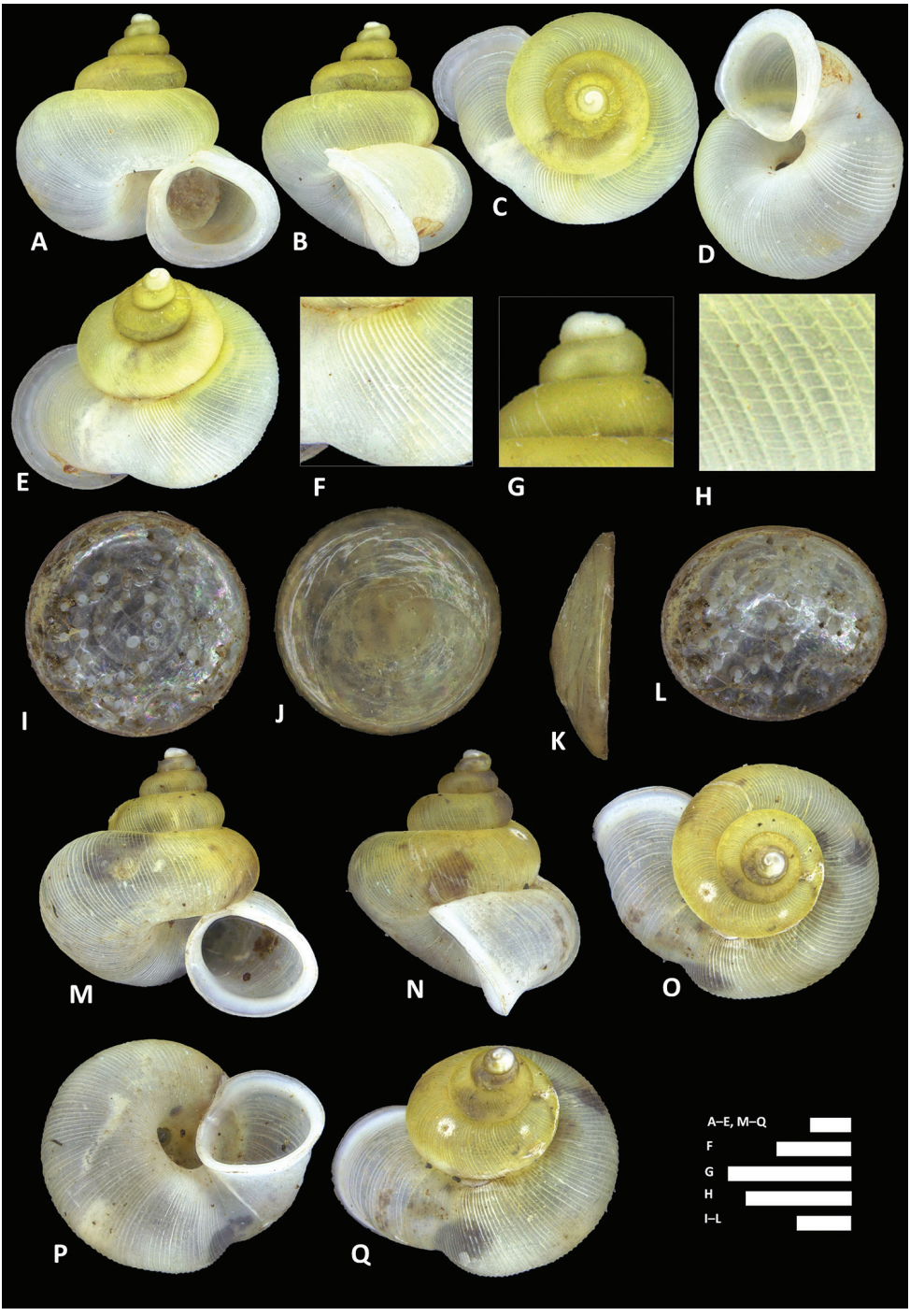

Figure 13. *Alycaeus clementsi* sp. n. **A–E** Shell of holotype, BOR/MOL 12970 **F–H** Close up of shell of holotype, BOR/MOL 12970 **I–L** Operculum of paratype, BOR/MOL 6865 **M–Q** Shell of paratype, BOR/MOL 8377. Scale bars: **A–G, M–Q** 1 mm; **H, I–L** 0.5 mm. All photographs by Junn Kitt Foon.

Operculum. Concave, rounded. Exterior covered with thin calcareous layer, surface finely granulated with a scattered arrangement of calcareous blunt spikes. Interior covered with proteinaceous coating, smooth, mamillated.

Shell colour. Yellow at the first 4 whorls. Fades to white towards aperture.

Living animal. Body cream-white. Head pink. Tentacles cream-white, tips pink.

Habitat and ecology. Lives on wet limestone rock walls and crevices. In shady forests on limestone hills.

Distribution range. In Perlis, retricted to limestone hills of the Nakawan Range. In Kedah, restricted to limestone hills of the Langkawi archipelago, Kodiang and Gunung Keriang.

Differential diagnosis. *Alycaeus clementsi* sp. n. is similar to *A. kelantanensis* in its shell colouration. Despite shell size of *A. clementsi* sp. n. being variable within populations across its range, *A. clementsi* sp. n. is distinguished from *A. kelantanensis* by its consistently large shell (larger by about 2.13 mm in shell height, 2.32 mm in shell width), thick expanded peristome, spiky operculum exterior as well as the animal colouration.

Discussion. Historically, *Alycaeus clementsi* sp. n. shells from Kaki Bukit, Perlis were misidentified as *A. perakensis* in Benthem Jutting (1960a). Shells of *A. clementsi* sp. n. in Perlis usually have thicker peristome compared to shells from Kedah albeit all other diagnostic characters remain identical. Shell size of *A. clementsi* sp. n. is variable within populations across its range and does not appear to have any geographical pattern. This species may occur in Thailand at areas adjacent to Perlis and northern Kedah.

Alycaeus conformis Fulton, 1902

Figures 7E, 14, 31D

Alycaeus conformis Fulton, 1902: 68–69; Sykes 1903: 198; Laidlaw 1928: 34; Laidlaw 1932: 36; Venmans 1956: 81, figure 1; Robertson et al. 1987: 2; Chan 1997: 37; Tarruella and Domènech 2011: 72; Páll-Gergely et al. 2016: 20160151; Foon et al. 2017: 10, figure 4B.

Alycaeus confirmis [sic]: Maassen 2001: 21.

Alycaeus coniformis [sic]: Tarruella and Domènech 2011: 72, figure. 1B.

Type locality. Perak.

Type material. *Syntypes.* Perak: ANSP 84690/2 (Seen), NHMUK 1902.5.28.22-23/2 (Seen).

Other examined materials. KTN 01 Gunung Reng, Kelantan: BOR/MOL 6836/2. KTN 66 Batu Tongkat, Kelantan: ZRC 1975.2.21.88/1. Lojing, Kelantan: BOR/MOL 6526/1. PHG 03 Gunung Jebak Puyuh, Pahang: BOR/MOL 6884/1. PHG 01 Kota Gelanggi, Pahang: BOR/MOL 6887/1, BOR/MOL 8396/2. Mykarst-122 Bukit Merah, Pahang: BOR/MOL 12986/1. PHG 02 Gunung Senyum, Pahang: BOR/MOL 12987/1. PHG 05 Bukit Cintamanis, Pahang: BOR/MOL 6893/1, BOR/MOL 8403/2, BOR/MOL 8404/2. PHG 72 Bukit Panching, Pahang: ANSP 439103/1. Per-

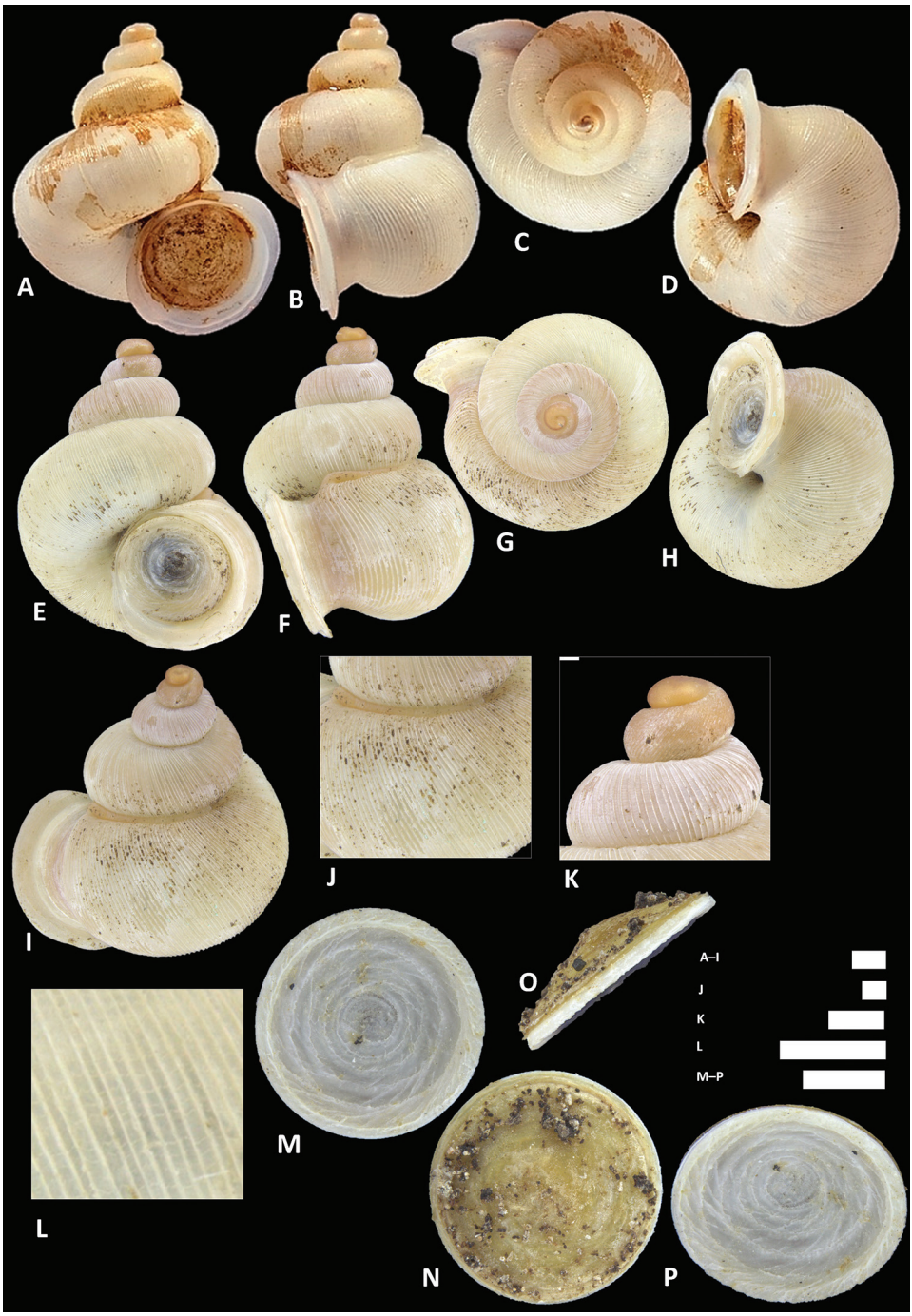

Figure 14. *Alycaeus conformis* Fulton, 1902. **A–D** Shell of syntype, NHMUK 1902.5.28.22-23 **E–I** Shell of BOR/MOL 6526 **J–L** Close up of shell of BOR/MOL 6526 **M–P** Operculum of BOR/MOL 12986. Scale bars: **A–P** 1 mm. Photographs **A–D** by Harold Taylor (copyright of NHM, reproduced with permission). Photographs **E–P** by Junn Kitt Foon.

ak: ZRC 1975.2.21.86/1, RMNH 153478/2. PRK 23 Gunung Rapat, Perak: BOR/MOL 10057/1. SGR 02 Bukit Takun, Selangor: BOR/MOL 6809/1, BOR/MOL 8316/2. SGR 01 Batu Caves, Selangor: ZRC 1975.2.21.87/1, ZRC 1990.10274-10288/14. Endau-Kluang, Johor: BOR/MOL 6458/1, BOR/MOL 6459/1.

Description. Protoconch. Smooth at first whorl, becomes grooved in the second whorl. Grooves arranged parallel to each other and tilted anteriorly at 45° to the coiling axis.

Shell shape. Conical. Shell height: 8.77–10.19 mm. Shell width: 7.16–8.19 mm.

Spire. Spire height: 2.37–3.21 mm. Spire width: 3.24–3.66 mm. Number of whorls: up to 4 ⅜. Spire shape: oblong conical. Whorl periphery rounded. Umbilicus open.

Whorl constriction. At about 4 ¼ whorls posterior of protoconch.

Breathing tube. Length: 4.70–5.76 mm.

Aperture and peristome. Aperture circular, moderately expanded. Aperture height: 4.11–5.14 mm. Aperture width: 4.27–4.93 mm. Peristome double, thickened, slightly notched at suture. Interspace narrow. Peristome orientation 10–16° oblique with respect to the coiling axis.

Spiral lines. Indistinct, regularly spaced. Approximately 11–59 lines per 1 mm.

Radial ribs running anterior of breathing tube. Radial ribs pronounced, evenly spaced. Approximately 10–17 ribs per 1 mm.

Radial ribs running perpendicular to breathing tube. Radial ribs more pronounced and thicker than those anterior of breathing tube, evenly spaced. Approximately 9–13 ribs per 1 mm.

Radial ribs running posterior of breathing tube. Ribs absent. Only radial growth lines.

Operculum. Concave, conical. Exterior covered by thick calcareous layer. Exterior has radially spiral lamellae of 6 revolutions. Interior covered by proteinaceous layer, mamillated.

Shell colour. First 3 whorls usually red or pink. All colours fade to white towards ultimate whorl.

Living animal. Body grey. Head grey. Tentacles dark grey to black.

Habitat and ecology. Lives under large rotten logs and on leaf litter. In wet, shady forests in both limestone and non-limestone areas.

Distribution. Localised in Perak but widespread in Kelantan, Pahang, Selangor and Johor. Elsewhere, in Phuket, southern Thailand (Páll-Gergely et al. 2016).

Differential diagnosis *Alycaeus conformis* is most similar to *Alycaeus gibbosulus* in shell shape but differs in having a less expanded penultimate whorl, finer radial ribs anterior of breathing tube, shorter constriction whorl, shorter breathing tube, less oblique peristome and multilamellated operculum exterior. The animal body is dark grey in *A. conformis* compared to brown in *A. gibbosulus*.

Discussion. Fulton (1902) stated the type locality of *A. conformis* as Perak without further specifying the location. Perak is a large state in western Peninsular Malaysia. During recent intensive sampling across limestone hills in Perak, *Alycaeus conformis* was only discovered at one locality, Gunung Rapat. *Alycaeus conformis* has also been reported from Kelantan (Sykes 1903, Laidlaw 1928), Selangor (Laidlaw 1932, Ven-

mans 1956), Pahang and Johor. Venmans (1956) described the radular morphology of *A. conformis* from Batu Caves, Selangor. Páll-Gergely et al. (2016) described the microstructures associated with the breathing tube of *A. conformis* from Phuket Island, Thailand. The shells of *A. conformis* are often coated in a layer of organic matter when alive (Figure 5E).

***Alycaeus costacrassa* sp. n.**
http://zoobank.org/A08F755C-2292-4CA7-92AD-75D78ED1B4B1
Figures 7M, 15, 31N

Alycaeus perakensis var. *minor* nomen nudum, Clements et al. 2008: 2760.

Type locality. Mykarst-065 Batu Balong, Pahang (3°42'41"N, 101°51'25"E).

Type material. *Holotype.* Mykarst-065 Batu Balong, Pahang: BOR/MOL 12995. *Paratypes.* Mykarst-065 Batu Balong, Pahang: BOR/MOL 8320/2, BOR/MOL 6811/4, BOR/MOL 8319/6.

Other examined materials. KTN 06 Gua Ikan, Kelantan: BOR/MOL 6631/1. KTN 148 unnamed hill, Kelantan: BOR/MOL 12993/1. KTN 95 Gua Panjang, Kelantan: BOR/MOL 12994/12. PHG 15 Gua Bama, Pahang: BOR/MOL 243/1, BOR/MOL 6235/4, BOR/MOL 6818/2, BOR/MOL 8323/2, BOR/MOL 8324/6. Mykarst-169 Gua Gajah, Pahang: BOR/MOL 6250/5, BOR/MOL 12992/1. PHG 03 Gunung Jebak Puyuh, Pahang: BOR/MOL 6628/3, BOR/MOL 6882/1. PHG 05 Bukit Cintamanis, Pahang: BOR/MOL 6634/2, BOR/MOL 6892/2. PHG 01 Kota Gelanggi, Pahang: BOR/MOL 6635/1, ZRC 1975.2.24.356-372/7, ZRC 1975.2.24.373-402/30. PHG 16 Gua Sai, Pahang: BOR/MOL 6637/80, BOR/MOL 6638/30, ZRC 1975.2.21.557-564/10. Ulu Keniyam Kechil, Pahang: ZRC 1975.2.22.660-692/32.

Etymology. In Latin – costa crassa, meaning thick ribbed. Named after the species' diagnostic widely spaced, pronounced radial ribbing of the whorls.

Description. Protoconch. Smooth.

Shell shape. Conical. Shell height: 3.47–6.37 mm. Shell width: 3.42–6.12 mm.

Spire. Spire height: 1.06–2.43 mm. Spire width: 1.53–2.79 mm. Number of whorls: up to 5 ¼. Spire shape: oblong conical. Whorl periphery rounded. Umbilicus open.

Whorl constriction. At about 5 whorls posterior of protoconch.

Breathing tube. Length: 0.30–0.67 mm.

Aperture and peristome. Aperture circular, moderately expanded. Aperture height: 1.79–2.89 mm. Aperture width: 1.62–2.84 mm. Peristome double, not thickened, winged at suture. Peristome orientation 26–39° oblique with respect to the coiling axis.

Spiral lines. Distinct. Regularly spaced. Approximately 19–52 lines per 1 mm.

Radial ribs running anterior of breathing tube. Radial ribs pronounced, evenly spaced. Approximately 9–18 ribs per 1 mm.

Radial ribs running perpendicular to breathing tube. Radial ribs pronounced, evenly spaced. Approximately 11–17 ribs per 1 mm.

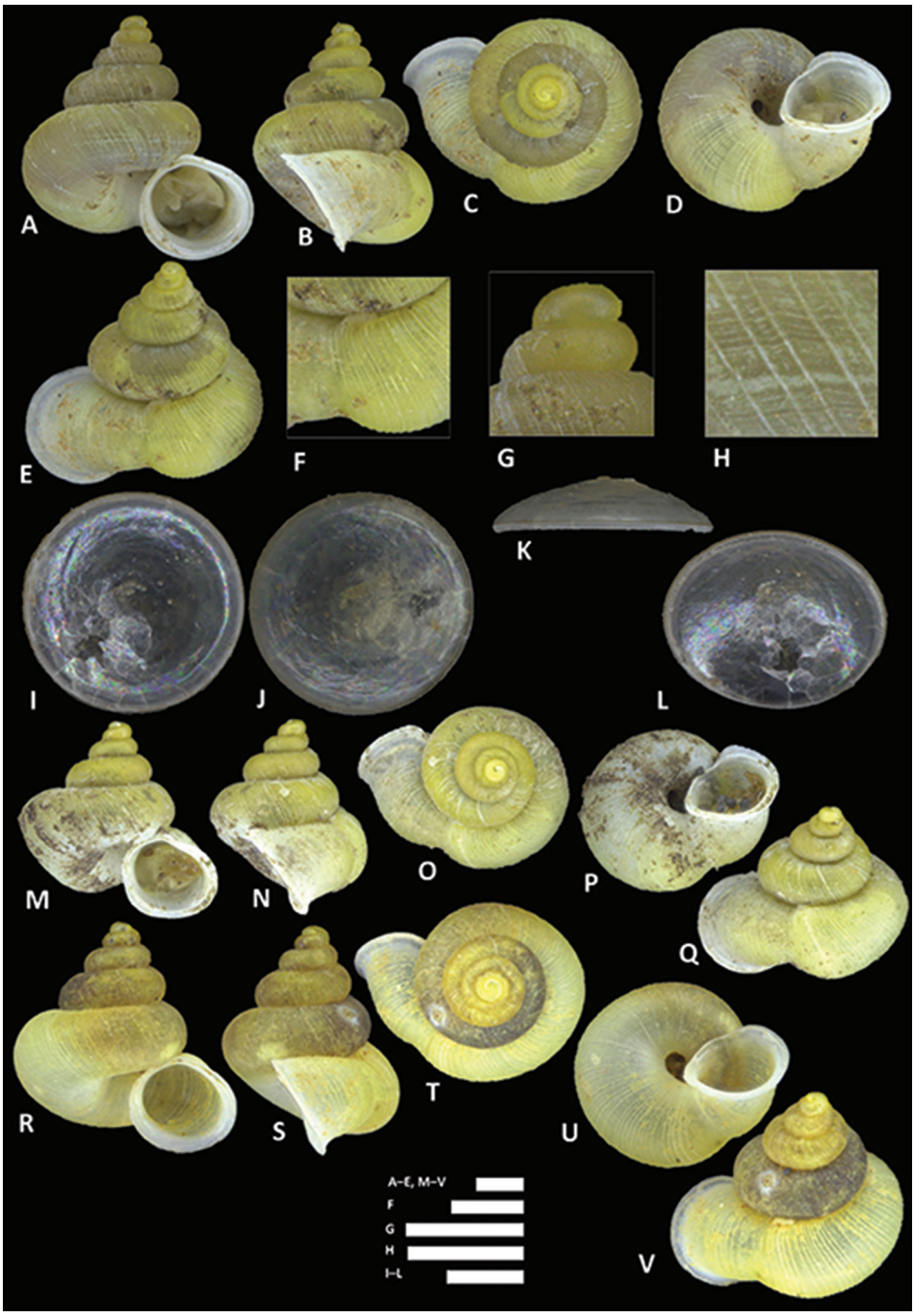

Figure 15. *Alycaeus costacrassa* sp. n. **A–E** Shell of holotype, BOR/MOL 6811 **F–H** Close up of shell of holotype, BOR/MOL 6811 **I–L** Operculum of holotype, BOR/MOL 6811 **M–Q** Shell of BOR/MOL 6818 **R–V** Shell of BOR/MOL 12992. Scale bars: **A–G** 1 mm; **H, I–L** 0.5 mm. All photographs by Junn Kitt Foon.

Radial ribs running posterior of breathing tube. Radial ribs pronounced and ueneven immediately posterior of constriction, becoming pronounced and evenly spaced towards the aperture. Approximately 10–21 ribs per 1 mm.

Operculum. Concave, rounded. Exterior covered with thick but flaky calcareous layer, surface finely granulated. Interior proteinaceous layered, smooth, with indistinct mamilla.

Shell colour. Whorls yellow, fading to white posterior of constriction. Peristome white.

Living animal. Body cream-white. Head pinkish brown. Tentacles reddish-brown.

Habitat and ecology. Lives on wet limestone walls covered with mosses. Occassionally found in crevices, on lower parts of tree trunks. In shady forests on limestone hills.

Distribution range. Widespread from southern Kelantan to central Pahang.

Differential diagnosis. *Alycaeus costacrassa* sp. n. most resembles *A. selangoriensis* sp. n. in its thick operculum, pronounced radial ribbing and spiral lines but has a narrower ultimate whorl and a more circular peristome without posterior folding at the upper palatal section. *Alycaeus costacrassa* sp. n. also resembles *A. kapayanensis* in shell shape but differs in its consistently more pronounced radial ribs as well as operculum with thicker calcareous exterior.

Discussion. Shells of *A. costacrassa* sp. n. are consistent in their diagnostic characters but vary considerably in shell size and whorl convexity across its range. Populations in Gua Sai and Gua Bama have the smallest shells (Shell height: 3.47–4.46 mm, Shell width: 3.42–4.27 mm, Figure 15M–Q) with less rounded whorls. Gua Gajah shells are intermediate in size (Shell height: 4.85 mm, Shell width: 4.67 mm, Figure 15R–V) with rounded whorls. Batu Balong and Gua Panjang have larger shells (Shell height: 4.99–5.94 mm, Shell width: 4.66–5.58 mm, Figure 15A–E) with rounded whorls. It is possible that *A. costacrassa* sp. n. may contain several cryptic species pending availability of molecular data for investigation.

***Alycaeus expansus* sp. n.**

http://zoobank.org/E2003BE4-BAD9-42B9-A89D-40ABB6EACED1

Figures 7N, 16, 31I

Type locality. PHG 74 Bukit Sagu, Pahang (3°58'54"N, 103°08'39"E).

Type material. *Holotype.* PHG 74 Bukit Sagu, Pahang: BOR/MOL 12983. *Paratypes.* PHG 74 Bukit Sagu, Pahang: BOR/MOL 269/2, BOR/MOL 6358/4. PHG 75 Bukit Tenggek, Pahang: BOR/MOL 273/2.

Other examined materials. PHG 72 Bukit Panching, Pahang: BOR/MOL 247/1, ZRC 1975.2.24.352-355/3, ANSP 439118/8. PHG 73 Bukit Charas, Pahang: BOR/MOL 245/1, BOR/MOL 6367/1, BOR/MOL 6890/1, BOR/MOL 8400/9, BOR/MOL 12984/1, ZRC 1975.2.21.956-1015/63, ZRC 1975.2.21.876-955/81, ZRC 1975.2.21.435-488/53, ZRC 1975.2.21.732-831/101. PHG 74 Bukit Sagu, Pahang: ZRC 1975.2.21.532-556/26. PHG 75 Bukit Tenggek, Pahang: ZRC 1975.2.24.723-725/2, ZRC 1975.2.21.489-531/44.

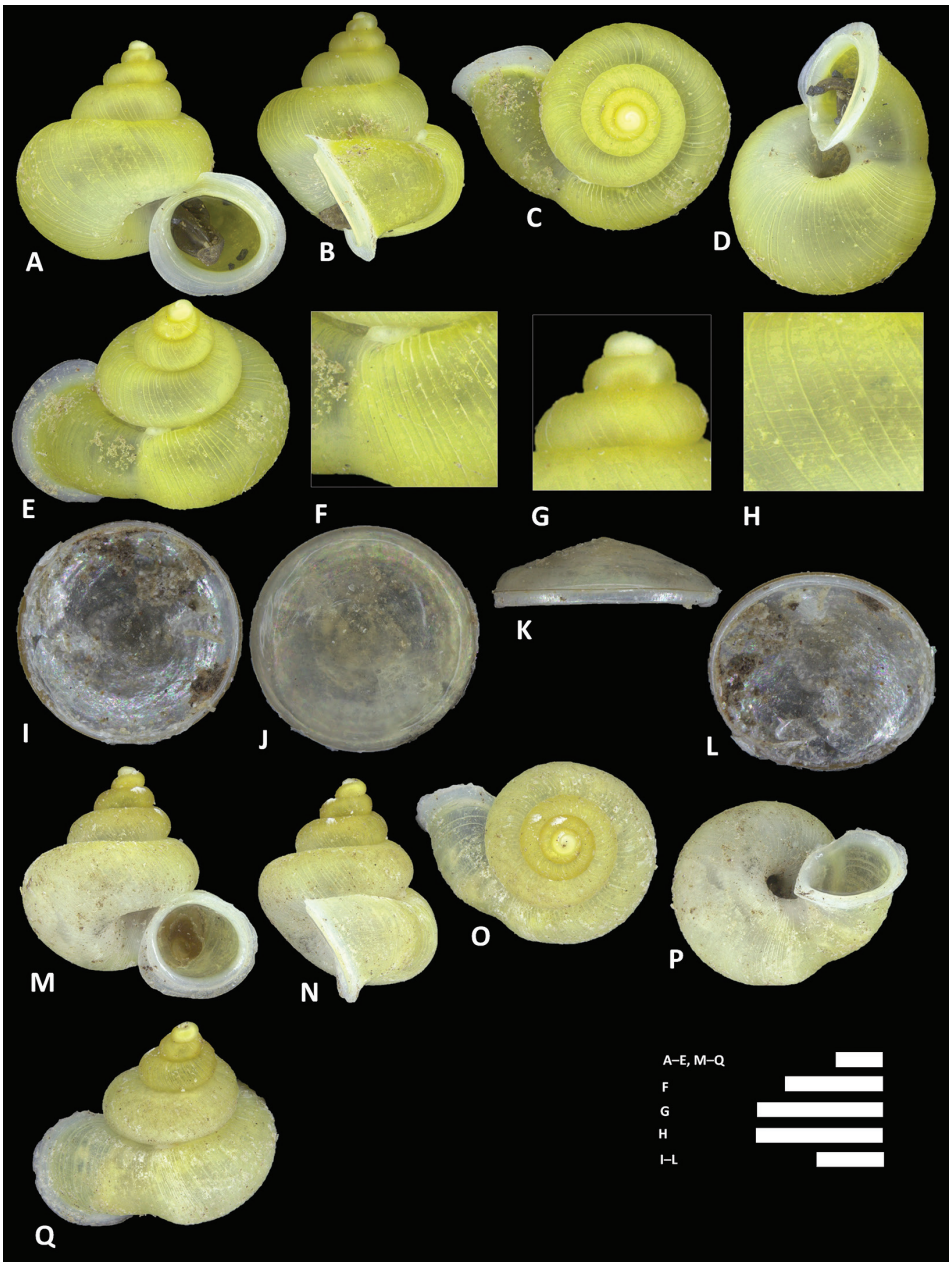

Figure 16. *Alycaeus expansus* sp. n. **A–E** Shell of holotype, BOR/MOL 12983 **F–H** Close up of shell of holotype, BOR/MOL 12983 **I–L** Operculum of holotype, BOR/MOL 12983 **M–Q** Shell of BOR/MOL 245. Scale bars: **A–H** 1 mm; **I–L** 0.5 mm. All photographs by Junn Kitt Foon**.**

Etymology. Latin, meaning expanded. In reference to the very expanded peristome and globose whorls.

Description. Protoconch. Smooth.

Shell shape. Conical. Shell height: 4.11–5.88 mm. Shell width: 3.87–5.96 mm.

Spire. Spire height: 1.33–1.85 mm. Spire width: 1.88–2.57 mm. Number of whorls: up to 4 ½. Spire shape: oblong conical. Whorl periphery rounded. Umbilicus open.

Whorl constriction. At about 4 ¼ whorls posterior of protoconch.

Breathing tube. Length: 0.44–0.62 mm.

Aperture and peristome. Aperture very expanded, ocassionally forming wing-like extensions at columellar and upper palatal sections. Wing-like extension at columellar section of the aperture is angular. Aperture height: 1.81–3.44 mm. Aperture width: 1.78–3.13 mm. Peristome double, not thickened, notched at suture. Peristome orientation 27–32° oblique with respect to the coiling axis.

Spiral lines. Indistinct. Regularly spaced. Approximately 18–40 lines per 1 mm.

Radial ribs running anterior of breathing tube. Radial ribs indistinct, evenly spaced. Approximately 6–15 ribs per 1 mm.

Radial ribs running perpendicular to breathing tube. Radial ribs pronounced and thicker than those anterior of breathing tube, evenly spaced. Approximately 11–17 ribs per 1 mm.

Radial ribs running posterior of breathing tube. Radial ribs indistinct, unevenly spaced to absent.

Operculum. Concave, conical. Exterior covered with thick calcareous layer, surface finely granulated. Interior covered with proteinaceous coating, smooth, mamillated.

Shell colour. Whorls yellow. Peristome white.

Living animal. Body cream-white. Head pink. Tentacles cream-white, tips pink.

Habitat and ecology. Lives on wet rock surfaces and crevices covered with mosses at higher areas and wang of limestone hills. In shaded forests.

Distribution range. Restricted to the Kuantan Hills of eastern Pahang (comprises of Bukit Tenggek, Bukit Sagu, Bukit Charas and Bukit Panching).

Differential diagnosis. *Alycaeus expansus* sp. n. is distinguished from all other Peninsular Malaysian *Alycaeus* by its very obtuse ultimate whorl, very expanded peristome with wing-like extensions at columellar and upper palatal sections, thick operculum and animal colouration.

Discussion. Prior to this study, shells of *A. expansus* sp. n. from Bukit Charas and Bukit Panching were labelled as *A. kelantanensis* (BOR/MOL and ZRC collection lots). Shells of *A. expansus* sp. n. is consistent in its diagnostic obtuse ultimate whorl and very expanded peristome across its range but varies in shell size and spire height for each hill population. Shells from Bukit Sagu and Bukit Tenggek (the northern two of the Kuantan Hills) tend to be larger with ultimate whorl always obtused and spire low. Shells from Bukit Charas and Bukit Panching (the southern two of the Kuantan Hills) tend to be slightly smaller and more variable in ultimate whorl shape (obtuse to normal) and spire height (tall to low). It is possible that *A. expansus* sp. n. may contain two cryptic species pending availability of molecular data for investigation. Unfortunately, populations on Bukit Panching, Bukit Tenggek and Bukit Sagu are now likely lost to limestone quarrying (see Discussion in *A. carinata*).

***Alycaeus gibbosulus* Stoliczka, 1872**
Figures 7F–G, 17, 31E

Alycaeus gibbosulus Stoliczka, 1872: 268–269, plate 10, figure 14; Pfeiffer 1876: 58; Nevill 1878: 295; Crosse 1879b: 339; Morgan 1885b: 402; Möllendorff 1886: 310; Tenison-Woods 1888: 1068; Kobelt 1902: 344; Sykes 1902: 62; Benthem Jutting 1960a: 13, 19; Davison 1995: 236; Maassen 2001: 21; Clements et al. 2008: 2760; Tarruella and Domènech 2011: 72, figure 1F; Foon et al. 2017: 12, figure 4C.
Alycaeus chaperi Morgan, 1885a: 70.
Alycaeus (*Orthalycaeus*) *gibbosulus*: Möllendorff 1891: 342; Kobelt and Möllendorff 1897: 150; Möllendorff 1902: 144.
Alycaeus gibbosulos [sic]: Berry 1963: plate 4.
Dioryx pyramidalis: Habe 1965: 111–112, plate 2, figures 3–4; Maassen 2001: 21. [not *Alycaeus pyramidalis* Benson, 1856]
Alycaeus (*Alycaeus*) *gibbosulus*: Laidlaw 1928: 34; Chan 1998b: 1.

Type locality. Penang Island.

Type material. *Syntypes.* Penang Island: 12 shells deposited at the Indian Museum, Kolkata (Nevill 1878) (Not seen).

Other examined materials. Botanic Garden, Penang Island: BOR/MOL 8525/1, BOR/MOL 8526/12. KDH 01 Bukit Baling, Kedah: BOR/MOL 6855/1, BOR/MOL 8358/1, BOR/MOL 8359/23, BOR/MOL 12996/1, ZRC 1975.2.21.182-207/25, ZRC 1975.2.21.144-150/6, ZRC 1997.17/4, ANSP 423057/2. KDH 02 Gunung Pulai, Kedah: BOR/MOL 6857/1, BOR/MOL 8362/16. KDH 10 Bukit Keplu, Kedah: BOR/MOL 6871/1, BOR/MOL 8375/51, BOR/MOL 8376/1, BOR/MOL 6190/1. PRK 62 Gua Dayak, Perak: BOR/MOL 279/1. Mykarst-171 Tasik Temenggor Hill S2, Perak: BOR/MOL 6244/1. PRK 55 Gunung Pondok, Perak: BOR/MOL 6850/1, BOR/MOL 8351/3, BOR/MOL 8352/7, BOR/MOL 11523/1, BOR/MOL 11538/2, ZRC 1972.2.21.140-142/3. Limestone outcrop 50m from roadside, Kampung Pahit, Klian Intan, Perak: BOR/MOL 6875/1, BOR/MOL 8381/3, BOR/MOL 8382/1. Mykarst-027 Gunung Kanthan North, Perak: BOR/MOL 9106/2. Mykarst-025, Perak: BOR/MOL 9382/10, BOR/MOL 9416/2, BOR/MOL 9436/17, BOR/MOL 9500/11. PRK 23 Gunung Rapat, Perak: BOR/MOL 10286/1. PRK 59 Bukit Batu Kurau, Perak: ZRC 1975.2.21.180-181/4. Sungai Siput, Perak: ZRC 1975.2.21.143/1. Capis, upper Perak: ZRC 1975.2.21.1020-1022/3. Gua Kelam, PRS 64 Wang Ulu, Perlis: BOR/MOL 278/1, BOR/MOL 6866/1, BOR/MOL 6868/1, BOR/MOL 8372/4, ZRC 1975.2.21.152-179/27. PRS 19 Bukit Chuping, Perlis: BOR/MOL 6860/3, ZRC 1975.2.21.151/1. Bukit Ayer, PRS 64 Wang Ulu, Perlis: BOR/MOL 6862/1, BOR/MOL 8366/5, BOR/MOL 8367/3, BOR/MOL 12960/1. PRS 17 Gunung Chabang, Perlis: BOR/MOL 6870/1. PRS 40 Bukit Merbok, Perlis: BOR/MOL 8139/1. TRG 01 Bukit Bewah, Terengganu: BOR/MOL 6662/10, BOR/MOL 13002/1. Malakka (= Peninsular Malaysia): RMNH 153521/2.

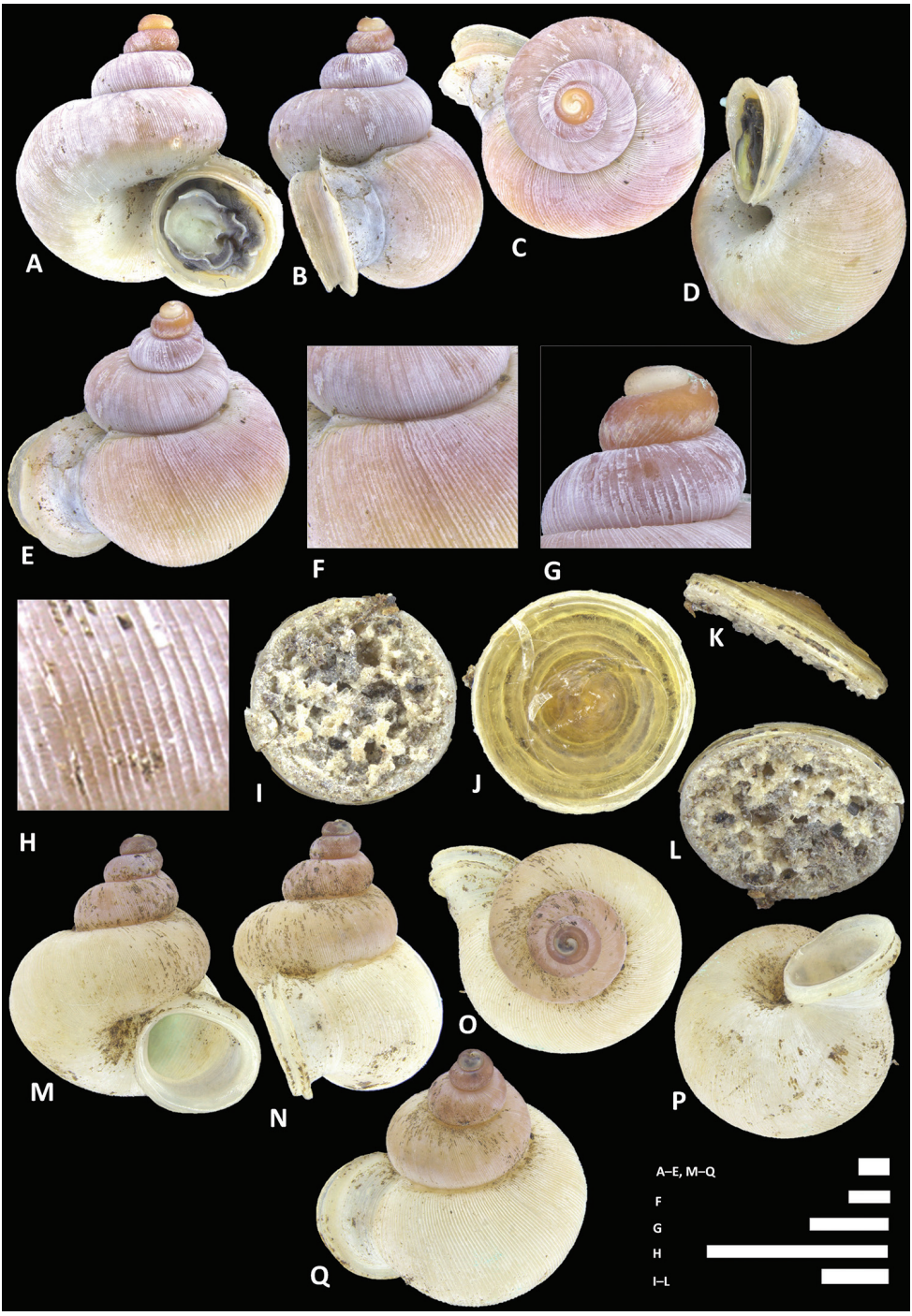

Figure 17. *Alycaeus gibbosulus* Stoliczka, 1872. **A–E** Shell of BOR/MOL 8525 **F–H** Close up of shell of BOR/MOL 8525 **I–L** Operculum of BOR/MOL 8525 **M–Q** Shell of BOR/MOL 12960. Scale bars: **A–Q** 1 mm. All photographs by Junn Kitt Foon.

Description. Protoconch. Smooth at first whorl, becomes grooved in the second whorl. Grooves arranged parallel to each other and tilted anteriorly at 45° to the coiling axis.

Shell shape. Conical. Shell height: 9.20–10.15 mm. Shell width: 8.46–9.75 mm.

Spire. Spire height: 2.32–3.07 mm. Spire width: 3.32–3.67 mm. Number of whorls: up to 4 ⅛. Spire shape: oblong conical. Whorl periphery rounded. Umbilicus open.

Whorl constriction. At about 4 whorls posterior of protoconch.

Breathing tube. Length: 5.28–6.52 mm.

Aperture and peristome. Aperture circular, moderately expanded. Aperture height: 4.11–5.14 mm. Aperture width: 4.27–4.93 mm. Peristome double, thickened, slightly notched at suture. Interspace narrow to wide. Peristome orientation 18–24° oblique with respect to the coiling axis.

Spiral lines. Indistinct, regularly spaced. Approximately 20–44 lines per 1 mm.

Radial ribs running anterior of breathing tube. Radial ribs pronounced, evenly spaced. Approximately 14–21 ribs per 1 mm.

Radial ribs running perpendicular to breathing tube. Radial ribs more pronounced and thicker than those anterior of breathing tube, evenly spaced. Approximately 8–14 ribs per 1 mm.

Radial ribs running posterior of breathing tube. Ribs absent. Only radial growth lines.

Operculum. Concave, conical. Exterior covered by thick calcareous layer. Exterior has scaffold-like calcareous deposits overlaid on radially spiral lamellae. Interior covered by proteinaceous layer, mamillated.

Shell colour. First 3 whorls usually red, purple or pink. All colours fade to white towards ultimate whorl.

