

Five million years in the darkness: A new troglomorphic species of *Cryptops* Leach, 1814 (Chilopoda, Scolopendromorpha) from Movile Cave, Romania

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Abstract

A new species of *Cryptops* Leach, 1814, *C. speleorex* **sp. nov.**, is described from Movile Cave, Dobrogea, Romania. The cave is remarkable for its unique ecosystem entirely dependent on methane- and sulfur-oxidising bacteria. Until now, the cave was thought to be inhabited by the epigean species *C. anomalans*, which is widespread in Europe. Despite its resemblance to *C. anomalans*, the new species is well-defined morphologically and molecularly based on two mitochondrial (cytochrome *c* oxidase subunit I COI and 16S rDNA) and one nuclear (28S rDNA) markers. *Cryptops speleorex* sp. nov. shows a number of troglomorphic traits such as a generally large body and elongated appendages and spiracles, higher number of coxal pores and saw teeth on the tibia of the ultimate leg. With this record, the number of endemic species known from the Movile Cave reaches 35, which ranks it as one of the most species-rich caves in the world.

Keywords

Biospeleology, *Cryptops speleorex* sp. nov., Dobrogea, molecular phylogenetics, new species, troglomorphy

Introduction

Located in the southeastern part of Romania not far from the Black Sea Coast, Movile Cave is the first known subterranean chemosynthesis-based ecosystem (Sarbu et al. 2019). Being completely isolated from the outside environment for 5.5 million years, the cave is remarkable for its unique ecosystem entirely dependent on methane- and sulfur-oxidising bacteria, which release nutrients through chemosynthesis for fungi and other cave animals along the food chain. This subterranean ecosystem is also notable for being rich in hydrogen sulfide, methane (1–2%), ammonia and CO₂ (1.5–3.5%) whereas it is poor in O₂ (7–16%). Relative humidity in the cave is 100% and there is no detectable air movement. The cave was first discovered in 1986 and since then, only a handful of people have visited it (Sarbu et al. 2019).

Despite its harsh living conditions, Movile Cave ecosystem is known to harbor a diverse and unique fauna. The cave hosts 51 invertebrate species, of which 34 species are endemic (Sarbu et al. 2019). Among these species, some present a number of unique adaptations to a troglobitic life in caves, such as the troglobiont water scorpion *Nepa anophthalma* Decu, Gruia, Keffer & Sarbu, 1994 (Hexapoda, Hemiptera, Nepidae); the nesticid and liocranid spiders *Kryptonesticus georgescuae* Nae, Serban & Weiss, 2018 (Araneae: Nesticidae) and *Agraeocina cristiani* (Georgescu, 1989) (Araneae, Liocranidae); the cave leech *Haemopsis caeca* Manoleli, Klemm & Sarbu, 1998 (Annelida, Hirudinea, Haemopidae) and the isopod *Armadillidium tabacarui* Gruia, Iavorschi & Sarbu, 1994 (Crustacea, Isopoda, Armadillidiidae) (Sarbu et al. 2019).

Five species of myriapods are hitherto discovered from the innermost parts of Movile viz. *Archiboreoiulus serbansarbui* Giurginca, Vănoaica, Šustr, & Tajovský, 2020 (Diplopoda), *Symphylella* Silvestri, 1902 sp. (Symphyla), *Geophilus alpinus* Meinert, 1870 and *Clinopodes carinthiacus* (Latzel, 1880) (Geophilomorpha) and a troglobitic population of *Cryptops anomalans* Newport, 1844 (Negrea 1993; Sarbu et al. 2019). It is worth mentioning that the latter taxon has been only studied morphologically (Negrea 1993, 2004).

Recently, we had the occasion to study freshly collected specimens of an undetermined species of the genus *Cryptops* Leach, 1814 from Movile Cave. Using both, morphological and molecular evidence, the cave specimens were compared with those of *C. anomalans* living on the surface, outside the cave. A phylogenetic analysis of 29 *Cryptops* specimens from different parts of Europe, including two from inside Movile Cave, based on two mitochondrial (cytochrome c oxidase subunit I COI and 16S rDNA) and one nuclear (28S rDNA) markers was performed. Morphological and molecular analyses confirmed that the cave specimens from Movile correspond to a new species, *Cryptops speleorex* sp. nov., that we describe herein. Additionally, we provide an annotated list and a key to the troglobitic *Cryptops* species in the world.

Material and methods

All *Cryptops* specimens from Movile Cave were hand-collected by the biospeleologists Serban Sarbu and A. Hillebrand and preserved in 70% or 96% ethanol.

Microphotographs were obtained with a Nikon DS-Ri-2 camera mounted on a Nikon SMZ25 stereomicroscope using NIS-Elements Microscope Imaging Software with an Extended Depth of Focus (EDF) patch. Images were edited in Photoshop CS6 and assembled in InDesign CS6. Material is shared between the **ISER** – Emil Racoviță Institute of Speleology, Bucharest, Romania; **IZB** – University of Belgrade – Institute of Zoology, Faculty of Biology, Belgrade, Serbia; **NHMW** – Naturhistorisches Museum Wien, Austria; **NMNHS** – National Museum of Natural History, Sofia, Bulgaria and the **ZMUT** – University of Turku – Zoological Museum, Finland. In addition to the type material of the new species we have morphologically studied material of *C. anomalans* from Serbia and Romania.

Morphological terminology follows Bonato et al. (2010).

Abbreviations: **T** – tergite, **S** – sternite.

Molecular methods

Altogether 29 specimens from both inside and outside the Movile Cave were included in the phylogenetic analysis. Of these, 14 were sequenced in this study. Total DNA was extracted from the legs using NucleoSpinTissue kit (Macherey-Nagel) according to the standard protocol for human or animal and cultured cells. Samples were incubated overnight. One nuclear (28S rRNA) and two mitochondrial (cytochrome *c* oxidase subunit I, COI, and 16S rRNA) fragments were chosen for amplification since they have proven informative between closely related taxa (Vahtera et al. 2012, 2013). 28S rRNA fragment was amplified with the primers 28Sa/28Sb (Whiting et al. 1997), COI fragment with the primers LCO1490/HCO2198 (Folmer et al. 1994) and 16S rRNA with the primers 16Sa/16Sb (Xiong and Kocher 1991; Edgecombe et al. 2002). All primers had a universal tail (T7Promoter/T3) attached to them.

Polymerase chain reaction (PCR) amplifications were performed with MyTaq™ HS Red Mix. PCR was performed in a total volume of 23 µL containing 7.5 µL of MQ, 12.5 µL of MyTaq HS Red Mix, 2×, 0.5 µL of each primer (10 µM) and 2 µL of DNA template. PCR started with initial denaturation at 95 °C for 1 min and was followed by denaturation at 95 °C for 15 s. Annealing temperature for 28S rRNA and COI was 49 °C and 43 °C for 16S rRNA. Annealing lasted for 15 s and was followed by extension at 72 °C for 10 s. The last three steps were repeated 35 times. A negative control was included. PCR products were run in electrophoresis on 1% Agarose gel using Midori Green Advanced DNA Stain (Nippon Genetics). Samples were purified with an A'SAP PCR clean-up kit (ArcticZymes). Sequencing was performed by MacroGen Europe. The resulting chromatograms were visualized and assembled using the software Sequencher 5 (Gene codes corporation, USA). All new sequences are deposited in GenBank (See Table 1 for accession numbers).

Phylogenetic analyses

Most specimens included in the analysis had all three markers successfully sequenced. To obtain more geographic variation in the dataset, 15 *Cryptops* specimens (mostly from Wesener et al. 2016) from GenBank (Table 1) were additionally included in

Table 1. Specimens used in the molecular phylogeny and their GenBank accession numbers (specimens sequenced in this study in bold). Institutional abbreviations: ISER–Emil Racoviță Institute of Speleology, Bucharest, Romania; IZBU–University of Belgrade–Faculty of Biology, Institute of Zoology, Belgrade, Serbia; MCZ–Museum of Comparative Zoology, Harvard University; ZFMK–Museum Koenig, Bonn; ZSM–Bavarian State Collection of Zoology, Munich; ZMUT–Zoological Museum, University of Turku, Finland.

Species	Lab code	Voucher ID number	Voucher	Country	COI	16S	28S
<i>Cryptops speleorex</i> sp. nov.	K3	http://mus.utu.fi/ZMUT.MYR-TYPE001	ZMUT	Romania	MW240507	MW243978	MW243648
<i>C. speleorex</i> sp. nov.	K4		ISER	Romania	MW240508	MW243977	MW243649
<i>C. anomalans</i>	1a		IZB	Serbia	MW240504	MW243967	MW243651
<i>C. anomalans</i>	1b		IZB	Serbia	MW240505	MW243968	MW243652
<i>C. anomalans</i>	2		IZB	Serbia	MW240511	–	MW243642
<i>C. anomalans</i>	3		IZB	Serbia	MW240515	MW243970	MW243643
<i>C. anomalans</i>	4		IZB	Serbia	MW240503	MW243979	MW243654
<i>C. anomalans</i>	7		IZB	Serbia	MW240506	MW243969	MW243653
<i>C. anomalans</i>	8		IZB	Serbia	MW240512	MW243971	MW243644
<i>C. anomalans</i>	9		IZB	Serbia	MW240514	MW243973	MW243645
<i>C. anomalans</i>	12		IZB	Serbia	MW240516	MW243974	MW243646
<i>C. anomalans</i>	13		IZB	Serbia	MW240513	MW243972	MW243647
<i>C. anomalans</i>	54a		ISER	Romania	MW240510	MW243975	MW243650
<i>C. anomalans</i>	57a		ISER	Romania	MW240509	MW243976	MW243641
<i>C. anomalans</i>		ZFMK-MYR 1048	ZFMK	Germany	KM491639	–	–
<i>C. anomalans</i>		ZFMK-MYR 1047	ZFMK	Germany	KM491699	–	–
<i>C. anomalans</i>		ZFMK-MYR 1379	ZFMK	Germany	KM491703	–	–
<i>C. anomalans</i>		ZFMK-MYR 4072	ZFMK	Germany	KM491706	–	–
<i>C. anomalans</i>		ZSM-ART-JSP130812-004	ZSM	Germany	KU497151	–	–
<i>C. anomalans</i>		ZSM-ART-JSP110624-001	ZSM	Germany	KU497158	–	–
<i>C. anomalans</i>		ZSM-ART-JSP141105-017	ZSM	Germany	KU497159	–	–
<i>C. anomalans</i>		IZ-131458	MCZ	UK	KF676499	KF676457	KF676353
<i>Cryptops</i> sp.		ZFMK-MYR-1185	ZFMK	Austria	KM491620	–	–
<i>Cryptops</i> sp.		ZFMK-MYR 3662	ZFMK	Germany	KU342042	–	–
<i>Cryptops</i> sp.		ZSM-ART-JSP150118-047	ZSM	Slovenia	KU497143	–	–
<i>Cryptops</i> sp.		ZSM-ART-JSP110425-008	ZSM	Croatia	KU497153	–	–
<i>C. croaticus</i>		ZFMK-MYR 3320	ZFMK	Austria	KU342049	–	–
<i>C. hortensis</i>		IZ-130582	MCZ	UK	JX422662	JX422684	JX422582
<i>C. parisi</i>		IZ-130592	MCZ	UK	KF676502	KF676460	KF676356
<i>Scelopendra cingulata</i>		IZ-131446	MCZ	Spain	HM453310	HM453220	AF000782

the phylogenetic analysis. Of these, 12 had only COI available. Multiple sequence alignments were performed in MAFFT7 online service (Katoh et al. 2019; Kuraku et al. 2013). Sequences were trimmed in Mesquite v 3.10 (Maddison and Maddison 2019) after which the three separate data sets were concatenated with SequenceMatrix (Vaidya et al. 2011) for the phylogenetic analyses. The final molecular matrix including all three data sets (COI, 16S, 28S) consisted of 1561 characters and 29 taxa (excluding outgroup).