Living animal. Body brown. Head brown. Tentacles light to dark grey.

Habitat and ecology. Lives under large rotten logs or on leaf litter. In wet, shady forests in both limestone and non-limestone areas.

Distribution. Widespread from Perlis to Perak on the west coast and in parts of Kelantan and Terengganu on the east coast but not found in Selangor, Pahang and the southern states of Peninsular Malaysia. Elsewhere, in Trang, southern Thailand (as *Dioryx pyramidalis* (Benson, 1856), in Habe (1965)).

Differential diagnosis. *Alycaeus gibbosulus* is most similar to *A. conformis* in shell shape but differs in having a more expanded penultimate whorl, coarser sculpture, more oblique peristome, longer constriction whorl, longer breathing tube (longer by 0.66 mm), ultimate whorl that is very obtused prior to constriction and scaffold-like calcareous deposits at the operculum exterior. The animal body is brown in *A. gibbosulus* compared to grey in *A. conformis*.

Discussion. The syntypes of *A. gibbosulus* is housed in the Indian Museum, Kolkata, India (Nevill 1878) but was not examined in this study. Nevertheless, topotypic specimens from Penang Island (BOR/MOL 8525, BOR/MOL 8526) match the illustration of the type by Stoliczka (1872). This is considered to be sufficient for positive species identification.

This species is closely related to *A. conformis* and has historically been confused with it. Studies that reported *A. gibbosulus* in various localities are as follows: Penang (Stoliczka 1872, Crosse 1879b, Tenison-Woods 1888, Kobelt 1902, Laidlaw 1928, Möllendorff 1891), Perlis (Benthem Jutting 1960a), Perak (Crosse 1879b, Möllendorff 1886, Möllendorff 1891, Davison 1995, Chan 1998b) and Kelantan (Sykes 1902, Möllendorff 1902). Möllendorff (1886) reported that Perak shells differ from Penang shells in being paler as well as possessing a wider ultimate whorl. These shell forms are well within the morphological variation of *A. gibbosulus*. An erroneous record of *Dioryx pyramidalis* Benson, 1856 in Peninsular Malaysia has been traced back to a mistake by Habe (1965) in which specimens of *A. gibbosulus* from northern Malay Peninsula were misidentified as *Alycaeus pyramidalis* Benson, 1856. The species *Alycaeus chaperi* Morgan, 1885b, is also a synonym of *Alycaeus gibbosulus* (Möllendorff 1886, Möllendorff 1891).

Alycaeus gibbosulus has been reported to exist sympatrically with *A. conformis* in Gunung Rapat, Perak (Foon et al. 2017). Elsewhere range overlaps between *A. gibbosulus* and *A. conformis* remain unresolved. In Kelantan, Sykes (1902) mentioned a collection of shells with typical *A. gibbosulus* characters and some which were "much less gibbous". These less gibbous shells are likely *A. conformis*, which is common in Kelantan. Hence, it is possible that both *A. gibbosulus* and *A. conformis* exist sympatrically in Kelantan. In Pahang where only *A. conformis* records are confirmed, an aberrant record of *A. gibbosulus* from Kuala Tahan (Benthem Jutting 1960a) warrants investigation. The shells of *A. gibbosulus* are sometimes coated in a layer of organic matter when alive (Figure 7F).

***Alycaeus ikanensis* sp. n.**
http://zoobank.org/DBC1A3CE-F85A-4F42-8188-63607F148C5C
Figures 18, 31L

Alycaeus perakensis var. *minor* nomen nudum, Clements et al. 2008: 2760.

Type locality. KTN 06 Gua Ikan, Kelantan (5°21'14"N, 102°01'33"E).

Type material. *Holotype.* KTN 06 Gua Ikan, Kelantan: BOR/MOL 12972. *Paratypes.* KTN 06 Gua Ikan, Kelantan: BOR/MOL 6834/23.

Other examined materials. KTN 06 Gua Ikan, Kelantan: BOR/MOL 6193/2, BOR/MOL 6632/17.

Etymology. Named after the type locality, Gua Ikan.

Description. Protoconch. Smooth.

Shell shape. Conical. Shell height: 4.02–4.58 mm. Shell width: 3.58–4.16 mm.

Spire. Spire height: 1.42–1.78 mm. Spire width: 1.83–2.03 mm. Number of whorls: up to 4 ½. Spire shape: oblong conical. Whorl periphery rounded. Umbilicus open.

Whorl constriction. At about 4 ¼ whorls posterior of protoconch.

Breathing tube. Length: 0.35–0.42 mm.

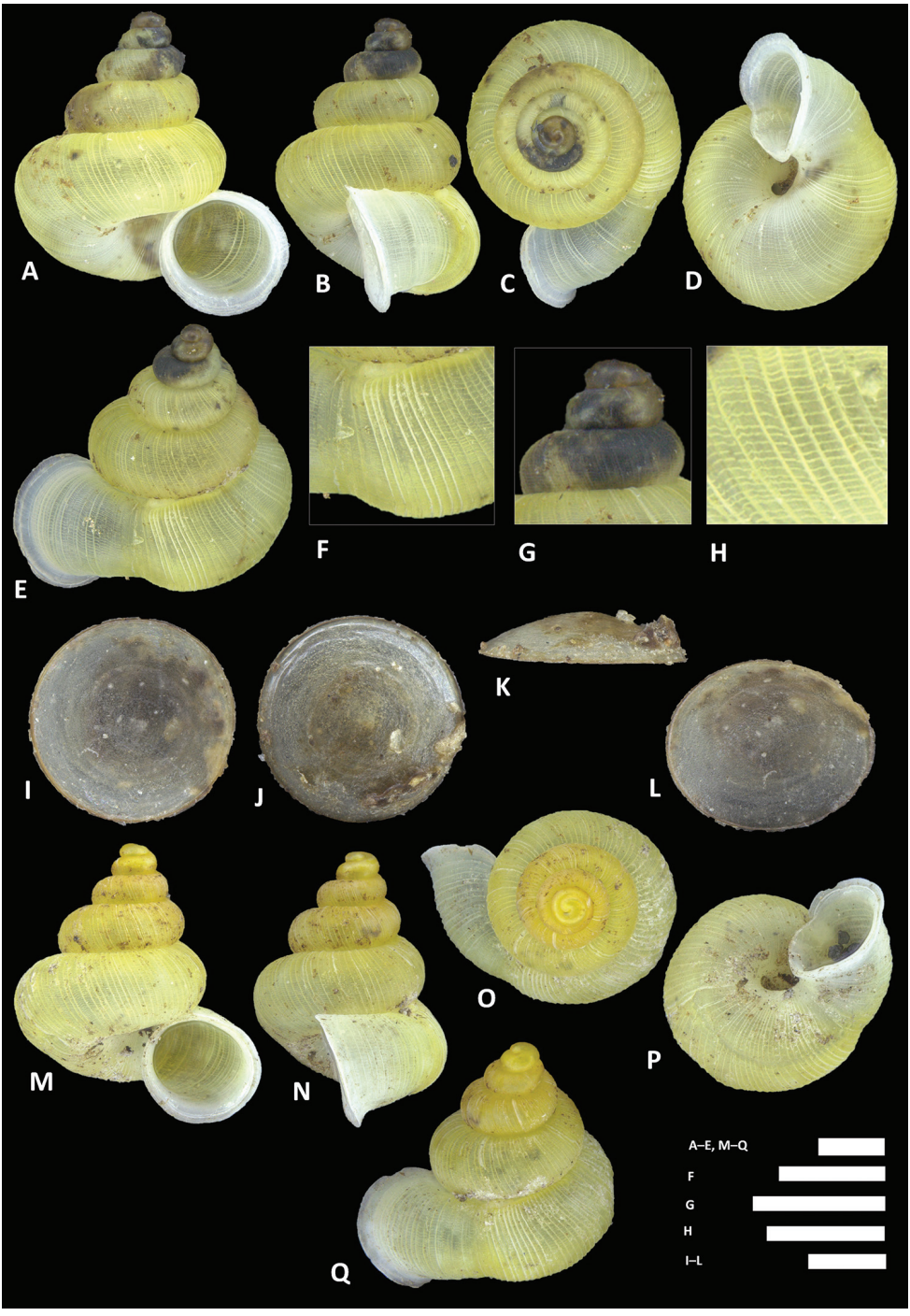

Figure 18. *Alycaeus ikanensis* sp. n. **A–E** Shell of holotype, BOR/MOL 12972 **F–H** Close up of shell of holotype, BOR/MOL 12972 **I–L** Operculum of holotype, BOR/MOL 12972 **M–Q** Shell of paratype, BOR/MOL 6834. Scale bars: **A–H, M–Q** 1 mm; **I–L** 0.5 mm. All photographs by Junn Kitt Foon.

Aperture and peristome. Aperture circular, moderately expanded. Aperture height: 1.59–1.87 mm. Aperture width: 1.60–1.96 mm. Peristome double, not thickened, notched at suture. Peristome orientation 16–27° oblique with respect to the coiling axis.

Spiral lines. Distinct. Regularly spaced. Approximately 22–30 lines per 1 mm.

Radial ribs running anterior of breathing tube. Radial ribs pronounced, evenly spaced. Approximately 9–19 ribs per 1 mm.

Radial ribs running perpendicular to breathing tube. Radial ribs pronounced, white and thicker than those anterior of breathing tube, evenly spaced. Approximately 13–18 ribs per 1 mm.

Radial ribs running posterior of breathing tube. Radial ribs absent immediately posterior of constriction, becoming pronounced and unevenly spaced towards the aperture.

Operculum. Concave, rounded. Exterior covered with very thin and indistinct calcareous layer, surface finely granulated, with very indistinct appressed multilamellae. Interior proteinaceous layered, smooth, very indistinct appressed multilamellae.

Shell colour. Whorls yellow, fading to white posterior of constriction. Peristome white.

Living animal. Unknown.

Habitat and ecology. Lives on limestone walls and boulders covered with mosses. In shady forests on limestone hills.

Distribution range. Restricted to Gua Ikan, central Kelantan.

Differential diagnosis. *Alycaeus ikanensis* sp. n. is distinctive in being the smallest species among conical, yellow shelled *Alycaeus* species in Peninsular Malaysia. *Alycaeus ikanensis* sp. n. is distinguished from *A. costacrassa* sp. n. by its consistently much smaller shell (smaller by about 0.62 mm in shell height, 0.90 mm in shell width) and narrower ultimate whorl**.**

Discussion. Limestone hills adjacent to the type locality Gua Ikan may also harbour populations of the species.

Alycaeus jousseaumei **Morgan, 1885a**

Figures 7H–I, 19, 31F

Alycaeus jousseaumei Morgan, 1885a: 70; Morgan 1885b: 402, plate 8, figure 4; Möllendorff 1886: 312; Möllendorff 1891: 343; Tarruella and Domènech 2011: 72, figure 2B; Foon et al. 2017: 12, figure 4D.

Alycaeus (*Chamalycaeus*) *jousseaumi* [sic]: Kobelt and Möllendorff 1897: 151.

Alycaeus (*Chamalycaeus*) *jousseaumei*: Kobelt 1902: 357; Laidlaw 1928: 36; Chan 1998a: 4; Chan 1998b: 1.

Chamalycaeus jousseaumei: Benthem Jutting 1960a: 13; Berry 1963: plate 4; Maassen 2001: 24; Clements et al. 2008: 2760.

Type locality. Mont Lano (= PRK 18 Gunung Lanno), Perak (4°31'31"N, 101°08'48"E).

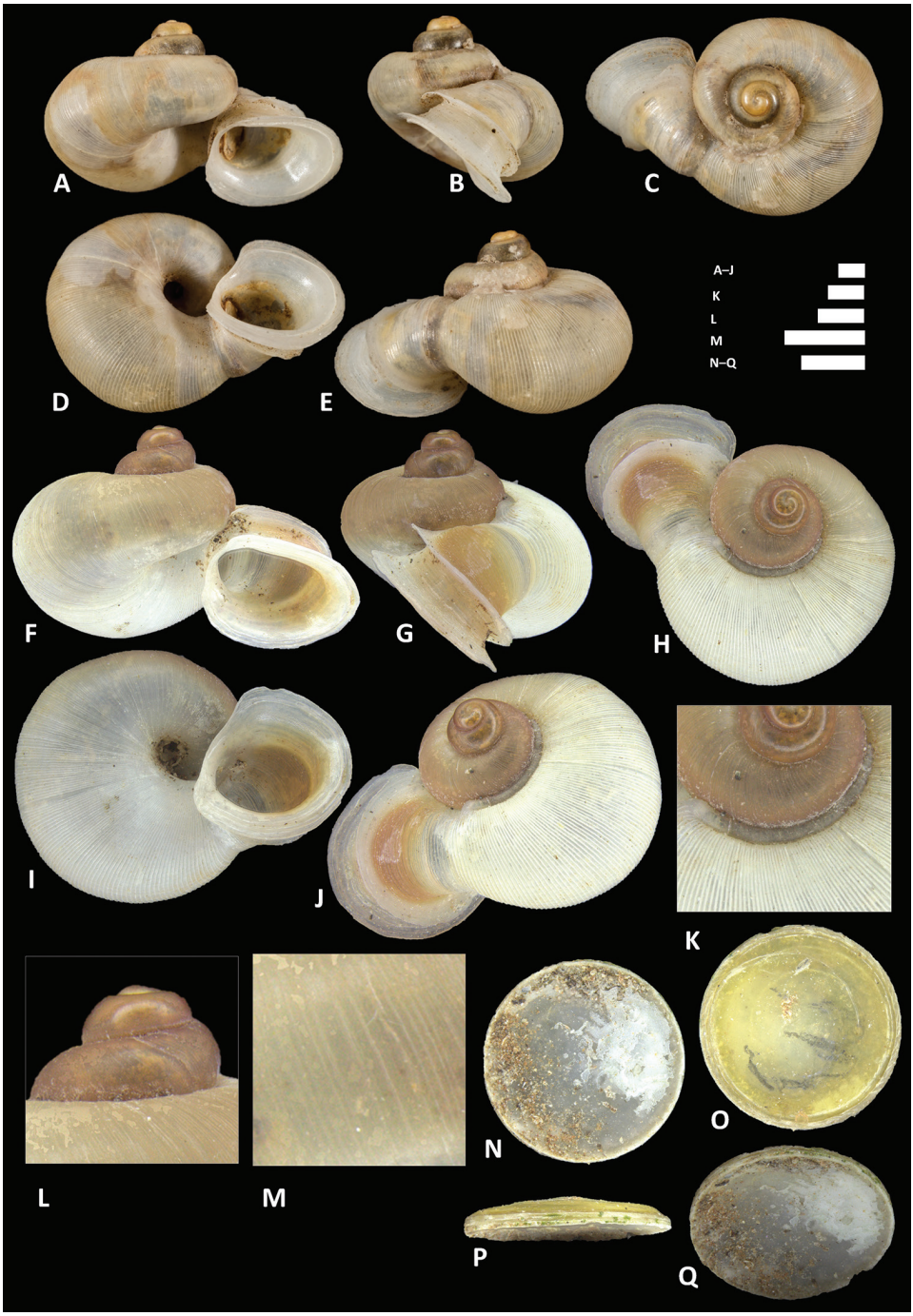

Figure 19. *Alycaeus jousseaumei* Morgan, 1885a. **A–E** Shell of syntype, MNHN-IM-2000-31801 **F–J** Shell of BOR/MOL 11211 **K–M** Close up of shell of BOR/MOL 11211 **N–Q** Operculum of BOR/MOL 11211. Scale bars: **A–Q** 1 mm. Photographs **A–E** by Manuel Caballer (reproduced herein under CC-BY 4.0 license, Project RECOLNAT, MNHN). Photographs **F–V** by Junn Kitt Foon.

Type material. *Syntypes*. Mont Lano (= PRK 18 Gunung Lanno), Perak: MNHN IM-2000-31800/1 (Not seen), MNHN IM-2000-31801/1 (Seen).

Other examined materials. PRK 01 Gunung Tempurung, Perak: BOR/MOL 6847/1, BOR/MOL 8346/3, BOR/MOL 11136/11, BOR/MOL 11211/37, BOR/MOL 11408/10. PRK 15 Gunung Keroh, Perak: ZRC 1975.2.21.247-248/2. PRK 18 Gunung Lanno, Perak: BOR/MOL 6841/1, BOR/MOL 6916/3, BOR/MOL 8337/2, BOR/MOL 8338/2. PRK 23 Gunung Rapat, Perak: BOR/MOL 293/5, BOR/MOL 6255/1, BOR/MOL 6844/1, BOR/MOL 6846/1, BOR/MOL 6848/1, BOR/MOL 7133/6, BOR/MOL 8341/14, BOR/MOL 8342/2, BOR/MOL 8345/22, BOR/MOL 8347/25, BOR/MOL 8348/4, BOR/MOL 10046/8, BOR/MOL 10202/3, BOR/MOL 10228/9, BOR/MOL 10253/10, BOR/MOL 12963/1, BOR/MOL 12998/2, ZRC 1997.18/2. PRK 27 Gunung Datok, Perak: BOR/MOL 10412/9, BOR/MOL 10441/8, BOR/MOL 10474/30, BOR/MOL 10494/8. PRK 34 Gunung Tasek, Perak: BOR/MOL 6839/1, BOR/MOL 8336/6, BOR/MOL 10788/7, BOR/MOL 11054/1. PRK 42 Gunung Bercham, Perak: BOR/MOL 10593/4. PRK 47 Gunung Kanthan South, Perak: BOR/MOL 9101/2, ZRC 1975.2.21.2/2. PRK 53 Hill KF, Perak: BOR/MOL 10658/12, BOR/MOL 10689/13, BOR/MOL 10717/5. Mykarst-189, Perak: BOR/MOL 6842/1, BOR/MOL 8339/8. Mykarst-068, Perak: BOR/MOL 6843/1, BOR/MOL 8340/1, RMNH 153708/3. Mykarst-025, Perak: BOR/MOL 9383/1. Mykarst-027 Gunung Kanthan North, Perak: BOR/MOL 9053/3, BOR/MOL 9374/1. Mykarst-070 Kramat Pulai, Perak: ZRC 1975.2.21.238-245/8. Perak: RMNH 153477/1.

Description. Protoconch. Smooth.

Shell shape. Flat. Shell height: 7.50–8.76 mm. Shell width: 12.42–15.03 mm.

Spire. Spire height: 1.77–2.27 mm. Spire width: 2.94–3.45 mm. Number of whorls: up to 3. Spire shape: oblong conical. Whorl periphery rounded. Umbilicus open.

Whorl constriction. At about 2 ¾ whorls posterior of protoconch.

Breathing tube. Length: 5.44–5.97 mm.

Aperture and peristome. Aperture circular, very expanded. Aperture height: 4.88–7.30 mm. Aperture width: 4.92–6.59 mm. Peristome triple. The first (most anterior) peristome is moderately expanded but not thickened. The second (outer) peristome is very expanded but not thickened. The second peristome is impressed on the thickened third (inner), non-expanded peristome. Interspace between first and second peristome wide. Interspace between second and third peristome narrow. Peristome orientation is 44–55° oblique with respect to the coiling axis.

Spiral lines. Absent.

Radial ribs running anterior of breathing tube. Radial ribs indistinct, evenly spaced. Approximately 10–18 ribs in 1 mm.

Radial ribs running perpendicular to breathing tube. Radial ribs pronounced and thick, evenly spaced. Approximately 8–15 ribs in 1 mm.

Radial ribs running posterior of breathing tube. Radial ribs pronounced, evenly spaced. Approximately 10–25 ribs per 1 mm.

Operculum. Flat, conical. Exterior calcareous, smooth but occasionally with calcareous deposits. Interior covered by proteinaceous layer, smooth.

Shell colour. First 3 whorls usually red, orange, purple or white. Ultimate whorl white. Whorl constriction generally white, occasionally red.

Living animal. Body light grey to light brown. Head pinkish-brown to dark grey. Tentacles brown.

Habitat and ecology. Lives on limestone rock surfaces and crevices. In wet, shady forests on limestone hills.

Distribution range. Restricted to the karsts of Kinta Valley, Perak. Its known northern limit is at Gunung Tchehel and southern limit at Gunung Tempurung.

Differential diagnosis. *Alycaeus jousseaumei* is distinguished from all other *Alycaeus* species in Peninsular Malaysia by its very low spire, very expanded, obtuse ultimate whorl and very expanded, double peristome with wide interspace.

Discussion. *Alycaeus jousseaumei* is morphologically unique and unmistakable among Peninsular Malaysian *Alycaeus*. *Alycaeus jousseaumei* has been subjected to attempts of supraspecific reclassification. Morgan (1885a) initially placed *A. jousseaumei* in the genus *Alycaeus* but Kobelt and Möllendorff (1897) reassigned *A. jousseaumei* in *Chamalycaeus* without any justification. The genus *Chamalycaeus* in Peninsular Malaysia is characterised by its small to minute shell (shell width <6.0 mm), discoid shell shape, strong radial ribs and a breathing tube of variable length (Kobelt 1902, Maassen 2001, Egorov 2013, Foon et al. 2017). *Alycaeus jousseaumei* is clearly not a *Chamalycaeus* species. Thus, *Alycaeus jousseaumei* is herein reassigned back to *Alycaeus*. *Alycaeus jousseaumei* is remarkably similar to *A. kapayanensis* in being range-restricted to the karsts of Kinta Valley (Morgan 1885a, 1885b, Möllendorff 1886, Möllendorff 1891, Benthem Jutting 1960a, Chan 1998a, 1998b).

Alycaeus kapayanensis Morgan, 1885b

Figures 7O, 20, 31M

Alycaeus kapayanensis Morgan, 1885b: 403, plate 8, figure 5; Benthem Jutting 1960a: 13; Maassen 2001: 22; Tarruella and Domènech 2011: 72.
Alycaeus (*Orthalycaeus*) *kapayensis* [sic]: Möllendorff 1891: 342.
Alycaeus (*Orthalycaeus*) *kapayanensis*: Kobelt and Möllendorff 1897: 150.
Alycaeus (*Alycaeus*) *kapayanensis*: Kobelt 1902: 346; Laidlaw 1928: 35.
Alycaeus perakensis var. *minor* nomen nudum, Clements et al. 2008: 2760.
Alycaeus kapayanesis [sic]: Foon et al. 2017: 12, figure 4E.

Type locality. Gunong Lano (= PRK 18 Gunung Lanno), Perak (4°31'31"N, 101°08'48"E).

Type material. *Syntype.* Perak, Gunong Lano (= PRK 18 Gunung Lanno), Perak: MNHN IM-2000-31792/45 (1 specimen seen).

Other examined materials. PRK 01 Gunung Tempurung, Perak: BOR/MOL 11142/11, BOR/MOL 11229/1, BOR/MOL 11385/2, BOR/MOL 11414/3. PRK 23 Gunung Rapat, Perak: BOR/MOL 241/2, BOR/MOL 6845/1, BOR/MOL

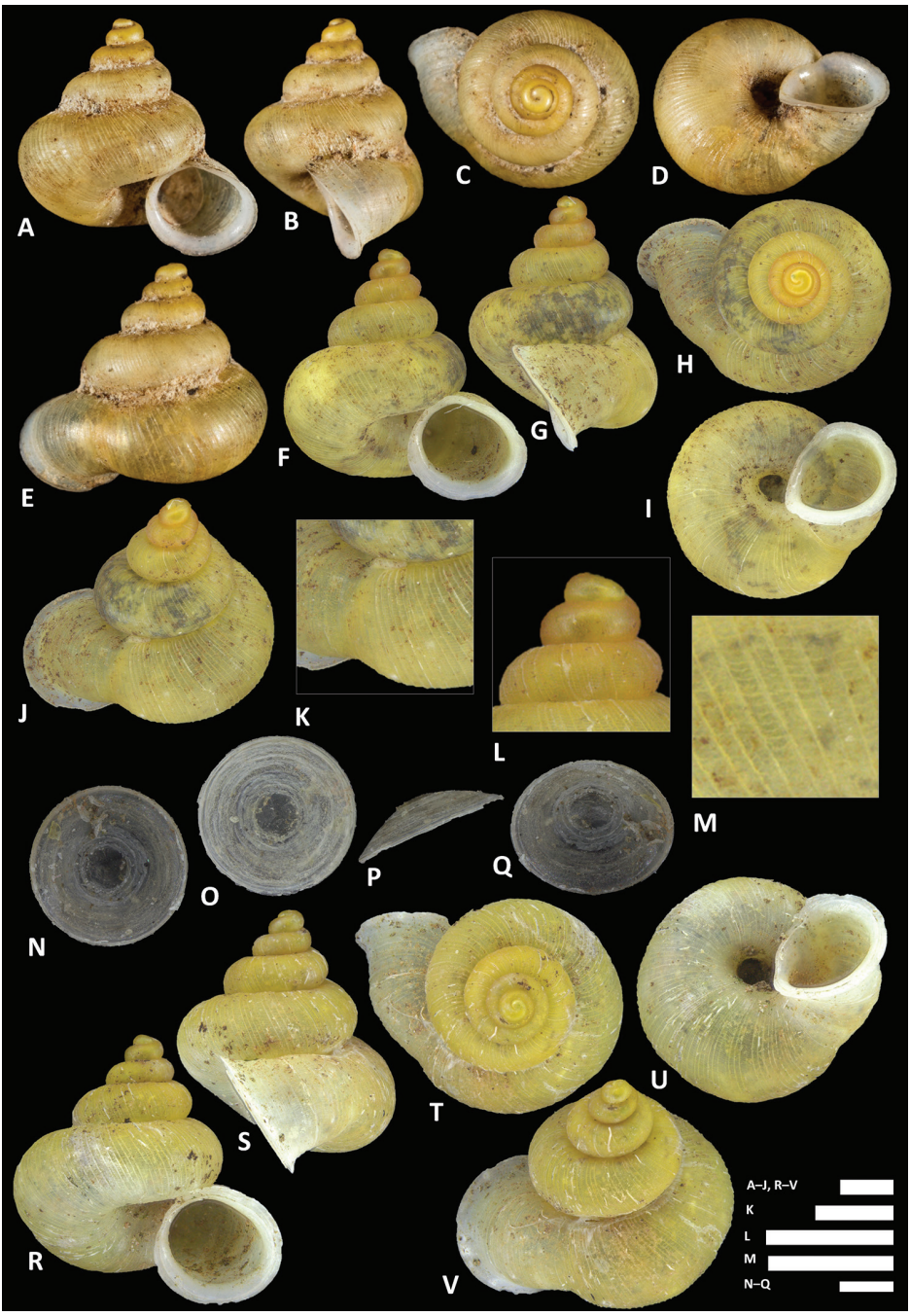

Figure 20. *Alycaeus kapayanensis* Morgan, 1885b. **A–E** Shell of syntype, MNHN-IM-2000-31792 **F–J** Shell of BOR/MOL 10793 **K–M** Close up of shell of BOR/MOL 10793 **N–Q** Operculum of BOR/MOL 6845 **R–V** Shell of BOR/MOL 11385. Scale bars: **A–L** 1 mm; **M–Q** 0.5 mm. Photographs **A–E** by Manuel Caballer (reproduced herein under CC-BY 4.0 license, Project RECOLNAT, MNHN). Photographs **F–V** by Junn Kitt Foon.

8343/4, BOR/MOL 8344/2, BOR/MOL 10031/4, BOR/MOL 10230/10, BOR/MOL 10259/4, BOR/MOL 12985/1. PRK 27 Gunung Datok, Perak: BOR/MOL 10482/4, BOR/MOL 10502/3. PRK 29 Gunung Lang, Perak: BOR/MOL 244/1, BOR/MOL 13005/13. PRK 34 Gunung Tasek, Perak: BOR/MOL 6840/5, BOR/MOL 6905/1, BOR/MOL 8405/11, BOR/MOL 8406/20, BOR/MOL 10793/52, BOR/MOL 11028/29, BOR/MOL 11065/5. PRK 42 Gunung Bercham, Perak: BOR/MOL 10629/1. PRK 47 Gunung Kanthan South, Perak: BOR/MOL 9081/38, BOR/MOL 9161/12, ZRC 1975.2.22.229/1. PRK 53 Hill KF, Perak: BOR/MOL 10671/3, BOR/MOL 10696/6. Hill 10 km NE of Sungai Siput town, Perak: BOR/MOL 246/1. Mykarst-025, Perak: BOR/MOL 9425/1, RMNH 153570/1. Mykarst-027 Gunung Kanthan North, Perak: BOR/MOL 9041/2. Limestone outcrop opposite Jalan Jalong-Lasah Chinese cemetery, NE of Sungai Siput, Perak; BOR/MOL 6876/1, BOR/MOL 8383/21, BOR/MOL 8384/1. Sungai Siput North, Perak: ZRC 1975.2.22.183-189/7, ZRC 1975.2.22.383-443/61, RMNH 153569/101, ZMA 33450/1.

Description. Protoconch. Smooth.

Shell shape. Conical. Shell height: 4.85–5.34 mm. Shell width: 4.44–5.09 mm.

Spire. Spire height: 1.66–2.03 mm. Spire width: 2.11–2.39 mm. Number of whorls: up to 5. Spire shape: oblong conical. Whorl periphery rounded. Umbilicus open.

Whorl constriction. At about 4 ⅝ whorls posterior of protoconch.

Breathing tube. Length: 0.29–0.51 mm.

Aperture and peristome. Aperture circular, moderately expanded. Aperture height: 2.01–2.77 mm. Aperture width: 2.13–2.36 mm. Peristome single, not thickened, notched at suture. Peristome orientation 29–32° oblique with respect to the coiling axis.

Spiral lines. Distinct. Regularly spaced. Approximately 27–48 lines per 1 mm.

Radial ribs running anterior of breathing tube. Radial ribs pronounced, evenly spaced. Approximately 11–15 ribs per 1 mm.

Radial ribs running perpendicular to breathing tube. Radial ribs pronounced, evenly spaced. Approximately 10–19 ribs per 1 mm.

Radial ribs running posterior of breathing tube. Radial ribs absent immediately posterior of constriction, becoming pronounced and evenly spaced at the middle until prior to aperture. Approximately 11–23 ribs per 1 mm.

Operculum. Concave, rounded. Exterior covered with very thin calcareous layer, with indistinct appressed multilamellae. Interior covered with proteinaceous coating, smooth indistinct appressed multilamellae.

Shell colour. Whorls yellow. Peristome white.

Living animal. Body yellow. Head orange. Tentacles red.

Habitat and ecology. Lives on both dry, bare rock and wet limestone walls covered with mosses or tree roots. Although it inhabits forested areas, *A. kapayanensis* has also been found on revegetated limestone walls at former quarries.

Distribution range. Restricted to the karsts of Kinta Valley, Perak. Its known northern limit is at the Sungai Kerdah karst region, northeast of Sungai Siput Utara town and southern limit at Gunung Tempurung.

Differential diagnosis. *Alycaeus kapayanensis* is similar to *A. costacrassa* sp. n. but differs consistently in having less pronounced spiral ribs and much thinner operculum. *Alycaeus kapayanensis* also resembles *A. selangoriensis* sp. n. but is consistently smaller shelled (smaller by about 0.96 mm in shell height, 1.6 mm in shell width), has less whorls, less expanded ultimate whorl and thinner operculum.

Discussion. Historically, many Peninsular Malaysian *Alycaeus* with small, yellow and conical shells were lumped under *A. kapayanensis* out of convenience (ZRC collection lots). We systematically and empirically examined these shells from across the peninsula and concluded that *A. kapayanensis* is restricted to Kinta Valley. Superficially similar species elsewhere differ consistently in shell, operculum and animal characters and are thus described as new taxa: *Alycaeus costacrassa* sp. n., *Alycaeus selangoriensis* sp. n., *Alycaeus ikanensis* sp. n., *Alycaeus alticola* sp. n. and *Alycaeus charasensis* sp. n. In Kinta Valley, many *A. kapayanensis* shells have previously been labelled as "*A. perakensis* var. *minor*", a nomen nudum (Clements et al. 2008, ZRC collection lots). The only morphological variability in *A. kapayanensis* is the degree of expansion of the ultimate whorl.

Alycaeus kelantanensis Sykes, 1902

Figures 7P–Q, 21, 31K

Alycaeus kelantanense Sykes, 1902: 60–62, Figure 11–12.
Alycaeus kelantanensis: Möllendorff 1902: 135–149; Laidlaw 1928: 35; Berry 1965: 28; Schilthuizen et al. 1999: 353; Maassen 2001: 22; Clements et al. 2008: 2760; Liew 2010: 101; Tarruella and Domènech 2011: 72, figure 2C.

Type locality. Kelantan, Malay Peninsula.

Type material. *Syntype.* Kelantan: RMNH 153594/1 (Seen).

Other examined materials. KTN 01 Gunung Reng, Kelantan: BOR/MOL 6837/1. KTN 45 unnamed hill at Kampung Bayu, Kelantan: BOR/MOL 6236/6, BOR/MOL 12974/1. KTN 66 Batu Tongkat, Kelantan: ZRC 1975.2.21.838-875/44. KTN 77 Bukit Sejuk, Kelantan: BOR/MOL 6199/3, BOR/MOL 6231/1. KTN 95 Gua Panjang, Kelantan: BOR/MOL 6200/6, BOR/MOL 6829/1, BOR/MOL 8329/13, BOR/MOL 8330/5. KTN 109 part of Gua Panjang, Kelantan: BOR/MOL 12973/1. KTN 134 Gua Batu Boh, Kelantan: BOR/MOL 6828/1, BOR/MOL 8328/3, BOR/MOL 8409/3. KTN 135 Gua Serai, Kelantan: BOR/MOL 242/1. KTN 136 Gua Musang, Kelantan: ZRC 1975.2.21.250-349/102, ZRC 1975.2.24.452-476/25, ZRC 1975.2.24.309-351/43. KTN 139 unnamed hill, Kelantan: BOR/MOL 6197/5. KTN 148 'Hill 001', Kelantan: BOR/MOL 12976/4. KTN 149 unnamed hill, Kelantan: BOR/MOL 6833/1, BOR/MOL 8333/11. KTN 176 Batu Lesong, Kelantan: BOR/MOL 6830/1, BOR/MOL 8331/7, BOR/MOL 8332/8. Mykarst-168, Kelantan: BOR/MOL 6189/2, BOR/MOL 6838/2. Mykarst-186 Gua Madu, Kelantan: BOR/MOL 6234/1, BOR/MOL 6825/1, BOR/MOL 8327/7, ZRC 1975.2.21.350-430/91. Limestone outcrop 3 km north of Felda Ciku 5 settlement,

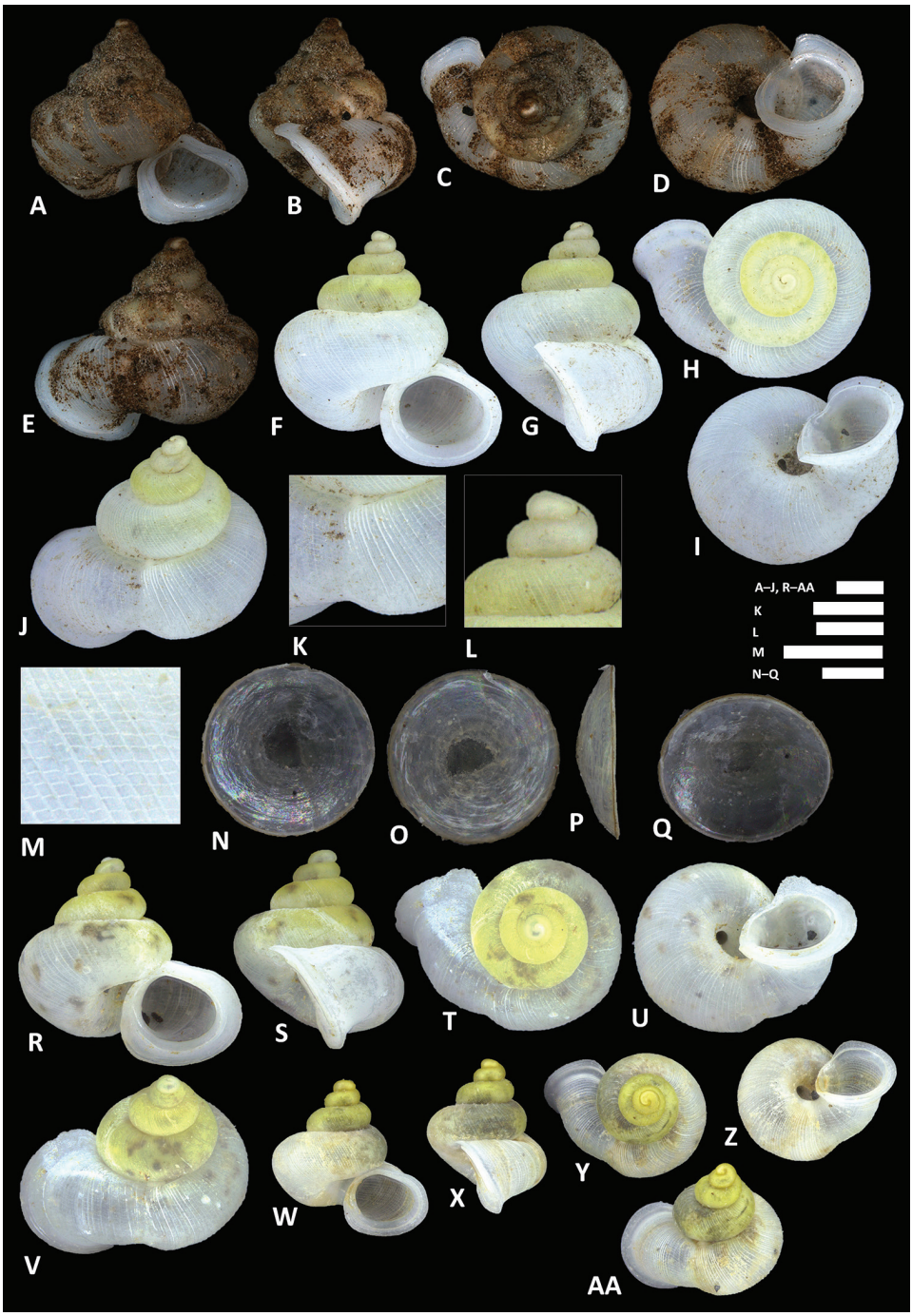

Figure 21. *Alycaeus kelantanensis* Sykes, 1902. **A–E** Shell of syntype, RMNH 153594 **F–J** Shell of BOR/MOL 8327 **K–M** Close up of shell of BOR/MOL 8327 **N–Q** Operculum of BOR/MOL 6825 **R–V** Shell of BOR/MOL 12973 **W–AA** Shell of BOR/MOL 12974. Scale bars: **A–J, K, R–AA** 1 mm; **L, M, N–Q** 0.5 mm. Photographs **A–E** by Thor Seng Liew. Photographs **F–AA** by Junn Kitt Foon.

Kelantan: BOR/MOL 6238/3. Bukit Gua Peraling, Kelantan: ZRC 2.24.440-451/12. Kelantan: RMNH 153593/3, ZMA 33451/2. PHG 40 Gua Layang, Pahang: BOR/MOL 6822/1, BOR/MOL 8325/2, BOR/MOL 8326/7. PHG 114 'Boomerang' Hill, Pahang: BOR/MOL 6188/2. Unnamed limestone hill north of Jalan Lipis-Gua Musang Lama, Felda Chegar Perah I and II, Pahang: BOR/MOL 6233/1, BOR/MOL 6814/1, BOR/MOL 8321/5, BOR/MOL 8322/3.

Description. Protoconch. Smooth.

Shell shape. Conical. Shell height: 3.33–5.04 mm. Shell width: 3.36–5.04 mm.

Spire. Spire height: 1.08–1.76 mm. Spire width: 1.40–2.25 mm. Number of whorls: up to 4. Spire shape: oblong conical. Whorl periphery rounded. Umbilicus open.

Whorl constriction. At about 3 ⅝ whorls posterior of protoconch.

Breathing tube. Length: 0.38–0.67 mm.

Aperture and peristome. Aperture circular, moderately expanded to very expanded. Aperture height: 1.82–2.73 mm. Aperture width: 1.69–2.46 mm. Peristome double, thickened, folded posteriorly into a wing-like upper palatal structure, notched at suture. Peristome orientation 26–34° oblique with respect to the coiling axis.

Spiral lines. Distinct. Regularly spaced. Approximately 15–28 lines per 1 mm.

Radial ribs running anterior of breathing tube. Radial ribs pronounced, evenly spaced. Approximately 12–18 ribs per 1 mm.

Radial ribs running perpendicular to breathing tube. Radial ribs pronounced, white and thicker than those anterior of breathing tube, evenly spaced. Approximately 12–29 ribs per 1 mm.

Radial ribs running posterior of breathing tube. Radial ribs absent immediately posterior of constriction, becoming pronounced and evenly spaced at the middle, absent again towards the aperture. Approximately 11–20 ribs per 1 mm.

Operculum. Concave, rounded. Exterior covered with thin calcareous layer, with very indistinct appressed multilamellae. Interior covered with proteinaceous coating, smooth, with indistinct mamilla.

Shell colour. Whorls white throughout. First 3 whorls occasionally yellow.

Living animal. Body cream-white. Head pinkish. Tentacles yellow, with red tips.

Habitat and ecology. Lives in rock crevices and limestone solution holes. In moist, shady forests. Occur on both limestone and non-limestone areas.

Distribution range. Widespread across southern Kelantan.

Differential diagnosis. *Alycaeus kelantanensis* varies in shell size and whorl convexity but can nevertheless be distinguished from other similar sized *Alycaeus* by its rather angular and winged double peristome, pronounced and widely-spaced radial ribs and spiral lines, as well as the red-tipped yellow tentacles of its soft body. *Alycaeus kelantanensis* is similar to *A. clementsi* sp. n. in shell colour but differs in being consistently smaller shelled (smaller by about 2.13 mm in shell height, 2.32 mm in shell width), having smooth operculum exterior and a more angular double peristome.

Discussion. The type specimen for *A. kelantanensis* was collected by John Waterstradt, likely from the Pulai Princess Cave hill (4°47'38"N, 101°56'31"E), south of Gua Musang, Kelantan (after Liew et al. 2014, Waterstradt 1902). *Alycaeus kelantanensis* shells from

across its range are consistent in their diagnostic characters but varies in shell size within and between populations. Aside from the locations listed above, this species has also been recorded from limestone hills near Kuala Betis, 25 km west of Gua Musang, Kelantan (Berry 1965) and in the non-limestone Lojing Highlands, Kelantan (Liew 2010).

***Alycaeus kurauensis* sp. n.**
http://zoobank.org/FFC4471A-0820-4048-9572-0C55BBF5F7F1
Figures 7R, 22, 31P

Type locality. PRK 59 Bukit Batu Kurau, Perak (4°55'45"N, 100°49'02"E).

Type material. *Holotype.* PRK 59 Bukit Batu Kurau, Perak: BOR/MOL 12967. *Paratypes.* PRK 59 Bukit Batu Kurau, Perak: BOR/MOL 6851/10, BOR/MOL 8408/2.

Other examined materials. PRK 59 Bukit Batu Kurau, Perak: BOR/MOL 8353/22, ZRC 1975.2.22.230-284/54.

Etymology. Named after the type locality, Batu Kurau.

Description. Protoconch. Smooth.

Shell shape. Conical. Shell height: 5.04–5.56 mm. Shell width: 5.34–6.06 mm

Spire. Spire height: 1.08–2.06 mm. Spire width: 2.34–2.52 mm. Number of whorls: up to 4. Spire shape: oblong conical. Whorl periphery rounded. Umbilicus open.

Whorl constriction. At about 3 ⅝ whorls posterior of protoconch.

Breathing tube. Length: 0.45–0.62 mm.

Aperture and peristome. Aperture circular, moderately expanded. Aperture height: 2.51–2.84 mm. Aperture width: 2.34–2.65 mm. Peristome double, thickened, notched at suture. Peristome orientation 35–45° oblique with respect to the coiling axis.

Spiral lines. Distinct. Regularly spaced. Approximately 24–36 lines per 1 mm.

Radial ribs running anterior of breathing tube. Radial ribs pronounced, evenly spaced. Approximately 7–16 ribs per 1 mm.

Radial ribs running perpendicular to breathing tube. Radial ribs pronounced and thicker than those anterior of breathing tube, evenly spaced. Approximately 9–16 ribs per 1 mm.

Radial ribs running posterior of breathing tube. Radial ribs absent immediately posterior of constriction. At the middle section, becoming pronounced and evenly spaced from the middle section until prior to aperture. Approximately 10–15 ribs per 1 mm.

Operculum. Concave, rounded. Exterior covered with thick calcareous layer, smooth. Interior covered with proteinaceous coating, smooth, mamillated.

Shell colour. Whorls yellow. Peristome white.

Living animal. Body cream-yellow. Head orange. Tentacles red.

Habitat and ecology. Lives on both dry and wet limestone walls. In shady forests and cliffs on limestone hills.

Distribution range. Restricted to Batu Kurau, Perak.

Differential diagnosis. *Alycaeus kurauensis* sp. n. is similar to *Alycaeus perakensis* in conical shell shape and radial ribs spacing but differs in being consistently smaller (by

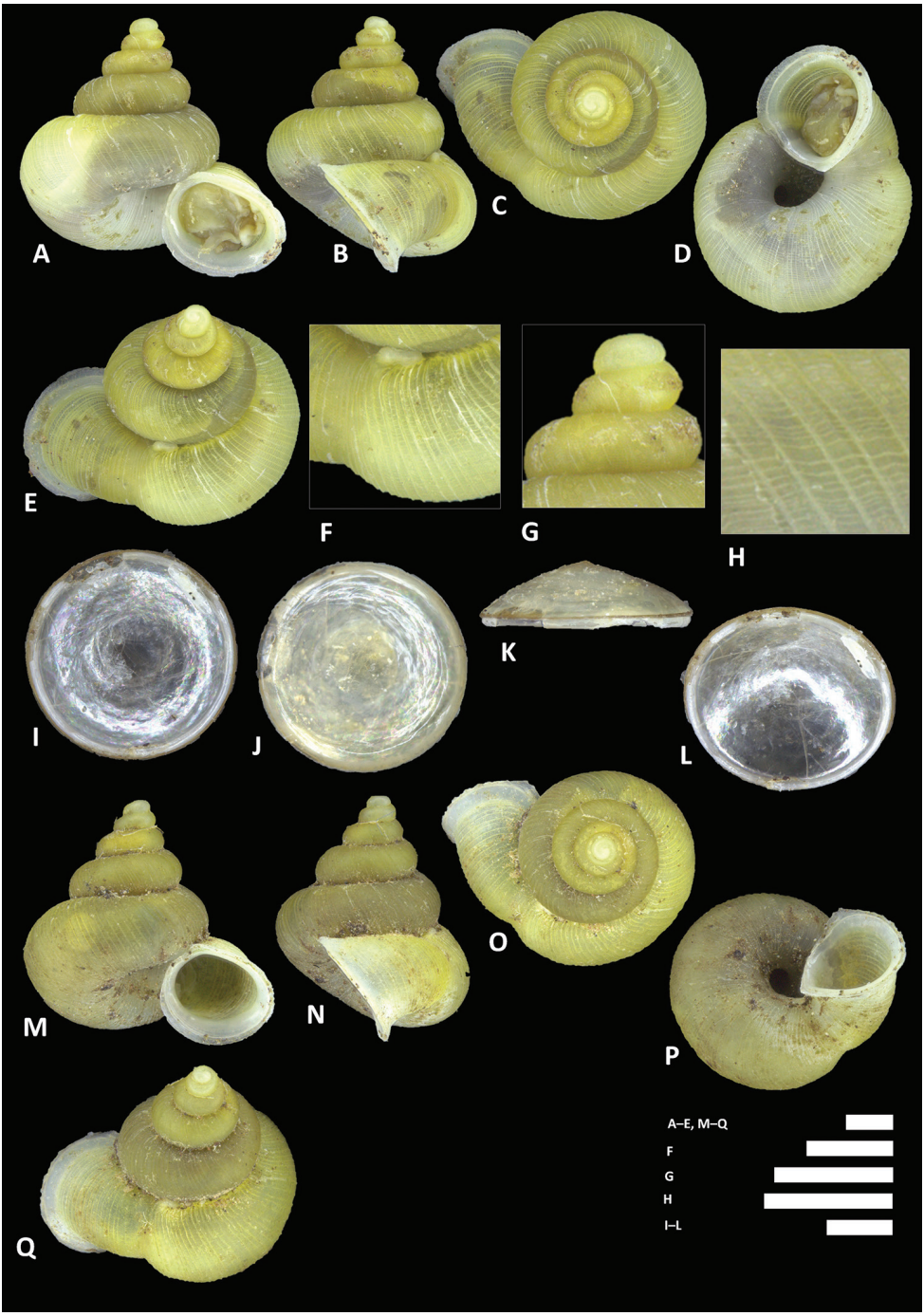

Figure 22. *Alycaeus kurauensis* sp. n. **A–E** Shell of holotype, BOR/MOL 12967 **F–H** Close up of shell of holotype, BOR/MOL 12967 **I–L** Operculum of paratype, BOR/MOL 6851 **M–Q** Shell of paratype, BOR/MOL 6851. Scale bars: **A–E, F, G, M–Q** 1 mm; **H, I–L** 0.5 mm. All photographs by Junn Kitt Foon.

about 1.33 mm in shell height, and by about 1.85 mm in shell width), has a less expanded ultimate whorl and peristome, a thick operculum with smooth exterior as well as body and tentacle colouration. *Alycaeus kurauensis* sp. n. is also similar to *Alycaeus kapayanensis* in size and colour but differs in having a wider ultimate whorl, thicker operculum with smooth exterior and more widely spaced radial ribs.

Discussion. A nomen nudum "*Alycaeus perakensis var. minor*" was used for this subspecies in the ZRC collection. *A. kurauensis* sp. n. is quite consistent in all aspects of shell shape except in the ultimate whorl, which varies in the degree of expansion but never as expanded as *A. perakensis*.

Alycaeus liratulus Preston, 1907

Figures 7C, 23, 31B

Alycaeus (Pincerna) liratula Preston, 1907: 206; Robertson et al. 1987: 4; Tarruella and Domènech 2011: 72; Mienis 2014: 37.
Alycaeus (*Alycaeus*) *liratulus*: Laidlaw 1928: 35; Benthem Jutting 1959: 77; Maassen 2001: 22; Clements et al. 2008: 2760.
Alycaeus liratulus: Marwoto 2016: 17.
Pincerna liratula: Páll-Gergely 2017: 213–219, figure 1C.

Type locality. Kelantan.

Type material. *Syntypes*. Ke-lan-tan (=Kelantan): ANSP 99391/1 (Seen), NHMUK 1907.5.20.191-192/2 (1 specimen seen), HUJ 22445 (Not seen).

Other examined materials. Mykarst-186 Gua Madu, Kelantan: BOR/MOL 6826/2. KTN 136 Gua Musang, Kelantan: ZRC 1975.2.22.4-7/4. KTN 176 Batu Lesong, Kelantan: BOR/MOL 6831/1. KTN 149 unnamed hill, Kelantan: BOR/MOL 6832/1, BOR/MOL 8334/3. Mykarst-168, Kelantan: BOR/MOL 8411/2.

Description. Protoconch. Smooth.

Shell shape and size. Globose. Shell height: 5.62–6.70 mm. Shell width: 5.195–6.08 mm.

Spire. Spire height: 1.42–2.01 mm. Spire width: 2.30–2.83 mm. Number of whorls: up to 4 ⅛. Spire shape: oblong conical. Whorl periphery rounded. Umbilicus open.

Whorl constriction. At about 3 ¾ whorls posterior of protoconch.

Breathing tube. Length: 1.13–1.25 mm.

Aperture and peristome. Aperture circular, moderately expanded. Aperture height: 2.78–3.16 mm. Aperture width: 2.88–3.43 mm. Peristome double, thickened, slightly notched at suture. No interspace. Peristome orientation 9–20° oblique with respect to the coiling axis.

Spiral lines. Distinct. Regularly spaced. Approximately 11–14 lines per 1 mm.

Radial ribs running anterior of breathing tube. Radial ribs pronounced, evenly spaced. Approximately 6–7 ribs per 1 mm.

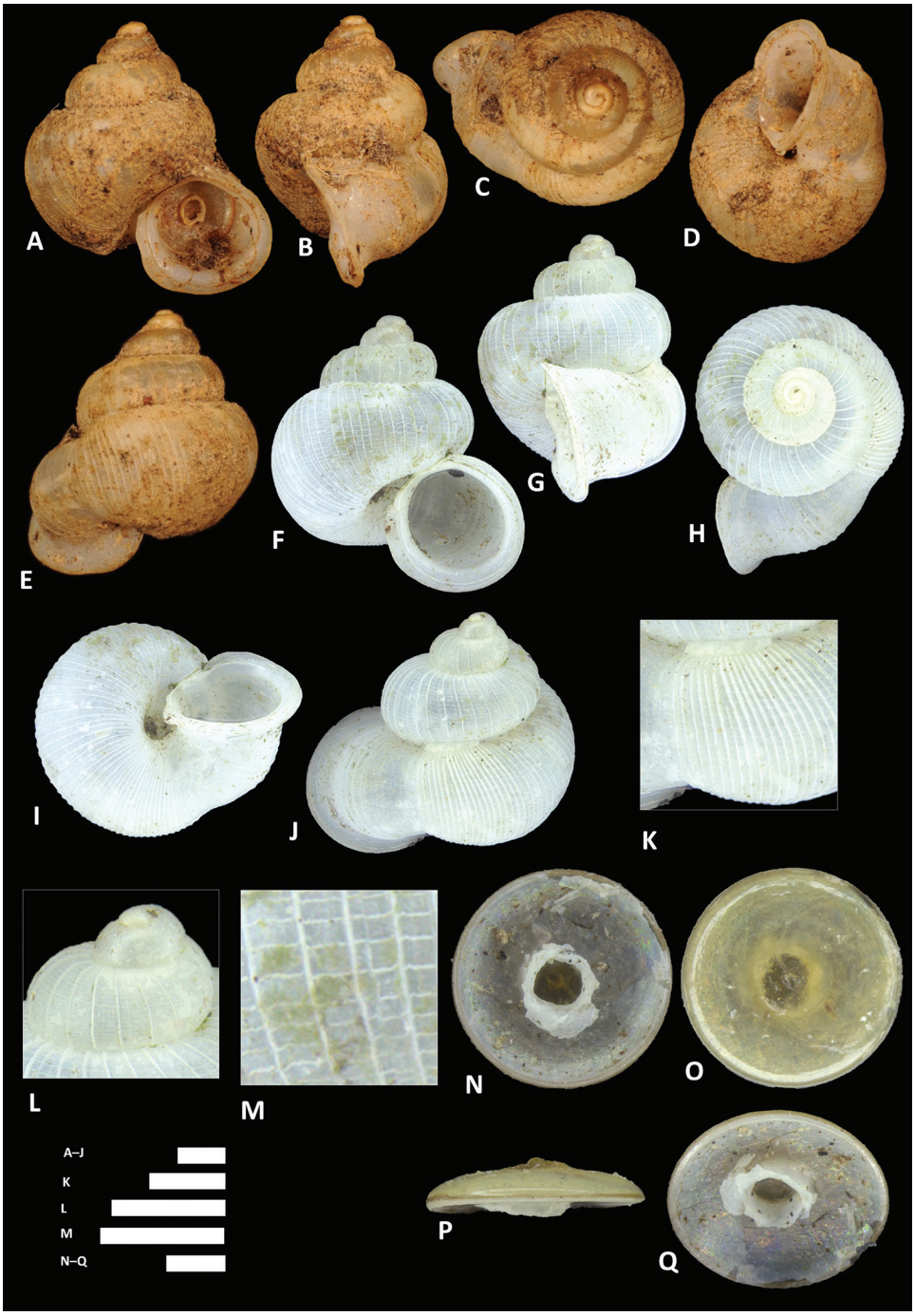

Figure 23. *Alycaeus liratulus* (Preston, 1907). **A–E** Shell of syntype, ANSP 99391 **F–J** Shell of BOR/MOL 6831 **K–M** Close up of shell of BOR/MOL 8357 **N–Q** Operculum of BOR/MOL 6832. Scale bars: **A–J** 1 mm; **K, L** 1 mm; **M, N–Q** 0.5 mm. Photographs **A–E** by the Malacology Department, ANSP. Photographs **F–Q** by Junn Kitt Foon.

Radial ribs running perpendicular to breathing tube. Radial ribs pronounced, evenly spaced. Approximately 9–12 ribs per 1 mm.

Radial ribs running posterior of breathing tube. Radial ribs absent immediately posterior of constriction, becoming distinct and unevenly spaced at the middle and then absent again prior to aperture.

Operculum. Concave, rounded. Exterior covered by calcareous layer. Exterior nucleus with calcareous, cup-like projection. Interior covered by proteinaceous layer, smooth, mamillated.

Shell colour. Off white, apical whorls occasionally pinkish white.

Living animal. Body maroon. Head maroon. Tentacles red or brown tipped.

Habitat and ecology. Lives on shrubs close to the ground. In forested areas of limestone hills.

Distribution. Restricted to central and southern Kelantan. Elsewhere, isolated records in northern Sumatra, Indonesia (Benthem Jutting 1959, Marwoto 2016) need to be verified.

Differential diagnosis. *Alycaeus liratulus* is most similar to *Alycaeus thieroti* in shell shape but differs in having a larger shell (larger by about 1 mm in shell height, 0.8 mm in shell width), wider-spaced radial ribs and spiral lines, longer breathing tube (longer by 0.65 mm) and flat operculum with cup-shaped calcareous extension at the nucleus exterior.

Discussion. Confusion between *A. liratulus* and *A. thieroti* due to similarity in shell shape and poor original descriptions have led to many misidentifications in the past (see Discussion in *Alycaeus thieroti*). Isolated records of *A. liratulus* from northern Sumatra (Benthem Jutting 1959, Marwoto 2016) have to be re-examined. Laidlaw (1928) considers *A. liratulus* as closely related to the *A. globosus* of Borneo, an opinion we concur based on its globose shell. However, *A. globosus* differs from *A. liratulus* in the arrangement and density of radial ribs, short breathing tube and absence of a cup-shaped projection at the operculum exterior.

Supraspecific classification was attempted for *A. liratulus* by Preston (1907), who created a new subgenus *Pincerna* based on the sole diagnostic character of the cup-shaped protrusion on the operculum exterior of *A. liratulus*. However, the operculum structure is an unsuitable diagnostic character because analogous structures have also been found in *Alycaeus kukenthali* Sarasin & Sarasin, 1899 and *Alycaeus ochraceus* Godwin-Austen, 1893, two species unrelated in shell shape to *A. liratulus* (Sarasin and Sarasin 1899, Laidlaw 1928, Páll-Gergely 2017). Note that we maintained *Pincerna* as a subgenus of *Alycaeus* although *Pincerna* was recently elevated to genus level (Páll-Gergely 2017). See Remarks section under genus *Alycaeus* for discussion.

Alycaeus perakensis Crosse, 1879a

Figures 7S, 24, 31V

Alycaeus perakensis Crosse, 1879a: 206–208, plate 7, figure 7; Crosse 1879b: 339–340; Möllendorff 1886: 310; Sykes 1903: 195; Tension-Woods 1888: 1068; Tielecke

1940: 345; Davison 1995: 236; Schilthuizen et al. 1999: 353; Clements et al. 2008: 2760; Foon et al. 2017: 13, figure 4F.

Alycaeus (*Orthalycaeus*) *perakensis*: Möllendorff 1891: 342; Kobelt and Möllendorff 1897: 150.

Alycaeus (*Alycaeus*) *perakensis*: Kobelt 1902: 348; Laidlaw 1928: 35; Chan 1998a: 4; Chan 1998b: 1.

Alycaeus perakensis perakensis: Maassen 2001: 23; Tarruella and Domènech 2011: 72.

Type locality. Buket Pondong (= PRK 55 Gunung Pondok), Perak (4°46'57"N, 100°50'01"E).

Type material. *Syntypes.* Buket Pondong (= PRK 55 Gunung Pondok), Perak: MNHN IM-2000-31793/1 (Seen), MNHN IM-2000-31794/1 (Seen), MNHN IM-2000-31795/1 (Seen).

Other materials. KDH 01 Bukit Baling, Kedah: BOR/MOL 6525/1, BOR/MOL 6854/5, BOR/MOL 8527/1, BOR/MOL 8528/2. KDH 02 Gunung Pulai, Kedah: BOR/MOL 6858/2. PRK 55 Gunung Pondok, Perak: BOR/MOL 272/1, BOR/MOL 6849/1, BOR/MOL 8349/29, BOR/MOL 8350/23, BOR/MOL 11479/46, BOR/MOL 11506/31, BOR/MOL 11539/50, BOR/MOL 11563/20, ZRC 1997.25/5, ZRC 1975.2.22.175-182/12, ZRC 1975.2.22.36-66/31, ANSP 423056/2. PRK 61 Gua Badak, Perak: ZRC 1975.2.22.160-174/15. PRK 62 Gunung Dayak, Perak: BOR/MOL 277/5, BOR/MOL 6201/3, ZRC 1975.2.22.127-159/33. PRK 64 Bukit Kepala Gajah, Perak: BOR/MOL 6852/1, BOR/MOL 8354/33, BOR/MOL 8355/5, BOR/MOL 10088/31, BOR/MOL 10124/15, BOR/MOL 10136/18, BOR/MOL 10166/21, BOR/MOL 13001/2. Mykarst-171 Tasik Temenggor Hill S2, Perak: BOR/MOL 6243/1. Hill 40 m east of Sungai Siput Hospital, Perak: BOR/MOL 271/1, BOR/MOL 6877/1, BOR/MOL 8385/24, BOR/MOL 8386/1. Limestone outcrop 50m from roadside, Kampung Pahit, Klian Intan, Perak: BOR/MOL 6874/1, BOR/MOL 8379/22, BOR/MOL 8380/9. 'Bat Cave' Hill, roadside towards Perlop 1 and 2 oil palm plantations, Perak: BOR/MOL 6878/1, BOR/MOL 8387/17, BOR/MOL 8388/5, BOR/MOL 9770/11, BOR/MOL 9799/3, BOR/MOL 9833/1, BOR/MOL 9877/4. Batu Kebelah, Kampung Kenang Baru, Jalong Tinggi, Perak: BOR/MOL 6879/1, BOR/MOL 8389/5, BOR/MOL 8390/5, BOR/MOL 9546/23, BOR/MOL 9565/2, BOR/MOL 9573/5, BOR/MOL 9585/17. Lenggong, Perak: ZRC 1997.24/4 specimens. Perak: RMNH 153573/3, RMNH 153574/2. Banang Pupo, Yala, Thailand: ANSP 446394/3.

Description. Protoconch. Smooth.

Shell shape. Conical. Shell height: 5.98–7.27 mm. Shell width: 6.48–8.62 mm.

Spire. Spire height: 1.83–2.64 mm. Spire width: 2.80–3.39 mm. Number of whorls: up to 4 ½. Spire shape: oblong conical. Whorl periphery rounded. Umbilicus open.

Whorl constriction. At about 4 ¼ whorls posterior of protoconch.

Breathing tube. Length: 0.61–0.88 mm.

Aperture and peristome. Aperture circular, expanded. Aperture height: 3.06–4.32 mm. Aperture width: 2.86–4.10 mm. Peristome double, not thickened, notched at suture. Peristome orientation 43–49° oblique with respect to the coiling axis.

Spiral lines. Distinct. Regularly spaced. Approximately 17–35 lines per 1 mm.

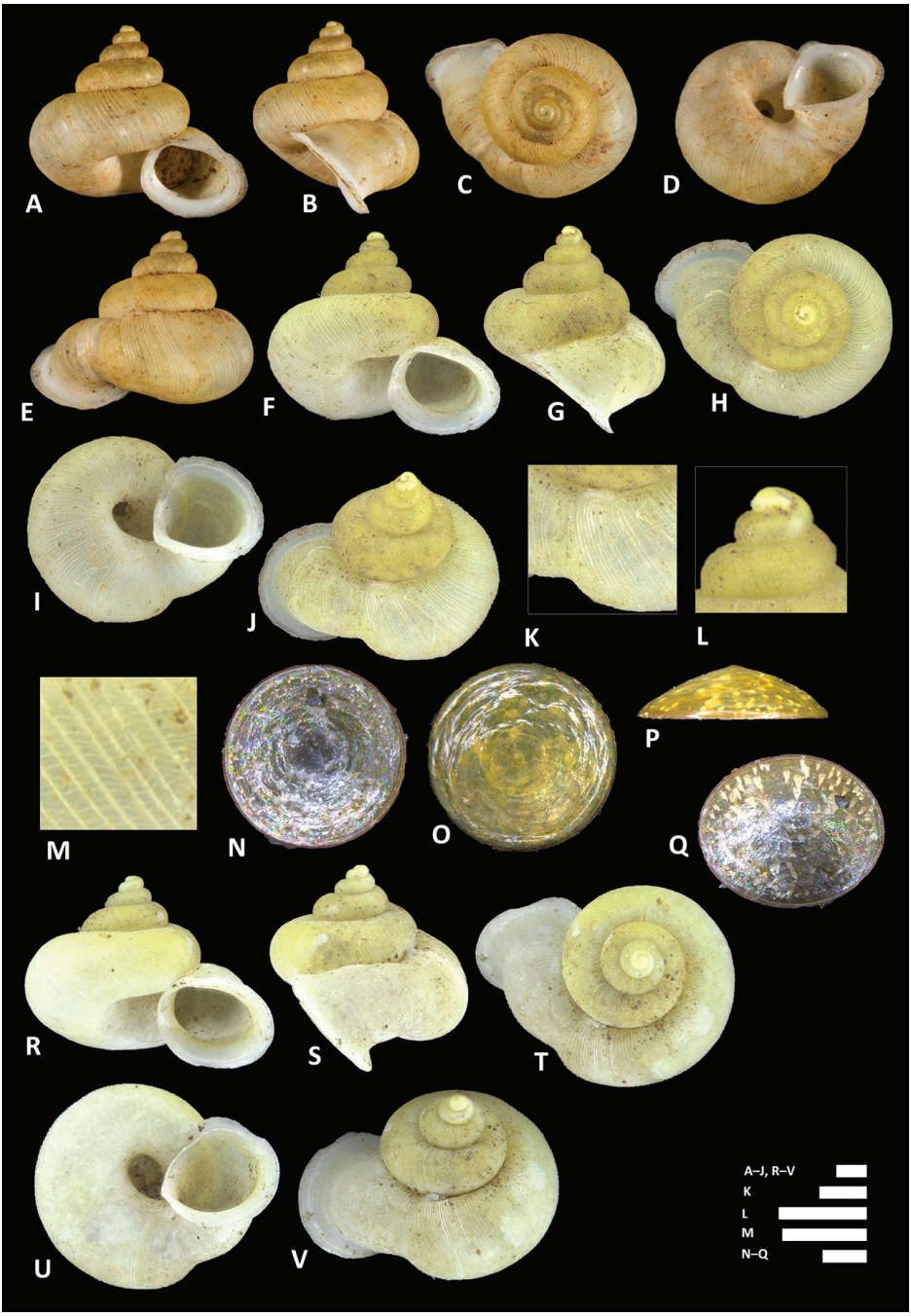

Figure 24. *Alycaeus perakensis* Crosse, 1879a. **A–E** Shell of syntype, MNHN-IM-2000-31793 **F–J** Shell of BOR/MOL 8350 **K–M** Close up of shell of BOR/MOL 8350 **N–Q** Operculum of BOR/MOL 8349 **R–V** Shell of BOR/MOL 8355. Scale bars: **A–J, K, L, R–V** 1 mm; **M, N–Q** 0.5 mm. Photographs **A–E** by Manuel Caballer (reproduced herein under CC-BY 4.0 license, Project RECOLNAT, MNHN). Photographs **F–V** by Junn Kitt Foon.

Radial ribs running anterior of breathing tube. Radial ribs pronounced, evenly spaced. Approximately 8–14 ribs per 1 mm.

Radial ribs running perpendicular to breathing tube. Radial ribs pronounced, white and thicker than those anterior of breathing tube, evenly spaced. Approximately 9–15 ribs per 1 mm.

Radial ribs running posterior of breathing tube. Radial ribs pronounced, widely and regularly spaced, approximately 9–16 ribs per 1 mm. Prior to aperture, radial ribs become absent.

Operculum. Concave, rounded. Exterior covered with thin calcareous layer, surface finely granulated with a scattered arrangement of calcareous spikes. Interior covered with proteinaceous coating, smooth.

Shell colour. Whorls yellow. Peristome white.

Living animal. Body cream-white. Head pink. Tentacles brown.

Habitat and ecology. Lives on both dry and wet limestone walls. Some individuals have been spotted on tree trunks and fallen logs beside limestone cliffs. In shady forests on limestone hills.

Distribution range and habitat. Restricted to central and northern Perak as well as northeastern Kedah (Bukit Baling and Gunung Pulai). Elsewhere, in Yala, Thailand (Sykes 1903, Laidlaw 1928, ANSP 446394).

Differential diagnosis. *Alycaeus perakensis* is most similar to *Alycaeus roebeleni* in conical shell shape but differs in being smaller (smaller by about 0.97 mm in shell height, 1.96 mm in shell width), aperture margins more circular and has a less expanded ultimate whorl. *Alycaeus perakensis* is distinguished from *Alycaeus kapayanensis* and *Alycaeus kurauensis* sp. n. by its much larger shell (larger by about 1.43 mm in shell height, 2.32 mm in shell width), more expanded penultimate whorl, operculum exterior with spikes and more oblique peristome. Shells of *A. perakensis* vary in the degree of expansion of the ultimate whorl.

Discussion. Historically, the lack of access to type specimens and poor original diagnosis have led to the misidentification of *A. selangoriensis* sp. n., *A. clementsi* sp. n. and *A. kapayanensis* as *A. perakensis* (Laidlaw 1932, van Bethem Jutting 1960a, Clements et al. 2008). *Alycaeus perakensis* shells are consistent in shell size and spire height but varies in the degree of expansion of the ultimate whorl with no particular geographic pattern. Tielecke (1940) used *A. perakensis* as a representative species for *Alycaeus* in his comparison of cyclophorid reproductive anatomy. Möllendorff (1894) considered *A. perakensis* to be closely related to *A. roebeleni*. *Alycaeus perakensis* shells were also collected from Biserat and Banang Pupo, Yala, southern Thailand (Sykes 1903, Laidlaw 1928, ANSP 446394).

***Alycaeus regalis* sp. n.**

http://zoobank.org/B8E836AE-F3D5-47B8-BA69-B7E866DCC10B
Figures 7T, 25, 31T

Alycaeus perakensis altispirus: Tarruella and Domènech 2011: figure 2E. [not *Alycaeus altispirus* (Möllendorff, 1902)]

Type locality. PHG 02 Gunung Senyum, Pahang (3°41'50"N, 102°26'04"E).

Type material. *Holotype.* PHG 02 Gunung Senyum, Pahang: BOR/MOL 12990. *Paratypes.* PHG 02 Gunung Senyum, Pahang: BOR/MOL 12991/11. PHG 03 Gunung Jebak Puyuh, Pahang: BOR/MOL 6629/14.

Other examined materials. PHG 02 Gunung Senyum, Pahang: BOR/MOL 6232/3, BOR/MOL 6240/4, BOR/MOL 6881/1, BOR/MOL 8393/5, ZRC 1975.2.22.581-600/20. PHG 03 Gunung Jebak Puyuh, Pahang: BOR/MOL 6883/1.

Etymology. Latin, meaning royal. In reference to the species' tall spire and colour reminiscent of the yellow royal parasol which is part of the regalia of Southeast Asian kingdoms.

Description. Protoconch. Smooth.

Shell shape. Conical. Shell height: 6.57–7.18 mm. Shell width: 5.86–6.87 mm.

Spire. Spire height: 2.32–2.90 mm. Spire width: 2.88–3.21 mm. Number of whorls: up to 5 ½. Spire shape: oblong conical. Whorl periphery rounded. Umbilicus open.

Whorl constriction. At about 5 ¼ whorls posterior of protoconch.

Breathing tube. Length: 0.62–0.81 mm.

Aperture and peristome. Aperture circular, very expanded. Aperture height: 2.91–3.66 mm. Aperture width: 2.95–3.59 mm. Peristome double, sometimes thickened, slightly notched at suture. Peristome orientation 4–17° oblique with respect to the coiling axis.

Spiral lines. Regularly spaced. Approximately 20–36 lines per 1 mm.

Radial ribs running anterior of breathing tube. Radial ribs pronounced, evenly spaced. Approximately 7–15 ribs per 1 mm.

Radial ribs running perpendicular to breathing tube. Radial ribs pronounced, white and thicker than those anterior of breathing tube, evenly spaced. Approximately 6–15 ribs per 1 mm.

Radial ribs running posterior of breathing tube. Radial ribs pronounced and uneven immediately posterior of constriction, becoming pronounced and evenly spaced from the middle section until prior to aperture. Approximately 8–16 ribs per 1 mm.

Operculum. Flat. Exterior with proteinaceous coating and indistinct appressed multilamellae. Interior with proteinaceous coating, smooth, mamillated. Operculum interior sometimes with a hard, ligament-like proteinaceous extension embedded within the columellar muscle of the animal when alive.

Shell colour. Whorls yellow. Peristome white.

Living animal. Body cream-white. Head pinkish-brown. Tentacle tips brown.

Habitat and ecology. This species lives on dry rock surfaces covered with powdery lichens. They never appear on wet and mossy sections of limestone rocks.

Distribution range. Restricted to limestone karsts at central Pahang (Gunung Senyum and Gunung Jebak Puyuh) only.

Differential diagnosis. *Alycaeus regalis* sp. n. is most similar to *A. altispirus* in shell size (shell height: 6.40–7.18 mm, shell width: 5.86–6.87 mm) and tall shell spire (spire height: 2.32–2.90 mm) but differs in the ultimate whorl periphery being rounder, upper palatal section lacking the posterior folding and peristome orientated parallel to the coiling axis.

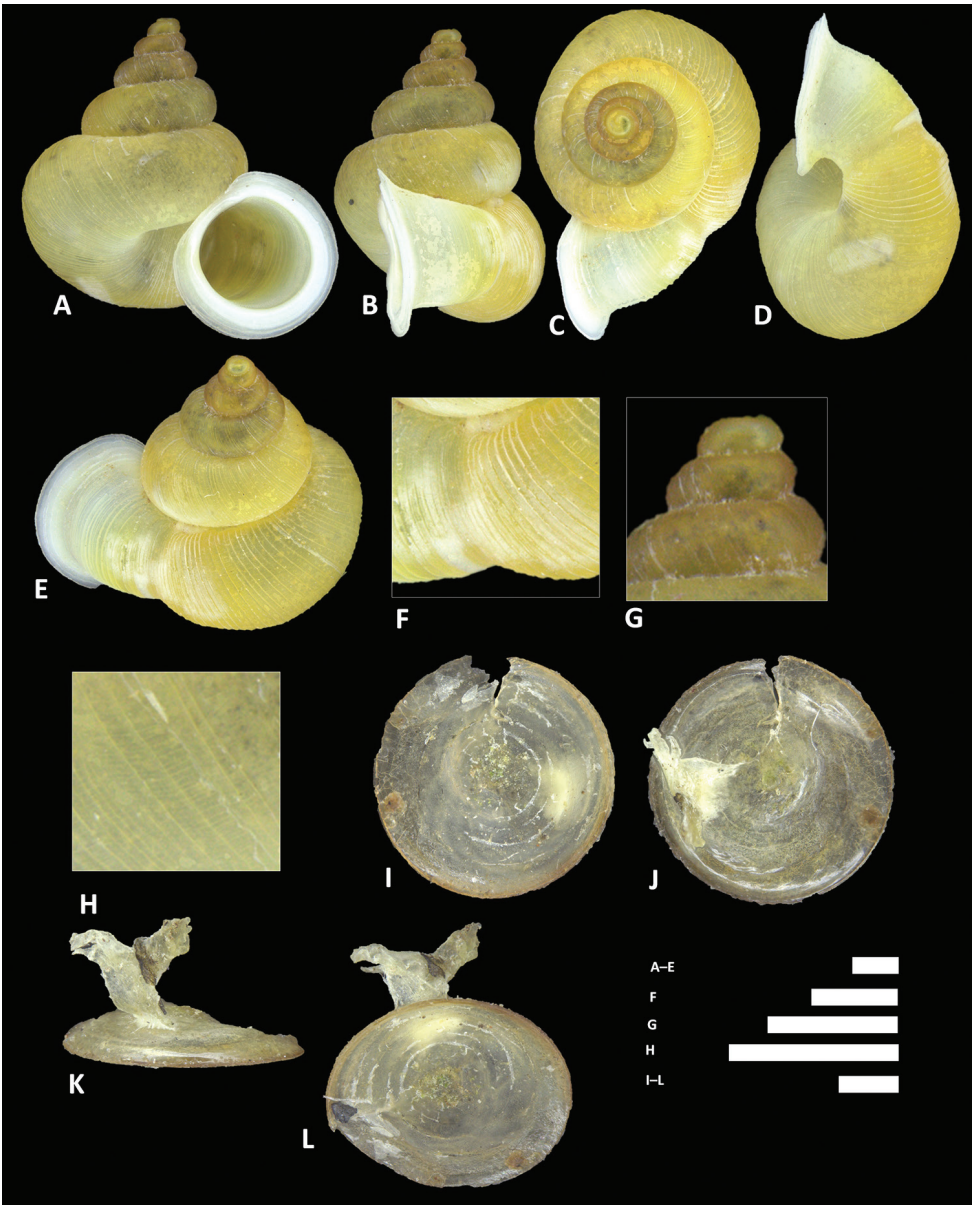

Figure 25. *Alycaeus regalis*, sp. n. **A–E** Shell of holotype, BOR/MOL 12990 **F–H** Close up of shell of holotype, BOR/MOL 12990 **I–L** Operculum of paratype, BOR/MOL 6881. Note operculum with proteinaceous interior extension. Scale bars: **A–E, F, G, H** 1 mm; **I–L** 0.5 mm. All photographs by Junn Kitt Foon.

Discussion. Prior to this study, specimens of *A. regalis* sp. n. from Gunung Senyum were always labelled as *Alycaeus perakensis altispirus* (Tarruella and Domènech 2011; ZRC collection lots) even though they clearly differ from each other, especially

in the aperture shape. *Alycaeus regalis* sp. n. occur sympatrically with *A. costacrassa* sp. n. and *A. senyumensis* sp. n. although the two are separated by their habitat preferences. *Alycaeus regalis* sp. n. appear to prefer drier habitats whereas *A. costacrassa* sp. n. and *A. senyumensis* sp. n. are always found on wet rocks with mosses.

Alycaues roebeleni Möllendorff, 1894

Figures 26, 31W

Alycaeus roebeleni Möllendorff, 1894: 146–156; Tarruella and Domènech 2011: 73, figure 3A.
Alycaeus (*Alycaeus*) *roebelini* [sic]: Laidlaw 1928: 35.
Alycaeus (*Alycaeus*) *roebeleni*: Zilch 1957: 147, plate 6, figure 27.

Type locality. Samui Islands (= Koh Samui archipelago), Thailand.

Type material. *Lectotype*. Koh Samui, Thailand: SMF 109317 (Seen).

Other examined materials. PRS 11 Bukit Tok Seri, Perlis: BOR/MOL 6863/1, BOR/MOL 8368/2. PRS 17 Gunung Chabang, Perlis: BOR/MOL 6230/1, BOR/MOL 6869/1, BOR/MOL 6873/6, BOR/MOL 8374/8. PRS 19 Bukit Chuping, Perlis: BOR/MOL 6859/1, BOR/MOL 8363/30, BOR/MOL 12980/1, ZRC 1975.2.22.99-126/29. Koh Samui, Thailand: RMNH 153575/2, ZMA 317517/1, ANSP 81380/2. Mountain north of Phatthalung, Thailand: ANSP 446393/1.

Description. Protoconch. Smooth.

Shell shape. Conical. Shell height: 7.20–8.01 mm. Shell width: 8.94–10.08 mm.

Spire. Spire height: 2.17–2.74 mm. Spire width: 3.13–3.68 mm. Number of whorls: up to 4 ½. Spire shape: oblong conical. Whorl periphery rounded. Umbilicus open.

Whorl constriction. At about 4 ¼ whorls posterior of protoconch.

Breathing tube. Length: 0.71–0.94 mm.

Aperture and peristome. Aperture circular, very expanded. Aperture height: 4.39–5.21 mm. Aperture width: 4.08–5.01 mm. Peristome single to double, not thickened. Peristome orientation 44–49° oblique with respect to the coiling axis.

Spiral lines. Indistinct. Regularly spaced. Approximately 23–37 lines per 1 mm.

Radial ribs running anterior of breathing tube. Radial ribs pronounced, evenly spaced. Approximately 8–9 ribs per 1 mm.

Radial ribs running perpendicular to breathing tube. Radial ribs pronounced, evenly spaced. Approximately 7–10 ribs per 1 mm.

Radial ribs running posterior of breathing tube. Radial ribs pronounced, unevenly spaced immediately posterior of constriction.

Operculum. Concave, rounded. Exterior covered with thin calcareous layer, smooth. Interior covered with thick proteinaceous coating, smooth, mamillated.

Shell colour. Yellow at apical whorls. Either fades to white towards ultimate whorl or remain yellow throughout.

Living animal. Unknown.

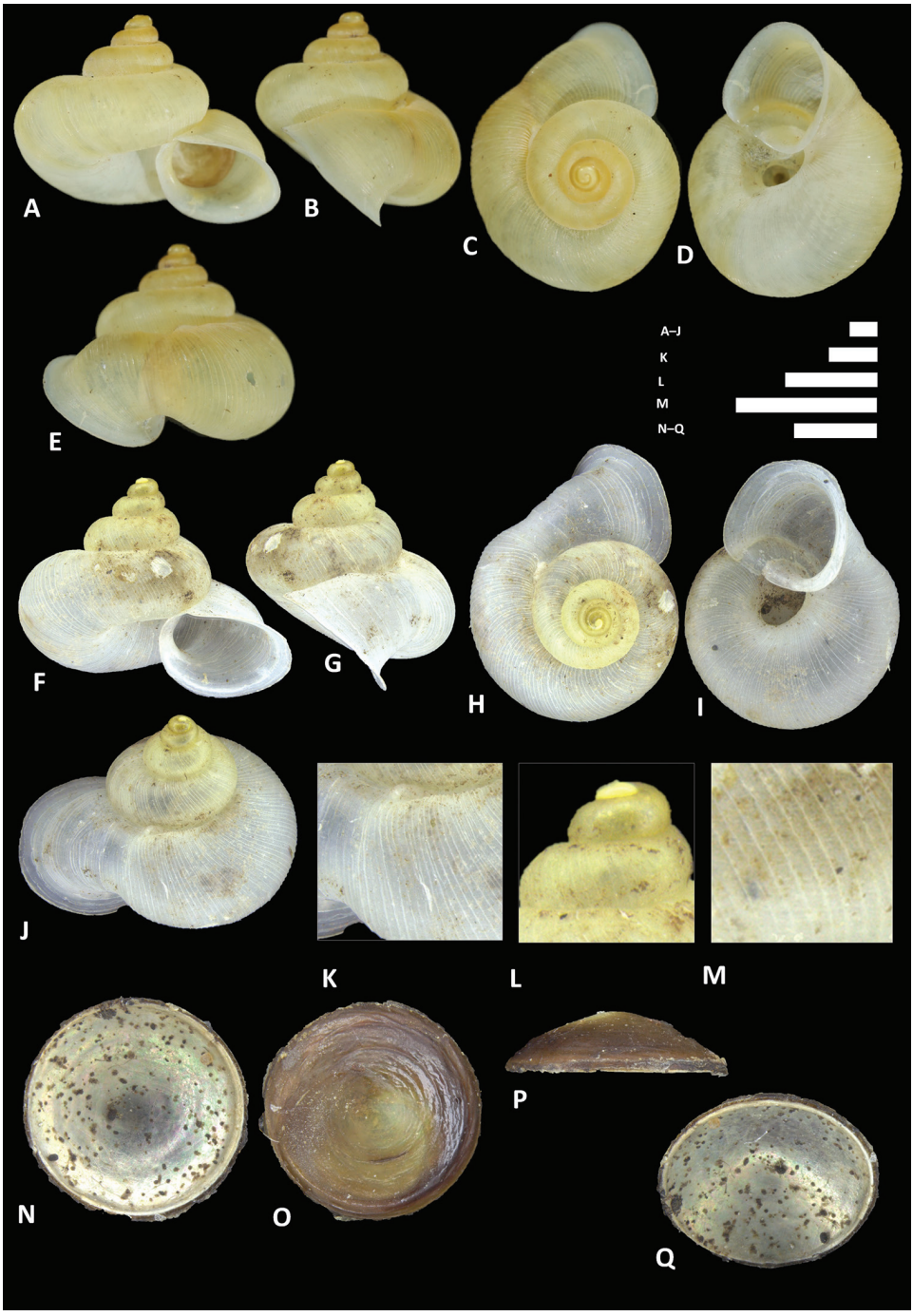

Figure 26. *Alycaeus roebeleni* Möllendorff, 1894. **A–E** Shell of syntype, SMF 109317 **F–J** Shell of BOR/MOL 8363 **K–M** Close up of shell of BOR/MOL 8363 **N–Q** Operculum of BOR/MOL 8363. Scale bars: **A–J, K, L, M, N–Q** 1 mm. Photographs **A–E** by Páll-Gergely Barna, courtesy of R. Janssen, SMF. Photographs **F–Q** by Junn Kitt Foon.

Habitat and ecology. Lives on limestone rock crevices covered by mosses. In shady forests on limestone hills.

Distribution range. Restricted to limestone hills of the Chuping geological formation in central Perlis. Elsewhere, in Koh Samui and Phatthalung, southern Thailand (Möllendorff 1894, materials examined).