Phylogenetic analysis was conducted using both parsimony and maximum likelihood as optimality criteria. Parsimony analysis was done with TNT v. 1.5 (Goloboff and Catalano 2016) treating gaps as missing data. The search strategy consisted of 100 replications, and of 10 rounds of both ratchet and tree drifting followed by tree fusing (Goloboff 1999). Command xmult was executed until 50 independent hits of the shortest tree were found. A strict consensus of the most-parsimonious trees was produced. The command 'blength' was used to report the branch lengths of the

resulting trees. Jackknife (Farris et al. 1996) resampling method with 1000 replicates and with a probability of a character removal being 0.36 was applied to estimate nodal support. Maximum likelihood analysis of the combined data was conducted RAxML v. 8 (Stamatakis 2014) in the CIPRES portal (Miller et al. 2010). The three genes were separated into different partitions. Unique general time-reversible (GTR) model of sequence evolution (RAxML implements only GTR-based models of nucleotide substitutions) with corrections for a discrete gamma distribution (GTR+ Γ) was used. Nodal support values were estimated using the rapid bootstrap algorithm with 1000 replicates together with GTR-CAT model (Stamatakis et al. 2008). The mitochondrial genes (16S+COI) and the nuclear ribosomal 28S were additionally analysed separately using the same search strategy as was used for the combined data.

Uncorrected p-distances of aligned COI, 16S and 18S data were calculated with MEGA v. 7.0.21 (Kumar et al. 2016).

Results

Order Scolopendromorpha Pocock, 1895

Family Cryptopidae Kohlrausch, 1881

Genus *Cryptops* Leach, 1814

Cryptops (*Cryptops*) *anomalans* Newport, 1844

Material examined. ROMANIA: SE Romania: Lalomița County, Călugărească Forest, 18.II.2016, leg. and det. S. Baba, 1 subad. ex. (ISER); Lalomița County, Călugărească Forest, oak forest, 28.II.2019, leg. and det. S. Baba, 2 ex. (ISER) (lab code 54a); Lalomița County, Călugărească Forest, rotten wood, 13.III.2016, leg. and det. S. Baba, 1 ex. (ISER); Bucharest, Herăstrău Park, under stones, 10.X.2019, leg. and det. S. Baba, 1 ex. (ISER) (lab code 57a); Mangalia, Obanul Mare, Cave Drilling, -3 m, 10.VIII.1999, det. St. and A. Negrea, 1 ex. (ISER); Mangalia, Obanul Mare, Cave Drilling, -8 m, 27.V.2000, det. St. and A. Negrea, 1 ex. (ISER); Mangalia, Obanul Mare, Cave Drilling, -8 m, 28.VI.2000, det. St. and A. Negrea, 1 ex. (ISER); Mangalia, Obanul Mare, Cave Drilling, -12 m, 27.V.2000, det. St. and A. Negrea, 1 ex. (ISER). SERBIA: Valley of the Izbice River, v. Izbice, near Novi Pazar, SW Serbia (43°07.333'N, 20°34.354'E; elevation about 700 m a.s.l.): 5♂, 5♀, collected in 2012 (May-October), leg. D. Stojanović (lab code 1) (IZB); Prolom Banja Spa, near Kuršumlija, southern Serbia (43°02.449'N, 21°23.448'E; elevation about 620 m a.s.l.): 3♀, collected 30.04.2016., leg. D. Stojanović (lab code 2) (IZB); village Kacabać, near Bojnik, Leskovac, southern Serbia (43°03.415'N, 21°46.368'E; elevation about 200 m a.s.l.): 2♂, 1♀, collected 01.05.2016., leg. D. Stojanović (lab code 3) (IZB); Pećina Rasnica 1 Cave, village Rasnica, near Pirot, SE Serbia: 1♂, 1♀, collected 18.07.2018., leg. D. Antić (lab code 4) (IZB); Novopazarska Banja Spa, near Novi Pazar, SW Serbia (43°09.269'N, 20°33.132'E; elevation about 650 m a.s.l.): 3♂, 4♀, collected 30.05.2012., leg. D. Stojanović (IZB);

Spomen Park, Leskovac, southern Serbia (42°59.051'N, 21°56.349'E; elevation about 200 m a.s.l.): 1♀, collected 28.07.2012., leg. D. Stojanović (IZB); pine forest near the Đurđevi Stupovi Monastery, Novi Pazar, SW Serbia (43°09.183'N, 20°30.049'E): 1♀, collected 15.05.2015., leg. D. Stojanović (lab code 7) (IZB); village Dobanovci, near Surčin, Belgrade, Serbia (44°49.197'N, 20°13.334'E): 1♀, collected 03.11.2013., leg. D. Stojanović (lab code 8) (IZB); Bojčinska šuma forest, village Progar-Jakovo, near Surčin, Belgrade, Serbia (44°43.528'N, 20°09.245'E): 3♀, 1♂, collected 09.06.2013., leg. D. Stojanović, K. Bjelanović (lab code 9) (IZB); Vrla River, Mt. Vlasina, near “Rosa” water factory, v. Topli Do, near Surdulica, SE Serbia (42°38.213'N, 22°17.565'E; elevation about 1070 m a.s.l.): 1♂, collected 07.07.2011, leg. D. Stojanović (IZB); Višnjička Banja, Belgrade, Serbia (44°49.073'N, 20°32.337'E; elevation about 350 m a.s.l.): 1♂, collected 09.06.2006, leg. Ž. Pavković (IZB); Spomen Park, Leskovac, southern Serbia (42°59.051'N, 21°56.349'E; elevation about 200 m a.s.l.): 3♀, 1♂, collected 14.04.2012., leg. D. Stojanović (lab code 12) (IZB). **BULGARIA:** Pirin Mts, between Sandanski and Lilyanovo, 12.8.1988, litter, mainly *Platanus*, P. Beron leg. 1 ex. (NM-NHS) (Figs 2B, 3B, 4B,D, 5B).

***Cryptops (Cryptops) speleorex* sp. nov.**

<http://zoobank.org/8A28E7DF-168B-485C-8A0C-CD7EB218E650>

Figs 1A, B, 2A, 3A, 4A, C, 5A, 6A–C

Previous records. *Cryptops anomalans*: Negrea, 1993: p. 87 and all subsequent records (Negrea 1994, 1997, 2004; Negrea and Minelli 1994; Sarbu et al. 2019).

Material examined. Holotype: ROMANIA: Constanța County, Mangalia, Movile Cave (Peștera Movile), Lake Hall, June, 2014, leg. S. Sarbu, 1 ex. (NMNHS, Myriapoda Collection Id: 10 812); **Paratypes:** same locality and collector leg. S. Serban, 1 ex. (NHMW10177); same locality, 22.XI.2017, leg. A. Hillebrand, 1 ad. ex., identified as *C. anomalans* by Stefan Baba (ISER); 1 ad. ex., same locality, date and collector, identified as *C. anomalans* by Stefan Baba (<http://mus.utu.fi/ZMUT.MYR-TYPE001>).

Diagnosis. A species morphologically similar to *Cryptops anomalans*, but differing from it by the much elongated antennae and legs, generally less setose forcipules and body, coxopleures with more than 300 coxal pores (vs. less than 100 in *anomalans*), ultimate leg with 13–17 saw teeth on tibia (usually 7–10, occasionally 12 in *anomalans*), and larger and elongated spiracles (see Table 2). Genetically, *Cryptops speleorex* sp. nov. differs from the *C. anomalans* specimens from Romania and Serbia by 9.2–12.2% in COI and 6.6–8.7% in 16S rDNA.

Description (holotype). Length (anterior margin of head plate to posterior margin of telson) approx. 52 mm (46 mm in an adult paratype) (Figs 1A, B). Head plate (Fig. 2A) 3.2 mm long, 3.4 mm broad; antenna approx. 10 mm long. Body yellow-brownish (Fig. 1A); antennae and legs pale yellow; posterior edge of head and tergites with irregular light brownish band, darker in the middle (Figs 1B, 2A); forcipular tarsungulum and leg claws dark brown. Head plate overlaps approx. 1/3 of tergite 1; head plate slightly broader than long (3.2 mm × 3.4 mm), posterior corners strongly

Table 2. Differences in morphological characters between *Cryptops anomalans* and *C. speleorex* sp. nov.

Morphological character	<i>Cryptops anomalans</i>	<i>Cryptops speleorex</i> sp. nov.
Body size (mm)	25–50	>46–52
Antennae length	Until posterior end of T3	Until mid of T5
Antennal article 7 L/W (mm)	0.5 × 0.25	1.0 × 0.5
Antennae: spines on basal articles	Present, numerous	Lacking or just a few
Ultimate leg length	7.65 mm	13.25 mm
Ultimate leg pretarsus (mm)	0.25	1
Ultimate leg saw teeth on tibia and tarsus 1	Tibia: 7–12 (usually 7–10); Tarsus: 3–5	Tibia: 13–17; Tarsus: 5–6
Legs	Short, compact, pretarsus short	Strongly elongated, pretarsus long
Spiracles	Ovoid, small to medium sized (Fig. 4D)	Strongly elongated, large (Fig. 4C)
Forcipular trochanteroprefemur	With spines medially (4–6)	Without spines, just stout setae
Coxopleural pore field	Approx. 2/3 of coxopleura; composed of less than 100 pores (86–90)	Approx. 4/5 of coxopleura; composed of more than 310 pores (317–320)

rounded, sides convex outwards, anterior apex slightly indented at the base of antennae, bisected by longitudinal median furrow; paramedian sutures diverging anteriorly on head plate; head punctate, sparsely covered with fine setae.

Antenna relatively long, extending to the middle of tergite 5 when folded backward (Figs 1A, 2A); composed of 17 articles; article length formula: $17 < 1 < 2 = 16 < 3 = 4 = 13 = 14 < 5 = 6 = 11 = 12 < 7 - 10$; basal two articles relatively stout, in general articles increase in length to a maximum at articles 7–10, then gradually shortening; article 17 is more than half length of article 16 (approx. 60%); articles 5–10 much longer than wide, length up to 3 times the width. All surfaces of antennal articles with scattered long setae, densest on articles 1–3; short, fine setae abundant on all articles except for articles 1 and 2, as well as basal part of 3.