Differential diagnosis. *Alycaeus roebeleni* is most similar to *A. perakensis* in shell shape but is larger (larger by about 0.97 mm in shell height, 1.96 mm in shell width), spire taller and wider (taller by about 0.22 mm in spire height, wider by about 0.31 mm in spire width), penultimate whorl wider as well as peristome more expanded (Möllendorff 1894). *Alycaeus roebeleni* also differs from *A. perakensis* in its operculum, which has a smooth exterior and thick, brown proteinaceous layer at the interior. The spire height of *A. roebeleni* is quite variable across its range but never as tall as *A. perakensis*.

Discussion. This species was considered closely related to *A. perakensis* by Möllendorff (1894), which we concur with, based on examined specimens. However, contrary to the Möllendorff (1894) claim that the operculum is entirely proteinaceous, we show that *A. roebeleni* has proteinaceous interior and calcareous exterior layers. Despite clear distinctions made between *A. roebeleni* and *A. perakensis* in Möllendorff (1894), the two species remain confused by past workers. An *A. roebeleni* collection lot in ZRC was originally labelled as *A. perakensis* (ZRC 1975.2.22.99-126). A specimen labelled as *A. roebeleni* from Banang Pupo, Yala, Thailand is actually *A. perakensis* (ANSP 446394). *Alycaeus roebeleni minor* Möllendorff, 1894, from Biserat, Yala, Thailand is also likely *A. perakensis* (see Remarks in *A. perakensis*). The Perlis population appears to be the southern-end of the distribution range for *A. roebeleni*.

***Alycaeus selangoriensis* sp. n.**
http://zoobank.org/B7390E20-CC8B-4893-BC8B-7DB15521E8CC
Figures 7U, 27, 31O

Alycaeus perakensis: Laidlaw 1932: 37. [not *Alycaeus perakensis* Crosse, 1879a]
Alycaeus (*Alycaeus*) *perakensis*: Chan 1997: 37. [not *Alycaeus perakensis* Crosse, 1879a]
Alycaeus kapayanensis: Venmans 1956: 83. [not *Alycaeus kapayanensis* Morgan, 1885b]
Alycaeus perakensis var. *minor* nomen nudum, Clements et al. 2008: 2760.

Type locality. SGR 01 Batu Caves, Selangor (3°14'17"N, 101°41'02"E).

Type material. *Holotype.* SGR 01 Batu Caves, Selangor: BOR/MOL 12988. *Paratypes.* SGR 01 Batu Caves, Selangor: BOR/MOL 6808/1, BOR/MOL 8314/9, BOR/MOL 12989/1. SGR 02 Bukit Takun, Selangor: BOR/MOL 6810/7, BOR/MOL 8318/2.

Other examined materials. SGR 01 Batu Caves, Selangor: BOR/MOL 268/2, BOR/MOL 6371/>1, BOR/MOL 8315/24, ZRC 1975.2.22.285-382/98, ZRC

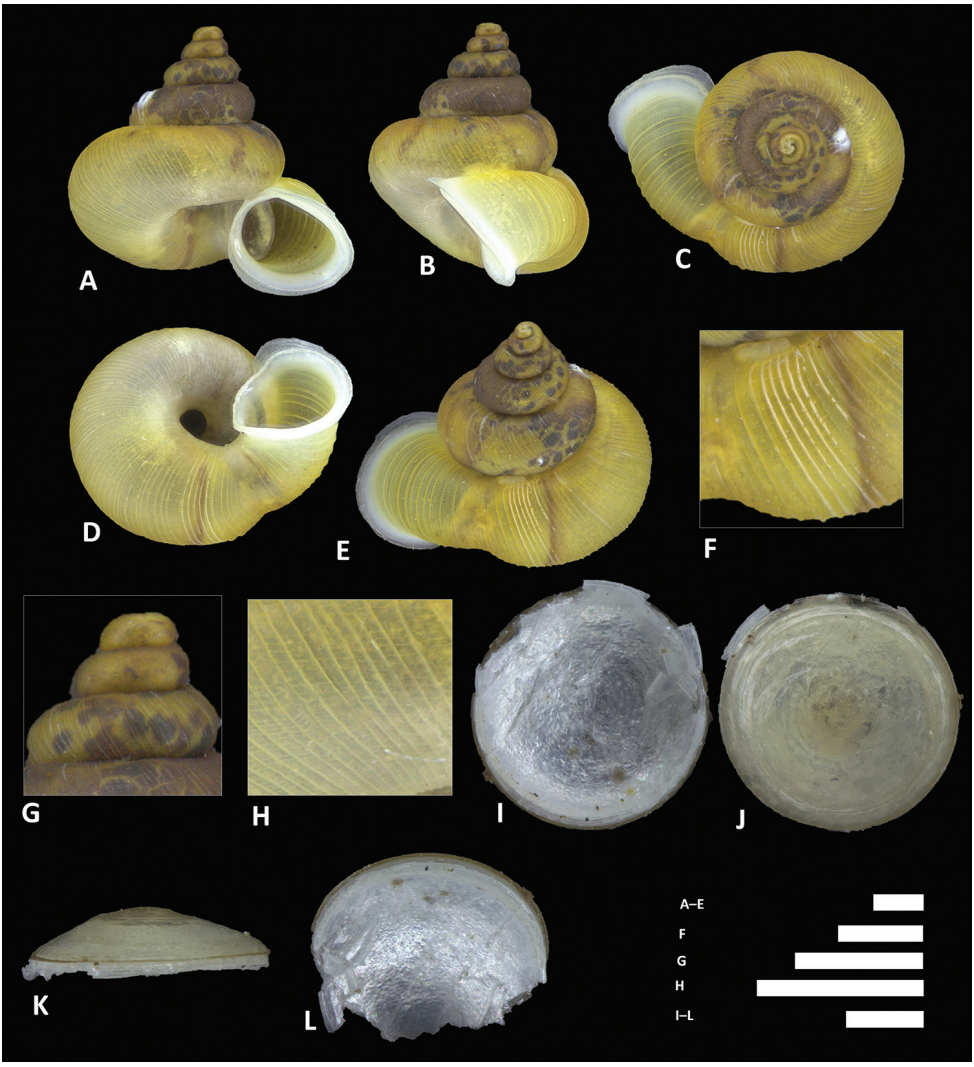

Figure 27. *Alycaeus selangoriensis* sp. n. **A–E** Shell of holotype, BOR/MOL 12988 **F–H** Close up of shell of holotype, BOR/MOL 12988 **I–L** Operculum of paratype, BOR/MOL 6808. Scale bars: **A–E, F, G, H** 1 mm; **I–L** 0.5 mm. All photographs by Junn Kitt Foon.

1997.23/5, RMNH 153568/16, ZMA 33474/1. SGR 02 Bukit Takun, Selangor: BOR/MOL 6627/14, BOR/MOL 8317/6, ZRC 1975.2.22.190-228/39, ZRC 1975.2.24.403-439/37, ZRC 1997.22/5.

Etymology. Named after Selangor, the state that the type locality of this species is part of.

Description. Protoconch. Smooth.

Shell shape. Conical. Shell height: 5.07–5.44 mm. Shell width: 5.06–5.88 mm.

Spire. Spire height: 1.81–2.00 mm. Spire width: 2.35–2.50 mm. Number of whorls: up to 5 ¼. Spire shape: oblong conical. Whorl periphery rounded. Umbilicus open.

Whorl constriction. At about 5 whorls posterior of protoconch.

Breathing tube. Length: 0.52–0.71 mm.

Aperture and peristome. Aperture circular, expanded. Aperture height: 2.68–2.37 mm. Aperture width: 2.33–2.61 mm. Peristome double, not thickened, upper palatal section folded posteriorly into a wing-like structure, notched at suture. Peristome orientation 35–40° oblique with respect to the coiling axis.

Spiral lines. Distinct. Regularly spaced. Approximately 20–33 lines per 1 mm.

Radial ribs running anterior of breathing tube. Radial ribs pronounced, evenly spaced. Approximately 7–20 ribs per 1 mm.

Radial ribs running perpendicular to breathing tube. Radial ribs pronounced, white and thicker than those anterior of breathing tube, evenly spaced. Approximately 11–21 ribs per 1 mm.

Radial ribs running posterior of breathing tube. Radial ribs absent immediately posterior of constriction, becoming pronounced and evenly spaced at the middle until prior to aperture. Approximately 9–14 ribs per 1 mm.

Operculum. Concave, rounded. Exterior covered with thick but flaky calcareous layer, surface finely granulated. Interior proteinaceous layered, smooth, with indistinct mamilla.

Shell colour. Whorls yellow. Peristome white.

Living animal. Body cream-white. Head pinkish-brown. Tentacles reddish-brown.

Habitat and ecology. Lives on wet limestone walls covered with mosses, in forested areas. It can also be found in areas with substantial human disturbance such as on the limestone walls of the temple at Batu Caves.

Distribution. Restricted to Batu Caves and Bukit Takun, Selangor.

Differential diagnosis. *Alycaeus selangoriensis* sp. n. is most similar to *A. kapayanensis* but differs in having a consistently larger shell (larger by about 0.96 mm in shell height, 1.6 mm in shell width), more expanded ultimate whorl and thicker operculum with calcareous exterior. The upper palatal section of the peristome in *A. selangoriensis* sp. n. is always folded posteriorly and downwards, creating a wing-like extension prior to the notch at the suture, a feature not present in the simple circular expanded peristome of *A. kapayanensis*. *Alycaeus selangoriensis* sp. n. resembles *A. perakensis* in having a moderately expanded ultimate whorl but differs in being smaller shelled (smaller by about 1.37 mm in shell height, 2.08 mm in shell width).

Discussion. Historically, *Alycaeus selangoriensis* sp. n. shells have been assigned to superficially similar congeners *A. perakensis* and *A. kapayanensis* (Laidlaw 1932, Venmans 1956, Chan 1997, ZRC and RMNH collection lots). *Alycaeus selangoriensis* sp. n. has also been labelled as "*Alycaeus kapayanensis var. minor*", a nomen nudum (Clements et al. 2008, ZRC collection lots). *Alycaeus selangoriensis* sp. n. is morphologically consistent in having a very expanded ultimate whorl but varies in spire height. Venmans (1956) described and found that the radula and jaw of *A. selangoriensis* sp. n. differ substantially from *A. thieroti* and *A. conformis*.

***Alycaeus senyumensis* sp. n.**
http://zoobank.org/78ADBCEF-599F-41D9-8CBE-C76DA77683ED
Figures 7V–W, 28, 31R

Alycaeus kelantanensis: Clements et al. 2008: 2760.

Type locality. PHG 02 Gunung Senyum, Pahang (3°41'50"N, 102°26'04"E).

Type material. *Holotype.* PHG 02 Gunung Senyum, Pahang: BOR/MOL 12965. *Paratypes.* PHG 02 Gunung Senyum, Pahang: BOR/MOL 6880/2, BOR/MOL 12966/69. PHG 03 Gunung Jebak Puyuh, Pahang: BOR/MOL 8395/6, BOR/MOL 12964/2.

Other examined materials. PHG 02 Gunung Senyum, Pahang: BOR/MOL 275/1, BOR/MOL 6195/6, BOR/MOL 6239/4, BOR/MOL 6249/11, BOR/MOL 8391/41, BOR/MOL 8392/29, ZRC 1975.2.22.444-543/100, ZRC 1975.2.22.626-632/7. PHG 03 Gunung Jebak Puyuh, Pahang: BOR/MOL 6630/13, BOR/MOL 8394/27.

Etymology. Named after the type locality, Gunung Senyum.

Description. Protoconch. Smooth.

Shell shape. Conical. Shell height: 4.49–5.01 mm. Shell width: 3.96–4.41 mm.

Spire. Spire height: 1.47–1.94 mm. Spire width: 2.05–2.28 mm. Number of whorls: up to 5 ¼. Spire shape: oblong conical. Whorl periphery rounded. Umbilicus partially closed.

Whorl constriction. At about 5 whorls posterior of protoconch.

Breathing tube. Length: 0.44–0.57 mm.

Aperture and peristome. Aperture circular, very expanded especially at columellar section. Aperture height: 2.17–2.36 mm. Aperture width: 2.02–2.20 mm. Peristome double, thickened, upper palatal section folded posteriorly into a wing-like structure, notched at suture. Peristome orientation 21–28° oblique with respect to the coiling axis.

Spiral lines. Indistinct. Regularly spaced. Approximately 14–24 lines per 1 mm.

Radial ribs running anterior of breathing tube. Radial ribs pronounced, evenly spaced. Approximately 8–15 ribs per 1 mm.

Radial ribs running perpendicular to breathing tube. Radial ribs pronounced, white and thicker than those anterior of breathing tube, evenly spaced. Approximately 14–21 ribs per 1 mm.

Radial ribs running posterior of breathing tube. Radial ribs unevenly spaced, sometimes distinct but usually absent.

Operculum. Concave, conical. Exterior covered with thin calcareous layer, surface finely granulated. Interior covered with proteinaceous layer, smooth.

Shell colour. Whorls yellow or brownish-red. Peristome white.

Living animal. Body cream-white. Head pink. Tentacles yellow or red.

Habitat and ecology. Lives on both wet, mossy limestone rock walls and boulders. In shady forests on limestone hills. Some living individuals were observed dangling on mucous threads under rock overhangs.

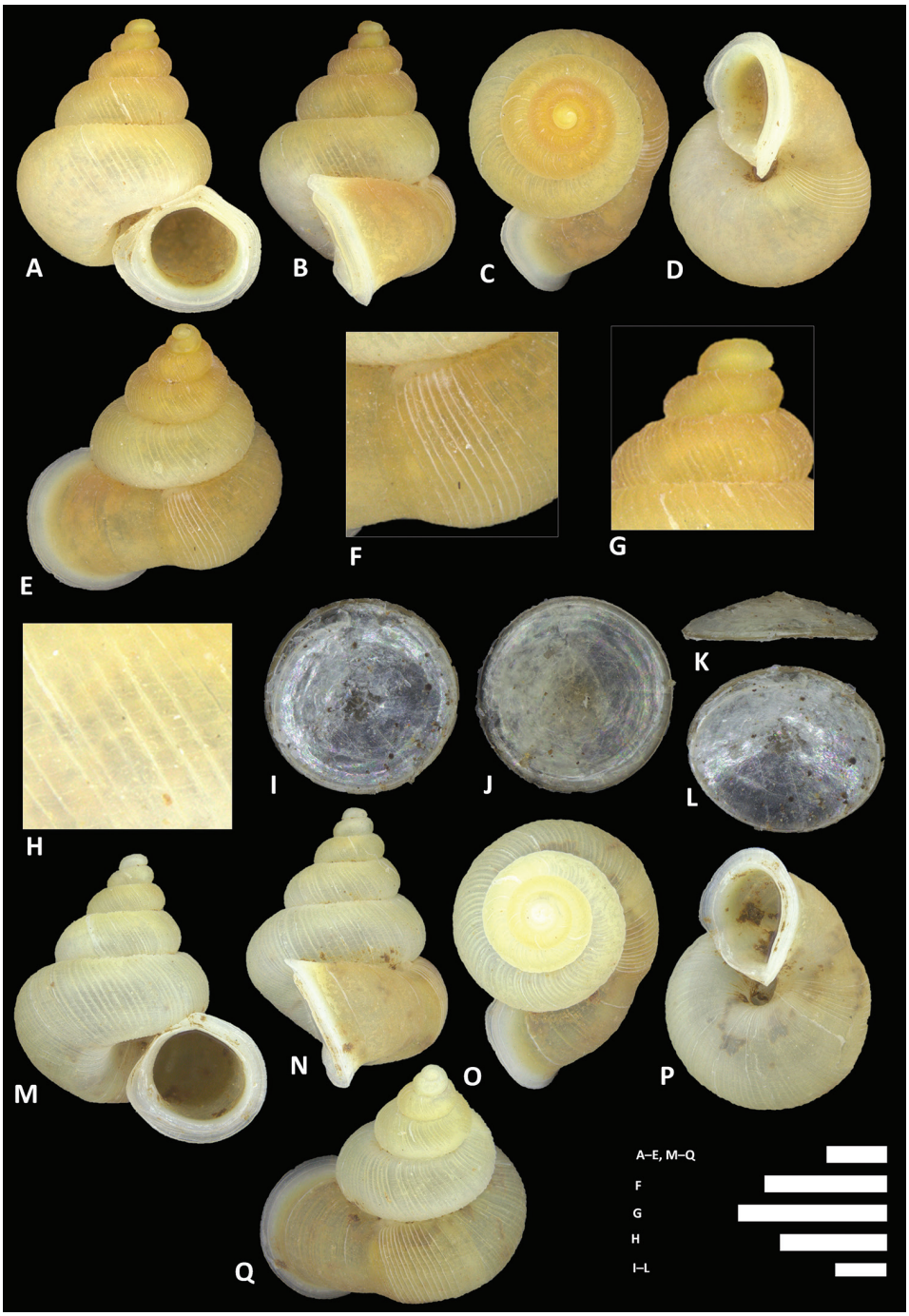

Figure 28. *Alycaeus senyumensis* sp. n. **A–E** Shell of holotype, BOR/MOL 12965 **F–H** Close up of shell of holotype, BOR/MOL 12965 **I–L** Operculum of paratype, BOR/MOL 6880 **M–Q** Shell of paratype, operculum of BOR/MOL 12966. Scale bars: **A–E, F, G, M–Q** 1 mm; **H, I–L** 0.5 mm. All photographs by Junn Kitt Foon.

Distribution range. Restricted to limestone karsts at central Pahang (Gunung Senyum and Gunung Jebak Puyuh) only.

Differential diagnosis. *Alycaeus senyumensis* sp. n. is distinguished from other *Alycaeus* by its peristome that is distinctly expanded and angled at the columellar section and partially obscuring the umbilicus, narrow ultimate whorl, strong radial ribs, shallow suture and small shell. *Alycaeus senyumensis* sp. n. is differentiated from the sympatric *A. regalis* sp. n. and *A. costacrassa* sp. n. by its much smaller shell and expanded peristome angled at the columellar base.

Discussion. Historically, *Alycaeus senyumensis* sp. n. specimens were labelled as *A. kelantanensis* (Clements et al. 2008, ZRC collection lots). *Alycaeus senyumensis* sp. n. occur sympatrically with *A. costacrassa* sp. n. and *A. regalis* sp. n. although syntopically only with *A. costacrassa* sp. n. This is the only *Alycaeus* species we observed dangling from mucous threads during our fieldwork. Such behaviour in *Alycaeus* has been recorded in Peninsular Malaysia and Borneo before (Schilthuizen et al. 1999, Deeleman-Reinhold 2009).

Alycaeus thieroti Morgan, 1885b

Figures 7D, 29, 31C

Alycaeus thieroti Morgan, 1885b: 403-404, plate 10; Venmans 1956: 82, figure 3; Benthem Jutting 1960a: 13; Sykes 1903: 197; Chan 1997: 37; Maassen 2001: 23; Clements et al. 2008: 2760; Tarruella and Domènech 2011: 73; Foon et al. 2017: 13, figure 5A.

Alycaeus (*Orthalycaeus*) *thieroti*: Möllendorff 1891: 342; Kobelt and Möllendorff 1897: 151.

Alycaeus (*Alycaeus*) *thieroti*: Kobelt 1902: 352; Laidlaw 1928: 35; Laidlaw 1932: 36.

Alycaeus liratulus: Liew 2010: 101. [not *Alycaeus liratulus* (Preston, 1907)]

Pincerna thieroti: Páll-Gergely 2017: 213–214.

Type locality. PRK 18 Gunung Lanno, Perak (4°31'31"N, 101°08'48"E).

Type material. *Syntype*. Gunong Lano (= PRK 18 Gunung Lanno), Perak: MNHN IM-2000-31799/5 (1 specimen seen).

Other examined materials. Endau-Kluang, Johor: BOR/MOL 6466/1, BOR/MOL 6467/1. KTN 01 Gunung Reng, Kelantan: BOR/MOL 6835/1, BOR/MOL 8335/6. KTN 95 Gua Panjang, Kelantan: BOR/MOL 12962/5. Lojing, Kelantan: BOR/MOL 6528/2. PHG 01 Kota Gelanggi, Pahang: BOR/MOL 6886/2, BOR/MOL 6636/1. PHG 02 Gunung Senyum, Pahang: BOR/MOL 12961/4. PHG 03 Gunung Jebak Puyuh, Pahang: BOR/MOL 6885/3. PHG 05 Bukit Cintamanis, Pahang: BOR/MOL 6633/1. PHG 75 Bukit Tenggek, Pahang: ZRC 1975.2.22.8-11/2. PHG 77 Bukit Mengapur, Pahang: BOR/MOL 6889/1. Unnamed limestone hill north of Jalan Lipis-Gua Musang Lama, Felda Chegar Perah I and II, Pahang: BOR/MOL 6815/1. Gunung Tangkup, Kenong Rimba, Pahang: BOR/MOL 6237/1.

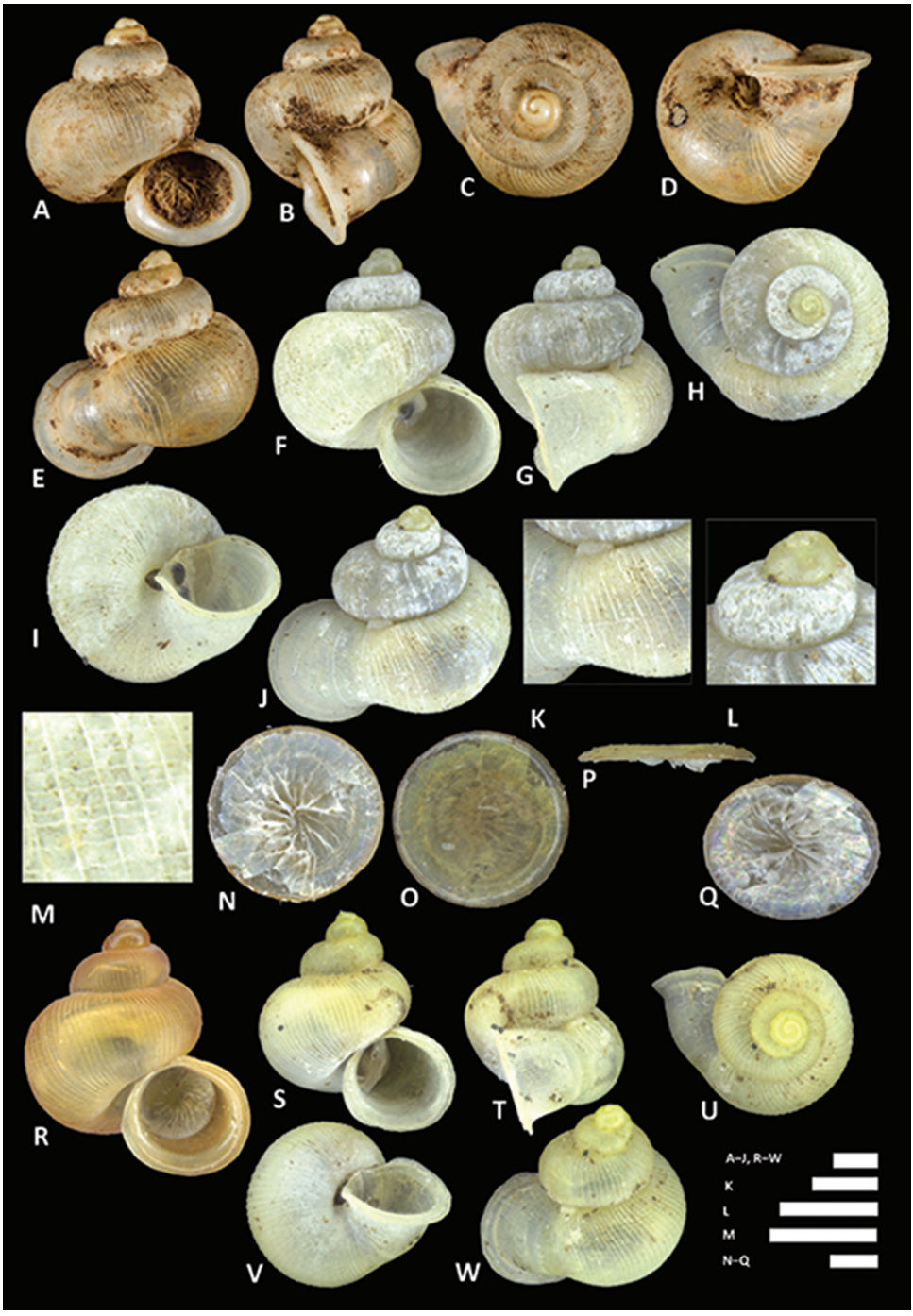

Figure 29. *Alycaeus thieroti* Morgan, 1885b. **A–E** Shell of syntype, MNHN-IM-2000-31799 **F–J** Shell of BOR/MOL 6835 **K–M** Close up of shell of BOR/MOL 6835 **N–Q** Operculum of BOR/MOL 6835 **R** Shell of BOR/MOL 6528a **S–W** Shell of BOR/MOL 6528b. Scale bars: **A–J, R–W** 1 mm; **K, L** 1 mm; **M, N–Q** 0.5 mm. Photographs **A–E** by Manuel Caballer (reproduced herein under CC-BY 4.0 license, Project RECOLNAT, MNHN). Photographs **F–W** by Junn Kitt Foon.

Gunung Kesong, Kenong Rimba, Pahang: BOR/MOL 6253/2. PRK 55 Gunung Pondok, Perak: BOR/MOL 8410/1. PRK 23 Gunung Rapat, Perak: BOR/MOL 10056/4, BOR/MOL 10258/2. PRK 62 Gunong Dayak, Perak: ZRC 1975.2.22.1/1. Mykarst-025, Perak: BOR/MOL 9415/1, BOR/MOL 12422/1. Lenggong, Perak: ZRC 1975.2.22.2-3/2. SGR 02 Bukit Takun, Selangor: ZRC 1997.27/5.

Description. Protoconch. Smooth.

Shell shape and size. Globose. Shell height: 4.55–5.68 mm. Shell width: 4.36–5.34 mm.

Spire. Spire height: 1.06–1.58 mm. Spire width: 1.73–2.30 mm. Number of whorls: up to 4. Spire shape: oblong conical. Whorl periphery rounded. Umbilicus open or partially closed.

Whorl constriction. At about 3 ⅝ whorls posterior of protoconch.

Breathing tube. Length: 0.40–0.53 mm.

Aperture and peristome. Aperture circular, moderately expanded. Aperture height: 2.28–2.76 mm. Aperture width: 2.42–2.98 mm. Peristome double, thickened, notched at suture. No interspace. Peristome orientation 15–18° oblique with respect to the coiling axis.

Spiral lines. Distinct. Regularly spaced. 20–37 lines per 1 mm.

Radial ribs running anterior of breathing tube. Radial ribs pronounced, evenly spaced. Approximately 8–15 ribs per 1 mm.

Radial ribs running perpendicular to breathing tube. Radial ribs pronounced, evenly spaced. Approximately 9–21 ribs per 1 mm.

Radial ribs running posterior of breathing tube. Ranges from absent to indistinct, unevenly spaced.

Operculum. Almost flat. Exterior covered by calcareous layer. Exterior has calcareous ridges radiating outwards of the nucleus. Interior covered by proteinaceous layer, smooth.

Shell colour. Variable – red, yellow or white.

Living animal. Body cream-white or maroon. Head pink. Tentacles red or brown tipped.

Habitat and ecology. Lives in crevices on wet limestone boulders and shrubs close to the ground. In thickly forested areas. Lives in both limestone and non-limestone areas.

Distribution. Widespread in Perak, Selangor, Kelantan and Pahang.

Differential diagnosis. *Alycaeus thieroti* is most similar to *Alycaeus liratulus* in shell shape but differs in having a smaller and more elongated shell (smaller by about 1 mm in shell height, 0.8 mm in shell width), narrowly-spaced radial ribs and spiral lines, shorter breathing tube (shorter by 0.65 mm) and flat operculum with calcareous ridges radiating out from the exterior nucleus.

Discussion. Morgan (1885b) first described *A. thieroti* with simple shell characters and an erroneous description of the operculum as smooth and proteinaceous. Möllendorff (1891) subsequently redescribed the species with additional shell characters but did not point out the error. The operculum is a critical diagnostic feature that clearly distinguishes *A. thieroti* from *A. liratulus*. Thus, this uncorrected error has led to the misidentification of *A. thieroti* as *A. liratulus* and vice versa (e.g. Liew 2010, ZRC collection lots). *Alycaeus thieroti* was known from Perak, Selangor and Kelantan prior to this study (Morgan 1885b, Möllendorff 1891, Sykes 1903, Laidlaw 1928, Laidlaw

1932, Benthem Jutting 1960a, Venmans 1956). *Alycaeus thieroti* in Pahang and Johor are new records. Venmans (1956) examined the radular and jaw features of *A. thieroti*, which is distinct from *A. selangoriensis* sp. n. but similar to *A. conformis* in teeth arrangement. Note that we maintained *Pincerna* as a subgenus of *Alycaeus* although *Pincerna* was recently elevated to genus level (Páll-Gergely 2017). See Remarks section under genus *Alycaeus* for discussion.

***Alycaeus virgogravida* sp. n.**
http://zoobank.org/5A58FAD8-6020-49FE-87CB-21D245D8EEC6
Figures 30, 31S

Type locality. Limestone hill at east side of Pulau Dayang Bunting, off Langkawi Island, Kedah (6°12'26"N, 99°47'04"E).

Type material. *Holotype.* Limestone hill at east side of Pulau Dayang Bunting, off Langkawi Island, Kedah: BOR/MOL 12978. *Paratypes.* Limestone hill at east side of Pulau Dayang Bunting, off Langkawi Island, Kedah: BOR/MOL 12979/1, BOR/MOL 6248/6.

Etymology. Latin, meaning pregnant maiden. Named after the type locality, Pulau Dayang Bunting, meaning island of the pregnant maiden.

Description. Protoconch. Smooth.

Shell shape. Conical. Shell height: 4.71–5.14 mm. Shell width: 4.44–4.97 mm.

Spire. Spire height: 1.68–1.77 mm. Spire width: 2.19–2.50 mm. Number of whorls: up to 4 ½. Spire shape: oblong conical. Whorl periphery rounded. Umbilicus open.

Whorl constriction. At about 4 ¼ whorls posterior of protoconch.

Breathing tube. Length: 0.49–0.51 mm.

Aperture and peristome. Aperture circular, expanded. Aperture height: 2.10–2.36 mm. Aperture width: 2.10–2.29 mm. Peristome double, not thickened, notched at suture. Peristome orientation 29–33° oblique with respect to the coiling axis.

Spiral lines. Distinct. Regularly spaced. Approximately 18–34 lines per 1 mm.

Radial ribs running anterior of breathing tube. Radial ribs pronounced, evenly spaced. Approximately 11–15 ribs per 1 mm.

Radial ribs running perpendicular to breathing tube. Radial ribs pronounced and thicker than those anterior of breathing tube, evenly spaced. Approximately 14–17 ribs per 1 mm.

Radial ribs running posterior of breathing tube. Radial ribs pronounced, unevenly spaced throughout.

Operculum. Concave, rounded. Exterior calcareous layer thick, smooth and polished. Exterior nucleus punctured through, with a cup-like projection. Four concentric ridges were distributed in the tunnel within the thick, cup-like projection. Interior calcareous, with dense concentric circles of multimellae, nucleus punctured through. Operculum edge teethed, etched with regularly spaced grooves.

Shell colour. Whorls yellow. Peristome white.

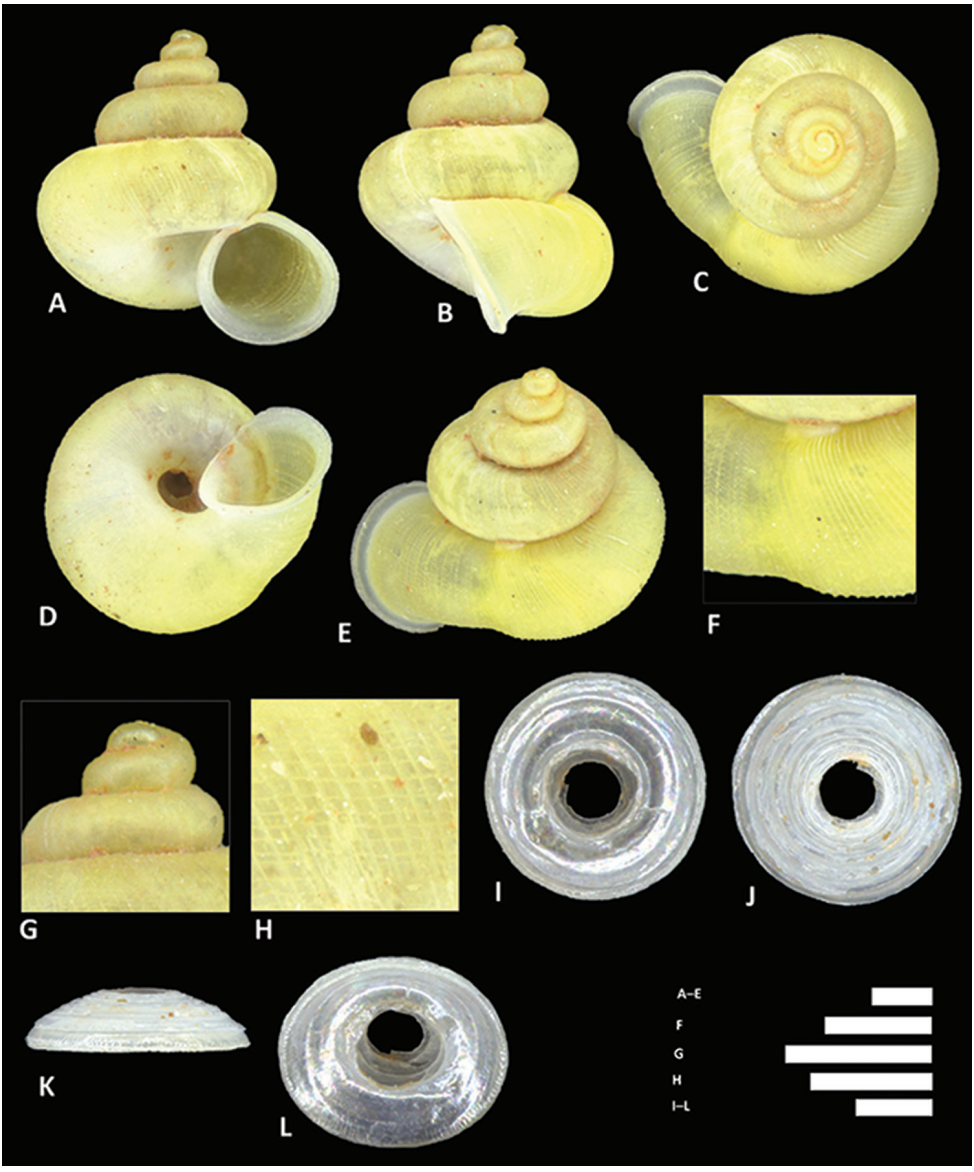

Figure 30. *Alycaeus virgogravida* sp. n. **A–E** Shell of holotype, BOR/MOL 12978 **F–H** Close up of shell of holotype, BOR/MOL 12978 **I–L** Operculum of holotype, BOR/MOL 12978. Scale bars: **A–E, F, G** 1 mm; **H, I–L** 0.5 mm. All photographs by Junn Kitt Foon.

Living animal. Unknown.

Habitat and ecology. Unknown.

Distribution range. Known only from the type locality Pulau Dayang Bunting, Langkawi archipelago.

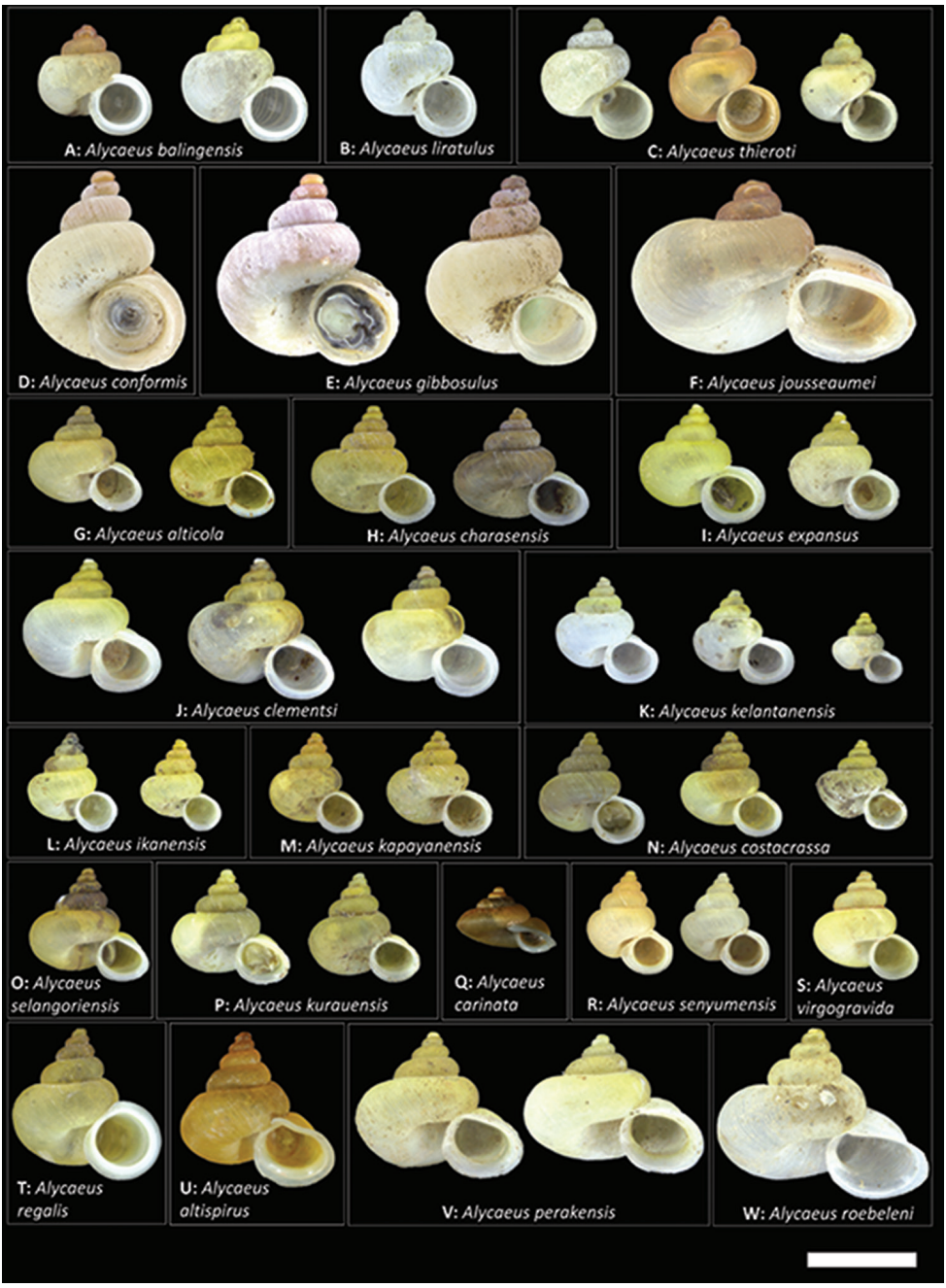

Figure 31. Synoptic view of the 23 *Alycaeus* taxa in Peninsular Malaysia. Scale bar: 5 mm. Photograph of *Alycaeus carinata* by Thor Seng Liew. Photograph of *Alycaeus altispirus* by Páll-Gergely Barna, courtesy of R. Janssen, SMF. All other photographs by Junn Kitt Foon.

Differential diagnsosis. *Alycaeus virgogravida* sp. n. is similar to *A. kapayanensis* in having a conical shell but is distinguished by its more expanded whorls, spacing of radial and spiral ribs, and notably, the thick, calcareous operculum with cup-shaped nucleus. *Alycaeus virgogravida* sp. n. is distinguished from the globose-shelled *Alycaeus liratulus*, the only other species in Peninsular Malaysia with cup-shaped operculum nucleus, by its conical shell.

Discussion. *Alycaeus virgogravida* sp. n. is the only small, conical and yellow *Alycaeus* species in Peninsular Malaysia with cup-shaped operculum.

Acknowledgements

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Supplementary material 1

List of names and coordinates of localities visited during fieldwork in 2016

Authors: Junn Kitt Foon, Thor-Seng Liew

Data type: Table in CSV file

Explanation note: A CSV file containing a list of name and coordinates of localities visited during fieldwork in 2016.

Link: https://doi.org/10.3897/zookeys.692.14706.suppl1

Supplementary material 2

List of specimen measurements used for this study

Authors: Junn Kitt Foon, Thor-Seng Liew

Data type: Table in Microsoft Excel file

Explanation note: A Microsoft Excel file containing a list of specimens and their measurements used in this study.

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RESEARCH ARTICLE

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Three new species of *Pinelema* from caves in Guangxi, China (Araneae, Telemidae)

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Abstract

Three new *Pinelema* species, *P. cunfengensis* Zhao & Li, **sp. n.** (♂♀), *P. podiensis* Zhao & Li, **sp. n.** (♂♀), and *P. qingfengensis* Zhao & Li, **sp. n.** (♂♀), are described from the Guangxi Zhuang Autonomous Region of China, bringing the total number of *Pinelema* species to eight. All occur in Yunnan Province or the Guangxi Zhuang Autonomous Region. The male palp of Telemidae was studied for the first time using scanning electron microscope.

Keywords

Haplogynae, karst region, SEM photographs, taxonomy, Yunnan-Guizhou Plateau

Introduction

Telemidae Fage, 1913 is a small family of haplogyne spiders with nine genera and sixty-six extant species, with one questionable fossil species, *Telema moritzi* Wunderlich, 2004 (Wunderlich 2004). Thirty-seven species in three genera have been described from China (World Spider Catalog 2017), and most of these species are distributed on

the Yunnan-Guizhou Plateau (Lin and Li 2010, Wang and Li 2010, 2016). Two species, *Telema cucphongensis* Lin & Li, 2009 and *Telema exiloculata* Lin & Li, 2009, were described from neighboring northern Vietnam (Lin et al. 2009).

The five described *Pinelema* Wang & Li, 2012 species are: *P. bailongensis* Wang & Li 2012, *P. curcici* Wang & Li, 2016, *P. huobaensis* Wang & Li, 2016, *P. xiushuiensis* Wang & Li, 2016, and *P. yaosaensis* Wang & Li, 2016. All are known from caves in southern China. Here, three new species of *Pinelema* are described, and the details of the male palp were examined using scanning electron microscope (SEM).

Materials and methods

All specimens were examined and measured using a Leica M205 C stereomicroscope. The bodies, male palps, and female receptacles were photographed using an Olympus C7070 digital camera mounted on an Olympus SZX12 stereomicroscope. Images were subsequently combined using Helicon Focus version 6.7.1 image stacking software (http://www. heliconsoft.com). Further morphological details were studied under an Olympus BX41 compound light microscope. The left palps of the male were photographed with a Hitachi SU8010 Scanning Electron Microscope. Vulvae were removed and treated in lactic acid before being photographed. All measurements are reported in millimeters. Leg measurements are shown as total length (femur, patella, tibia, metatarsus, tarsus).