Clypeus with 2 setae; prelabral setae in one row of 21–22; 4 short setae between clypeus and prelabral row, irregularly or more evenly scattered. Labral mid piece with a short, but well-developed tooth; side pieces rounded (Fig. 3A).

Forcipular segment anterior margin of coxosternite convex on each side, with a weak median diastema, fringed by 2 marginal setae on each side. Surface of coxosternite (Fig. 3A) covered with scarce short setae, 10–15 in total; trochanteroprefemur stout, median margin slightly expanded proximally, with 4 setae; femur and tibia very short; tarsungulum long, curved, almost equal in length to trochanteroprefemur's height.

Maxilla 2 with a well-developed pretarsus; dorsal brush white, dense, situated on the distalmost part of article 3 of telopodite. Proximal side of first maxillary telopodite covered by 10–15 setae (Fig. 3A).

Tergites Tergite 1 with a complete anterior transverse suture and cruciform sutures (Figs 1A, 2A). Oblique sutures present on tergites 2–8; complete paramedian sutures on tergites 2–20; lateral crescentic sulci visible on tergites 6–20; all tergites nearly devoid of setae, occasionally individual scattered short setae. Tergite 21 longer than wide, posterior margin subtriangular, with rounded apex; shallow median depression along posterior half of tergite (Fig. 1B).

Sternites 1–2 and 19–21 without transverse and median sutures; S 3–18 with median longitudinal and curved transverse sutures, more prominent from sternite 5 onward (Fig. 4A). All sternites covered by minute setae. Endosternite: subtrapezoidal,

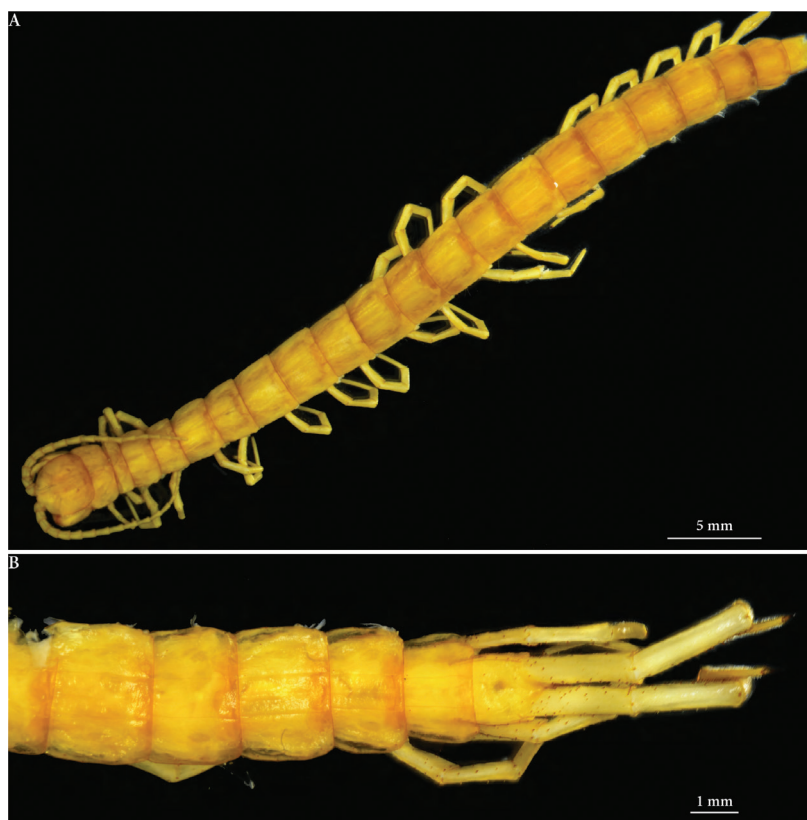


Figure 1. *Cryptops speleorex* sp. nov. **A** holotype, habitus, dorsal view **B** paratype (ZMUT), posterior-most segments and ultimate legs, dorsal view.



Figure 2. *Cryptops* spp., head and anteriormost segments **A** *Cryptops speleorex* sp. nov., holotype, dorsal view **B** *Cryptops anomalans*, Pirin Mts (Bulgaria), dorsolateral view (slightly apical).

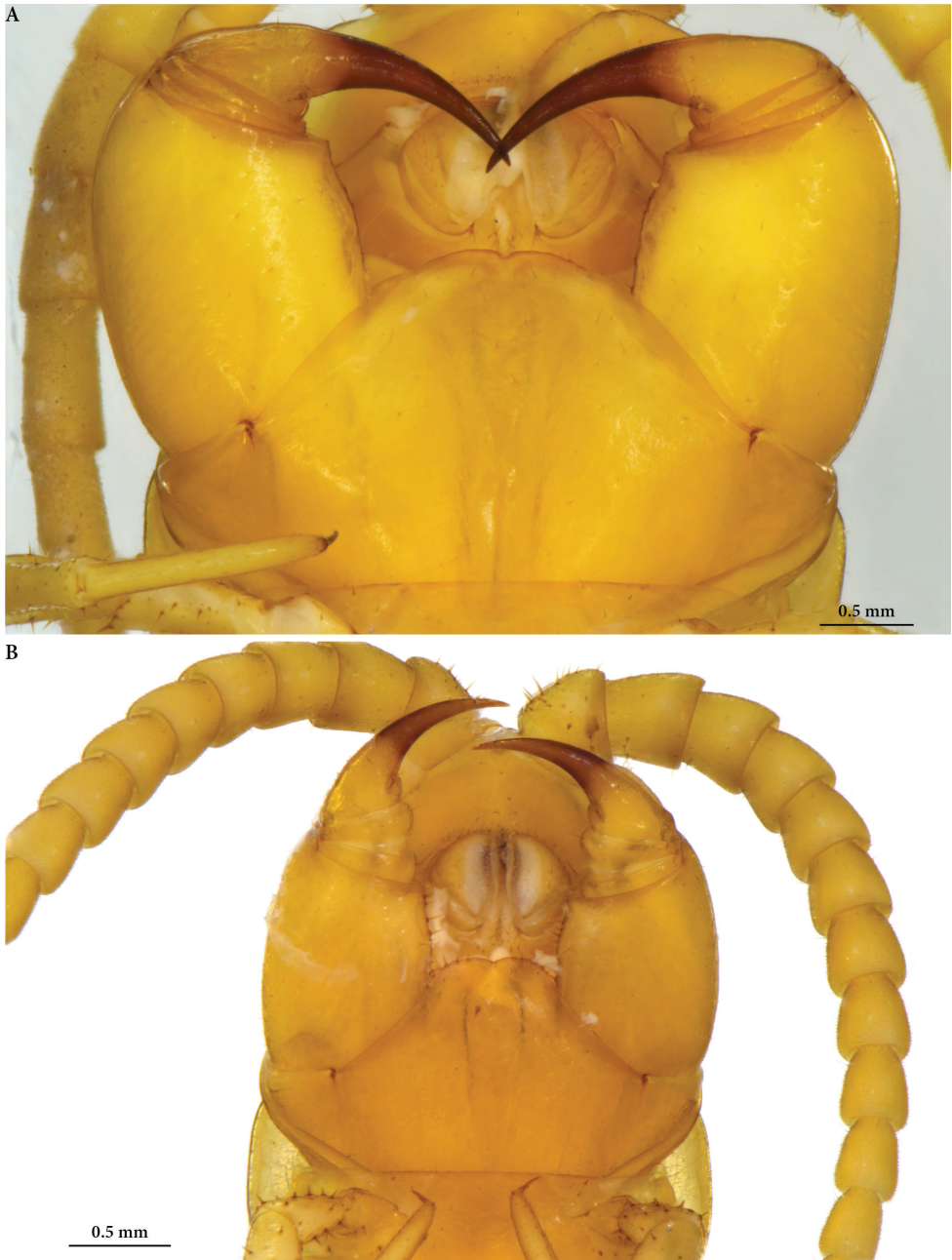


Figure 3. *Cryptops* spp., forcipular coxosternum, ventral view **A** *Cryptops speleorex* sp. nov., holotype **B** *Cryptops anomalans*, Pirin Mts (Bulgaria).

lateral margins very slightly convex, posterior margin slightly concave in the middle; surface with several (6–10) moderately long and sparse setae.

Spiracles strongly elongated on T3, reducing in size towards the posterior end of the body; slit-like (Fig. 4C).

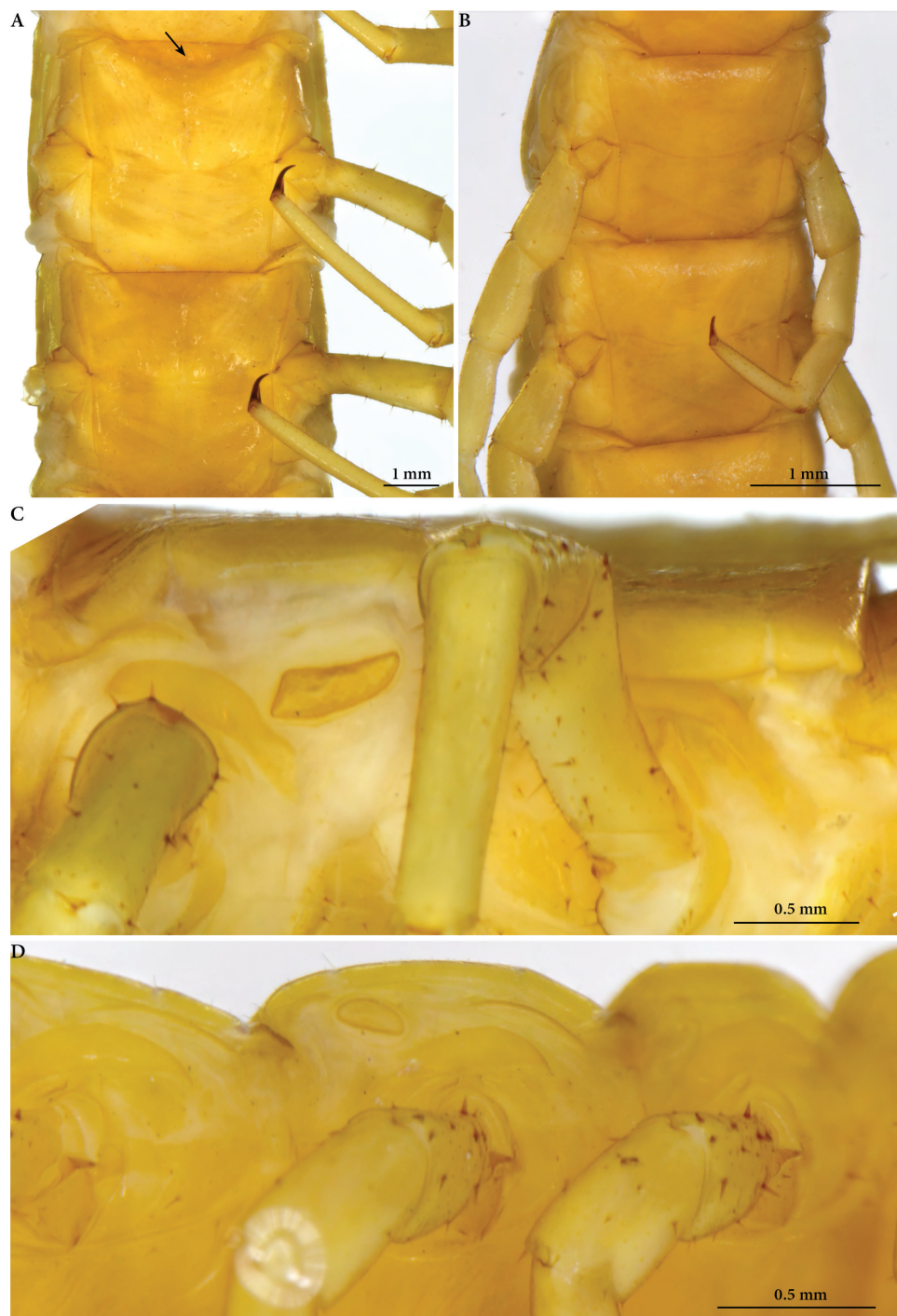


Figure 4. *Cryptops* spp., sternites 8–9 and spiracles **A, B** sternites 8–9 **A** *Cryptops speleorex* sp. nov., holotype, arrow indicating the endosternite **B** *Cryptops anomalans*, Pirin Mts (Bulgaria) **C, D** spiracles **C** *Cryptops speleorex* sp. nov., holotype **D** *Cryptops anomalans*, Pirin Mts (Bulgaria).