Abbreviations: **CA**, cymbial apophysis; **Em**, embolus; **Re**, receptacle; **Pa**, papillae; **SR**, spiral ridge; **SS**, spine-like structures.

Type specimens were preserved in 95% ethanol and deposited in the Institute of Zoology, Chinese Academy of Sciences (IZCAS), Beijing, China.

Taxonomy

Family Telemidae Fage, 1913

Genus *Pinelema* Wang & Li, 2012

Type species. *Pinelema bailongensis* Wang & Li, 2012 from Guangxi.

Diagnosis and description. See Wang and Li (2012, 2016).

Composition. *Pinelema* currently comprises eight species, including three new species described here. Five of them occur in the Guangxi Zhuang Autonomous Region: *P. bailongensis*, *P. cunfengensis* sp. n., *P. podiensis* sp. n., *P. qingfengensis* sp. n., *P. xiushuiensis*; the others are known from Yunnan Province in southern China: *P. curcici*, *P. huobaensis*, *P. yaosaensis*.

***Pinelema bailongensis* Wang & Li, 2012**
Figs 7A, 8A, 9A, 10A, 11A, 12A

Pinelema bailongensis Wang & Li, 2012: 82, figs 1–17 (♂♀).

Material examined. 1♂ (IZCAS), China: Guangxi Zhuang Autonomous Region: Baise Prefecture: Pingguo County, Bailong Cave, N23°19', E107°34', 111 m, 1.VIII.2009, C. Wang & Z. Yao.

Diagnosis. The species is similar to *P. xiushuiensis* and can be distinguished by a kidney-shaped palpal bulb, many fine papillae at the retrolateral posterior part of the bulb (noted by arrows on Fig. 8A) and spine-like structures on the tip of the embolus (noted by arrows on Figs 8A, 10A) (the bulb is ovoid, and papillae and spine-like structures are absent in *P. xiushuiensis*).

Description. Described by Wang and Li (2012). Here we add the description of the male palp: embolus long, tube shaped, outer margin distinctly protuberant, forming a spiral ridge (Figs 7A, 8A, 9A, 10A, 11A), continuing for approximately 180° around the embolus (Fig. 11A); the groove of the embolus has a cluster of spine-like structures (Figs 8A, 10A) (Wang and Li 2012: figs 1, 4); a distinct slit occurs in the groove, from the tip to the mesal part of the embolus (Figs 8A, 10A).

Distribution. Known only from the type locality.

***Pinelema cunfengensis* Zhao & Li, sp. n.**
http://zoobank.org/7F7662ED-985B-46CB-8AF3-D8719E7DA786
Figs 1–2, 7–12, 13

Type material. Holotype ♂: China: Guangxi Zhuang Autonomous Region: Nanning Prefecture: Longan County: Cunfeng Cave, N23°12.58', E107°35.43', 115 m, 13.V.2015, Z. Chen & Y. Li. **Paratypes:** 3♂ and 5♀, same data as holotype.

Etymology. The specific name refers to the type locality; adjective.

Diagnosis. The new species is similar to *P. podiensis* sp. n., and can be distinguished by the well-developed eyes and greenish abdomen (Figs 1A, 2A) (eyes reduced to white spots, abdomen pale yellow in *P. podiensis* sp. n.); relatively shorter embolus (about 0.33 of bulbal length) (Figs 1C–D, 7B, 8B, 9B, 10B) (0.38 of kidney shaped bulb in *P. podiensis* sp. n.); cymbial apophysis with 3 setae (Fig. 12B) (4 setae in *P. podiensis* sp. n.); receptacle slightly curved at anterior 1/3 (Fig. 2C) (almost straight in *P. podiensis* sp. n.).

Description. Male (holotype): Total length 1.33. Carapace 0.50 long, 0.49 wide. Abdomen 0.79 long, 0.60 wide. Carapace dark yellow with purple-brown pattern (Fig. 1A). Six eyes, all well-developed, ringed with black. Chelicerae, legs, labium and endites dark yellow. Sternum dark brown, with sparse setae. Leg measurements: I 4.11 (1.18, 0.19, 1.33, 0.85, 0.56); II 3.59 (1.08, 0.19, 1.13, 0.69, 0.51); III 2.56 (0.81,

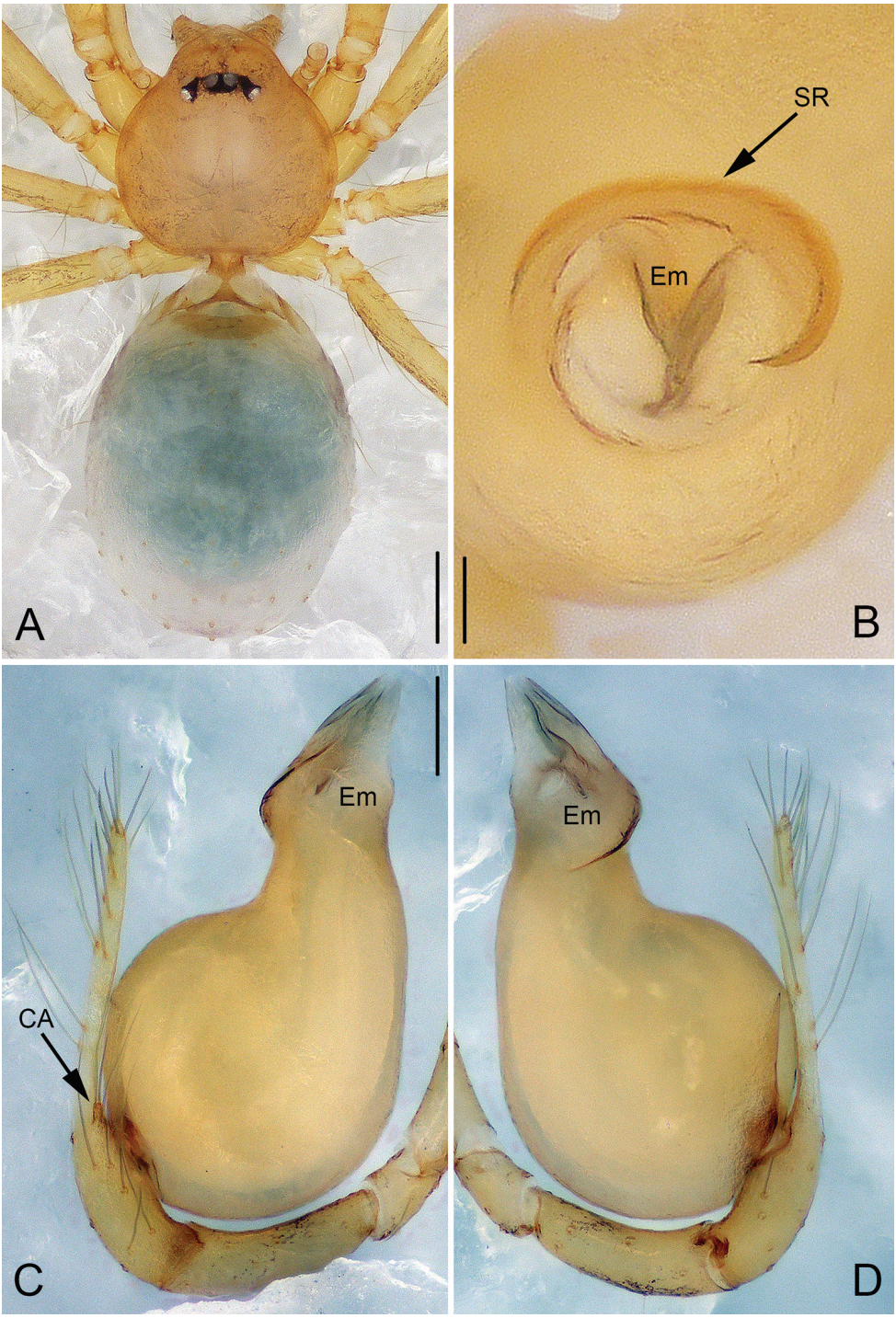

Figure 1. *Pinelema cunfengensis* sp. n., male holotype. **A** Habitus, dorsal view **B** Tip of embolus, apical view **C** Palp, prolateral view **D** Palp, retrolateral view. Scale bars: 0.2 mm (**A**), 0.05 mm (**B**), 0.1 mm (**C–D**).

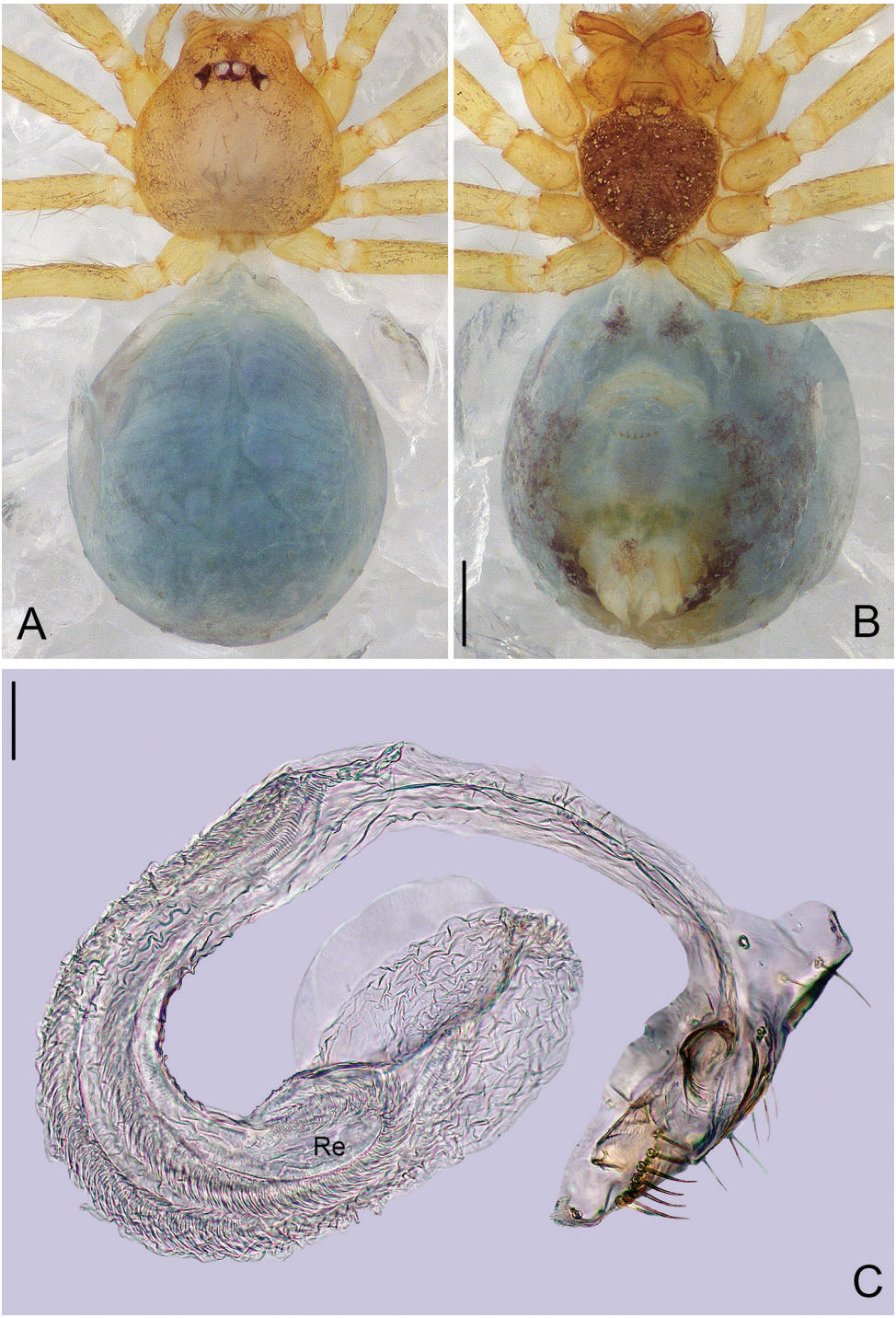

Figure 2. *Pinelema cunfengensis* sp. n., female paratype. **A** Habitus, dorsal view **B** Habitus, ventral view **C** Vulva, lateral view. Scale bars: 0.2 mm (**A–B**), 0.05 mm (**C**).

0.17, 0.75, 0.46, 0.36); IV 3.08 (0.99, 0.18, 0.92, 0.60, 0.38). Abdomen blue-green with purple-brown pattern ventrally.

Palp: tibia 2.5 times longer than patella, cymbium approximately two times longer than tibia, cymbial apophysis with 3 setae (Fig.12B); bulb almost pear shaped (Figs 1C–D, 7B, 8B, 9B, 10B), the spiral ridge makes a continues approximately 180° around the embolus (Figs 1B, 11B); tip of embolus with two grooves, embolus opening slit-like, with the slit originating from the tip and terminating mesally (Figs 8B, 10B).

Female: Total length 1.42. Carapace 0.48 long, 0.48 wide. Abdomen 0.87 long, 0.71 wide. Coloration and pattern as in male (Figs 2A–B). Leg measurements: I 3.67 (1.08, 0.18, 1.15, 0.75, 0.51); II 3.08 (0.95, 0.16, 0.98, 0.61, 0.38); III 2.30 (0.69, 0.17, 0.65, 0.41, 0.38); IV 2.94 (0.92, 0.16, 0.89, 0.56, 0.41).

Distribution. Known only from the type locality (Fig. 13).

Pinelema podiensis Zhao & Li, sp. n.

http://zoobank.org/E3DCFA2B-7B62-440D-AFA1-AD19A6450AB6
Figs 3–4, 7–12, 13

Type material. Holotype ♂: China: Guangxi Zhuang Autonomous Region: Baise Prefecture: Debao County: Podi Cave, N23°23.51', E106°38.40', 578 m, 4.VIII.2011, C. Wang. **Paratypes:** 1♂ and 4♀, same data as holotype.

Etymology. The specific name refers to the type locality; adjective.

Diagnosis. The new species is similar to *P. bailongensis*, and can be distinguished by the strongly reduced eyes and pale yellow abdomen (Figs 3A, 4A) (eyes well-developed and abdomen greenish in *P. bailongensis*); shorter embolus, about 0.38 of the bulb length (0.59 of the bulb length in *P. bailongensis*) (Figs 3C–D, 7C, 8C, 9C, 10C); receptacle coiled approximately 270° (Fig. 4C) (approximately 450° in *P. bailongensis*); the 1st and 2nd setae on cymbial apophysis located at the same height (Fig. 12C) (setae at different heights in *P. bailongensis*).

Description. Male (holotype): Total length 1.25. Carapace 0.48 long, 0.48 wide. Abdomen 0.73 long, 0.56 wide. Carapace yellow, with black yellow margins (Fig. 3A). Reduced eyes appear as white spots. Chelicerae, legs, labium and endites yellow. Sternum pale yellow, with sparse long setae. Leg measurements: I 4.35 (1.25, 0.20, 1.41, 0.89, 0.60); II 3.67 (1.06, 0.20, 1.10, 0.75, 0.56); III 2.64 (0.80, 0.20, 0.72, 0.53, 0.40); IV 3.23 (1.03, 0.19, 0.93, 0.63, 0.46). Abdomen pale yellow, with some green stripes.

Palp: tibia approximately two times longer than patella, cymbium 2.2 times longer than tibia, cymbial apophysis with 4 setae (Fig. 12C); bulb almost kidney shaped, with many fine papillae at the retrolateral posterior part of the bulb (Figs 3D, 8C); embolus long, tube shaped (Figs 3C–D, 7C, 8C, 9C, 10C); the spiral ridge continues approximately 180° around the embolus (Figs 3B, 11C); the opening of the embolus is distinct and as long as 2/3 of the embolus length (Figs 8C, 10C).

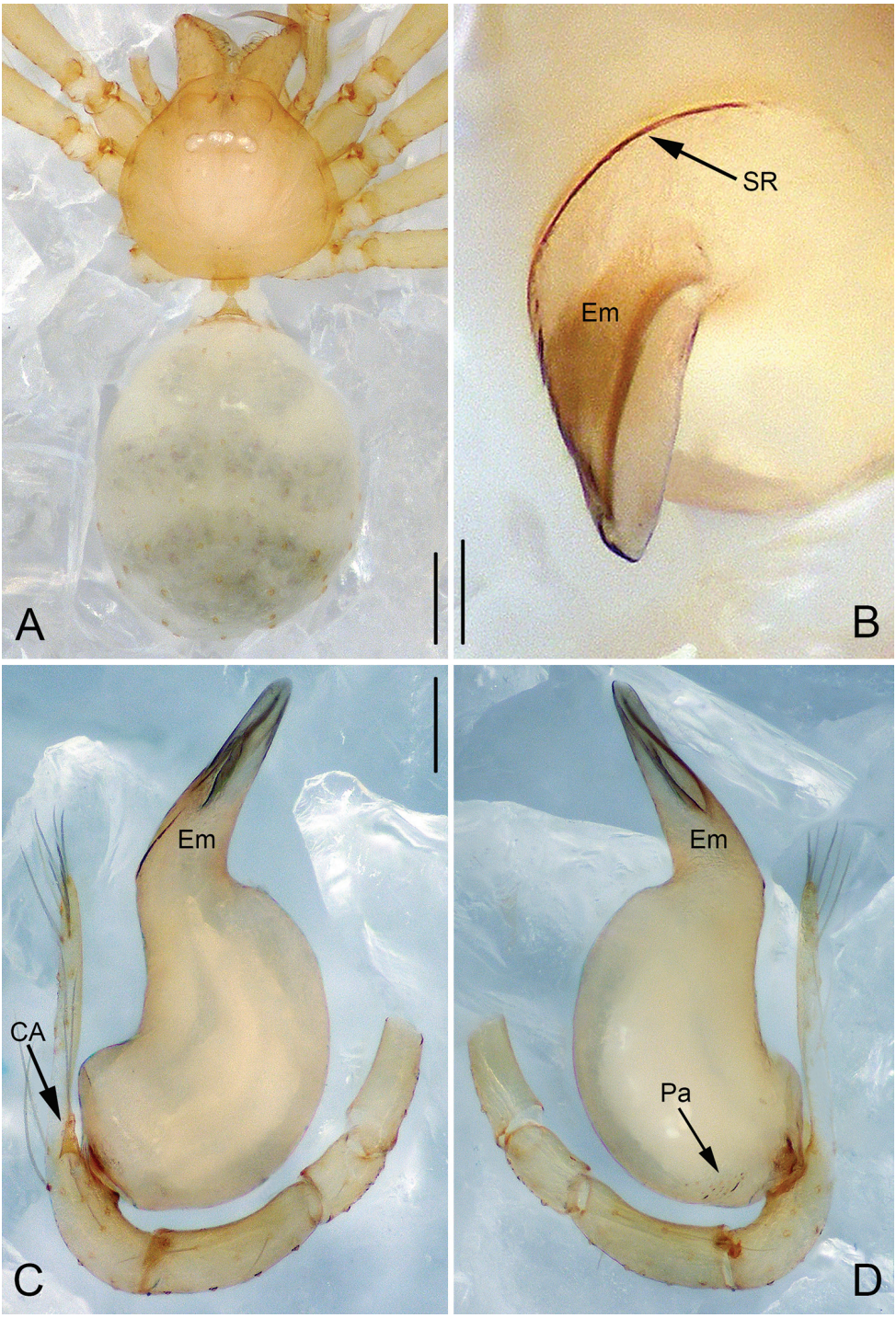

Figure 3. *Pinelema podiensis* sp. n., male holotype. **A** Habitus, dorsal view **B** Tip of embolus, apical view **C** Palp, prolateral view **D** Palp, retrolateral view. Scale bars: 0.2 mm (**A**), 0.05 mm (**B**), 0.1 mm (**C–D**).

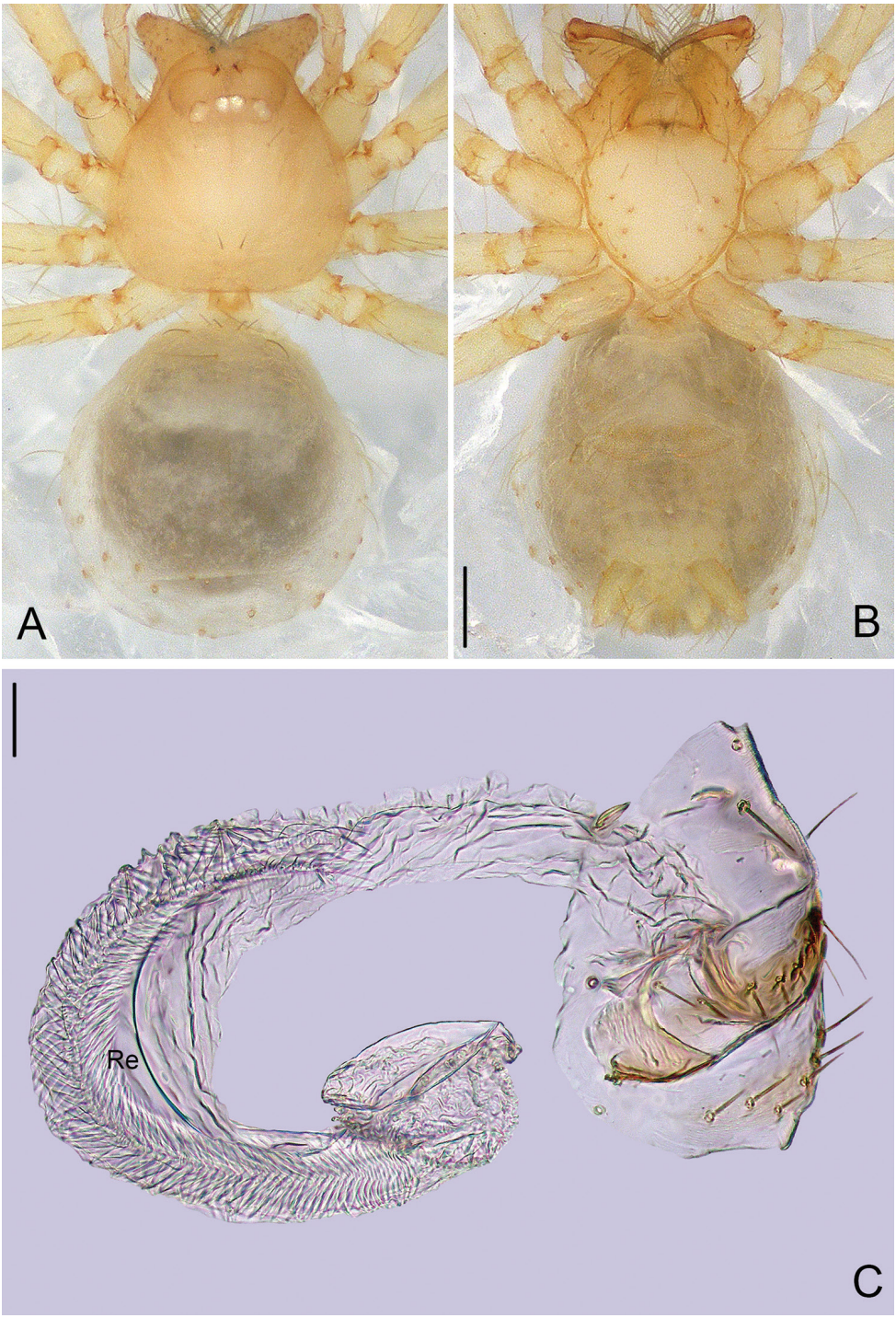

Figure 4. *Pinelema podiensis* sp. n., female paratype. **A** Habitus, dorsal view **B** Habitus, ventral view **C** Vulva, lateral view. Scale bars: 0.2 mm (**A–B**), 0.05 mm (**C**).

Female: Total length 1.45. Carapace 0.46 long, 0.45 wide. Abdomen 0.60 long, 0.60 wide. Coloration and pattern as in male (Figs 4A–B). Leg measurements: I 4.25 (1.22, 0.23, 1.34, 0.84, 0.61); II 3.59 (1.08, 0.20, 1.09, 0.71, 0.51); III 2.59 (0.83, 0.16, 0.71, 0.48, 0.41); IV 3.36 (1.10, 0.19, 0.97, 0.64, 0.46). Receptacle bent at anterior 2/3, curved approximately 270°, with a swollen sac at distal part (Fig. 4C).

Distribution. Known only from the type locality (Fig. 13).

***Pinelema qingfengensis* Zhao & Li, sp. n.**

http://zoobank.org/996421D3-0873-47F3-99D3-2EF4CA739C78

Figs 5–12, 13

Type material. Holotype ♂: China: Guangxi Zhuang Autonomous Region: Chongzuo Prefecture: Tiandeng County: Qingfeng Cave, N23°10.31', E107°09.38', 444 m, 26.XII.2012, Z. Chen & Z. Zhao. **Paratypes:** 1♂ and 6♀, same data as holotype.

Etymology. The specific name refers to the type locality; adjective.

Diagnosis. The new species is similar to *P. bailongensis* and can be distinguished by the completely reduced eyes and yellow abdomen (Figs 5A, 6A) (eyes well-developed and abdomen greenish in *P. bailongensis*); the shorter embolus, 0.40 of bulb length (Figs 5C–D, 7D, 8D, 9D, 10D) (0.59 of bulb length in *P. bailongensis*); receptacle curves approximately 450° (Fig. 6C) (receptacle curves approximately 540° in *P. bailongensis*) and cymbial apophysis with five setae (Fig. 12 D) (four setae in *P. bailongensis*).

Description. Male (holotype): Total length 1.72. Carapace 0.71 long, 0.59 wide. Abdomen 1.00 long, 0.80 wide. Carapace yellow (Fig. 5A). Eyes entirely reduced. Chelicerae, legs, labium, and endites yellow. Sternum pale yellow. Leg measurements: I 6.53 (2.00, 0.25, 2.08, 1.44, 0.77); II 5.91 (1.76, 0.26, 1.90, 1.28, 0.71); III 4.23 (1.47, 0.23, 1.16, 0.84, 0.53); IV 4.60 (1.56, 0.23, 1.33, 0.92, 0.56). Abdomen pale yellow, with sparse long setae.

Palp: tibia 2.2 times longer than patella, tarsus 1.9 times longer than tibia, cymbial apophysis with five setae (Fig. 12D); bulb subconical; embolus long, tube shaped (Figs 5C–D, 7D, 8D, 9D, 10D); the spiral ridge makes a complete 360° turn around the embolus (Figs 5B, 11D), opening of embolus indistinct, as long as half length of embolus (Figs 8D, 10D).

Female: Total length 1.72. Carapace 0.65 long, 0.65 wide. Abdomen1.04 long, 0.89 wide. Coloration and pattern as in male (Figs 6A–B). Leg measurements: I 5.94 (2.13, 0.27, 2.13, 1.42, 0.75); II 5.23 (1.86, 0.26, 1.88, 1.24, 0.63); III 3.81 (1.41, 0.24, 1.31, 0.85, 0.51); IV 4.67 (1.72, 0.24, 1.60, 1.11, 0.59). Receptacle curved, 450° (Fig. 6C).

Distribution. Known only from the type locality (Fig. 13).

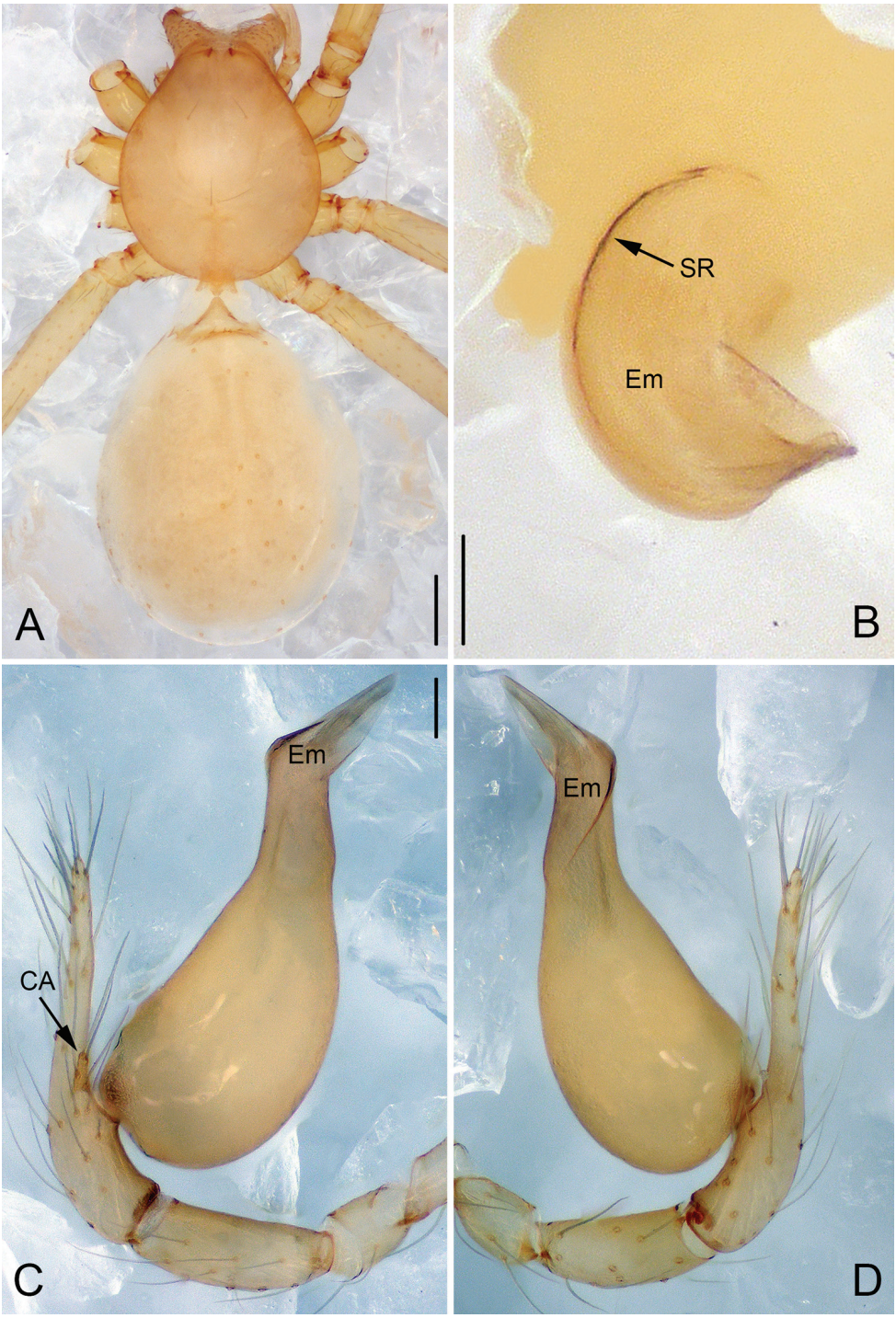

Figure 5. *Pinelema qingfengensis* sp. n., male holotype. **A** Habitus, dorsal view **B** Tip of embolus, apical view **C** Palp, prolateral view **D** Palp, retrolateral view. Scale bars: 0.2 mm (**A**), 0.05 mm (**B**), 0.1 mm (**C–D**).

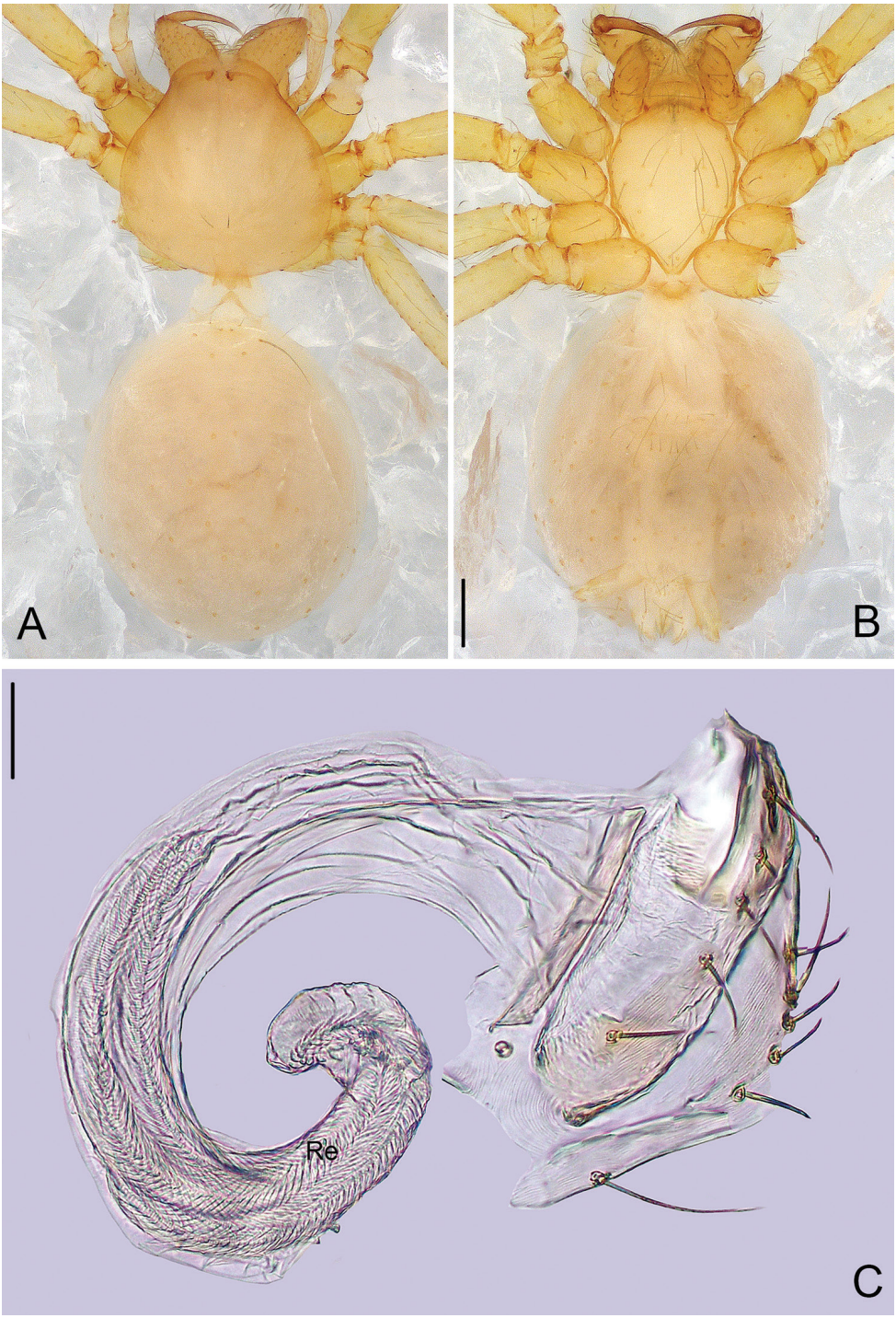

Figure 6. *Pinelema qingfengensis* sp. n., female paratype. **A** Habitus, dorsal view **B** Habitus, ventral view **C** Vulva, lateral view. Scale bars: 0.2 mm (**A–B**), 0.05 mm (**C**).

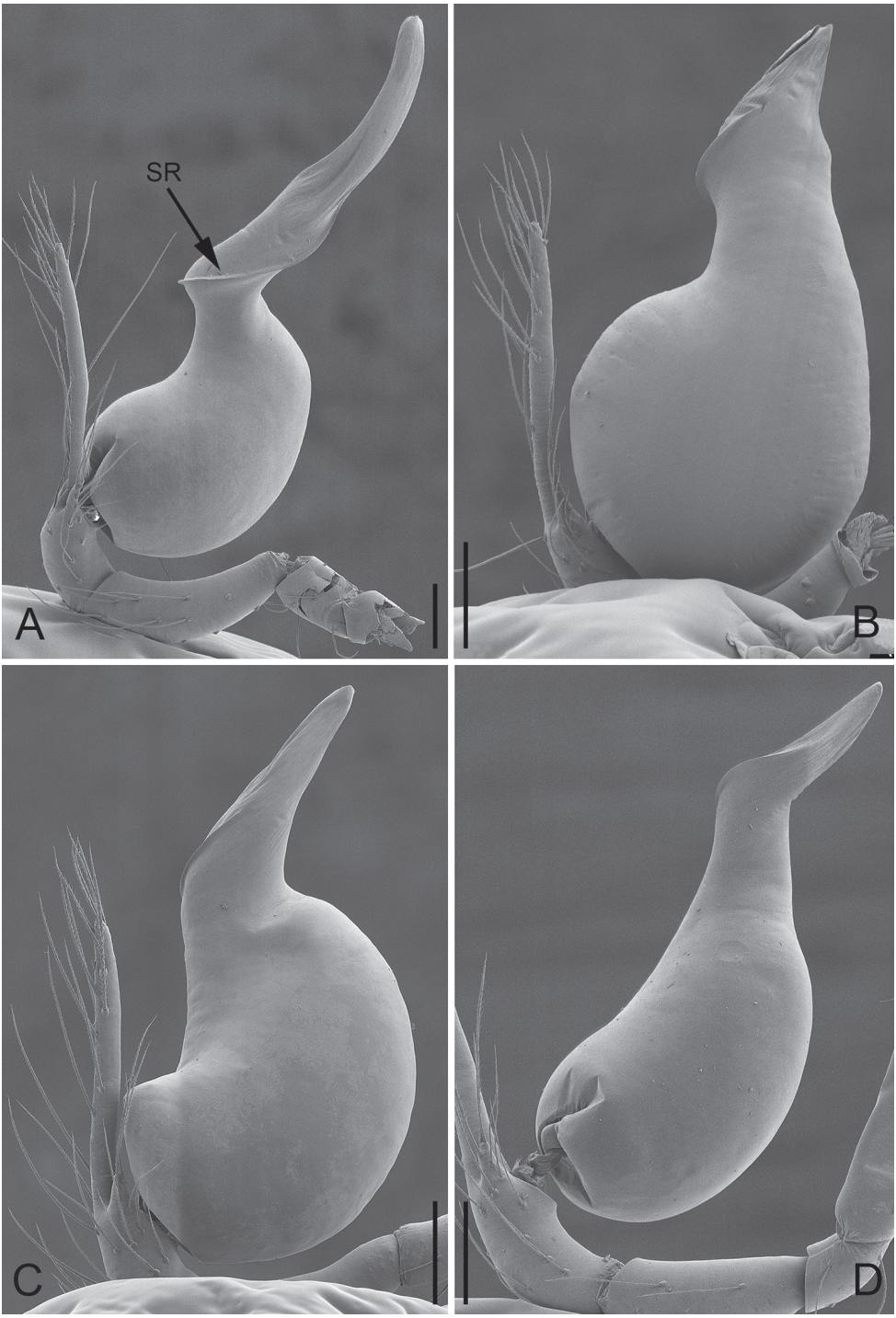

Figure 7. Prolateral view of male palp of *P. bailongensis* (**A**); *P. cunfengensis* sp. n. (**B**); *P. podiensis* sp. n. (**C**); *P. qingfengensis* sp. n. (**D**). Scale bars: 0.1 mm.

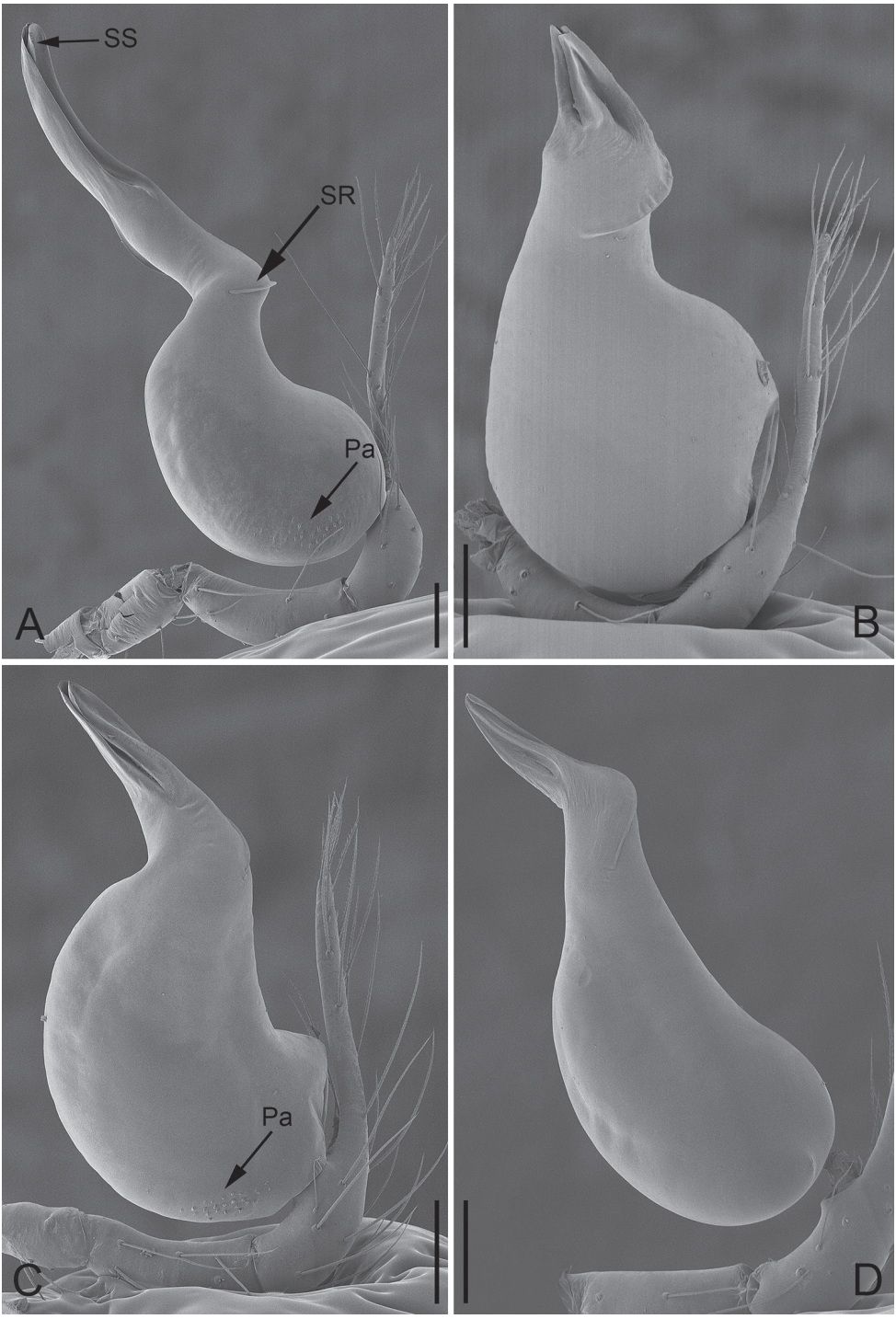

Figure 8. Retrolateral view of male palp of *P. bailongensis* (**A**); *P. cunfengensis* sp. n. (**B**); *P. podiensis* sp. n. (**C**); *P. qingfengensis* sp. n. (**D**). Scale bars: 0.1 mm.