Coxopleural pore field elliptical, covering 4/5 of surface, with more than 310 coxal pores (317–320), extending nearly to posterior margin of coxopleuron (Fig. 5A). Approx. 15–20 sparse spiniform setae emerging between pores and from the dorsal and posterior margins of coxopleuron.

Legs generally long; leg 10: prefemur 1.47 mm long, femur 1.59 mm, tibia 1.76 mm, tarsus 2.35 mm, pretarsus 0.7 mm. All tarsi single (Fig. 6A). Walking legs (Fig. 6A, B) smooth, generally poor in setae; spiniform setae sparsely present on the surface of prefemur, and occasionally also on the femur; all pretarsi long, with an anterior and posterior accessory spines of different size, the larger being 2/3rd of pretarsus; accessory spines absent on leg 21; 20 leg: prefemur, femur and tibia slightly swollen; femur and tibia being slightly concave at midlength; a specific field of dense, minute setae present on the ventral, lateral and mesal sides of prefemur, femur and part of tibia.

Ultimate leg (Fig. 6C): prefemur 3.61 mm long, femur 3.05 mm, tibia 1.94 mm, tarsus 1: 1.28 mm, tarsus 2: 2.22, pretarsus 0.56 mm.; numerous robust spiniform setae on the ventral, mesal and less so on lateral and dorsal sides of prefemur; spiniform setae present also on the ventral and mesal sides of femur; tibia, tarsus 1 and tarsus 2 covered by tiny dense setae on all sides; 13–14 saw teeth on tibia (17 in an adult paratype) and 5–6 on tarsus 1.

Etymology. The species epithet is a noun in apposition, meaning "king of the cave", referring to the species top position in the food chain of the Movile ecosystem.

Distribution. The species is hitherto known only from the aphotic zone of the Cave Movile in the southern part of Romanian Dobrogea.

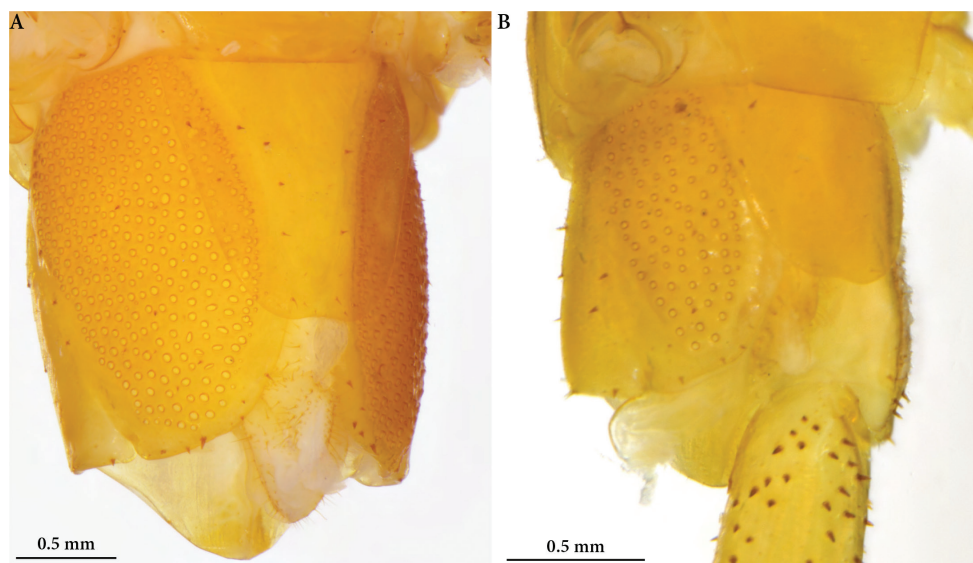


Figure 5. *Cryptops* spp., Coxopleural pore field **A** *Cryptops speleorex* sp. nov., holotype **B** *Cryptops anomalans*, Pirin Mts (Bulgaria).

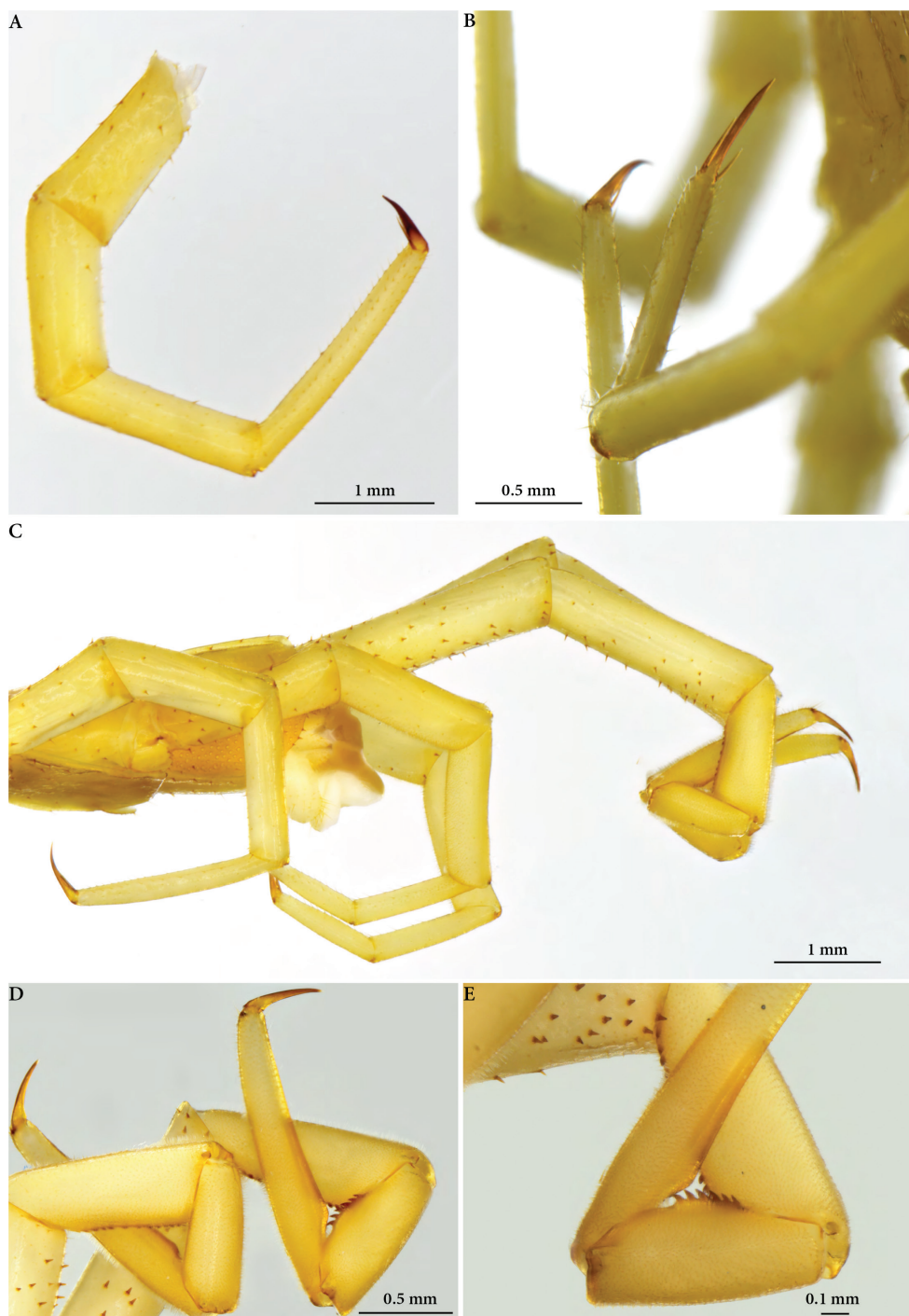


Figure 6. *Cryptops speleorex* sp. nov., legs. **A** holotype, walking leg **B** paratype (ZMUT), walking leg, close-up of apical claw **C** holotype, ultimate legs, lateral view **D, E** paratype (NHMW), distal articles of ultimate teeth showing saw teeth.

Ecological remarks. *Cryptops speleorex* sp. nov. is the largest invertebrate species in Movile Cave. It has been observed feeding on terrestrial isopods (*Trachelipus troglolobius* Tabacaru & Boghean, 1989, *Armadillidium tabacarui* Gruia, Iavorschi & Sarbu, 1994), smaller beetles, Diplura or spiders (Sarbu et al. 2019).

Phylogenetic analyses

Parsimony analysis resulted in a single most-parsimonious (MP) tree of length 1586 steps (Fig. 7). Two *C. speleorex* sp. nov. specimens collected from Movile Cave (samples K3 and K4) group within *C. anomalans* as a separate clade supported by jackknife resampling value (hereafter JF) of 99. The phylogeny shows the Movile Cave clade being evolutionary most closely related to the clade (JF = 75) including *C. anomalans* samples from southern Serbia and Belgrade area (JF = 100) and Romania and SW Serbia (JF = 84). This Serbian/Romanian clade forms a sister group with the clade (JF = 95) containing a single *C. anomalans* specimen (lab code 4) from southeast Serbia (collected from a cave) and identical sequences of *C. anomalans* from London, UK and different parts of Germany (JF = 100). All specimens above form a clade with strong support (JF = 92). Outside this clade are *Cryptops* sp. from Austria and an unsupported clade containing *Cryptops* spp. from Croatia and Slovenia together with *C. hortensis* (Donovan, 1810). Basal to these are resolved *C. parisi* Brolemann, 1920 and *C. croaticus* Verhoeff, 1931 (JF = 82) followed by *Cryptops* sp. from Germany.

Regarding the placement of *C. speleorex* sp. nov. and the relationships among the *C. anomalans* specimens, the likelihood analysis (Fig. 8) resulted in a mostly congruent tree topology with the parsimony tree, the only difference being that in the parsimony analysis *C. speleorex* sp. nov. is resolved basal to the Serbian/Romanian clade whereas in the likelihood tree it is resolved within it. The *C. speleorex* sp. nov. specimens form a clade supported by bootstrap value (hereafter BS) of 100. *Cryptops speleorex* sp. nov. groups together with the *C. anomalans* specimens from Serbia (excluding a single Serbian *C. anomalans* specimen, lab code 4) and Romania. All the specimens above form a sister clade to a group including *C. anomalans* specimens from Serbia (lab code 4), Germany and the UK. As in the parsimony analysis, the additional *Cryptops* species (other than *C. anomalans*) were resolved as basal to *C. anomalans*. Their internal grouping varies from that in the parsimony tree, which is not surprising due to the lack of nodal support in the basal-most nodes.

When analyzed separately (only likelihood, tree not shown), the mitochondrial COI and 16S resolved *C. speleorex* sp. nov. as a distinct clade (BS = 100) within *C. anomalans* specimens, the tree topology regarding *C. speleorex* sp. nov./*C. anomalans* being identical to that of the parsimony tree. Not surprisingly, the level of variation in the nuclear 28S was low and the likelihood analysis based on it could not resolve the relationships among the *C. anomalans*/*C. speleorex* sp. nov. specimens (tree not shown).

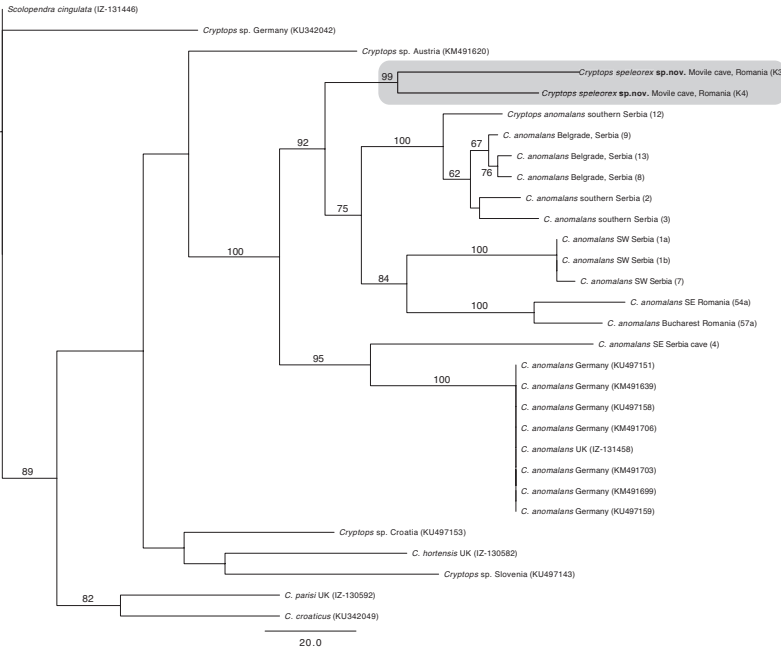


Figure 7. The single most parsimonious tree of length 1586 steps with jackknife resampling values > 50% shown on the nodes. Branch lengths represent the number of optimized character-state changes.

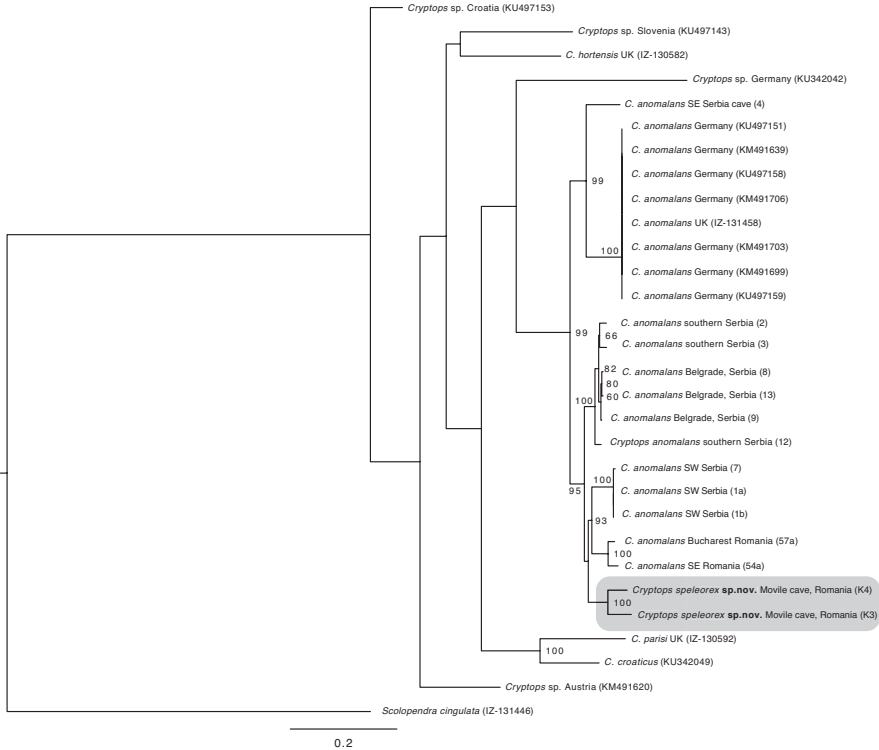


Figure 8. Likelihood tree with bootstrap values > 50% shown for each node.

Pairwise distances

Pairwise distances between the samples by each marker are shown in Tables 3–5. The differences between *C. speleorex* sp. nov. and the closest clade (Fig. 7) comprising of *C. anomalans* specimens from Romania and Serbia are 9.2–12.2% (COI) and 6.6–8.7% (16S rDNA). Nuclear 28S rDNA was conservative and showed almost no variation (0–0.3%) between these specimens. The difference between the new species and the rest of the *C. anomalans* specimens (Serbia (lab code 4), Germany and UK) is 13.8–15.5% (COI). In respect to 16S the differences were 10.7–12.5% and 9.9–11.2% between the new species and the Serbian (lab code 4) and *C. anomalans* from London, UK, respectively. Intraspecific difference between the two *C. speleorex* sp. nov. specimens is 8.5% in COI and 6.6% in 16S.

Key for identification of cave-specialized (troglomorphic/troglophilic) *Cryptops*

- 1 Forcipular coxosternal margin with blunt, rounded or slightly flattened, hyaline lobes; tarsungulum very short ***C. (Paracryptops) indicus***
- Forcipular coxosternal margin without hyaline lobes; tarsungulum moderate or long **3**
- 3 Trigonal sutures present on the posterior part of sternites. Tarsus of most legs bipartite ***Cryptops (Trigonocryptops)****
- Sternal trigonal sutures absent. Tarsus of most legs a single article ***Cryptops (Cryptops)***
- 5 Ultimate legs with saw teeth present from prefemur to tarsus 2, saw teeth formula: 28-30-14-17-17 ***C. spelaeoraptor* Ázara & Ferreira, 2014**
- Ultimate legs with saw teeth present on tibia and tarsus 1 only **7**
- 7 T1 with transverse suture only **9**
- T1 with transverse and other sutures **11**
- 9 Head without paramedian sutures; length: 19 mm, antennae short, 3+3 saw teeth on tibia and tarsus of ultimate legs ***C. beroni***
- Head with incomplete paramedian sutures on the posterior half and the anteriormost quarter of the cephalic plate; length: 28–29 mm; antennae long, 4+9 saw teeth on tibia and tarsus 1 of ultimate leg ***C. illyricus***
- 11 T1 with inverted Y-shaped sutures ***C. legagus* Edgecombe, Akkari, Netherlands, Du Preez, 2020**
- T1 with transverse and/or paramedian sutures **13**
- 13 T1 with transverse suture and two paramedian sutures; prefemur and femur of ultimate legs with dorsodistal spinous process; small species, ca 15 mm, cave in India ***C. kempi***
- T1 with transverse suture and U-shaped or cruciform suture; prefemur and femur of ultimate legs without dorsodistal spinous process; caves in Europe **15**

* Here belong: *C. camoowealensis*, *C. cavernicolus*, *C. hephaestus*, *C. iporangensis*, *C. longicornis*, *C. roeplainsensis*, *C. troglobius*

- 15 T1 with transverse and cruciform sutures; head with 2 complete paramedian sutures, large species ***Cryptops speleorex* sp. nov.**
- T1 with transverse suture and characteristic U-shaped suture attached to it; head with incomplete paramedian sutures 17
- 17 Labrum tridentate 19
- Labrum unidentate 21
- 19 Antennae short, head plate with incomplete anterior and posterior paramedian sutures; saw teeth on tibia and tarsus in combination 13+6 ***C. diana***
- Antennae long, head plate with posterior paramedian sutures only ***C. umbricus umbricus***
- 21 Head with two incomplete posterior paramedian sutures only; anterior margin of forcipular coxosternite strongly convex and covered by spiniform setae, cave in France ***C. umbricus lewisi***
- Head with two incomplete short posterior paramedian sutures only; anterior margin of forcipular coxosternite slightly rounded and barely protuberant; spiniform setae missing, cave on Tenerife ***C. vulcanicus***

Discussion

Scolopendromorphs are strictly terrestrial and most species are found in forest leaf litter, decomposed wood, under bark of dead trees, in the soil, under stones or in caves in the temperate and tropical areas of the world. Few species are well adapted to eremic environments (Minelli and Golovatch 2013), occasionally in atypical habitats such as forest canopy (Lewis 1982; Phillips et al. 2020) or tropical rivers (Siriwut et al. 2016). Although less common than lithobiomorphs, scolopendromorphs may occur in caves, where they are represented with some highly adapted species, mainly from the family Cryptopidae. Other families are only marginally recorded in caves: Scolopocryptopidae (genera *Thalckethops* Crabill, 1960 and *Newportia* Gervais, 1847 with several species from American caves, including several troglobites), Plutoniu-midae (genera *Plutonium* Cavanna, 1881 and *Theatops* Newport, 1844) in European caves and Scolopendridae (genus *Otostigmus* Porat, 1876; *O. cooperi* Chamberlin, 1942 inhabits Chilibrilo caves in Panama (Chamberlin 1942); *Otostigmus troglodytes* Ribaut, 1914 found in a cave near Tanga, Tanzania (Ribaut 1914)). The genus *Cryptops* is by far the most frequent in the caves worldwide with some 18–20 species found in caves in South Europe (Spain, France, Italy, Greece), Canary Islands, Cuba, Brazil, Australia and Africa. Troglomorphic species are known from the nominate subgenus, and the subgenera *Trigonocryptops* and *Paracryptops* (see Table 6).