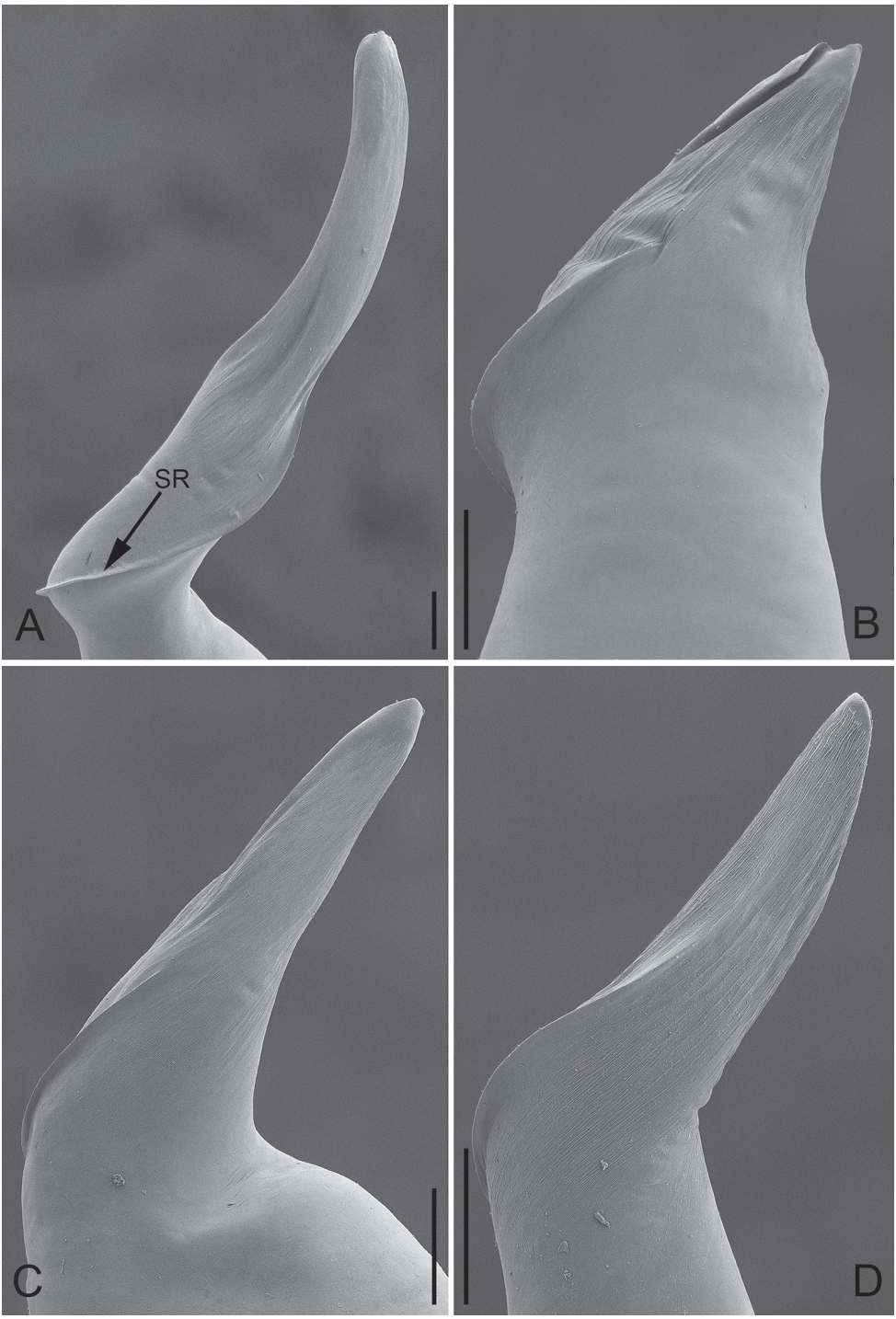

Figure 9. Prolateral view of embolus of *P. bailongensis* (**A**); *P. cunfengensis* sp. n. (**B**); *P. podiensis* sp. n. (**C**); *P. qingfengensis* sp. n. (**D**). Scale bars: 0.05 mm.

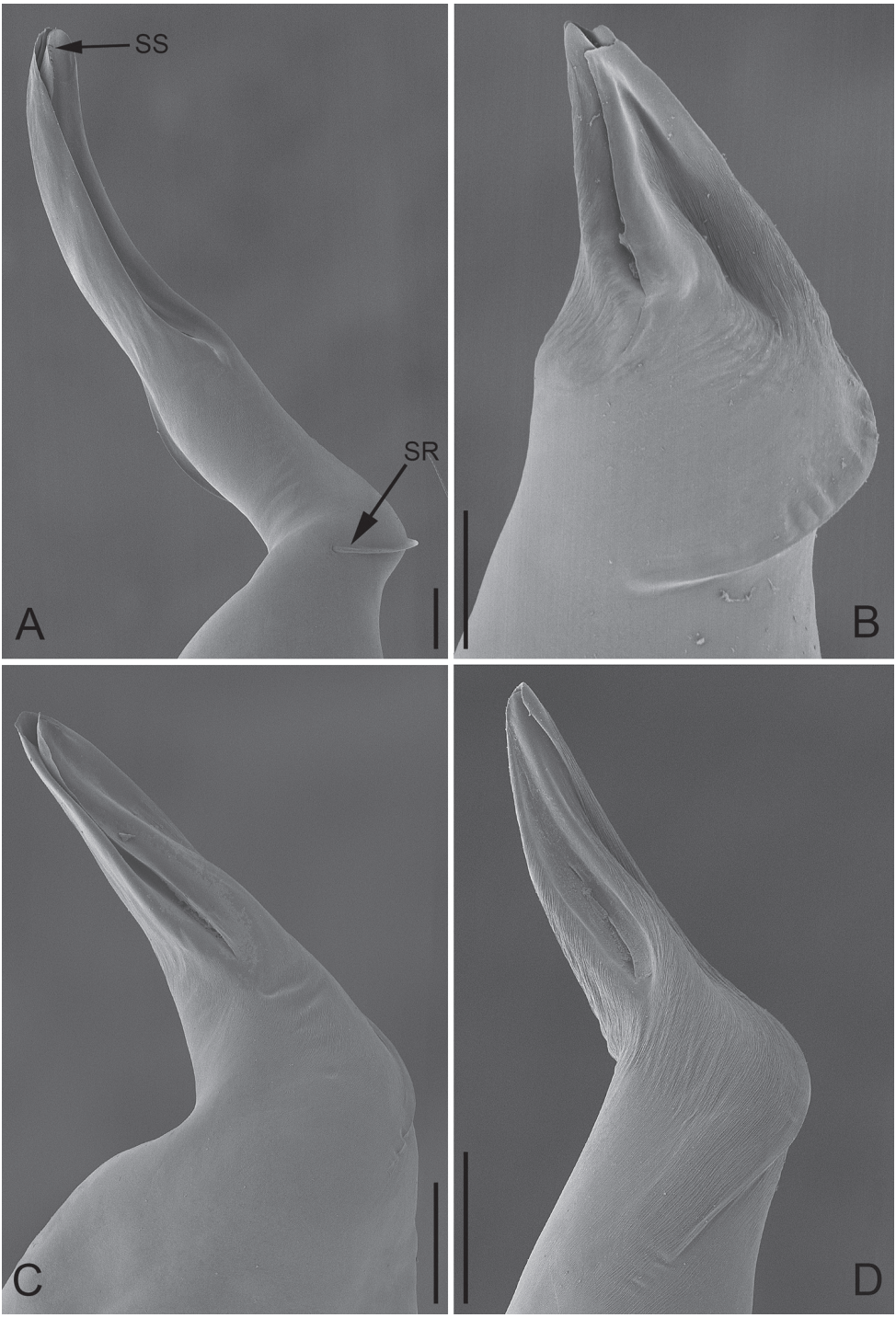

Figure 10. Retrolateral view of embolus of *P. bailongensis* (**A**); *P. cunfengensis* sp. n. (**B**); *P. podiensis* sp. n. (**C**); *P. qingfengensis* sp. n. (**D**). Scale bars: 0.05 mm.

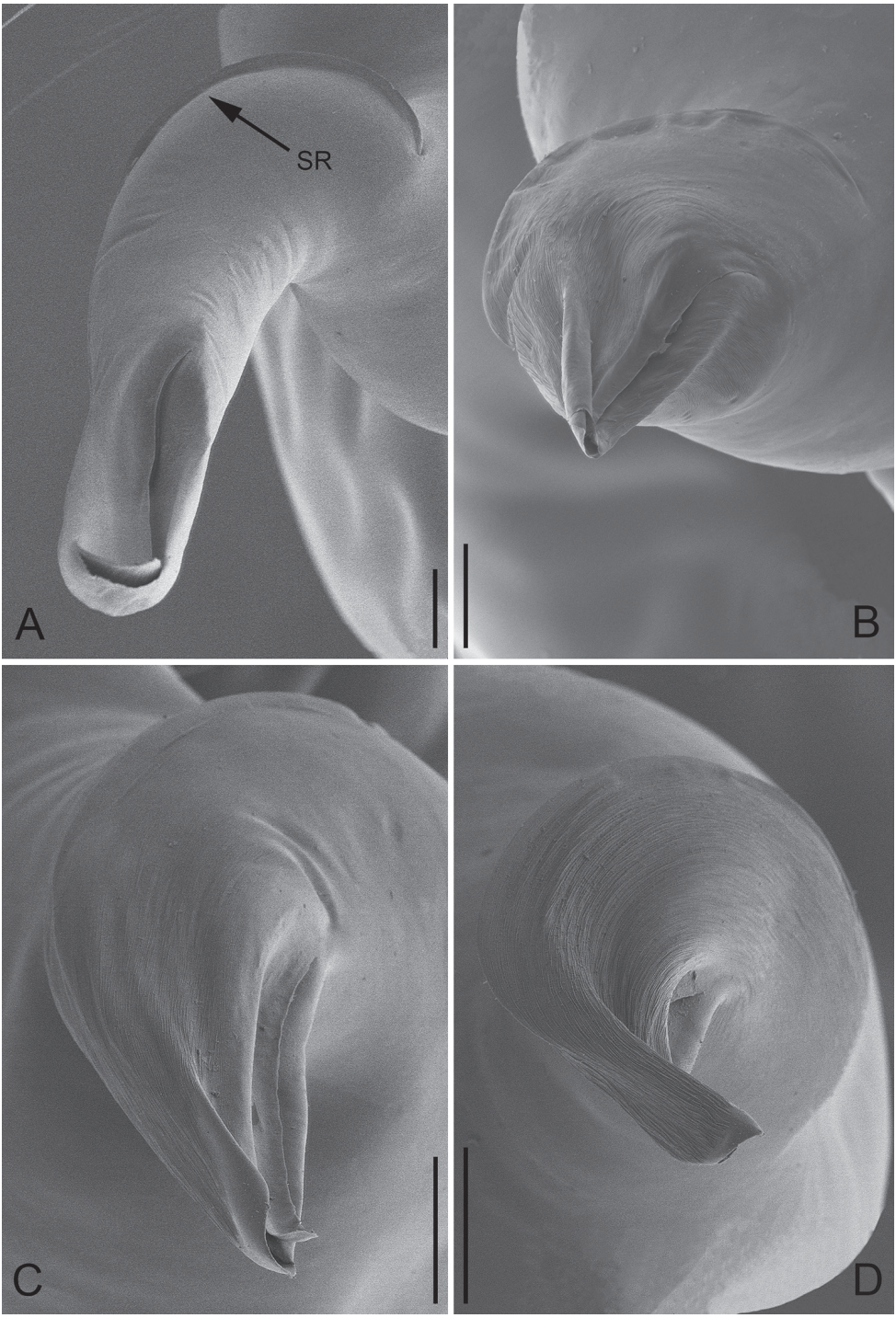

Figure 11. Apical view of embolus of *P. bailongensis* (**A**); *P. cunfengensis* sp. n. (**B**); *P. podiensis* sp. n. (**C**); *P. qingfengensis* sp. n. (**D**). Scale bars: 0.04 mm.

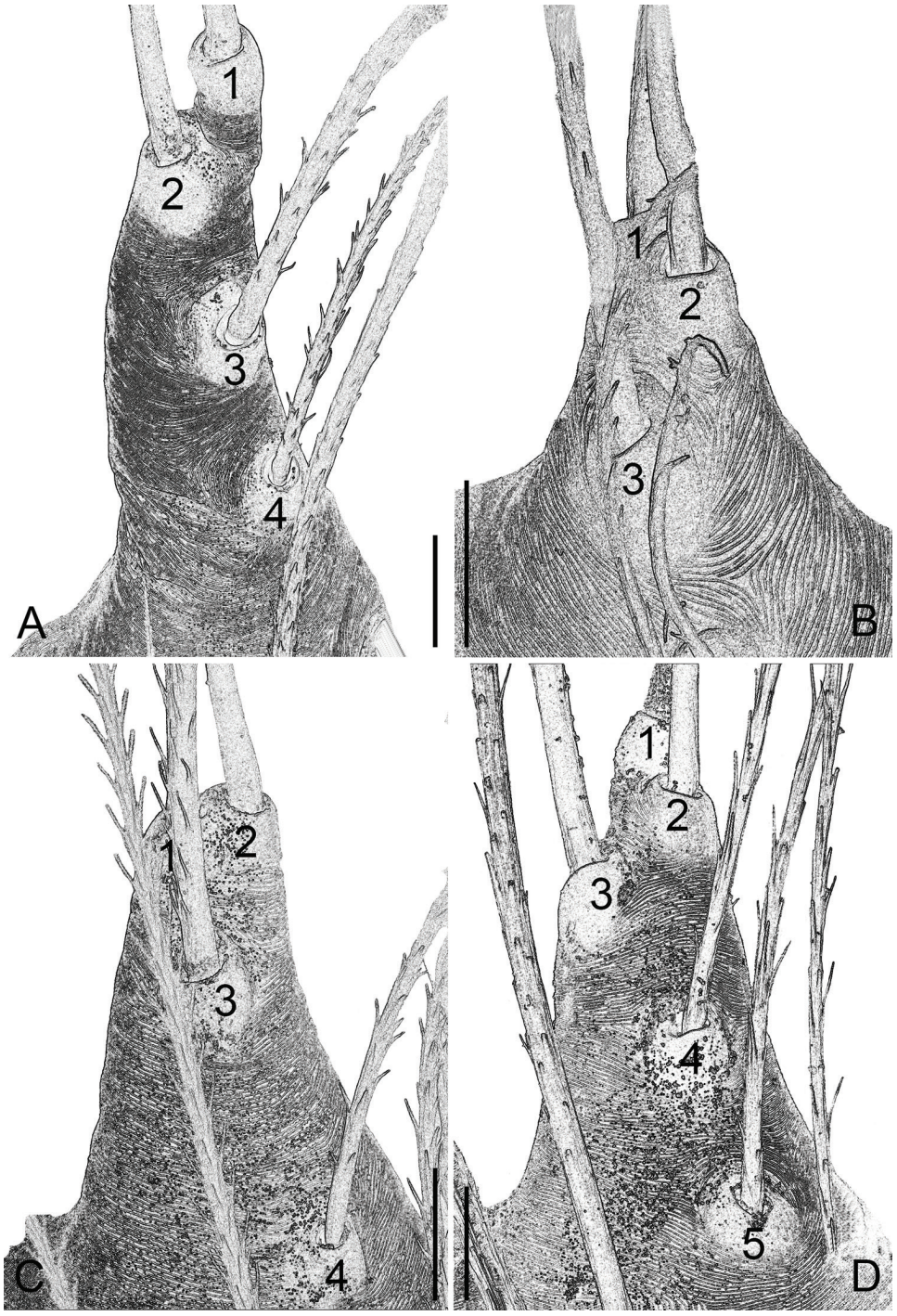

Figure 12. Cymbial apophysis of male palp of *P. bailongensis* (**A**); *P. cunfengensis* sp. n. (**B**); *P. podiensis* sp. n. (**C**); *P. qingfengensis* sp. n. (**D**). Scale bars: 0.01 mm. Arabic numerals refer to 1st–5th setae. First seta in *P. podiensis* sp. n. is lost.

Figure 13. Type localities of three new *Pinelema* species from caves in Guangxi, China.

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RESEARCH ARTICLE

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Discovery of the genus *Nipponodipogon* Ishikawa in the Oriental region, with description of two new species from China (Hymenoptera, Pompilidae)

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Abstract

The genus *Nipponodipogon* Ishikawa, 1965 is newly recorded from China (Guangdong, Hainan, and Yunnan) and the Oriental Region. Two new species, *N. orientalis* Loktionov, Lelej & Xu, **sp. n.** (Guangdong, Hainan, Yunnan) and *N. shimizui* Loktionov, Lelej & Xu, **sp. n.** (Guangdong, Yunnan), are described and illustrated. The updated key to the species based on Shimizu et al. (2015) is given.

Keywords

China, Deuterageniini, new species, *Nipponodipogon*, Oriental Region, Pepsinae

Introduction

The family Pompilidae (spider wasps) is one of the largest families among the aculeate wasps in Hymenoptera. The family numbers around 5000 recent species in 125 genera and five subfamilies in the World (Aguiar et al. 2013, Waichert et al. 2015), 650 species in the Palaearctic (Lelej and Loktionov 2012a). The spider wasps are distributed worldwide, but mostly in the tropical regions (Pitts et al. 2006). The spider wasps

† Deceased

are parasitoids that use spiders as host provisioning each cell with a single paralyzed spider on which they lay an egg (Iwata 1976). Some genera have evolved the mode of cleptoparasitism (Wasbauer 1995, Shimizu 2000, O'Neill 2001, Shimizu et al. 2012).

One of such cleptoparasitic genera is *Nipponodipogon* Ishikawa, 1965, a representative of brood parasitic wasps. Shimizu and Ishikawa (2002) pointed out the peculiar features in their antennal structure: the antenna is short, stout, and thickened toward middle of flagellum, and F2–F10 are somewhat flattened on the anteroventral side. Shimizu et al. (2012) confirmed the brood parasitism of *N. nagasei* and *N. iwatai* by using trap-nest technique. Based on several pieces of circumstantial evidence obtained from the contents of trap nests, they concluded that both species brood-parasitize species of *Deuteragenia* Šustera, 1912 (tribe Deuterageniini), and *N. iwatai* brood-parasitizes species of *Auplopus* Spinola, 1841 (tribe Auplopodini). They also discovered, that female of *N. nagasei* routinely lays up to five eggs on a single host spider, all of which develop into adult wasps without larval cannibalism; instead all spider wasps previously studied lay only one egg on a host spider (Shimizu et al. 2012).

Nipponodipogon, from the tribe Deuterageniini, subfamily Pepsinae, is distributed so far in the Eastern Palaearctic: in the Japanese Archipelago and the south of the Russian Far East. Ishikawa (1965) created this taxon as a subgenus of the genus *Dipogon* Fox, 1897, based on three species from Japan, *Dipogon* (*Nipponodipogon*) *iwatai* Ishikawa, 1965 (Honshu), *D.* (*N.*) *nagasei* Ishikawa, 1965 (Honshu and Kyushu) and *D.* (*N.*) *mandibularis* Ishikawa, 1965 (Honshu), the first of which is the type species. Later, Ishikawa (1968) described one species, *D.* (*N.*) *hayachinensis* Ishikawa from Japan, and Lelej (1986) described two species: *D.* (*N.*) *rossicus* Lelej and *D.* (*N.*) *kurilensis* Lelej from the Russian Far East. In the phylogenetic analysis of the tribe Deuterageniini (Lelej and Loktionov 2012b), *Nipponodipogon*, as well as, other subgenera of the genus *Dipogon* were proposed as separated genera. Shimizu et al. (2015) revised the genus *Nipponodipogon*, and described *N. sudai* Shimizu from Japan. Before this study, the genus included seven species that have been known from Japan and the Russian Far East (Loktionov and Lelej 2014, Shimizu et al. 2015).

In this paper we describe two new species of *Nipponodipogon* from China and enlarge the distribution of the genus to include China and the Oriental Region.

Materials and methods

During the study of hymenopteran collection in South China Agricultural University, we examined more than 2300 specimens of Chinese spider wasps collected during last two decades from Jilin, Inner Mongolia, Ningxia, Gansu, Shaanxi, Henan, Zhejiang, Hebei, Fujian, Hunan, Guangdong, Hainan, Guangxi, Yunnan, Sichuan, and Guizhou. Of them only 14 specimens belonging to the genus *Nipponodipogon* were collected in 2006, 2010, and 2011 years in the Oriental part of China (Guangdong, Hainan and Yunnan) by yellow pan traps and sweeping nets. The following acronyms are used for the collections where type specimens are deposited:

IBSS Federal Scientific Center of the East Asia Terrestrial Biodiversity, Far Eastern Branch of the Russian Academy of Sciences (former Institute of Biology and Soil Science), Vladivostok, Russia (curator Prof. Arkady Lelej).

SCAU Hymenopteran Collection of South China Agricultural University, Guangzhou, China (curator Prof. Zai-fu Xu).

To study male genitalic characters, genitalia were extracted after being previously softened. The muscles were removed in a sodium hydroxide solution (NaOH 10%). The genitalia were later placed in water to neutralize the NaOH and stored in micro vials filled with glycerin. Male genitalia were studied under a stereomicroscope in a depression slide.

Photographs of imagos and genitalia were taken with stereomicroscope SteREO Discovery.V12 and stacked using CombineZM software (Hadley 2008). The final illustrations were post-processed for contrast and brightness using Adobe® Photoshop® software.

The terminology for morphology is mostly based on the glossary provided by the Hymenoptera Anatomy Consortium (2013) and Shimizu et al. (2015). The terminology of wing venation and cells follows Day (1988). The following abbreviations are used for morphological terms:

F1, **F2**, **F3** etc., the first, second, third flagellomeres, etc.;
MID the middle interocular distance;
OOD the distance between posterior ocellus and compound eye which is measured from above;
POD the postocellar distance which is measured from above;
S1, **S2**, **S3** etc., the first, second, third metasomal sterna, etc.;
SMC2 the second submarginal cell of fore wing;
SMC3 the third submarginal cell of fore wing;
T1, **T2**, **T3** etc., the first, second, third metasomal terga etc.;
UID the upper interocular distance.

Systematics

Genus *Nipponodipogon* Ishikawa, 1965

Dipogon (*Nipponodipogon*) Ishikawa, 1965: 89. Type species: *Dipogon* (*Nipponodipogon*) *iwatai* Ishikawa 1965, ♀ (Japan: Honshu), by original designation.

Nipponodipogon: Lelej and Loktionov 2012a: 413; 2012b: 11; Loktionov and Lelej 2014: 153; Shimizu et al. 2015: 498.

Diagnosis. *Female*. Maxillary cardo with a few thin, pale bristles, the apex of these not extending beyond the maxillary lacinia. Antenna short, stout, and thickened to-

ward middle of flagellum (fusiform); F1 less than 3× its width. Supra-antennal area of frons produced anteriorly into a frontal ledge overhanging the antennal radicle. Apical margin of labrum not or slightly emarginated medially. Metapleuron strongly convex above level of lateral face of pronotum and metapleuron (dorsal view). Metapostnotum narrow and practically linear, deeply sunken between the metanotum and propodeum. Crossvein *cu-a* of hind wing short and almost straight, forming obtuse angle with vein *1A*. *Male*. Antenna slightly thickened medially, usually with F3–F11 triangularly produced beneath (except for *N. orientalis* Loktionov, Lelej & Xu, sp. n. and *N. shimizui* Loktionov, Lelej & Xu, sp. n.); F1 1.3–2.0× its width. Mandible with one subapical inner tooth. Body punctate. Exposed portion of hypopygium stick-like, compressed laterally; subbasal portion strongly widened (Figs 21, 42, 48).

Species included. Nine species. *Nipponodipogon hayachinensis* (Ishikawa, 1968), ♀ (Japan: Honshu); *N. iwatai* (Ishikawa, 1965), ♀ & ♂ (Japan: Hokkaido and Honshu); *N. kurilensis* (Lelej, 1986), ♀ (Russia: Kuril Islands); *N. mandibularis* (Ishikawa, 1965), ♀ (Japan: Honshu); *N. nagasei* (Ishikawa, 1965), ♀ & ♂ (Japan: Hokkaido, Honshu and Kyushu); *N. rossicus* (Lelej, 1986), ♀ & ♂ (Russia: Primorskij Terr.); *N. sudai* Shimizu *in* Shimizu, Lelej & Loktionov, 2015, ♀ & ♂ (Japan: Hokkaido and Honshu) (Shimizu et al. 2015 and Shimizu and Terayama 2016); *N. orientalis* Loktionov, Lelej & Xu, sp. n., ♀ & ♂ (China: Guangdong, Hainan and Yunnan); *N. shimizui* Loktionov, Lelej & Xu, sp. n., ♀ & ♂ (China: Guangdong and Yunnan).

Distribution. Palaearctic Region (Russia: Primorskij Terr., Kuril Islands; Japan: Hokkaido, Honshu, Kyushu) and Oriental Region (new record) (China: Guangdong, Hainan, Yunnan).

Biology. The representatives of the genus *Nipponodipogon* are brood parasitic wasps. *Nipponodipogon nagasei* and *N. iwatai* brood-parasitize species of *Deuteragenia* Šustera, 1912 (tribe Deuterageniini), and *N. iwatai* brood-parasitizes species of *Auplopus* Spinola, 1841 (tribe Auplopodini). Female of *N. nagasei* routinely lays up to five eggs on a single host spider, all of which develop into adult wasps without larval cannibalism, instead all spider wasps previously studied lay only one egg on a host spider (Shimizu et al. 2012).

Nipponodipogon orientalis Loktionov, Lelej & Xu, sp. n.

http://zoobank.org/006909A8-2FEC-4B94-95AF-766C7B128E5F
Figs 1–22

Material examined. Holotype. CHINA: ♀, Guangdong, Nankunshan, 4–6.VI.2011, Zai-fu Xu, No. 2016001247 (SCAU). **Paratypes**. CHINA: 2 ♀, with the same data as holotype, No. 2016001227 and 2016001217 (SCAU); 1 ♀, with the same data as holotype, No. 2016001255 (SCAU); 1 ♀, Hainan, Diaoluoshan, 12–13.VII.2010, Hua-yan Chen, No. 2016000370 (SCAU); 1 ♂, Yunnan, Gaoligongshan, 20–21. VII.2006, Zai-fu Xu, No. 2016000480 (IBSS); 1 ♂, Yunnan, Gaoligongshan, 20–21. VII.2006, Zai-fu Xu, No. 2016000479 (SCAU).

Figure 1. *Nipponodipogon orientalis* Loktionov, Lelej & Xu, sp. n., female, holotype, habitus, lateral view. Scale bar 1 mm.

Diagnosis. *Female*. Mesosoma completely yellow orange (Figs 1, 7). Posterolateral portion of propodeum with strong transverse rugae (Figs 5–7). T1 with long petiole basally (Fig. 6). Outer apicoventral corner of the metafemur produced triangularly (Fig. 8). *Male*. T1 distinctly petiolate basally (Fig. 15). F3–F11 not produced triangularly beneath, not forming serrated profile. Propodeum matt, with weak dense transverse striae posterolaterally (Fig. 15). Subbasal portion of hypopygium with round sublateral carina (Fig. 21, arrow).

Description. ***Female***. Body length 6.1–8.0 mm; fore wing length 4.7–6.2 mm. Head and metasoma black; sometimes clypeus along anterior margin brownish; antenna black, except flagellomeres 3–10 muddy yellow ventrally and sometimes scape and pedicel yellowish-brown ventrally; mandible brownish subapically. Mesosoma completely yellow orange (Figs 1, 7). Legs brown with abundant yellowish-brown (Fig. 1) to completely muddy yellowish. Fore wing weakly infuscate or sometimes more or less yellowish, with distinct two fuscous bands (Fig. 9). Hind wing weakly infuscate (Fig. 10).

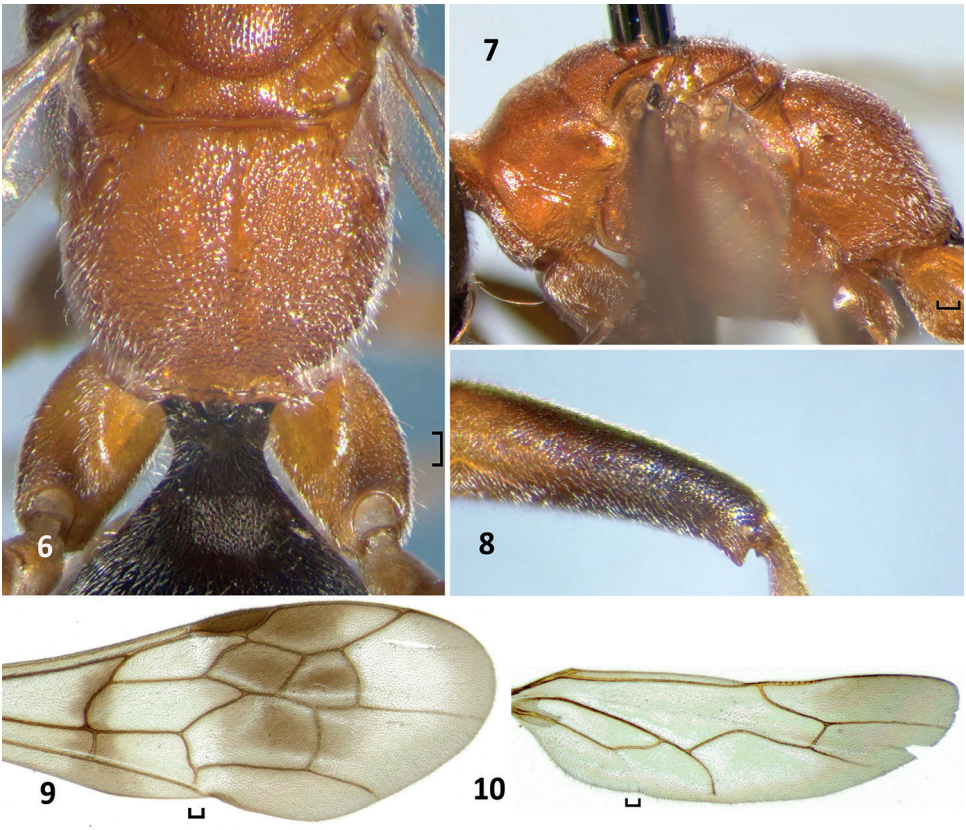
Head and mesosoma matt. Frons, vertex, and mesosoma, except propodeum, finely and densely punctate. Pronotum anteriorly, laterally and collar finely striate and punctate. Mesopleuron with denser punctures. Upper mesopleuron and metapleuron finely

Figures 2–5. *Nipponodipogon orientalis* Loktionov, Lelej & Xu, sp. n., female, paratype. **2** Head and pronotum, dorsal view **3** Head, frontal view **4** Head, lateral view **5** Propodeum, dorsolateral view. Scale bars 0.1 mm.

and densely striate. Lateral side of metanotum with several regular oblique striae. Propodeum strongly and densely punctate with fine transverse rugae posteriorly and much stronger rugae posterolaterally (Figs 5–7). Metasoma somewhat polished. T1–T5 with fine punctures; T6 and S6 less polished than other segments, with scattered setiferous pores located on all exposed portion; S1–S5 with somewhat larger punctures than on T1–T5. S1 with several longitudinal rugae baso-medially. Transverse groove on S2 gently arcuate.

Body with gray pubescence mostly short, but longer on clypeus, mesopleuron, propodeum posterolaterally and coxae. Body without setae except the following: upper frons sometimes with one long erect setae and a few shorter ones; clypeus with a few long suberect setae anteriorly; coxae and T1 basally with scattered short erect setae; S2–S5 with scattered longer erect setae posteriorly; T6 and S6 with denser long erect pale setae.

Width of *head* in frontal view 1.1–1.2× its height. Vertex weakly convex between eye tops (Fig. 3). Upper frons gently convex (Fig. 4). Frons without median line, but sometimes with indistinct elongate concavity medially. Supra-antennal area of frons



Figures 6–10. *Nipponodipogon orientalis* Loktionov, Lelej, Xu, sp. n., female, paratype. **6** Mesoscutellum, metanotum, metapostnotum, propodeum and T1, dorsal view **7** Mesosoma, lateral view **8** Metafemur, outer lateral view **9** Fore wing **10** Hind wing. Scale bars 0.1 mm.

produced anteriorly into a frontal ledge overhanging the antennal radicle (Fig. 4). Inner orbits weakly convergent above and subparallel below (Fig. 3). Half of MID 1.3–1.4× eye width. Ocelli large, slightly raised; ocellar triangle acute-angled (Fig. 2); POD/OOD=0.8–1.1. Posterior margin of vertex roundly concave (dorsal view) (Fig. 2). Clypeus convex medially with distinct concavity basolaterally; anterolateral corner broadly rounded; anterior margin almost straight or weakly emarginate medially; width 2.7–2.9× its length. Apical margin of labrum broadly rounded. Mandible with subapical tooth. Maxillary cardo with two tufts of thin, light brown bristles. Malar space short. Gena strongly narrowing posteriorly (Fig. 2, dorsal view; Fig. 4, lateral view). Antenna short, stout, and thickened toward middle of flagellum; F1–F3 distinctly widening toward apex; apex of apical flagellomere pointed; F1 length 0.95–1.0× F2 length; F1 length 2.2–2.4× its width and 0.50–0.65× UID.

Pronotum with anterior declivity flattened, not distinctly differentiated from dorsum; dorsum in dorsal view slightly narrowing anteriorly; shoulder gently rounded;

juncture between dorsal and lateral faces narrowly and roundly raised; posterior margin weakly and arcuately emarginate medially. Mesoscutum slightly sloped anteriorly; posterolateral margin not reflexed; parapsidal sulcus finely impressed. Discs of mesoscutellum and metanotum barely raised above level of mesoscutum and propodeum (Fig. 7). Metapostnotum narrow and practically linear, deeply sunken between metanotum and propodeum (Fig. 6). Propodeum evenly convex with flattened posterior declivity not well differentiated from dorsum (Fig. 7).

Fore wing (Fig. 9) with SMC2 receiving crossvein *1m-cu* at almost middle; SMC3 1.1–1.2× longer than SMC2 on vein *M*, and 0.6–0.7× longer than SMC2 on vein *Rs*; receiving crossvein *2m-cu* at almost middle; crossvein *2rs-m* almost straight or sometimes barely curved; crossvein *3rs-m* distinctly curved; crossvein *cu-a* barely postfurcal. Hind wing (Fig. 10). Outer apicoventral corner of metafemur produced triangularly (Fig. 8). Claws symmetrical with large subapical inner tooth. T1 distinctly petiolate (Fig. 6). S6 with a longitudinal median rounded carina posteriorly.

Male. Body length 3.7–4.6 mm; fore wing length 3.5–4.1 mm. Body black; antenna black with scape brown or black ventrally and flagellum weakly brown ventrally; mandible brown subapically; pro- tibia and tarsi brown; spurs of pro- and mesotibia brown, spurs of metatibia dark brown (Fig. 11). Fore wing weakly infuscate, with weak subapical fuscous band (Fig. 16). Hind wing weakly infuscate (Fig. 17).

Body mostly punctate and somewhat polished. Frons, discs of pronotum, mesoscutum, mesoscutellum, and metanotum finely and densely punctate. Pronotum laterally polished and indistinctly punctate. Mesopleuron with coarser punctures than frons. Upper mesopleuron striate. Lateral side of metanotum with several regular oblique striae. Metapleuron finely punctate. Propodeum more or less matt, finely and densely punctate with weak dense transverse striae posterolaterally. Metasomal segments finely punctate. S1 with several longitudinal rugae basally. Transverse groove on S2 weak, gently arcuate, not connected medially. S6 with scattered setiferous pores (Fig. 18). Body with gray pubescence mostly short, but longer on lower face, clypeus, propleuron, propodeum posteriorly and mesepisternum. Body without setae except the following: upper frons with one long erect setae; T7 and S6 with long erect brown setae.

Width of *head* in frontal view 1.1× its height. Vertex moderately convex between eye tops (Fig. 13). Upper frons gently convex (Fig. 14). Frons without median line, with indistinct elongate concavity medially. Supra-antennal area of frons produced anteriorly into weak frontal ledge overhanging the antennal radicle (Fig. 14). Inner orbits subparallel above and barely convergent below (Fig. 13). Half of MID 1.4–1.6× eye width. Ocelli large, noticeably raised; ocellar triangle right-angled (Fig. 12); POD/OOD=0.75–0.85. Posterior margin of vertex straight (dorsal view) (Fig. 12). Clypeus weakly convex medially; anterolateral corner broadly rounded; anterior margin barely broadly rounded, almost straight medially. Mandible with subapical tooth. Malar space short. Gena narrowing posteriorly (Fig. 12, dorsal view; Fig. 14, lateral view). Antenna shortened; flagellum filiform; flagellomeres indistinctly convex ventrally, not forming triangle projection; apex of apical flagellomere pointed; F1 length 0.9–1.0× F2 length; F1 length 1.85–1.90× its width and 0.30–0.36× UID.

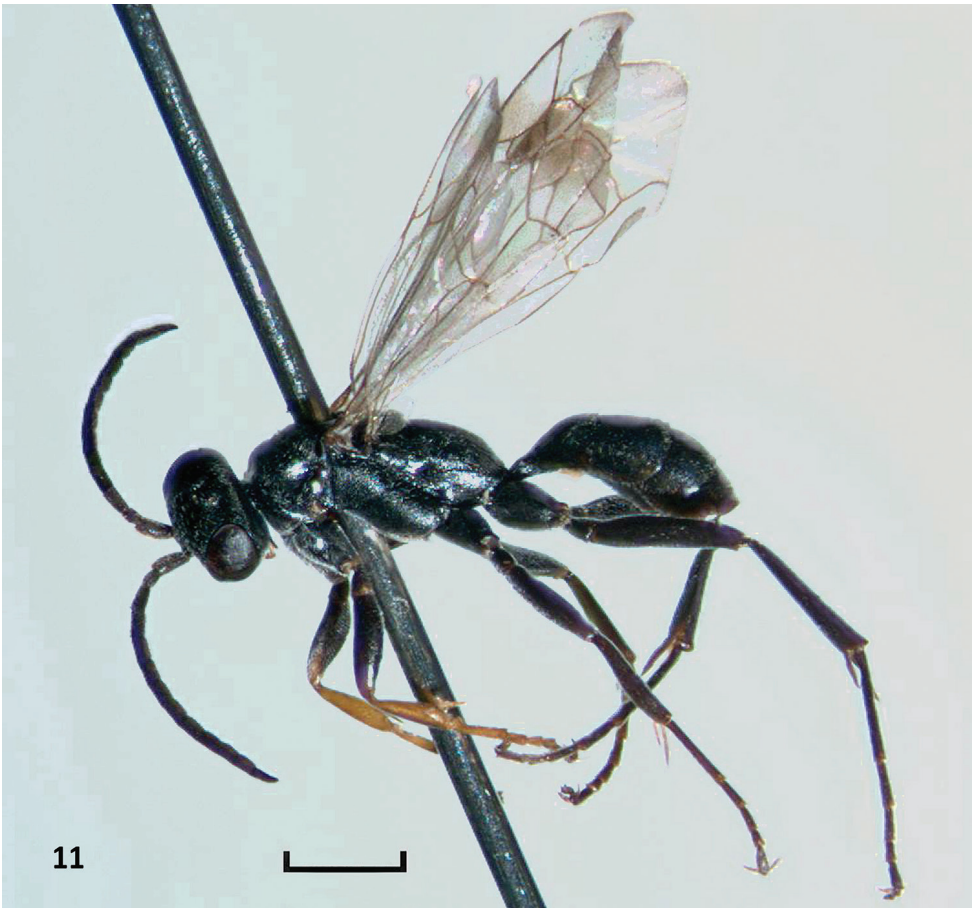
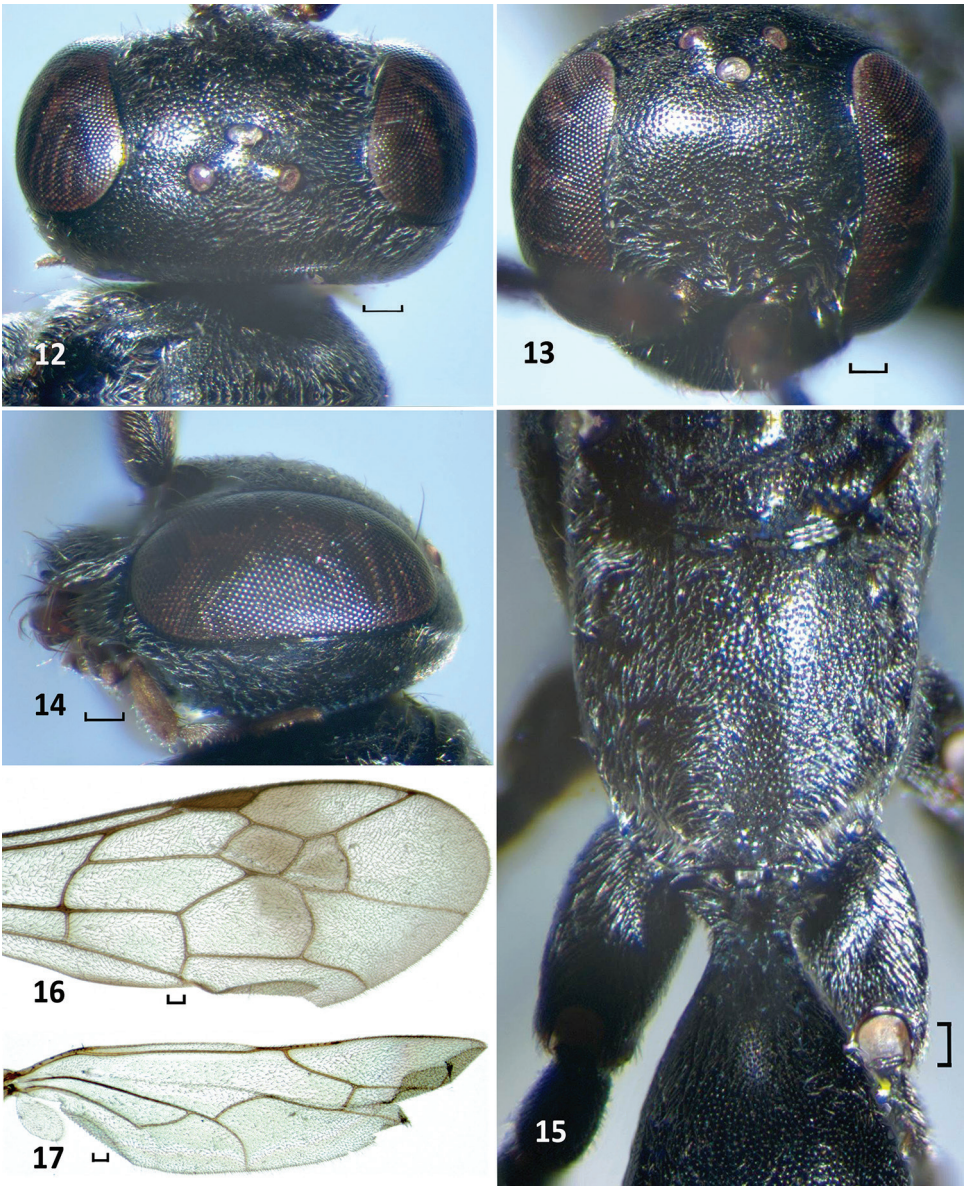


Figure 11. *Nipponodipogon orientalis* Loktionov, Lelej & Xu, sp. n., male, paratype, habitus, lateral view. Scale bar 1 mm.