Several morphological characters traditionally used in centipedes taxonomy could be subject to intraspecific variation related to postembryonic development, animal life stage and ecology (Akkari et al. 2017). This might render species identification problematic in some cases and generates taxonomic errors. This is also true for such

a highly variable and widely distributed species as *C. anomalans*. In fact, nine species and subspecies were hitherto synonymised with this species (see Krapelin 1903; Verhoeff 1931; Crabill 1962; Zapparoli 2002). Three subspecies are still listed as valid for it (Chilobase 2.0). Now the identity of these taxa and the presence of any possible cryptic species within *C. anomalans* could only be revealed via an integrative study combining morphological and molecular markers. Whereas clear molecular differences are here indicated by the different markers and the high interspecific distance between *C. anomalans* and the newly described species *C. speleorex* sp. nov., the morphological comparison was not as straightforward since both species show several similarities, including an overlapping in size. While several of the differences observed between both species (Table 2) could be understood as a clear indication of troglomorphism in *C. speleorex* sp. nov. such as the elongation of appendages, a few other characters including the number of saw teeth on tibia and tarsus 1 of the ultimate legs, number of coxal pores and the shape of spiracles were diagnostic to separate both species.

Intraspecific distance between the two sequenced *Cryptops speleorex* sp. nov. specimens is relatively high in comparison to the detected interspecific variation (Tables 3–5) raising a question whether these two specimens could actually be interpreted as two separate species. However, this variation is only shown in the two mitochondrial markers – there are no morphological differences (or any difference in their nuclear 28S marker) between the *C. speleorex* sp. nov. specimens. As Morgan-Richards et al. (2017) well explains, cryptic speciation should never be used as a null hypothesis in the absence of phenotypic or nuclear data supporting it. Instead, “the origin of the divergent mtDNA haplogroups might result from complex biogeographical scenarios or they might simply represent normal, stochastic processes of mutation and extinction of a non-recombining locus within a large population”.

Taxonomic and evolutionary implications of *C. speleorex* sp. nov.

The type locality of *C. anomalans* is unknown and therefore it is impossible to conclude which part (if any) of the studied population is the actual *C. anomalans* described by Newport (1844). Before this study, only a handful of *C. anomalans* specimens from a limited geographic range had been sequenced (Spelda et al. 2011; Vahtera et al. 2013; Wesener et al. 2016). We acknowledge that describing *C. speleorex* sp. nov. as a new species leaves *C. anomalans* paraphyletic and that monophyly is violated by this taxonomic act. However, we view this as an inevitable consequence of speciation with a particular evolutionary implication, i.e., that *C. speleorex* sp. nov. evolved within what is currently known as *C. anomalans*. It is worth noting that the closest evolutionary relatives of *C. speleorex* sp. nov. appear to be the *C. anomalans* specimens from Serbia (excluding the sample number 4) and Romania (Figs 8, 9). This means that they are most closely related to each other than either of them is to the rest of the studied *C. anomalans* populations. The current situation with *C. anomalans* should not be seen as a failed taxonomy but as a natural consequence when new data from a widespread species is obtained.

All positions containing gaps and missing data were eliminated. There were a total of 556 positions in the final dataset.

[illegible]

All positions containing gaps and missing data were eliminated. There were a total of 556 positions in the final dataset.																													
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29
15 <i>Cryptops spelaeox</i> sp. nov. Mivile cave, Romania (K4)	0.225	0.138	0.138	0.138	0.138	0.138	0.138	0.138	0.138	0.142	0.095	0.095	0.101	0.085															
16 <i>C. anomalans</i> Bucharest Romania (57a)	0.212	0.138	0.138	0.138	0.138	0.138	0.138	0.138	0.138	0.135	0.074	0.074	0.079	0.112	0.103														
17 <i>C. anomalans</i> SE Romania (54a)	0.225	0.146	0.146	0.146	0.146	0.146	0.146	0.146	0.146	0.142	0.092	0.092	0.097	0.122	0.117	0.040													
18 <i>C. anomalans</i> southern Serbia (2)	0.243	0.129	0.129	0.129	0.129	0.129	0.129	0.129	0.129	0.138	0.103	0.103	0.108	0.104	0.097	0.088	0.099												
19 <i>C. anomalans</i> Belgrade, Serbia (8)	0.239	0.133	0.133	0.133	0.133	0.133	0.133	0.133	0.133	0.140	0.097	0.097	0.103	0.110	0.094	0.086	0.094	0.023											
20 <i>C. anomalans</i> Belgrade, Serbia (13)	0.239	0.131	0.131	0.131	0.131	0.131	0.131	0.131	0.131	0.138	0.095	0.095	0.101	0.108	0.092	0.085	0.092	0.022	0.002										
21 <i>C. anomalans</i> Belgrade, Serbia (9)	0.239	0.131	0.131	0.131	0.131	0.131	0.131	0.131	0.131	0.138	0.095	0.095	0.101	0.108	0.092	0.085	0.092	0.022	0.002	0.000									
22 <i>C. anomalans</i> southern Serbia (3)	0.239	0.131	0.131	0.131	0.131	0.131	0.131	0.131	0.131	0.138	0.104	0.104	0.110	0.112	0.092	0.099	0.106	0.032	0.027	0.025	0.025								
23 <i>C. anomalans</i> southern Serbia (12)	0.241	0.137	0.137	0.137	0.137	0.137	0.137	0.137	0.137	0.135	0.094	0.094	0.099	0.106	0.090	0.090	0.101	0.040	0.029	0.027	0.027	0.043							
24 <i>C. borensis</i> UK (IZ-130582)	0.243	0.203	0.203	0.203	0.203	0.203	0.203	0.203	0.203	0.182	0.174	0.174	0.178	0.173	0.189	0.180	0.187	0.198	0.200	0.198	0.198	0.191	0.191						
25 <i>Cryptops</i> sp. Austria (KM491620)	0.228	0.178	0.178	0.178	0.178	0.178	0.178	0.178	0.178	0.167	0.182	0.182	0.185	0.174	0.167	0.176	0.183	0.180	0.173	0.173	0.173	0.185	0.182	0.169					
26 <i>Cryptops</i> sp. Croatia (KU497153)	0.230	0.182	0.182	0.182	0.182	0.182	0.182	0.182	0.182	0.180	0.200	0.200	0.203	0.201	0.191	0.203	0.209	0.198	0.196	0.194	0.194	0.194	0.192	0.156	0.156				
27 <i>C. parisi</i> UK (IZ- 130592)	0.221	0.192	0.192	0.192	0.192	0.192	0.192	0.192	0.192	0.173	0.176	0.176	0.182	0.191	0.182	0.171	0.180	0.171	0.169	0.167	0.167	0.167	0.171	0.196	0.192	0.185			
28 <i>C. croaticus</i> (KU342049)	0.239	0.201	0.201	0.201	0.201	0.201	0.201	0.201	0.201	0.185	0.173	0.173	0.176	0.192	0.178	0.174	0.180	0.194	0.194	0.192	0.192	0.196	0.196	0.169	0.192	0.192	0.137		
29 <i>Cryptops</i> sp. Slovenia (KU497143)	0.255	0.192	0.192	0.192	0.192	0.192	0.192	0.192	0.192	0.185	0.189	0.189	0.192	0.201	0.203	0.189	0.203	0.201	0.205	0.207	0.207	0.201	0.196	0.173	0.207	0.180	0.187	0.165	
30 <i>Cryptops</i> sp. Germany (KU342042)	0.223	0.201	0.201	0.201	0.201	0.201	0.201	0.201	0.201	0.187	0.192	0.192	0.196	0.210	0.194	0.178	0.192	0.198	0.194	0.194	0.194	0.205	0.198	0.210	0.185	0.187	0.196	0.203	0.216

Table 4. Estimates of evolutionary divergence between sequences. 16S: The number of base differences per site from between sequences are shown. The analysis involved 17 nucleotide sequences. All positions containing gaps and missing data were eliminated.

There were a total of 392 positions in the final dataset.																
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
1 <i>Scelopendra tinguata</i> (IZ-131446)																
2 <i>Cryptops anomalans</i> UK (IZ-131458)	0.390															
3 <i>C. anomalans</i> SW Serbia (1a)	0.372	0.092														
4 <i>C. anomalans</i> SW Serbia (1b)	0.372	0.092	0.000													
5 <i>C. anomalans</i> SW Serbia (7)	0.372	0.094	0.003	0.003												
6 <i>C. anomalans</i> southern Serbia (3)	0.372	0.082	0.036	0.036	0.038											
7 <i>C. anomalans</i> Belgrade, Serbia (8)	0.367	0.092	0.041	0.041	0.041	0.018										
8 <i>C. anomalans</i> Belgrade, Serbia (13)	0.372	0.089	0.043	0.043	0.043	0.020	0.008									
9 <i>C. anomalans</i> Belgrade, Serbia (9)	0.372	0.087	0.041	0.041	0.041	0.010	0.008	0.010								
10 <i>C. anomalans</i> southern Serbia (12)	0.365	0.084	0.033	0.033	0.036	0.018	0.031	0.033	0.023							
11 <i>C. anomalans</i> SE Romania (54a)	0.372	0.092	0.059	0.059	0.059	0.048	0.054	0.051	0.048	0.051						
12 <i>C. anomalans</i> Bucharest Romania (57a)	0.372	0.099	0.066	0.066	0.066	0.054	0.059	0.056	0.054	0.059	0.013					
13 <i>Cryptops speteorex</i> sp. nov. Movile cave, Romania (K4)	0.365	0.099	0.082	0.082	0.082	0.066	0.074	0.071	0.069	0.071	0.066	0.069				
14 <i>Cryptops speteorex</i> sp. nov. Movile cave, Romania (K3)	0.383	0.112	0.087	0.087	0.084	0.071	0.077	0.074	0.069	0.082	0.079	0.082	0.066			
15 <i>C. anomalans</i> SE Serbia cave (4)	0.385	0.084	0.094	0.094	0.097	0.077	0.087	0.084	0.082	0.079	0.097	0.107	0.107	0.125		
16 <i>C. parisi</i> UK (IZ-130592)	0.355	0.217	0.209	0.209	0.212	0.214	0.227	0.224	0.222	0.219	0.224	0.227	0.232	0.235	0.232	
17 <i>C. hortensis</i> UK (IZ-130582)	0.360	0.230	0.217	0.217	0.219	0.222	0.235	0.230	0.232	0.224	0.235	0.245	0.230	0.219	0.230	0.260

Table 6. An annotated list of the troglobitic/troglophilic *Cryptops* species in the world.