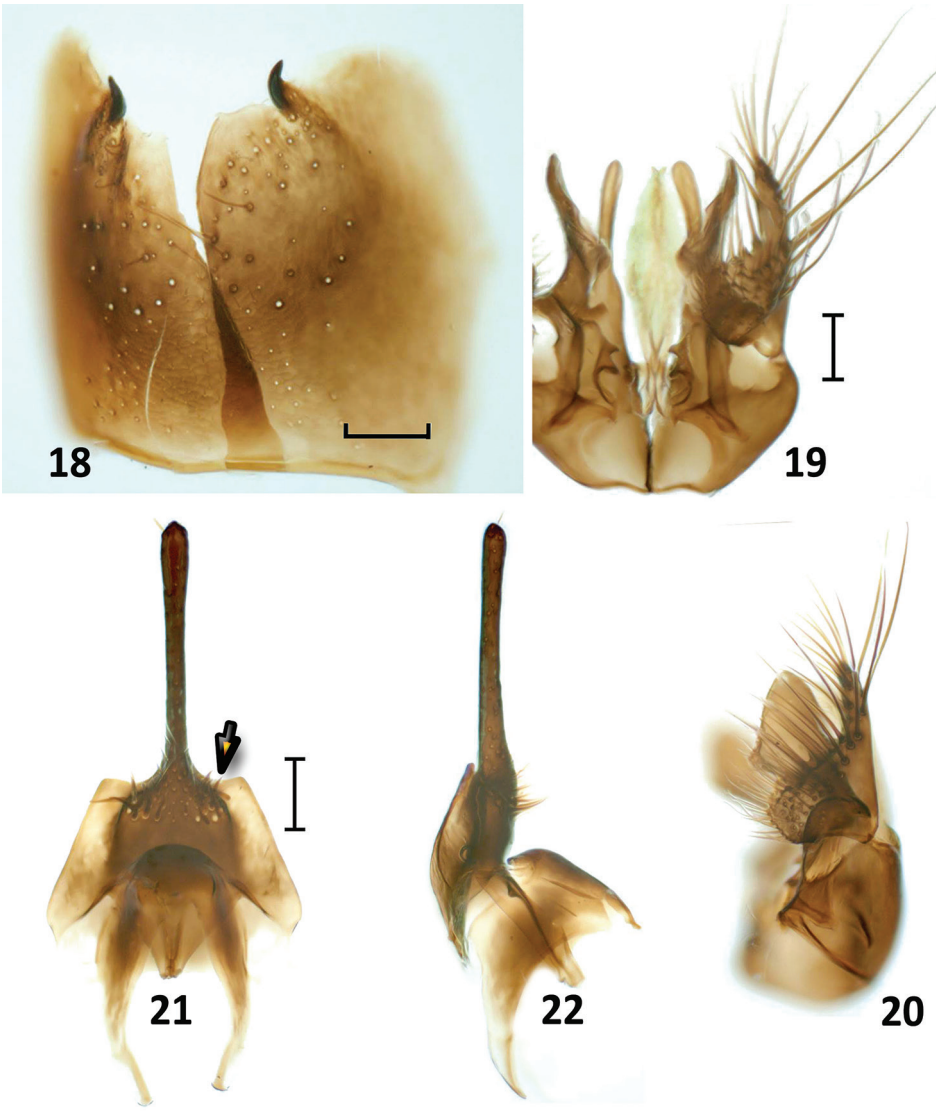
Pronotum with anterior declivity weakly concave, more differentiated from dorsum than in female; dorsum in dorsal view narrowing anteriorly; shoulder gently rounded; juncture between dorsal and lateral faces roundly raised; posterior margin weakly and arcuately emarginate. Mesoscutum slightly sloped anteriorly; parapsidal sulcus finely impressed. Discs of mesoscutellum and metanotum somewhat more strongly raised above level of mesoscutum and propodeum than in female. Metapostnotum (Fig. 15) longer and not deeply sunken between metanotum and propodeum, as in female; somewhat narrowing in middle; metapostnotum length 0.15–0.25× metanotum length medially. Propodeum evenly convex with posterior declivity not differentiated from dorsum; posterior surface evenly convex.

Fore wing (Fig. 16), hind wing (Fig. 17). Claws symmetrical with large subapical inner tooth. T1 distinctly petiolate; petiole long (Fig. 15). S6 deeply and arcuately emarginate posteriorly; lateral hook small, curved and pointed to apex (Fig. 18). Exposed portion of hypopygium stick form, compressed laterally, narrow (both in lateral and ventral views),



Figures 12–17. *Nipponodipogon orientalis* Loktionov, Lelej & Xu, sp. n., male, paratype. **12** Head, dorsal view **13** Head, frontal view **14** Head, lateral view **15** Mesoscutellum, metanotum, metapostnotum, propodeum and T1, dorsal view **16** Fore wing **17** Hind wing. Scale bars 0.1 mm.

weakly widened apically; subbasal portion extended laterally, with short erected stout spines (Figs 21, 22). Paramere broadly widened basally and narrowing toward apex (lateral view), with long bristles, longer bristle as long as paramere; volsella broad apically (lateral view) (Figs 19, 20).



Figures 18–22. *Nipponodipogon orientalis* Loktionov, Lelej & Xu, sp. n., male, paratype. **18** S6, ventral view **19** Genitalia, ventral view **20** Genitalia, lateral view **21** Hypopygium and S7, ventral view **22** Hypopygium and S7, lateral view. Scale bars 0.1 mm.

Remarks. The female of new species is similar to those of *Nipponodipogon kurilensis*, *N. sudai*, and *N. shimizui* sp. n. by having outer apicoventral corner of metafemur produced triangularly (Fig. 8) and T1 petiolate basally (Fig. 6), but can be separated from all of them in having mesosoma completely yellow orange (Figs 1, 7) (*vs* completely or mostly black (Figs 23, 29)) and posterolateral portion of propodeum with strong transverse rugae (Figs 5–7) (*vs* with fine transverse striae or/and punctures (Figs 27–29, 44)).

Female of *N. orientalis* sp. n. differs from that of *N. kurilensis* in having T1 with long petiole (Fig. 6) (*vs* short one in *N. kurilensis* (Shimizu et al. 2015: fig. 3D)); and from that of *N. shimizui* sp. n. in having crossvein *3rs-m* distinctly curved (Fig. 9) and T6 somewhat polished, not shagreened, with distinct scattered setiferous pores (*vs* crossvein *3rs-m* almost straight and T6 matt, shagreened, without distinct setiferous pores in *N. shimizui* sp. n. (Figs 31, 39)).

Male of new species is closely related to that of *N. shimizui* sp. n. by some morphological characters including shape of hypopygium and genitalia, but easily distinguishes in propodeum with fine transverse striae posterolaterally (Fig. 15) (*vs* propodeum without any striae in *N. shimizui* sp. n. (Fig. 38)); exposed portion of hypopygium narrow in lateral view (Fig. 22) (*vs* noticeably wider in *N. shimizui* sp. n. (Fig. 43)); subbasal portion of hypopygium in ventral view with round sublateral carina (Fig. 21, arrow) (*vs* with angulate sublateral carina in *N. shimizui* sp. n. (Fig. 42, arrow)); S6 with setiferous pores posteromedially (Fig. 18) (*vs* without setiferous pores posteromedially in *N. shimizui* sp. n. (Fig. 39)). Male of new species is also similar to that of *N. sudai* in having petiole on T1 basally (Fig. 15), but can be easily differentiated by having F3–F11 not producing triangularly beneath, not forming serrated profile (*vs* F3–F11 produced triangularly beneath, forming serrated profile in *N. sudai*); lateral hook on S6 small, claw-like, curved and pointed to apex (Fig. 18) (*vs* lateral hook on S6 large, strongly compressed laterally and thin, subtriangular in profile in *N. sudai* (Fig. 46)); and exposed portion of hypopygium without long erect setae (Figs 21, 22) (*vs* with long erect setae in *N. sudai* (Fig. 48)).

Sex association. In spite of the fact that females and males were collected in different locations (two males from Yunnan and five females from Guangdong and Hainan) and have different coloration (mesosoma completely yellow orange in female *vs* completely black in male), we consider that they are opposite sexes of same species. Male of new species has propodeum with fine transverse striae posterolaterally that correlates with strong transverse rugae on propodeum posteriorly, especially in posterolateral portion in female (*vs* male without any striae, female with fine transverse striae in *Nipponodipogon shimizui* sp. n.). Such coloration differences in female and male of new species are not exception and occur in widely distributed Palaearctic species *Arachnotheutes rufithorax* (Costa, 1881) (Loktionov and Lelej 2017: figs 87, 88).

Etymology. The name of the new species refers to the first record of the genus in the Oriental Region.

Distribution. China (Guangdong, Hainan, Yunnan).

Nipponodipogon shimizui Loktionov, Lelej & Xu, sp. n.

http://zoobank.org/C4D684DE-E576-49AD-8300-B403CE1E5F78
Figs 23–43

Material examined. Holotype. CHINA: ♀, Guangdong, Nanling, 8–17.VIII.2010, Hua-yan Chen, yellow pan traps, No. 2016001839 (SCAU). **Paratypes**. CHINA: 3

Figure 23. *Nipponodipogon shimizui* Loktionov, Lelej & Xu, sp. n., female, holotype, habitus, lateral view. Scale bars 1 mm.

♀, with the same data as holotype, No. 2016001836, 2016001840 and 2016001842 (SCAU); 1 ♀, with the same data as holotype, No. 2016001837 (IBSS); 1 ♀, Guangdong, Nanling, 5–7.VI.2010, Hua-yan Chen, No. 2016000023 (SCAU); 1 ♂, Yunnan, Lushui, 19.VII.2006, Zai-fu Xu, No. 2016000326 (SCAU).

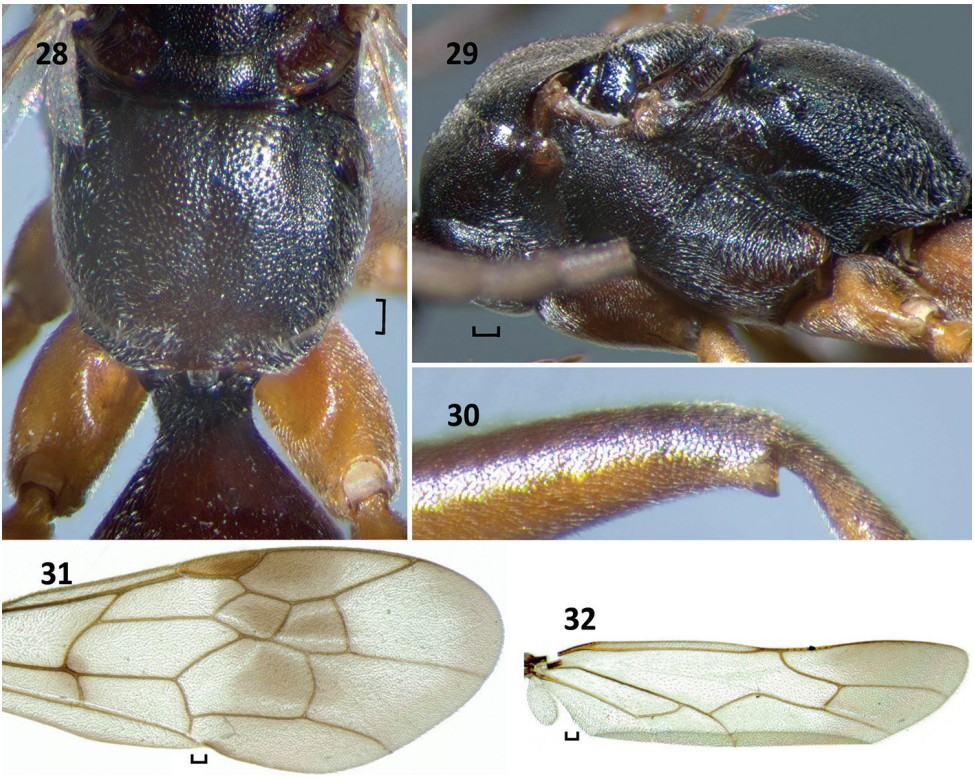
Diagnosis. *Female*. Outer apicoventral corner of metafemur produced triangularly (Fig. 30). T1 with distinct petiole basally (Fig. 28). Crossvein *2rs-m* almost straight or sometimes barely curved; crossvein *3rs-m* straight or almost straight (Fig. 31). Mesoscutum raised along midline (Fig. 29). Head and mesosoma matt; metasoma somewhat polished. *Male*. T1 distinctly petiolate basally (Fig. 38). F3–F11 not produced triangularly beneath, not forming serrated profile. Propodeum polished, without any striae (Fig. 38). Subbasal portion of hypopygium with angulate sublateral carina (Fig. 42, arrow).

Description. ***Female***. *Body* length 5.2–6.4 mm; fore wing length 4.3–5.1 mm. Head, mesosoma and metasoma black; sometimes clypeus along anterior margin dark brown; antenna black, except F3–F10 muddy yellow ventrally and scape yellowish-brown ventrally; mandible brownish subapically. Legs yellowish-brown or brown with

Figures 24–27. *Nipponodipogon shimizui* Loktionov, Lelej & Xu, sp. n., female, paratype. **24** Head and pronotum, dorsal view **25** Head, frontal view **26** Head, lateral view **27** Propodeum, dorsolateral view. Scale bars 0.1 mm.

procoxa laterally, profemur externally, meso- and metafemur, tibiae apically and tarsi somewhat darker (Fig. 23). Fore wing weakly infuscate, with weak subbasal and preapical fuscous bands (Fig. 31). Hind wing weakly infuscate (Fig. 32).

Head and mesosoma matt. Frons, vertex and mesosoma, except propodeum, finely and densely punctate. Pronotum laterally and finely striate and punctate. Mesopleuron with denser and coarser punctures then on disc of pronotum. Upper mesopleuron rugose. Metapleuron finely and densely striate. Lateral side of metanotum with several regular oblique striae. Propodeum strongly and densely punctate with fine transverse rugae posteriorly. Metasoma somewhat polished, except T6 and S6 matt. T1–T5 with fine punctures; T6 finely shagreened, without distinct setiferous pores; S6 less shagreened, than T6, with scattered setiferous pores located posteriorly and posterolaterally; S1–S5 with somewhat larger punctures than on T1–T5. S1 with several longitudinal rugae medially. Transverse groove on S2 gently arcuate.



Figures 28–32. *Nipponodipogon shimizui* Loktionov, Lelej & Xu, sp. n., female, paratype. **28** Mesoscutellum, metanotum, metapostnotum, propodeum and T1, dorsal view **29** Mesosoma, lateral view **30** Metafemur, outer lateral view **31** Fore wing **32** Hind wing. Scale bars 0.1 mm.

Body with gray pubescence mostly short, but longer on propodeum posterolaterally. Body without setae except the following: upper frons sometimes with one long erect setae; clypeus with a few long suberect setae anteriorly; S2–S5 with scattered long or short erect setae posteriorly; T6 and S6 with denser long erect pale setae.

Width of *head* in frontal view 1.1–1.2× its height. Vertex weakly convex between eye tops (Fig. 25). Upper frons gently convex (Fig. 26). Frons with indistinct median line and fine elongate concavity medially. Supra-antennal area of frons produced anteriorly into a frontal ledge overhanging the antennal radicle (Fig. 26). Inner orbits weakly convergent above and subparallel below (Fig. 25). Half of MID 1.3–1.6× eye width. Ocelli large, slightly raised; ocellar triangle barely acute-angled (Fig. 24); POD/OOD=0.6–0.8. Posterior margin of vertex roundly concave (dorsal view) (Fig. 24). Clypeus convex medially with distinct concavity basolaterally; anterolateral corner broadly rounded; anterior margin almost straight or weakly emarginate medially; width 2.7× its length. Apical margin of labrum broadly rounded. Mandible with large subapical tooth and indistinct basal tooth. Maxillary cardines with two tufts of thin,

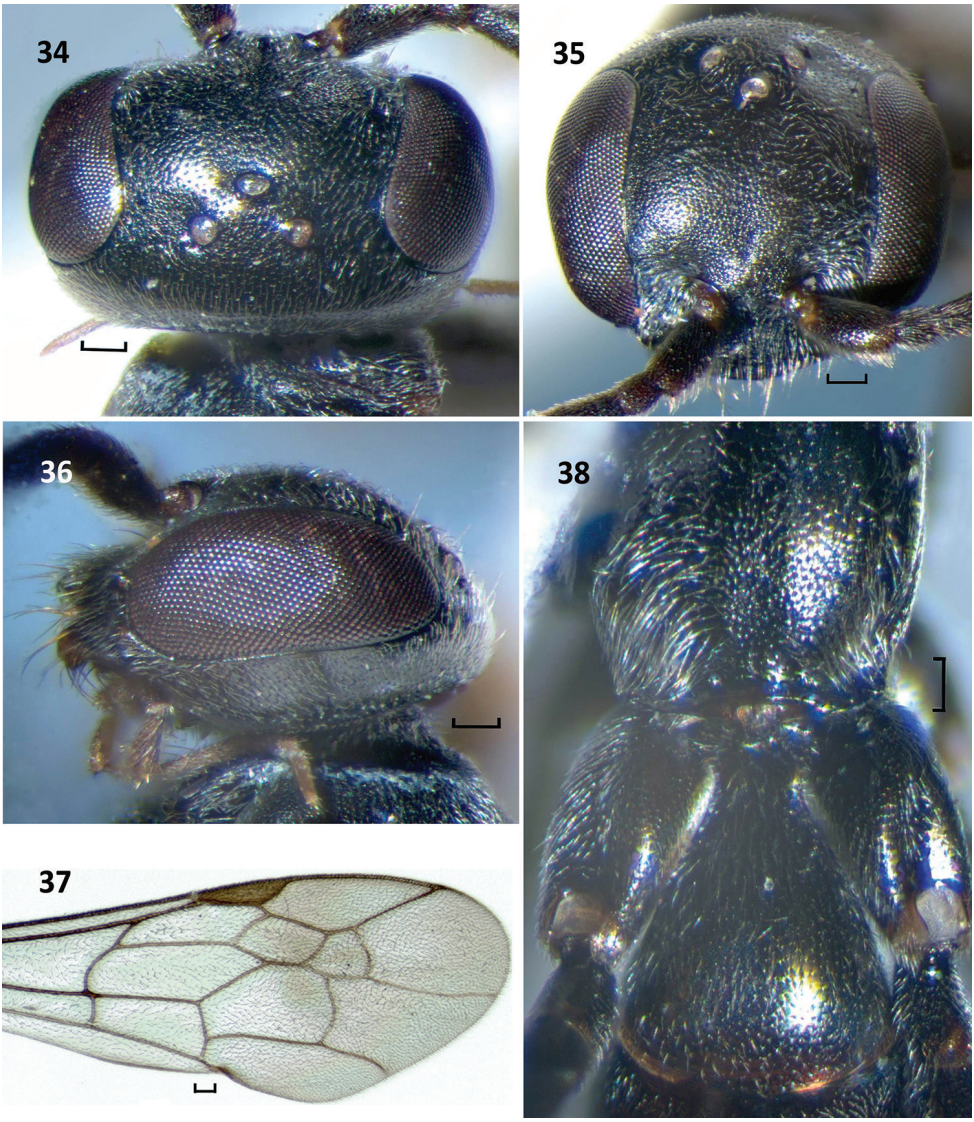
Figure 33. *Nipponodipogon shimizui* Loktionov, Lelej & Xu, sp. n., male, paratype, habitus, lateral view. Scale bar 1 mm.

light brown bristles. Malar space short. Gena narrowing posteriorly (Fig. 24, dorsal view; Fig. 26, lateral view). Antenna short, stout, and thickened toward middle of flagellum; F1–F4 distinctly widening toward apex; apex of apical flagellomere pointed; F1 length 0.90–0.95× F2 length; F1 length 2.2–2.6× its width and 0.5× UID.

Pronotum with anterior declivity flattened, not distinctly differentiated from dorsum; dorsum in dorsal view slightly narrowing anteriorly; shoulder gently rounded; juncture between dorsal and lateral faces narrowly and roundly raised; posterior margin weakly and arcuately emarginate medially (Fig. 24). Mesoscutum slightly sloped anteriorly; disc along median line slightly convex; posterolateral margin not reflexed; parapsidal sulcus finely impressed. Discs of mesoscutellum and metanotum barely raised above level of mesoscutum and propodeum (Fig. 29). Metapostnotum narrow and practically linear, deeply sunken between metanotum and propodeum (Fig. 28). Propodeum evenly convex with flattened posterior declivity not well differentiated from dorsum (Fig. 29).

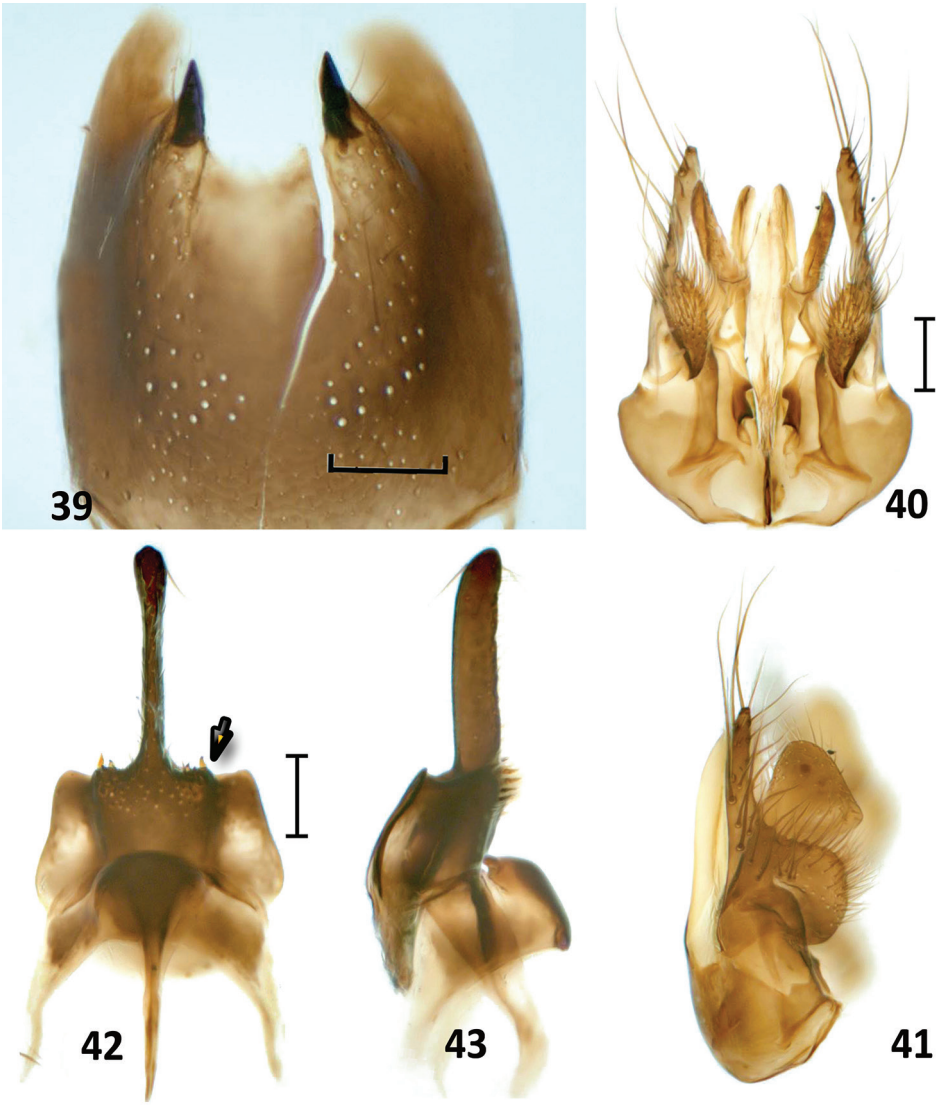
Fore wing (Fig. 31) with SMC2 receiving crossvein *1m-cu* at almost middle; SMC3 1.2–1.5× longer than SMC2 on vein *M*, and 0.8–1.1× longer than SMC2 on vein *Rs*; receiving crossvein *2m-cu* at almost middle; crossvein *2rs-m* almost straight or sometimes barely curved; crossvein *3rs-m* straight, sometimes barely curved; crossvein *cu-a* barely postfurcal. Hind wing (Fig. 32). Outer apicoventral corner of metafemur produced triangularly (Fig. 30). Claws symmetrical with large subapical inner tooth. T1 distinctly petiolate (Fig. 28). S6 with a longitudinal median rounded carina posteriorly.

Male. *Body* length 3.8 mm; fore wing length 3.4 mm. Body black; antenna black with scape brown ventro-apically and flagellum indistinctly brownish ventrally; mandible brown subapically; protibia and protarsi brown; spurs of tibia brown (Fig. 33). Fore



Figures 34–38. *Nipponodipogon shimizui* Loktionov, Lelej & Xu, sp. n., male, paratype. **34** Head, dorsal view **35** Head, frontal view **36** Head, lateral view **37** Fore wing **38** Propodeum and T1, dorsal view. Scale bars 0.1 mm.

wing weakly infuscate, with darker apical portion, fuscous band indistinct (Fig. 37). Hind wing weakly infuscate. Body mostly punctate and somewhat polished. Frons, discs of pronotum, mesoscutum, mesoscutellum, metanotum finely and densely punctate. Pronotum laterally polished and indistinctly punctate. Mesopleuron with coarser punctures than frons. Upper mesopleuron without striate. Lateral side of metanotum with several regular oblique striae. Metapleuron indistinctly punctate. Propodeum



Figures 39–43. *Nipponodipogon shimizui* Loktionov, Lelej & Xu, sp. n., male, paratype. **39** S6, ventral view **40** Genitalia, ventral view **41** Genitalia, lateral view **42** Hypopygium and S7, ventral view **43** Hypopygium and S7, lateral view. Scale bars 0.1 mm.

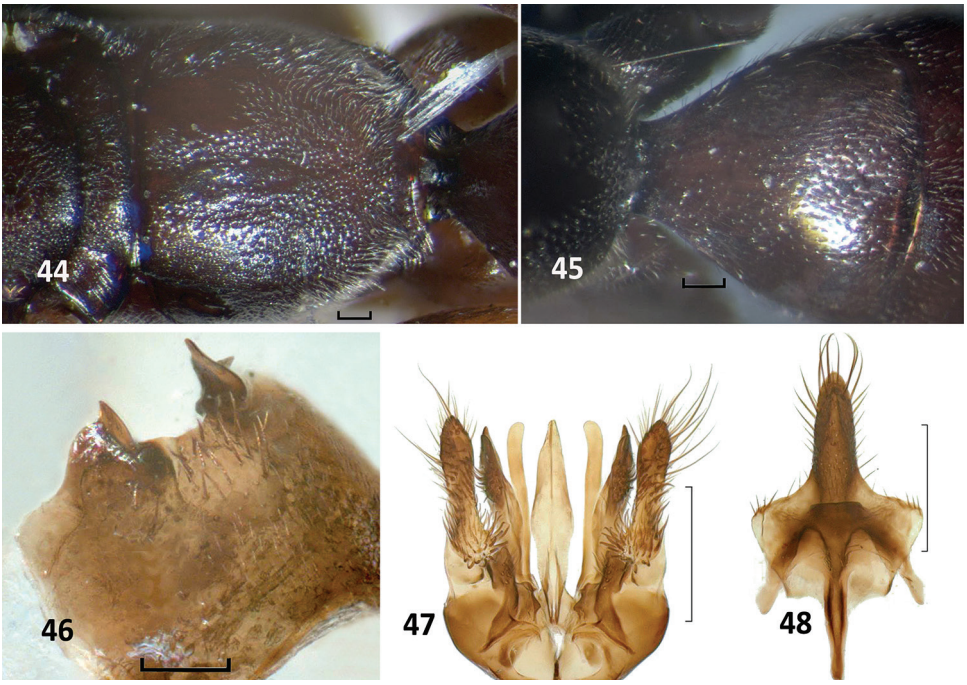
basolaterally polished with fine punctures larger than on frons, without any striae. Metasomal segments finely punctate. S1 with several longitudinal rugae basally. Transverse groove on S2 weak. S6 lacking setiferous pores posteromedially (Fig. 39). Body with gray pubescence mostly short, but longer on lower face, clypeus, and propodeum posteriorly. Body without setae except upper frons with one long erect setae and clypeus with a few long suberect setae anteriorly.

Width of *head* in frontal view 1.1× its height. Vertex moderately convex between eye tops (Fig. 35). Upper frons gently convex (Fig. 36). Frons without median line, with indistinct elongate concavity medially. Supra-antennal area of frons produced anteriorly into weak frontal ledge overhanging antennal radicle (Fig. 36). Inner orbits subparallel above and barely convergent below (Fig. 35). Half of MID 1.6× eye width. Ocelli large, noticeably raised; ocellar triangle right-angled (Fig. 34); POD/OOD=0.9. Posterior margin of vertex straight (dorsal view) (Fig. 34). Clypeus weakly convex medially; anterolateral corner rounded; anterior margin broadly rounded. Mandible with subapical tooth. Malar space short. Gena weakly narrowing posteriorly (Fig. 34, dorsal view; Fig. 36, lateral view). Antenna shortened; flagellum filiform; flagellomeres indistinctly convex ventrally, not forming triangle projection; apex of apical flagellomere pointed; F1 length 1.0× F2 length; F1 length 1.8× its width and 0.3× UID.

Pronotum with anterior declivity weakly concave, more differentiated from dorsum than in female; dorsum in dorsal view narrowing anteriorly; shoulder gently rounded; juncture between dorsal and lateral faces roundly raised; posterior margin arcuately emarginate. Parapsidal sulcus finely impressed. Discs of mesoscutellum and metanotum somewhat stronger raised above level of mesoscutum and propodeum than in female. Metapostnotum longer and not deeply sunken between metanotum and propodeum, as in female; somewhat narrowing in middle; metapostnotum length 0.25× metanotum length medially. Propodeum evenly convex with posterior declivity not differentiated from dorsum; posterior surface evenly convex.

Fore wing (Fig. 37). Claws symmetrical with small subapical inner tooth. T1 distinctly petiolate (Fig. 38). S6 deeply and arcuately emarginate posteriorly; lateral hook barely curved and pointed to apex (Fig. 39). Exposed portion of hypopygium stick form, compressed laterally, narrow and widened apically (ventral view); subbasal portion extended laterally, with short stout erect spines on two angulate sublateral carinae (Figs 42, 43). Paramere broadly widened basally and strongly narrowing toward apex (lateral view), with long bristles, longer bristle 0.7× longer than paramere; volsella broad apically (lateral view) (Figs 40, 41).

Remarks. The female of new species is similar to those of *Nipponodipogon kurilensis*, *N. sudai* and *N. orientalis* sp. n. by having outer apicoventral corner of metafemur produced triangularly (Fig. 30) and T1 petiolate basally (Fig. 28), but can be distinguished from them by following characters: posterolateral portion of propodeum with fine transverse striae and punctures (Figs 27–29) (*vs* with strong transverse rugae in *N. orientalis* sp. n. (Figs 5, 7)); mesosoma completely black (Figs 23, 29) (*vs* completely yellow orange in *N. orientalis* sp. n. (Figs 1, 7)); T6 matt and shagreened, without distinct setiferous pores (*vs* somewhat polished, not shagreened, with distinct scattered setiferous pores in *N. orientalis* sp. n.); vertex between eye tops slightly convex (Fig. 25) (*vs* distinctly convex in *N. kurilensis* (Shimizu et al. 2015: fig. 3A)); petiole of T1 long (Fig. 28) (*vs* very short in *N. kurilensis* (Shimizu et al. 2015: fig. 3D)); head and mesosoma matt, metasoma somewhat polished (*vs* head and mesosoma somewhat polished, metasoma distinctly polished in *N. kurilensis*); mesoscutum raised along midline (Fig. 29) (*vs* not raised in *N. sudai* (Shimizu et al. 2015: fig. 8D)); crossvein *3rs-m* almost straight (Fig. 31)



Figures 44–48. *Nipponodipogon sudai* Shimizu, paratype. **44** Mesoscutellum, metanotum, metapostnotum, propodeum and base of T1, dorsal view **45** T1, dorsal view **46** S6, ventral view **47** Genitalia, ventral view **48** Hypopygium and S7, ventral view **44** Female **45–48** Male. Scale bars 0.1 mm for **44–46**; 0.25 mm for **47, 48**.

(*vs* gently or moderately curved in *N. sudai* (Shimizu et al. 2015: fig. 9J)); propodeum anteromedially punctate (Fig. 28) (*vs* not punctate in *N. sudai* (Fig. 44)).

Male of new species is closely related to that of *N. orientalis* sp. n. by having some morphological characters including shape of hypopygium and genitalia, but can be easily distinguished in having propodeum without any striae posterolaterally (Fig. 38) (*vs* with fine transverse striae posterolaterally in *N. orientalis* sp. n. (Fig. 15)); exposed portion of hypopygium noticeably wider in lateral view (Fig. 43) (*vs* narrow in *N. orientalis* sp. n. (Fig. 22); subbasal portion of hypopygium in ventral view with angulate sublateral carina (Fig. 42, arrow) (*vs* with round sublateral carina in *N. orientalis* sp. n. (Fig. 21, arrow)); and S6 without setiferous pores posteromedially (Fig. 39) (*vs* with setiferous pores in *N. orientalis* sp. n. (Fig. 18)). Male of new species is also similar to that of *N. sudai* in having petiole in T1 basally (Fig. 38), but can be separated in having F3–F11 not producing triangularly beneath, not forming serrated profile (*vs* F3–F11 produced triangularly beneath, forming serrated profile in *N. sudai*); lateral hook on S6 claw-like, weakly curved and pointed to apex (Fig. 39) (*vs* lateral hook on S6 strongly compressed laterally and thin, subtriangular in profile in *N. sudai* (Fig. 46));

and exposed portion of hypopygium without long erect setae (Figs 42, 43) (*vs* with long erect setae in *N. sudai* (Fig. 48)).

Sex association. In spite of females and males were collected in different locations (one male in Yunnan and six females in Guangdong), we consider that they are opposite sexes of the same species. Male S6 of new species lacks setiferous pores posteromedially (Fig. 39), which correlates with female S6 of similar condition medially (*vs* with scattered setiferous pores in male and female of *Nipponodipogon orientalis* sp. n.).

Etymology. It is a pleasure to name this species after the well-known taxonomist Dr. Akira Shimizu (Tokyo Metropolitan University, Japan).

Distribution. China (Guangdong, Yunnan).

The updated key of *Nipponodipogon* species

(based on Shimizu et al. 2015)

Females

1 Outer apicoventral corner of metafemur produced triangularly (Figs 8, 30). T1 petiolate basally (Figs 6, 28, 44) **2**

– Outer apicoventral corner of metafemur rounded (Shimizu et al. 2015: fig. 2D). T1 not petiolate basally (Shimizu et al. 2015: fig. 6E)..... **5**

2 Posterolateral portion of propodeum with strong transverse rugae (Figs 5, 7). Mesosoma completely yellow orange (Figs 1, 7)..... ..... ***N. orientalis*** **Loktionov, Lelej & Xu, sp. n.**

– Posterolateral portion of propodeum with fine transverse striae or punctures (Figs 27–29, 44). Mesosoma completely black (Figs 23, 29), sometimes posterior margin of pronotum and posterolateral margin of metapostnotum brownish..... **3**

3 Vertex between eye tops strongly convex (Shimizu et al. 2015: fig. 3A). Petiole of T1 very short (Shimizu et al. 2015: fig. 3D). Head and mesosoma somewhat polished; metasoma distinctly polished. Ocelli forming right-angle triangle (Shimizu et al. 2015: fig. 3B) ..... ***N. kurilensis*** **(Lelej)**

– Vertex between eye tops slightly convex (Fig. 25). Petiole of T1 long (Fig. 28). Head and mesosoma matt; metasoma not distinctly polished. Ocelli usually forming acute-angle triangle (Fig. 24)..... **4**

4 Mesoscutum not raised along midline (Shimizu et al. 2015: fig. 7D). Crossvein *3rs-m* gently or moderately curved (Shimizu et al. 2015: fig. 9J). Disc of propodeum without punctures anteromedially (Fig. 44) ... ***N. sudai*** **Shimizu**

– Mesoscutum raised along midline (Fig. 29). Crossvein *3rs-m* almost straight (Fig. 31). Disc of propodeum with punctures anteromedially (Fig. 28)..... ..... ***N. shimizui*** **Loktionov, Lelej & Xu, sp. n.**

5 Transverse groove on S2 nearly straight (Shimizu et al. 2015: fig. 2E, arrow). T1 with long parallel-sided portion basally (Shimizu et al. 2015: fig. 8C) ..... ***N. iwatai* (Ishikawa)**

– Transverse groove on S2 subangulate (Shimizu et al. 2015: fig. 6F) or arcuate. T1 without parallel-sided portion basally (Shimizu et al. 2015: fig. 8D) **6**

6 Mandible short, its apex and two additional teeth rounded, basal tooth vestigial (Shimizu et al. 2015: fig. 8A) ..... ***N. mandibularis* (Ishikawa)**

– Mandible normal-sized, its apex and two additional teeth pointed, basal tooth distinct (Shimizu et al. 2015: fig. 8B) **7**

7 Vertex strongly convex between eye tops; hence head in frontal view nearly circular in outline (Shimizu et al. 2015: fig. 1A). Posterior margin of vertex remarkably concave in dorsal view (Shimizu et al. 2015: fig. 1B). Gena strongly developed. F1 length 2.7–2.9× its width. Propodeum gently convex in profile (Shimizu et al. 2015: fig. 1C). S6 not carinate along midline. Fore wing inner fascia along crossvein *cu-a* broad and distinct (Shimizu et al. 2015: fig. 9A) ..... ***N. hayachinensis* (Ishikawa)**

– Vertex not very strongly convex between eye tops; hence head in frontal view not circular in outline (Shimizu et al. 2015: figs 5A, 6A). Posterior margin of vertex not remarkably concave in dorsal view (Shimizu et al. 2015: figs 5B, 6C). Gena not strongly developed. F1 length 2.1–2.4× its width. Propodeum strongly convex in profile (Shimizu et al. 2015: figs 5C, 6D). S6 carinate along midline. Fore wing inner fascia along crossvein *cu-a* indistinct (Shimizu et al. 2015: figs 9F, 9H) **8**

8 Ocelli forming right- or obtuse-angled triangle and gena strongly receding posteriorly (Shimizu et al. 2015: fig. 5B) ..... ***N. nagasei* (Ishikawa)**

– Ocelli usually forming acute-angled triangle and gena roundly receding posteriorly (Shimizu et al. 2015: fig. 6C) ..... ***N. rossicus* (Lelej)**

Males (unknown for *N. kurilensis*, *N. mandibularis,* and *N. hayachinensis*)

1 T1 distinctly petiolate basally (Figs 15, 38); if petiole not distinct (as in *N. sudai*, Fig. 45), then lateral hook on S6 strongly compressed laterally and thin, subtriangular in profile (Fig. 46) **2**

– T1 not petiolate basally. Lateral hook on S6 not compressed laterally and not thin, but claw-like, curved and pointed to apex **4**

2 F3–F11 produced triangularly beneath, forming serrated profile. Lateral hook on S6 large, strongly compressed laterally and thin, subtriangular in profile (Fig. 46). Exposed portion of hypopygium with long erect setae (Fig. 48) ..... ***N. sudai* Shimizu**

– F3–F11 not produced triangularly beneath, not forming serrated profile. Lateral hook on S6 not compressed laterally nor thin, but claw-like, curved and pointed to apex (Figs 18, 39). Exposed portion of hypopygium without long erect setae (Figs 21, 22, 42, 43) 3

3 Propodeum with fine transverse striae posterolaterally (Fig. 15). Exposed portion of hypopygium narrow (lateral view) (Fig. 22); subbasal portion (ventral view) with round sublateral carina (Fig. 21, arrow) ..... ***N. orientalis* Loktionov, Lelej & Xu, sp. n.**

– Propodeum without any striae (Fig. 38). Exposed portion of hypopygium wide (lateral view) (Fig. 43); subbasal portion (ventral view) with angulate sublateral carina (Fig. 42, arrow) ..... ***N. shimizui* Loktionov, Lelej & Xu, sp. n.**

4 Ocellar triangle acute- to right-angled. Meso- and metatibial spurs dark brown. Exposed portion of hypopygium compressed laterally with ventral face flattened and polished, broad basally, tapering apically (Shimizu et al. 2015: figs 2F, 8F) ..... ***N. iwatai* (Ishikawa)**

– Ocellar triangle obtuse-angled; or if right-angled, meso- and metatibial spurs stramineous. Exposed portion of hypopygium completely compressed laterally and very thin, its ventral face linear (Shimizu et al. 2015: figs 5E, 8G–H) **5**

5 Genitalia with long setae on anterior margin of paramere (Shimizu et al. 2015: fig. 5G) ..... ***N. nagasei* (Ishikawa)**

– Genitalia with short setae on anterior margin of paramere (Shimizu et al. 2015: fig. 6J) ..... ***N. rossicus* (Lelej)**

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July 18, 2017 Prof. Xu Zai-fu died suddenly after a serious illness. He was only 52 years old. We indebted him for his kindness and support of Hymenoptera research in China.

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RESEARCH ARTICLE

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A new species of wasp-mimicking clearwing moth from Peninsular Malaysia with DNA barcode and behavioural notes (Lepidoptera, Sesiidae)

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Abstract

A new species of clearwing moth, *Pyrophleps ellawi* Skowron Volponi, **sp. n.**, is described from Peninsular Malaysia. Information on the habitat, time and conditions of occurrence, flight and mud-puddling behaviour, functional morphology, and DNA barcode are also provided. Photographs and a supplementary video from the wild demonstrate the postures and behaviour of this species of *Pyrophleps*, whose remaining members were described only on the basis of pinned specimens. This is the first record of this genus in Peninsular Malaysia.

Keywords

Sesiidae, clearwing moth, *Pyrophleps ellawi*, mimicry, mud-puddling, behaviour, Malaysia

Introduction

Until now the genus *Pyrophleps* Arita & Gorbunov, 2000 comprised seven species. Three were described more than one hundred years ago, namely *Adixoa cruentata* Swinhoe, 1896, *Aegeria ruficrista* Rothschild, 1912 and *Aschistophleps haematochrodes* Le Cerf, 1912. Revised by Arita and Gorbunov (2000), they were transferred to the genus *Pyrophleps*.