Species	Distribution	Category	References
<i>Cryptops (Cryptops) beroni</i> Matic & Stavropoulos, 1988	Greece: Crete, Acrotiri, Cave Katholiko	Troglobite?	Matic and Stavropoulos (1988)
<i>Cryptops (Trigonocryptops) camoowealensis</i> Edgecombe, 2006	Australia: Queensland, Camooweal area, Five O’Clock Cave	Troglobite	Edgecombe (2006)
<i>Cryptops (Trigonocryptops) cavernicolus</i> Negrea & Fundora Martinez, 1977	Cuba	Troglobite	Matic et al. (1977)
<i>Cryptops (Cryptops) diana</i> Matic & Stavropoulos, 1990	Greece: Thassos Island, cave Dracotrypa	unknown	Matic and Stavropoulos (1990)
<i>Cryptops (Trigonocryptops) hephaestus</i> Ázara & Ferreira, 2013	Brazil: known from three iron ore caves of the “Quadrilátero Ferrífero” (Iron Quadrangle) in Minas Gerais in Mariana and Itabirito municipalities	Troglophile	Ázara and Ferreira (2013), Chagas-Jr and Bichuette (2018)
<i>Cryptops (Cryptops) illyricus</i> Verhoeff, 1933	Caves only?; Slovenia and Croatia		Verhoeff 1933
<i>Cryptops (Trigonocryptops) iporangensis</i> Ázara & Ferreira, 2013	Brazil: known from four caves (Ressurgência das Areias de Água Quente, Gruta Monjolinho, Caverna Alambari de Baixo, Caverna Santana) in Iporanga, São Paulo	Troglobite	Ázara and Ferreira (2013), Chagas-Jr and Bichuette (2018)
<i>Cryptops (Paracryptops) indicus</i> (Silvestri, 1924)	India: Assam, Garo Hills, Siju Cave	Troglophile	(Silvestri 1924)
<i>Cryptops (Cryptops) kemp</i> Silvestri, 1924	India: Assam, Garo Hills, Siju Cave	Troglophile	(Silvestri 1924)
<i>Cryptops (Cryptops) legagus</i> Edgecombe, Akkari, Netherlands, Du Preez, 2020	Botswana: Diviner’s Cave (Koanaka Hills) and Dimapo Cave (Gcwihaba Hills)	Epigean/ Troglophile?	Edgecombe et al. (2020)
<i>Cryptops (Trigonocryptops) longicornis</i> (Ribaut, 1915)	Caves in Spain	Troglobite	Ribaut (1915)
<i>Cryptops (Cryptops) speleorex</i> sp. nov.	Romania: Mangalia, Movile Cave	Troglobite	This paper (see also Negrea 1993)
<i>Cryptops (Trigonocryptops) roeplainsensis</i> Edgecombe, 2005	Australia: known from three caves (Nurina Cave 6N-46, Burnabbie Cave, cave 6N-1327), Roe Plains	Troglobite	Edgecombe (2005)
<i>Cryptops (Cryptops) spelaeoraptor</i> Ázara & Ferreira, 2014	Brazil: Bahia, Campo Formoso, only known from the type locality, Toca do Gonçalves Cave		Ázara and Ferreira (2014), Chagas-Jr and Bichuette (2018).
<i>Cryptops (Trigonocryptops) troglolobius</i> Matic, Negrea & Fundora Martinez, 1977	Cuba	Troglobite	Matic et al. (1977)
<i>Cryptops (Cryptops) umbricus umbricus</i> Verhoeff, 1931	Caves in France and Italy but also found outside caves	Troglophile	Verhoeff (1931), Matic (1960), Iorio and Minelli (2005), Iorio and Geoffroy (2007, 2008), Iorio (2010)
Syn. <i>Cryptops jeanneli</i> Matic, 1960			
<i>Cryptops umbricus ischianus</i> Verhoeff, 1942			
<i>Cryptops (Cryptops) umbricus lewisi</i> Iorio, 2010	France: Alpes-Maritimes, Gourdon, Aven du Fourchu Cave	Troglobite	Iorio (2010)
<i>Cryptops (Cryptops) vulcanicus</i> Zapparoli, 1990	Spain: Tenerife Island, Cueva Felipe Reventón	Troglobite	Zapparoli (1990)

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Figure 9. Map of Europe showing geographic distribution of *Cryptops* specimens analyzed herein. Asterisk – *C. speleorex* sp. nov. Dot – other *Cryptops* spp. used in the study (see Table 1 for details).

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A phylogenetic and taxonomic review of baviine jumping spiders (Araneae, Salticidae, Baviini)

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Abstract

The systematics and taxonomy of the tropical Asian jumping spiders of the tribe Baviini is reviewed, with a molecular phylogenetic study (UCE sequence capture, traditional Sanger sequencing) guiding a reclassification of the group's genera. The well-studied members of the group are placed into six genera: *Bavia* Simon, 1877, *Indopadilla* Caleb & Sankaran, 2019, *Padillothorax* Simon, 1901, *Piranthus* Thorell, 1895, *Stagetillus* Simon, 1885, and one new genus, *Maripanthus* Maddison, **gen. nov.** The identity of *Padillothorax* is clarified, and *Bavirecta* Kanesharatnam & Benjamin, 2018 synonymized with it. *Hyctiota* Strand, 1911 is synonymized with *Stagetillus*. The molecular phylogeny divides the baviines into three clades, the *Piranthus* clade with a long embolus (*Piranthus*, *Maripanthus*), the genus *Padillothorax* with a flat body and short embolus, and the *Bavia* clade with a higher body and (usually) short embolus (remaining genera). In general, morphological synapomorphies support or extend the molecularly delimited groups. Eighteen new species are described: *Bavia nes-sagyna*, *Indopadilla bamilin*, *I. kodagura*, *I. nesinor*, *I. redunca*, *I. redynis*, *I. sabivia*, *I. vimedaba*, *Maripanthus draconis* (type species of *Maripanthus*), *M. jubatus*, *M. reinholdae*, *Padillothorax badut*, *P. mulu*, *Piranthus api*, *P. bakau*, *P. kobi*, *P. mandai*, and *Stagetillus irri*, all **sp. nov.**, with taxonomic authority W. Maddison. The distinctions between baviines and the astioid *Nungia* Żabka, 1985 are reviewed, leading to four species being moved into *Nungia* from *Bavia* and other genera. Fifteen new combinations are established: *Bavia maurerae*

(Freudenschuss & Seiter, 2016), *Indopadilla annamita* (Simon, 1903), *I. kahariana* (Prószyński & Deeleman-Reinhold, 2013), *I. sonzorol* (Berry, Beatty & Prószyński, 1997), *I. subartoi* (Prószyński & Deeleman-Reinhold, 2013), *Maripanthus menghaiensis* (Cao & Li, 2016), *M. smedleyi* (Reimoser, 1929), *Nungia hata-mensis* (Thorell, 1881), *N. modesta* (Keyserling, 1883), *N. papakula* (Strand, 1911), *N. xiaolonghaensis* (Cao & Li, 2016), *Padillothorax casteti* (Simon, 1900), *P. exilis* (Cao & Li, 2016), *P. flavopunctus* (Kanesharatnam & Benjamin, 2018), *Stagetillus banda* (Strand, 1911), all **comb. nov.** One combination is restored, *Bavia capistrata* (C. L. Koch, 1846). Five of these new or restored combinations correct previous errors of placing species in genera that have superficially similar palps but extremely different body forms, in fact belonging in distantly related tribes, emphasizing that the general shape of male palps should be used with caution in determining relationships. A little-studied genus, *Padillothorus* Prószyński, 2018, is tentatively assigned to the Baviini. *Ligdus* Thorell, 1895 is assigned to the Ballini.

Keywords

Classification, molecular phylogeny, new genus, new species, Salticidae, Salticoida

Introduction

Baviines are tropical Asian jumping spiders with elongate medium to large bodies, living above ground on leaves or branches of vegetation or in suspended litter (Maddison 2015a). The Baviini is by far the smallest of the four major groups that compose the clade Salticoida (Maddison, 2015a), with far fewer described species (31 to date) than the other three groups (Astioida, ~ 600 species; Marpissoida, ~ 850; Saltafresia, ~ 3500). Baviines have been little studied, but recent works have begun to add to our knowledge quickly (Caleb and Sanap 2017; Kanesharatnam and Benjamin 2018; Malamel et al. 2019; Caleb et al. 2019; Nafin et al. 2020), resulting so far in at least six genera currently placed in the Baviini (*Bavia* Simon, 1877, *Bavirecta* Kanesharatnam & Benjamin, 2018, *Indopadilla* Caleb & Sankaran, 2019, *Padillothorax* Simon, 1901, *Piranthus* Thorell, 1895, and *Stagetillus* Simon, 1885; Maddison 2015a; Kanesharatnam and Benjamin 2018; Malamel et al. 2015, 2019; Caleb et al. 2019). The frequency of new species in recent collecting suggests that the group is much more diverse than it appears; e.g., *Piranthus* includes only two South Asian species described, but there are at least three new species in Singapore alone. The purpose of this paper is to describe some of the recently discovered species, and to present the first phylogeny for the group. The phylogenetic work leads to a revised classification of species into genera, one of which is new.

Materials and methods

Material examined

Spider specimens examined for this study are stored in the University of British Columbia Spencer Entomological Collection, Canada (**UBCZ**), the Lee Kong Chian

Natural History Museum, Singapore (**LKCNHM**, <https://lkcnhm.nus.edu.sg>), the Research Collections at National Centre for Biological Sciences, Bengaluru, Karnataka, India (**NCBS**, <http://collections.ncbs.res.in>), the Florida State Collection of Arthropods (**FSCA**), and the Senckenberg Museum, Frankfurt, Germany (**SMF**). Work on Indian material was done at the National Centre for Biological Sciences, Bengaluru. Work on Sri Lankan material was done at the National Institute of Fundamental Studies, Kandy. Data for specimens collected during fieldwork by WPM and colleagues includes a code beginning “WPM#” representing not a specimen identification, but a collecting event of location and time.

Morphology

Preserved specimens were examined under both dissecting microscopes and a compound microscope with reflected light. Drawings were made with a drawing tube on a Nikon ME600L compound microscope. Most photographs of living specimens were made with either a Pentax Optio 33WR digital camera with a small lens glued to it for macro capability (2016 and earlier) or an Olympus OM-D E-M10 II camera with 60 mm macro lens (2017 and later). Microscope photographs were made either on a Nikon ME600L compound microscope or an Olympus SZX12 stereoscope and focus stacked using Helicon Focus 4.2.7.

All measurements are given in millimeters. Descriptions of color pattern are based on the alcohol-preserved specimen. Carapace length was measured from the base of the anterior median eyes not including the lenses to the rear margin of the carapace medially; abdomen length to the end of the anal tubercle. The following abbreviations are used:

- ALE** anterior lateral eyes;
- ECP** epigynal coupling pocket (also known as a hood or notch);
- PLE** posterior lateral eyes;
- PME** posterior median eyes (the “small eyes”);
- RTA** retrolateral tibial apophysis;
- TmA** terminal apophysis.

Molecular data

Molecular data was gathered for three gene regions by traditional Sanger PCR methods, and for many genes by Ultra-Conserved Element (UCE) target enrichment sequencing methods (Faircloth 2017), combined with data from the literature, to assemble a dataset of nine outgroup species and 22 baviine species. Table 1 lists the specimens used in the molecular study; Table 2 lists the data gathered for each. Table 3 lists specimens used for a small auxiliary study of *Nungia* Żabka, 1985 and *Capeyorkia* Richardson, 2016.

Table 1. Specimens from which molecular data were used in phylogenetic analysis of baviines.