The remaining four species, mostly caught with the use of synthetic pheromones, were described fairly recently: *P. nigripennis* Arita & Gorbunov, 2000, *P. vitripennis* Arita & Gorbunov, 2000, *P. cucphuonganae* Arita & Gorbunov, 2000 and *P. bicella* Xu & Arita, 2015. Thus, nothing was known until now about the behaviour of members of this genus. An identification key to the species of *Pyrophleps* has been published by Xu et al. (2015).

A wasp-mimicking sesiid was observed and collected in lowland dipterocarp forests of Peninsular Malaysia. Its flight and mud-puddling behaviour, as well as functional morphology, are described and shown in a video. Time and conditions of occurrence are provided. Based on morphological analyses as well as DNA barcode, it is described here as a new species, which leads the genus *Pyrophleps* to now count eight species.

Materials and methods

The behaviour of the new species was observed and filmed in its habitat. Using an electronic thermo-hygrometer placed in the shade, temperature and air humidity were measured. Two specimens were collected near Merapoh, Pahang, Malaysia without the use of synthetic pheromones. A further three individuals were observed and photographed but were not collected (the species was observed in total seven times; however, as three observations were made three days in a row, they could relate to the same individual, and only three were photographed in the wild). Morphological details were studied with a Leica M80 stereomicroscope and photographed using a Leica M205A. Wingspan, body and antenna length were measured on a computer screen from photographs of mounted specimens taken next to a scale. Genitalia were prepared by maceration of the abdomen in boiling 10% KOH, dissection in 10% ethanol, and pieces dehydrated by passing through 30%, 60%, and 100% ethanol and mounted in Euparal. DNA barcoding was conducted on total DNA isolated from a single leg of the paratype in the Canadian Centre for DNA Barcoding, University of Ontario, Guelph, Canada following Ivanova et al. (2006). The barcode sequence (available in the Barcode of Life Database, BIN number: BOLD:ACS2287) was analyzed through the Basic Local Alignment Search Tool (BLAST), Barcode of Life Data System Identification tool (Ratnasingham and Hebert 2007), CLC Sequence Viewer and SnapGene 3.3.4. Barcodes for comparisons were taken from BOLD.

Results

***Pyrophleps ellawi* Skowron Volponi, sp. n.**
http://zoobank.org/78854E0D-F0CE-4515-9581-4E06959411A5
Figs 1–4

Type material. Holotype ♂ (Fig. 3): "Malaysia: Pahang, Merapoh, 04°39.04'N, 102°01.80'E, 21 III 2017, Skowron Volponi M.A." / "Holotype, *Pyrophleps ellawi* sp. n., des. Skowron Vol-

Figure 1. *Pyrophleps ellawi* has a strong blue sheen in sunlight. Representatives of this species vary in the number of orange scales on the thorax. The scales form two longitudinal stripes, either dashed or solid.

poni M.A. 2017". Paratype ♂: "Malaysia: Pahang, Kuala Tahan, 04°22.98'N 102°23.98'E, 07 VIII 2014, Skowron Volponi M.A." / "Paratype, *Pyrophleps ellawi* sp. n., des. Skowron Volponi M.A. 2017". In coll. Marta Skowron Volponi (Gdansk).

Description. Alar expanse: 16–19.5 mm. Body length: 9.5–12 mm.

Head: antenna 6–6.5 mm, clavate, black dorsally, admixture of brick orange scales ventrally, several pale yellow or white scales at base, acuminate seta at apex; frons

Figure 2. *Pyrophleps ellawi* puddling on a river bank. Note the curled-up hind leg tarsi.

smoothly scaled, black with silver sheen; vertex covered with elongated, hair-like scales, bright orange mixed with pale yellow and several black scales between ocelli; smooth white scales adjacent to compound eye; ocelli brown; eyes red; proboscis orange, well-developed, functional; labial palpus long, upturned, with elongated black, orange and white scales dorsally and apically, shorter white scales ventrally; pericephalic hairs white with several orange ones dorsally, black ventrally.

Thorax: smoothly scaled, black with blue sheen, narrow longitudinal orange stripes (solid or dashed) dorsally; patch of white and individual orange scales laterally; elongated hair-like scales at wing insertion, white mixed with black; patagia black. Legs: fore coxa white with several orange scales ventrally; fore- and mid-femora smoothly scaled, black; fore tibia orange dorsally and black ventrally, tufted with hair-like scales (Fig. 2), smooth white scales dorsally at base; 1st tarsomere black with orange and yellow scales basally, tarsomeres 2–3 black with white scales dorsally at base, tarsomeres 4–5 black; mid tibia smooth-scaled ventrally, black with admixture of white scales, dorsally elongated scales white basally, orange medially and black distally; spurs black away from body and white towards body; tarsomeres black dorsally and white proximally but black distally on ventral side; hind femur black; hind tibia smooth-scaled, black in proximal half, tuft of hair-like scales covering distal half of tibia away from body and towards body and 1st and 2nd tarsomere only towards body: tibia with outer scale vestiture black with admixture of white, inner scale vestiture black and brick orange, on 1st tarsomere orange and black, on 2nd tarsomere shorter black scales; tarsomeres black with several white scales at base of 1st and 2nd tarsomere or only 1st. Spurs black away from body, white towards body. All legs with metallic sheen in sunlight. Forewing: hyaline; transparent areas covered with semi-hyaline scales

Figure 3. Male holotype of *Pyrophleps ellawi*.

with strong blue sheen (Fig. 1); veins, margins and fringe black; discal spot broad, black, with black extensions into anterior transparent area (ATA) along discal cell boundary and into external transparent area (ETA) between middle of cell M2-M3 and vein R3. ETA divided into nine cells, of which the two between veins R4-R3 and M3-CuA1 are additionally divided by narrow longitudinal stripes. Hindwing: transparent with semi-hyaline scales with blue sheen in distal half between veins 1A and M1, and at base. Discal spot narrow.

Abdomen: black with blue sheen, brighter strongly light-reflecting bands on margin of each tergite; admixture of white scales ventrally; anal tuft very small, black. Male genitalia (Fig. 4): tegumen broad proximally, gradually tapered towards uncus; saccus short with broad, slightly bifurcate base; valva broadening from 1/3 length, margins densely covered with long setae, sparser hair-like setae medially;

uncus with ring of brown setae; gnathos narrow, long, pointed distally; aedeagus about 1.5 length of valva.

Variability. The new species varies in the number of orange scales on thorax which form two, either dashed or solid, longitudinal stripes (Figs 1–2, Suppl. material 1 video TC: 00:40–00:57). On the hind legs white scales are present on the 2nd tarsomere in the holotype, in the paratype 2nd tarsomere is entirely black. It also differs in size.

Diagnosis. The new species is superficially most similar to *Pyrophleps vitripennis,* from which it can easily be distinguished by the configuration of male genitalia (compare Fig. 4 herein with Arita and Gorbunov 2000, Fig. 15), presence of hair-like scales on labial palpi (smoothly scaled in species compared), presence of orange hair-like scales on fore- and mid tibiae and lack of orange scales on wings, broader external transparent area of forewing. Apart from morphological features, *P. ellawi* shows 8% COI sequence divergence from *P. vitripennis* (Table 1). Based on genitalia configuration, this species is most similar to *P. nigripennis*. However, it differs in the shape of the valva and gnathos. Besides that, it can immediately be distinguished by the well-developed transparent areas of forewing (compare Fig. 3 herein with Arita and Gorbunov 2000, fig. 8), narrow discal spot on hindwing and by the colouration of the hind leg tuft (extensive red both externally, on tibia, and internally, on tibiae and tarsi, in *P. nigripennis*). From *P. ruficrista* it differs in more developed forewing ATA and PTA and less developed ETA and in the hind leg tuft (cinnabar red with two black spots and patches of blue scales in *P. ruficrista*). From *P. cruentata*, *P. haematochrodes* , *P. cucphuonganae* and *P. bicella*, it can be distinguished by the entirely transparent hindwings and absence of red scales on wings and abdomen.

Etymology. The species is named after our dear friend El Law, a dedicated conservation activist with sincere sensibility for Malaysian nature who, over the years of our studies on Malaysian Sesiidae, offered us his help in countless aspects.

Distribution and habitat. In addition to the type locality, the species is known also from the Taman Negara National Park, Malaysia, where it was observed and filmed in two locations approx. 50 km from each other. All observations were done on sandy and pebble river banks exposed to sunlight, in a lowland dipterocarp forest (Fig. 5)

Behaviour. *Pyrophleps ellawi* was observed flying around sandy and pebble beaches on a river bank and stopping now and again to mud-puddle (Suppl. material 1 video TC: 00:12–00:32). The flight is rapid, very similar to that of Eumeninae wasps. Many individuals of the wasp *Coeleumenes burmanicus* Bingham, 1897 were seen puddling in the same area. When flying, the wasp and the sesiid were impossible to distinguish. Both the flight path and velocity were very similar. When on land, *P. ellawi* moved around frantically, searching for moisture with its long proboscis (Suppl. material 1 video TC: 00:33–01:04). It usually landed for a moment only and never stayed for more than a few minutes on the same beach. When puddling, it keeps its wings folded back (Figs 1–2) and uses its fore and mid legs for locomotion (Suppl. material 1 video). The long hind legs do not seem to be fully functional in terms of locomotion. *Pyrophleps ellawi* keeps the hind tarsi curled upwards (Fig. 2) and occasionally it makes flapping movements which sometimes end in tapping the ground (Suppl. material 1 video

Table 1. COI pairwise sequence divergence of species closely related to *Pyrophleps ellawi* with Barcode of Life BIN numbers. Multiple alignment of the compared sequences is shown in Supplementary material 2.

Species	BIN number	Pairwise sequence divergence from *Pyrophleps ellawi*
Pyrophleps vitripennis	BOLD:ABX4445	7.90%
Heterosphecia pahangensis	BOLD:ACJ6445 BOLD:ACV6125	10.03% 9,68%
Heterosphecia bantanakai	BOLD:ABU6338	9.88%
Heterosphecia tawonoides	BOLD:ACJ6387	11.70%
Aschistophleps longipoda	BOLD:ABW9181	11.09 %

Figure 4. Male genitalia of *Pyrophleps ellawi*.

Figure 5. Habitat of *Pyrophleps ellawi*: sandy/pebble river banks in a lowland dipterocarp forest, Malaysia.

ACCTTATACTTTATTTTCGGAATTTGAGCTGGAATATTAGGTACATCTT
TAAGTTTACTAATTCGAGCAGAGCTTGGAACTCCAGGATCATTAATTG
GTGATGACCAAATTTATAATACAATTGTTACAGCTCATGCTTTCATTATA
ATTTTCTTTATAGTAATACCTATTATAATTGGAGGATTTGGAAATTGATTA
GTGCCCTTAATATTAGGAGCTCCTGATATAGCTTTCCCCCGAATAAATA
ATATAAGATTTTGACTTCTTCCTCCCTCTATTACCTTATTAGTTTCAAGA
AGAATTATTGAAAGTGGAACAGGAACAGGATGAACAGTTTACCCCCC
TCTTTCATCTAATATTGCTCATGGTGGCAGTTCTGTAGATCTTTCAATT
TTTTCTCTTCATTTAGCTGGAATTTCTTCAATTTTAGGAGCTATTAATTT
TATTACTACAATTATTAATATACGACCTAAAAATATATCCTTTGATCAAATA
CCTCTATTCGTTTGAGCTGTTGGAATTACAGCTCTTTTATTACTTTTATC
ATTACCTGTATTAGCGGGAGCTATTACTATACTTTTAACTGATCGAAATT
TAAATACTTCTTTTTTTGACCCTATTGGAGGAGGAGATCCAATTCTTTAT
CAACATTTATTT

Figure 6. 658-bp DNA sequence of the mitochondrial cytochrome c oxidase subunit I gene of *Pyrophleps ellawi* paratype. Barcode of Life BIN (BOLD Identification Number): BOLD:ACS2287.

TC: 00:48–00:54; 01:05–01:24). *Pyrophleps ellawi* was first seen in August 2014 (one observation), then in May 2016 (three observations 2 and 5 days apart) and in March 2017 app. one week after an extended period of heavy rains associated with the North-east Monsoon (3 observations 3 days in a row and 1 in a different location approx. 50 km away). It flies in the afternoon, between 1:30 and 4:00 pm with temperature 30–32°C and air humidity 60–80%. Each observation was of a single individual.

Discussion

Pyrophleps ellawi is associated with river banks in primary rainforests of Peninsular Malaysia. It was repeatedly observed mud-puddling, in the same location as *Heterosphecia pahangensis* Skowron, 2015 and *H. tawonoides* Kallies, 2003 (personal observations). In a different location, the authors also observed *P. cruentata* and *P. ruficrista* puddling on a river bank. Taking this into account, as well as the fact that Le Cerf (1912) collected *P. haematochrodes* near a river in Vietnam, it is possible that puddling on river banks is a typical behaviour of representatives of this genus, and perhaps of other Oriental Sesiidae.

Members of the family Sesiidae are very rarely filmed in their habitats. Most often, only their morphology is described in detail. This is also the case in Oriental Sesiidae, including the genus *Pyrophleps*; nearly nothing is known about their behaviour. Observations of sesiids in the wild provide priceless information on their biology and even on their true posture, which is lost once the insects are pinned. The video included in this publication allowed the authors to note the intense blue sheen of the sesiid in sunlight, its natural resting position, the functionality of its legs and mud-puddling behaviour, aspects entirely unknown for other species of *Pyrophleps*. Thus, we encourage other entomologists to film sesiids instead of collecting them straight away.

Arita and Gorbunov (2000) state that species of *Pyrophleps* fly from April to July, and in September, and suggest they have two generations per year. *Pyrophleps ellawi* was seen in March, May and August. *H. pahangensis* and *H. tawonoides* also occurred in this period. The authors of this work monitored the location also in April, June and July and although *H. pahangensis* and *H. tawonoides* were seen repeatedly during this time, *P. ellawi* was absent. This indicates it has a different life cycle than the observed *Heterosphecia*, and might have three generations per year. However, there might as well be additional generations in periods which we did not study. Moreover, voltinism may differ from year to year depending on the amount of rainfall and subsequent dry periods, associated with both monsoons and variable El Niño events affecting Malaysia (Corlett and Primack 2011). Due to the complex climate of Malaysia and also based on our observations, caution is needed when making conclusions about the number of generations Sundanian species of Sesiidae have per year, e.g. *P. ellawi* or *P. ruficrista*. *Pyrophleps ellawi* appeared after only several days of sunshine and high temperature following a long period of rain. This may mean that a rise of temperature and end of rain trigger emergence of *Pyrophleps* (perhaps after an extended period spent as a larvae or pupae during the monsoon). Other factors, such as the moon phase, may also influence timing of emergence, which would be an interesting topic for future studies. It is also worth noting that all observed individuals seemed to have freshly emerged.

Although *P. ellawi* occurs in the same locations as *H. pahangensis* and *H. tawonoides*, which are known to be bee mimics in both morphology and behaviour (Skowron et al. 2015; Skowron Volponi and Volponi 2017), and shows similar mud-puddling behaviour, it flies in a completely different manner and cannot be confused with these two species. However, in the field, it had been repeatedly confused with Eumeninae (potter) wasps, whose rapid flight it closely resembles. Adding to this the slender body,

long legs (with hind leg tuft much smaller than in *Heterosphecia*, barely visible from underneath the wings when the sesiid perches, thus unlike the pollen-laden hind legs of bees) and strong blue sheen of *P. ellawi* (Figs 1–2), it seems that the new species is a mimic of Eumeninae wasps.

Conclusion

The new wasp-mimicking species of Sesiidae, *Pyrophleps ellawi*, represents the first record of the genus *Pyrophleps* in Peninsular Malaysia and the first filmed in the wild. The video realized in its habitat provided valuable information on its authentic habitus, functional morphology, and behaviour.

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Supplementary material 1

Video of *Pyrophleps* ellawi in natural habitat

Authors: Marta Agnieszka Skowron Volponi, Paolo Volponi

Data type: multimedia

Explanation note: Supplementary video from the wild shows the behaviour and authentic postures of *Pyrophleps ellawi*. High resolution video available from Vimeo on: https://vimeo.com/230445159

Link: https://doi.org/10.3897/zookeys.692.13587.suppl1

Supplementary material 2

Multiple alignment of barcode sequences

Authors: Marta Agnieszka Skowron Volponi, Paolo Volponi

Data type: mollecular data

Explanation note: Multiple alignment of barcode sequences of the following species: *Pyrophleps ellawi*, *P. vitripennis*, *Heterosphecia pahangensis* (3 specimens), *H. bantanakai*, *H. tawonoides*, *Aschistophleps longipoda*.

Link: https://doi.org/10.3897/zookeys.692.13587.suppl2

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RESEARCH ARTICLE

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The acoustic repertoire of the Atlantic Forest Rocket Frog and its consequences for taxonomy and conservation (*Allobates*, Aromobatidae)

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Abstract

The use of acoustic signals is a common characteristic of most anuran species to mediate intraspecific communication. Besides many social purposes, one of the main functions of these signals is species recognition. For this reason, this phenotypic trait is normally applied to taxonomy or to construct evolutionary relationship hypotheses. Here the acoustic repertoire of five populations of the genus *Allobates* from the Brazilian Atlantic Forest are presented for the first time, on a vulnerable to extinction Neotropical taxon. The description of males' advertisement and aggressive calls and a female call emitted in a courtship context are presented. In addition, the advertisement calls of individuals from distinct geographical regions were compared. Differences in frequency range and note duration may imply in taxonomic rearrangements of these populations, once considered distinct species, and more recently, proposed as a single species, *Allobates olfersioides*. Calls of the male from the state of Rio de Janeiro do not overlap spectrally with calls of males from northern populations, while the shorter notes emitted by males from Alagoas also distinguishes this population from the remaining southern populations. Therefore, it is likely that at least two of the junior synonyms should be revalidated. Similarities among male advertisement and female calls are generally reported in other anuran species; these calls may have evolved from a preexisting vocalization common to both sexes. Male aggressive calls were different from

both the male advertisement and female calls, since it was composed by a longer and multi-pulsed note. Aggressive and advertisement calls generally have similar dominant frequencies, but they have temporal distinctions. Such patterns were corroborated with the Atlantic Forest Rocket Frogs. These findings may support future research addressing the taxonomy of the group, behavioral evolution, and amphibian conservation.

Keywords
Anuran communication, bioacoustics, conservation, female vocalization, taxonomy

Introduction

Acoustic communication is the most used channel of intraspecific information transference in anurans (Walkowiak 2007; Wells 2007). Diverse social functions are mediated by such acoustic signals, for example during territorial conflicts and mate attraction (Wells 2007; Toledo et al. 2015). Sounds are generally emitted by males, which present complex vocal apparatus, generally including the vocal sac, an adaptive structure for resonance (Duellman and Trueb 1986; Wells and Schwartz 2007), and multimodal communication (Starnberger et al. 2014). The mating system in anurans is the most likely explanation for this fact, since females usually represent the selective sex and have to discriminate among potential mates using acoustic evidence from male calls (Wells 1977). However, even without a vocal sac, some females of different species are able to produce sounds, mainly during short-range interactions (Preininger et al. 2016). Females basically use acoustic signals to advertise receptivity for a candidate male during courtship (Márquez and Verrel 1991; Bosch 2002), but sometimes, female calls are used in aggressive (Preininger et al. 2016) or defensive contexts (Toledo and Haddad 2009). Considering the intraspecific social functions, these acoustic signals potentially carry important evidence of species recognition, and the appropriate calls description is useful for taxonomic decisions and future evolutionary studies (Robillard et al. 2006; Padial et al. 2008; Köhler et al. 2017).

Information that elucidates taxonomy is especially useful in the case of the Atlantic Forest populations of *Allobates* Zimmermann & Zimmermann, 1988. This genus has been facing some taxonomic instability: based on morphology, a previous study (Verdade and Rodrigues 2007, Frost 2016) placed three other available specific names for these geographically widespread populations into junior synonymy of *A. olfersioides* (Lutz, 1925): *A. alagoanus* (Bokermann, 1967), *A. capixaba* (Bokermann, 1967), and *A. carioca* (Bokermann, 1967). However, other authors still considered these three disconnected populations as different species, *A. olfersioides* in the state of Rio de Janeiro, *A. capixaba* in the states of Espírito Santo, and *A. alagoanus* in the state of Alagoas (e.g., Haddad et al. 2013, MMA 2014). The clarification of whether these populations are distinct species or lineages of the same species is essential as, if they are considered apart, the different populations

are threatened (*A. olfersioides* is VU) or data deficient (*A. alagoanus* and *A. capixaba*) (MMA 2014). If all populations are considered as one species, the conservation status of the species may change.

These species are morphologically cryptic, the argument that justified the synonymy (Verdade and Rodrigues 2007). Nevertheless, acoustic traits have often revealed differences among morphologically cryptic species (e.g. Toledo et al. 2007, Köhler et al. 2015, Andrade et al. 2016). Especially for these populations, some acoustic differences were suggested (see Bokermann 1967), but never tested. Therefore, a comparative analysis of the acoustic communication among different populations would enlighten the group taxonomy. In spite of this, populations of the Atlantic Forest *Allobates* are showing evidence of decline in the states of Rio de Janeiro and Espírito Santo (Weygoldt 1989, Verdade 2010, Carvalho et al. 2017), and hence, multiple acoustic recordings are scarce.

Therefore, in trying to provide further information on the acoustic signals of these populations, we collected recordings of the two distinct regions: Southeast and Northeast Brazil. These calls, emitted in three different social contexts, are described, and comparisons are made between the advertisement calls of individuals from five populations. This comparison exposed striking differences between some populations, indicating three putative species.

Materials and methods

Sixteen audio files were obtained with calls emitted in three different social contexts: (1) advertisement calls; (2) territorial calls; and (3) female amplectant calls (*sensu* Toledo et al. 2015). These recordings come from populations of five municipalities from southeastern and northeastern Brazil (Figure 1).

Our sample from southeastern Brazil was based on the advertisement calls of one male from Teresópolis, Rio de Janeiro, recorded on 14 Dec 1977 by Ronald W. Heyer (microphone and recorder data are not available) and deposited in Fonoteca Neotropical Jacques Vielliard, FNJV (FNJV32824). Recordings from Bahia come from 12 males from the municipalities of Igrapiuna (n = 9 males), Ituberá (n = 1 male), and Porto Seguro (n = 1 female and 2 males). Using an Edirol recorder and a Sony microphone, recordings from Igrapiuna were obtained in August to September 2008, and May to July 2009, while the male from Ituberá was recorded on 04 April 2005. These audio files, with advertisement and territorial calls, can be accessed upon request in the sound collection of the Universidade Estadual de Feira de Santana, following the codes: 100.18, 100.203, 100.206, 100.209, 100.218, 100_324, 100_325, 100_326, 100_334, 100_335, 100_287. We deposited the same files referring to their original collection (mentioned above) in FNJV (FNJV 33311-33320). The calls from Porto Seguro were recorded with a DAT recorder on February 2002 at Reserva Particular Estação Veracel. Female calls were recorded while in amplexus with a conspecific male. The observer was 1 m from the calling female. This recording is also deposited in FNJV

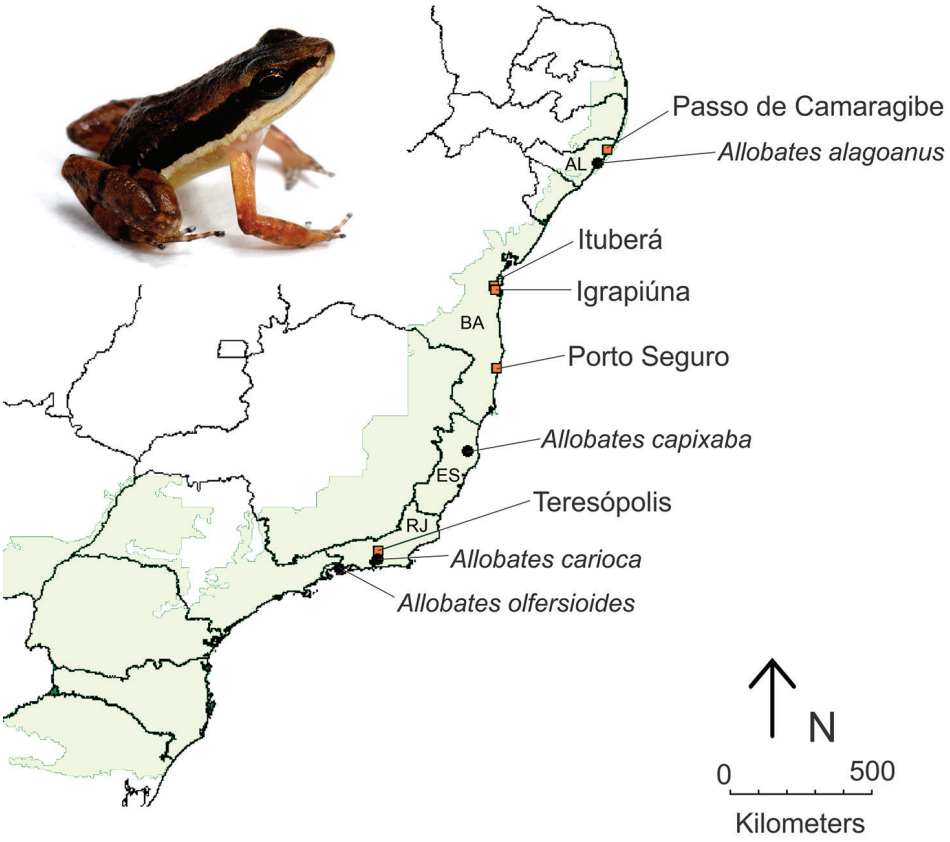

Figure 1. Sampled *Allobates* populations (orange squares - indicating the municipality name) and type localities of four available specific names for the Atlantic forest populations of the genus *Allobates* (black circles - indicating their specific names). Brazilian state names are abbreviated: AL - Alagoas, BA - Bahia, ES - Espírito Santo, and RJ - Rio de Janeiro. The light green shade indicates the original distribution of the Atlantic Forest. The upper left photograph of an adult male *Allobates* was taken in Igrapiúna, BA.

(FNJV32825). Advertisement calls of the two males from Bahia are deposited in the Scientific Collection of Amphibians Vocalizations from the National Museum of Rio de Janeiro with the following access codes: MNVOC_57_04 and MNVOC_57_06. Two males were recorded between 12 and 14 September 2004, at municipality of Passo de Camaragibe, Alagoas, Brazil. These individuals were on the forest floor, approximately 50 m from a rivulet, inside a forest remnant, nearly 100 m from the coastal shore. Advertisement and territorial calls of two males were recorded using a Marantz cassette tape recorder (PMD222) equipped with an external directional microphone (Audiotecnica AT835b) positioned approximately 50 cm from the calling male. Recordings were deposited in FNJV (FNJV12681 and 12685).

All recordings were digitized at 22 kHz of frequency sampling and 16 bits of resolution for standardize the analyzed audio files. Vocalizations were analyzed with Raven Pro 1.4 (Bioacoustic Research Program, 2011). We analyzed such acoustic properties: Note duration (s), Minimum frequency (Hz), Peak of dominant frequency (Hz), Maximum frequency (Hz), and Frequency bandwidth (as maximum subtracted by minimum) (Hz). Spectral measurements were obtained using a FFT (Fast Fourier Transform) of 1024. For acoustic measurements, we selected the calls using the spectrogram. The acoustic traits analyzed and the respective Raven functions used for measurements are present in the Suppl. material 1, Table S1. Figures were prepared with FFT of 256, with 50 % of overlap in a Hann window. Power spectrums for individual notes were generated in the software Goldwave v6.24, using the spectrum filter function. No filtering was applied in the spectrograms.

One-Way Analysis of Variance (ANOVA) was performed with post hoc test of Fisher LSD (Least Significant Difference), for comparing notes duration among different populations. We carried the analysis in the software Statistica, where we adopted the significance level of 0.05.

Results

The advertisement call of all populations is composed by one single note, generally repeated inside a sequence with discrete intervals (Figure 2a). Notes are composed of one or two fused pulses.

Many males (60 %) presented interval between notes decreasing along the sequence (Figure 2b and c), with stronger patterns most observed in calls of males from Alagoas. Female amplectant call sequence presents the same structure. A slight spectral modulation can be observed between notes for both call types. However, the call produced by females has more pronounced spectral modulations (Figure 3). Advertisement calls from different regions had distinct band frequency occupation: calls from Rio de Janeiro (Southeastern) are lower (not overlapping) than calls from populations of Northeastern Brazil (Figure 2). In addition, we found difference (One-Way ANOVA, $F_{(4,308)} = 27.888$; $P < 0.0001$, followed by Fisher LSD: Suppl. material 1, Table S2) between the note duration of the population of Alagoas and all others (shorter in Alagoas), and between the population of Ituberá and all others (intermediate between Alagoas and all others) (Suppl. material 1, Figure S1). A clinal variation on notes duration was observed, in which southern populations has longer notes than northern populations.

Male aggressive calls are different from advertisement and female amplectant calls since they are composed by a single multi-pulsed note (Figure 3). In two occasions, we registered males combining aggressive calls among sequences of advertisement calls. A detailed comparison of acoustic properties among these three types of calls and geographic variation among advertisement calls is available in the Table 1.

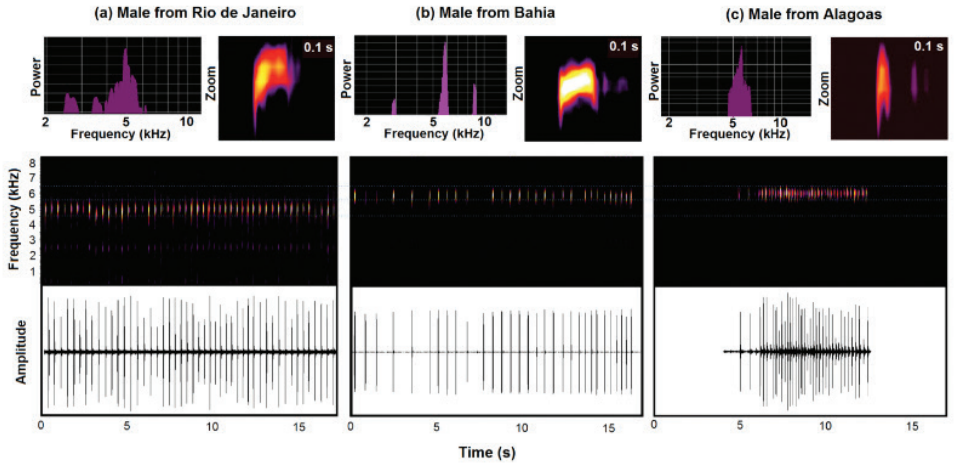

Figure 2. Power spectrum (above left), spectrogram (middle and detail of one note highlighted above right) and oscillogram (below) of vocalizations of three populations of the Atlantic Forest Rocket Frogs: Rio de Janeiro, state of Rio de Janeiro (a; FNJV32824); Igrapiuna, state of Bahia (b; FNJV33312); and Passo de Camaragibe, state of Alagoas (c; FNJV12685).

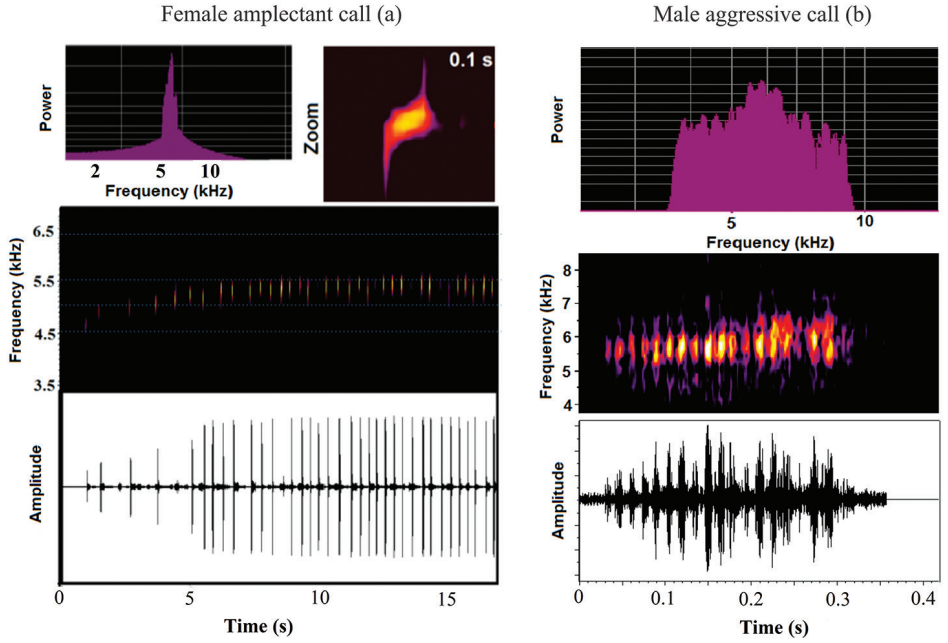

Figure 3. Female amplectant call of the Atlantic Forest Rocket Frog from the state of Bahia: power spectrum (above left), spectrogram (middle and detail of one note highlighted above right) and oscillogram (below) (FNJV32825) (a); and Male aggressive call of the Atlantic Forest Rocket Frog from the state of Alagoas: power spectrum (above), spectrogram (middle), and oscillogram (below) (FNJV12681) (b).

Table 1. Acoustic properties of three types of calls of the Atlantic Forest populations of *Allobates*. Values presented as mean ± SD (range) number of calls.

Call type	**Male advertisement call**					**Male aggressive call**		**Female amplectant call**
Municipality (State)	**Rio de Janeiro (RJ)**	**Igrapiuna (BA)**	**Ituberá (BA)**	**Porto Seguro (BA)**	**Passo de Camaragibe (AL)**	**Igrapiuna (BA)**	**Passo de Camaragibe (AL)**	**Porto Seguro (BA)**
Individuals	**1**	**9**	**1**	**2**	**2**	**1**	**1**	**1**
Interval between notes (s)	0.328 ± 0.039 (0.296 – 0.449) 15	0.666 ± 0.387 (0.203 – 2.958) 180	0.308 ± 0.035 (0.262 – 0.381) 23	0.396 ± 0.530 (0.076 – 2.921) 37	0.190 ± 0.100 (0.083 – 0.624) 48	not applicable	not applicable	0.423 ± 0.254 (0.229 – 1.163) 19
Note or call duration (s)	0.046 ± 0.003 (0.039 – 0.053) 25	0.042 ± 0.016 (0.024 – 0.089) 180	0.032 ± 0.002 (0.028 – 0.038) 23	0.044 ± 0.012 (0.030 – 0.068) 37	0.022 ± 0.006 (0.007 – 0.039) 48	0.64 ± 0.042 (0.611 – 0.706) 4	0.28 ± 0.11 (0.15 – 0.35) 3	0.032 ± 0.006 (0.026 – 0.044) 25
Minimum frequency (kHz)	4.83 ± 0.08 (4.48 – 4.91) 25	5.67 ± 0.15 (5.40 – 5.94) 180	5.82 ± 0.11 (5.55 – 6.00) 23	5.83 ± 0.08 (5.68 – 5.98) 37	5.91 ± 0.16 (5.44 – 6.31) 48	4.22 ± 0.011 (4.07 – 4.32) 4	5.41 ± 0.53 (5.36 – 5.47) 2	5.34 ± 0.76 (5.21 – 5.51) 25
Peak of dominant frequency (kHz)	4.91 ± 0.08 (4.60 – 5.06) 25	5.80 ± 0.15 (5.49 – 6.03) 180	6.01 ± 0.10 (5.64 – 6.09) 23	5.99 ± 0.04 (5.94 – 6.05) 37	6.14 ± 0.14 (5.90 – 6.35) 48	6.03 ± 0.13 (5.83 – 6.13) 4	6.04 ± 0.48 (5.55 – 6.52) 2	5.47 ± 0.78 (5.21 – 5.51) 25
Maximum frequency (kHz)	5.04 ± 0.08 (4.71 – 5.10) 25	5.86 ± 0.15 (5.55 – 6.09) 180	6.07 ± 0.06 (5.85 – 6.13) 23	6.09 ± 0.06 (5.98 – 6.30) 37	6.24 ± 0.16 (6.00 – 6.54) 48	6.56 ± 0.13 (6.37 – 6.67) 4	6.92 ± 0.42 (6.50 – 7.34) 2	5.52 ± 0.08 (5.38 – 5.72) 25
Range frequency (kHz)	0.21 ± 0.03 (0.10 – 0.28) 25	0.18 ± 0.05 (0.08 – 0.32) 180	0.24 ± 0.07 (0.08 – 0.36) 23	0.25 ± 0.06 (0.12 – 0.41) 37	0.33 ± 0.20 (0.15 – 1.07) 48	2.33 ± 0.19 (2.15 – 2.60) 4	1.50 ± 0.36 (1.14 – 1.87) 2	0.18 ± 0.05 (0.08 – 0.26) 25

Discussion

Although the comparisons are limited due to small sample sizes, these results do not corroborate the proposed synonymy between, at least, *A. olfersioides* and the northeastern populations (Verdade and Rodrigues 2007). While the morphological data showed that these populations are cryptic, the observed variation on frequency band and note duration of the advertisement call represents a strong evidence that these populations are indeed, at least, three distinct species. This finding is in agreement with the suggested in Bokermann (1967), who indicated possible acoustics differences in regards to temporal properties (interval between notes) between *A. olfersioides* and *A. capixaba*. As we did not have access to the recordings from the state of Espírito Santo, we now face different possible taxonomic resolutions: i) the populations from Bahia are attributed to *A. capixaba*, which is distinct from the northern populations, which should be *A. alagoanus*; or ii) the populations from Bahia represents a new species, considering the population in Rio de Janeiro as *A. olfersioides*, in Alagoas as *A. alagoanus*, and in Espírito Santo as *A. capixaba* (for which we did not have call recordings). The clinal variation on note duration give margins for both interpretations.

If our evidence is questionable, due to the limited sample size, we stress the need of further recordings (mainly from Southeast populations) coupled with molecular analysis to increase resolution in the taxonomy of the Atlantic Forest Rocket Frogs. Targeting these populations in future studies are critical, as if the different populations are considered distinct species, the occurrence range of *A. olfersioides* will be restricted to the state of Rio de Janeiro, where declines and local extinctions were reported (Weygoldt 1989, Verdade 2010, Carvalho et al. 2017). In such case, *A. olfersioides* conservation status (today considered as "Least Concern") would change to "Vulnerable", and *A. capixaba*, and *A. alagoanus* would be considered as "Data Deficient", as currently is classified in the Brazilian list of Threatened Species (MMA 2014). Therefore, this evaluation is not only of taxonomic interest, but may also reflect directly in anuran (and Atlantic Forest) conservation.

Some congeneric species present similar advertisement calls, with one note repeated several times in a discrete interval. It is the case in *A. algorei* Barrio-Amorós & Santos, 2009, *A. flaviventris* Melo-Sampaio, Souza & Peloso, 2013, *A. goianus* (Bokermann, 1975), *A. magnussoni* Lima, Simões & Kaefer, 2014, *A. masniger* (Morales, 2002), and *A. nidicola* (Caldwell & Lima, 2003) (Barrio-Amorós and Santos 2009, Bastos et al. 2011, Tsuji-Nishikido et al. 2012, Lima et al. 2014). However, many other species may present a complex call composed by a series of notes, as we can find in *A. brunneus* (Cope, 1887), *A. crombiei* (Morales, 2002), *A. femoralis* (Boulenger, 1884), *A. granti* (Kok, MacCulloch, Gaucher, Poelman, Bourne, Lathrop & Lenglet, 2006), *A. grillisimilis* Simões, Sturaro, Peloso & Lima, 2013, *A. kingsburyi* (Boulenger, 1918), *A. myersi* (Pyburn, 1981), *A. paleovarzensis* Lima, Caldwell, Biavati & Montanarin, 2010, and *A. talamancae* (Cope, 1875) (Kok et

al. 2006, Castillo-Trenn and Coloma 2008, Simões et al. 2008, Simões and Lima 2011, Lima et al. 2012, Kaefer and Lima 2012, Simões et al. 2013, Lechelt et al. 2014, Lima et al. 2014).

A modulated interval between notes (decreasing intervals between notes during the call) observed mainly in the advertisement calls of northeast males and in the female call has not been observed in other species, except for *A. talamancae* (Lechelt et al. 2014). A similar frequency modulation observed among notes in the advertisement call of all populations was observed in the advertisement call of *A. femoralis* and *A. paleovarzensis* from Central and South-West Brazilian Amazonia (Kaefer and Lima 2012, Simões et al. 2008). Therefore, this genus is interesting and useful for testing the evolution of call structure.

Female calls (with intraspecific social context) are present in more than 50 species belonging to 12 families (Preininger et al. 2016). Our study extends this information to an additional family, providing the first female call in Aromobatidae. Females may use acoustic signals in four social contexts: advertisement, courtship, aggressiveness (Preininger et al. 2016), and defense (Toledo and Haddad 2009). Although a female calling during amplexus was registered, the signal's social function is not clear and should still be the subject of observations and future playback experiments. Except for the pronounced spectral modulation, female calls are similar to advertisement calls of males from the same population. Emerson and Boyd (1999) suggested that in species where females vocalize during courtship, the calls might have evolved by a preexisting pathway that appears to be common to both sexes. Similarity between male and female calls are common (Bosch and Márquez 2001); however, female calls are generally less intense (in sound pressure levels) and of shorter duration than male advertisement calls (Tobias and Kelley 1987, Preininger et al. 2016).

Aggressive calls in anurans are generally different from advertisement calls in a temporal structure, and sometimes the aggressive calls are considered adjustments of the male advertisement call (Wells 2007, Wells and Schwartz 2007). As in the Atlantic Forest Rocket Frog, the aggressive calls of *A. caeruleodactylus* (Lima and Caldwell 2001) are shorter and louder than their advertisement calls (Lima et al. 2002). Therefore, it is possible that this pattern is conserved in congeneric species.

The current study presents novel acoustic information about five distinct populations of the Atlantic Forest Rocket Frogs, which may stimulate further comprehensive studies focusing on the taxonomy and systematics of the Atlantic Forest populations or even among the Neotropical congenerics. Bioacoustic characterization of different populations has been proven to be useful for both taxonomy and conservation (e.g. Méndez-Cárdenas et al. 2008, Forti et al. 2016, Köhler et al. 2017). That is especially relevant for the populations considered presently as they are already categorized as threatened (MMA 2014), population declines have been reported (Weygoldt 1989, Verdade 2010, Carvalho et al. 2017), and the Atlantic Forest itself is one of the biodiversity hotspots in the world (Myers et al. 2000).

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Supplementary material 1

The acoustic repertoire of the Atlantic Forest Rocket Frog (*Allobates*, Aromobatidae) and its consequences for taxonomy and conservation.

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Data type: acoustic measurements and results of specific comparing analysis

Explanation note: Here, we presented complementary methodology information and additional results with statistical differences of note duration among populations.

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