Species	Specimen ID	Sex	Locality	Lat-Long
Amycoida				
<i>Attulus floricola</i> (C. L. Koch, 1837)	d545	♂	Poland: Narew	52.9, 23.5
	d030	♂	Canada: Nova Scotia	44.4318, -64.6075
<i>Breda bicruciatata</i> (Mello-Leitão, 1943)	d471	♀	Uruguay: Lavalleja	-34.426, -55.195
<i>Colonus hesperus</i> (Richman & Vetter, 2004)	d472	♂	U.S.A.: Arizona	34.5847, -112.5707
Astioida				
<i>Helpis minitabunda</i> (L. Koch, 1880)	NZ19-9152	♀	New Zealand	-40.994, 172.994
	S194, S195		New Zealand	
<i>Ligurra latidens</i> (Doleschall, 1859)	AS19.3412	♂	Singapore	1.4438, 103.7334
	d175		Singapore	
Marpissoida				
<i>Afromarengo</i> sp.	MRB262		Gabon	
<i>Phidippus johnsoni</i> (Peckham & Peckham, 1883)	d549	♂	Canada: Iona Beach	49.222, -123.216
Saltafresia				
<i>Menemerus bivittatus</i> (Dufour, 1831)	d559	♀	Singapore	1.4438, 103.7334
	S13/S225		Ecuador	
<i>Saliciscus scenicus</i> (Clerck, 1757)	NA19-2676	♀	Canada: Iona Beach	49.222, -123.216
	d003, S107		U.S.A.	
Baviines				
<i>Bavia aericaps</i> Simon, 1877	2008PNG-2407	♂	Papua New Guinea	-5.231, 142.532
<i>Bavia</i> cf. <i>intermedia</i> (Karsch, 1880)	d079	♂	Malaysia: Sabah: Poring Hot Springs	
<i>Bavia nessagyna</i> , sp. nov.	SWK12-4087	♀	Malaysia: Lambir Hills	4.20, 114.037
<i>Bavia sexpunctata</i> (Doleschall, 1859)	AS19.2183	♀	Singapore	1.36, 103.77
<i>Indopadilla bamilin</i> , sp. nov.	SWK12-1618	♂	Malaysia: Mulu	4.06, 114.829
<i>Indopadilla kahariana</i> (Prószyński & Deeleman-Reinhold, 2013)	SWK12-1163	♂	Malaysia: Mulu	4.047, 114.825
	SWK12-1876	♀	Malaysia: Mulu	4.041, 114.817
<i>Indopadilla kodagura</i> , sp. nov.	AS19.4314	♂	India: Kodagu	12.22, 75.66
<i>Indopadilla nesinor</i> , sp. nov.	MRB076	♀	Singapore	1.39, 103.81
<i>Indopadilla redunca</i> , sp. nov.	SWK12-1831	♀	Malaysia: Mulu	4.040, 114.815
<i>Indopadilla redynis</i> , sp. nov.	SWK12-0080	♀	Malaysia: Kubah	1.61, 110.19
<i>Indopadilla sabivia</i> , sp. nov.	d107	♂	Malaysia: Sabah: Kiabau	5.832, 117.225
<i>Indopadilla vimedaba</i> , sp. nov.	SWK12-3620	♀	Malaysia: Mulu	4.042, 114.814
<i>Stagetillus irri</i> , sp. nov.	S202	♀	Philippines: Luzon	
<i>Stagetillus</i> cf. <i>opaciceps</i> Simon, 1885	MRB079	♀	Malaysia: Ulu Gombak	3.325, 101.753
<i>Padillothorax badut</i> , sp. nov.	d548	♀	Malaysia: Lambir Hills	4.200, 114.035
<i>Padillothorax flavopunctus</i> (Kanesharatnam & Benjamin, 2018)	IFS_SAL_1017	j	Sri Lanka	7.2833, 80.6303
<i>Padillothorax</i> cf. <i>flavopunctus</i>	IFS_SAL_679	♀	Sri Lanka	7.3611, 80.8333
<i>Padillothorax mulu</i> , sp. nov.	SWK12-2556	♂	Malaysia: Mulu	4.049, 114.86
<i>Maripanthus draconis</i> , sp. nov.	d547	♀	Singapore	1.36, 103.77
	d176	♂	Malaysia: Genting Highlands	3.400, 101.777
<i>Maripanthus reinholdae</i> , sp. nov.	SWK12-1991	♀	Malaysia: Mulu	4.023, 114.813
	SWK12-1934	♀	Malaysia: Mulu	4.04, 114.817
<i>Piranthus bakau</i> , sp. nov.	d424	♂	Malaysia: Bako	1.722, 110.446
<i>Piranthus</i> cf. <i>kohi</i> , sp. nov.	MRB109	j	Malaysia: Ulu Gombak	3.325, 101.753
<i>Piranthus planolancis</i> Malamel, Nafin, Sudhikumar & Sebastian, 2019	AS19.5940	♀	India: Mysuru	12.223, 76.627
	AS19.5970	♂	India: Mysuru	12.223, 76.627

	S	SRR12832794	3940528	189254	1225	1162	912384	6782- β	14324- β	854- σ (ML14)	972- σ (MBN8)
Bavines											
<i>Bavia acirreps</i>	2008PNG-2407 d079	S	SRR12832794	3940528	189254	1225	1162	912384	6782- β	14324- β	
<i>Bavia cf. intermedia</i>	SWK12-4087	S	SRR12832793	497179	5132	894	860	410659	754- σ (MBN8)		
<i>Bavia nesagyna</i>	AS19.2183	S	SRR12832792	1638329	77954	1236	1179	911457	2772- β		
<i>Bavia sexspunctata</i>	SWK12-1618	S	SRR12832791	2410712	16408	1187	1145	820455	5677- β	14346- β	
<i>Indopadilla bamilin</i>	SWK12-1163	S	SRR12832791	2410712	16408	1187	1145	820455	4759- β	687- σ MW081881	
<i>Indopadilla kalahiana</i>	SWK12-1876	S	SRR12832806	542868	4171	895	863	525638	1042- σ MW081869	675- σ MW081883	596- β
<i>Indopadilla kodagura</i>	AS19.4314	S	SRR12832806	542868	4171	895	863	525638	6758- β	632- σ MW081882	1083- β

Species	Specimen ID	UCE Probes	SRA	Reads pass QC	Contigs	UCE loci	filtered UCE loci	filtered UCE length	28S	mtDNA	16/SND1	COI
<i>Attalus floricola</i>	d545	A	SRR12832808	4519623	40309	468	129	78353	4797-β			
	d030										770-σ (MN06)	972-σ (MN06)
<i>Breda bicruciatata</i>	d471	A	SRX7739885 (MMDH20)		38487	399	87	35038	6720-β	14305-β		
<i>Colonus hesperus</i>	d472	A	SRX7739887 (MMDH20)		56975	331	78	28801	6688-β	12586-β		
<i>Helpis miniitubunda</i>	NZ19-9152	S	SRR12832807	4037736	210843	1096	1031	757228	6751-β	15601-β		
	S194, S195										956-σ (MH03)	1047-σ (MH03)
<i>Ligurga latidens</i>	AS19.3412	S	SRR12832798	3565247	25016	1118	1076	760567	5415-β			
	d175										909-σ (BM12)	
<i>Afromarengo sp.</i>	MRB262								1049-σ (BM12)		730-σ (BM12)	946-σ (BM12)
<i>Phidippus johnsoni</i>	d549	S	SRR12832797	2954316	133630	1103	1038	779778	6734-β	14319-β		
<i>Menemerus bivittatus</i>	d559	S	SRR12832796	5327638	74123	1203	1136	770717	5639-β			
	S13/S225										956-σ (MH03)	956-σ (MH03)
<i>Salicicus scuticus</i>	NA19-2676	A	SRR12832795	2854670	25200	462	122	73552	6651-β		909-σ (MH03)	972-σ (BM12)
	d003, S107											
<i>Bavirines</i>												
<i>Bavia ariceps</i>	2008PNG-2407	S	SRR12832794	3940528	189254	1225	1162	912384	6782-β	14324-β		
<i>Bavia cf. intermedia</i>	d079								754-σ (MBN8)		854-σ (ML14)	972-σ (MBN8)
<i>Bavia nesagyna</i>	SWK12-4087	S	SRR12832793	497179	5132	894	860	410659	2772-β			
<i>Bavia sexpunctata</i>	AS19.2183	S	SRR12832792	1638329	77954	1236	1179	911457	5677-β	14346-β		
<i>Indopadilla bamilin</i>	SWK12-1618											
<i>Indopadilla kahariana</i>	SWK12-1163	S	SRR12832791	2410712	16408	1187	1145	820455	4759-β		687-σ MW081881	
	SWK12-1876								1042-σ MW081869		675-σ MW081883	596-β
<i>Indopadilla kodaguana</i>	AS19.4314	S	SRR12832806	542868	4171	895	863	525638	6738-β		632-σ MW081882	1083-β

Species	Specimen ID	UCE Probes	SRA	Reads pass QC	Contigs	UCE loci	filtered UCE loci	filtered UCE length	28S	mtDNA	16S/ND1	COI
<i>Indopadilla nesor</i>	MRB076										920-σ MW081884	960-σ MW081865
<i>Indopadilla redunca</i>	SWK12-1831								1061-σ MW081871		650-σ MW081885	
<i>Indopadilla redynis</i>	SWK12-0080	S	SRR12832805	307232	4791	917	879	483961	435-β			
<i>Indopadilla salvina</i>	d107								771-σ MW081872			
<i>Indopadilla vimeadaba</i>	SWK12-3620											952-σ MW081866
<i>Stagetillus irri</i>	S202								656-σ (MH03)	608-σ MW081886		
<i>Stagerillus cf. opaticeps</i>	MRB079	S	SRR12832804	1033936	9649	1077	1047	772184	6894-β	963-σ (MH03)		969-σ (MH03)
<i>Padillothorax badut</i>	d548	S	SRR12832803	3504035	217449	1238	1175	906962	5682-β	967-βσ (MBN8,β)		467-β
<i>Padillothorax flavopunctus</i>	IFS_SAL_1017								729-σ MW081874	14231-β		
<i>Padillothorax cf. flavopunctus</i>	IFS_SAL_679								695-σ MW081875			557-σ MW081867
<i>Padillothorax mulu</i>	SWK12-2556								1033-σ MW081873			544-σ MW081868
<i>Maripanthus draconis</i>	d547	S	SRR12832802	2632437	127899	1207	1159	881761	5622-β	14399-β	659-σ MW081887	
	d176								821-σ MW081878			
<i>Maripanthus reinholdae</i>	SWK12-1991	S	SRR12832801	1554841	72255	1170	1139	890576	5243-β	1653-β		
	SWK12-1934								1043-σ MW081877			
<i>Piranthus bakau</i>	d424								1044-σ MW081879		720-σ MW081888	
<i>Piranthus cf. kohi</i>	MRB109								1067-σ MW081880			
<i>Piranthus planolancis</i>	AS19.5940	S	SRR12832800	3050561	135553	1217	1173	924020	6749-β	14872-β		
	AS19.5970	S	SRR12832799	1235845	56562	1186	1157	895555	6749-β	14683-β		

Table 3. *Nungia* and *Capeyorkia* specimens sequenced for phylogenetic study, with Genbank accession numbers.

Species	Specimen ID	Sex	Locality	Lat-Long	28S	16SND1
<i>Nungia hatamensis</i> (Thorell, 1881)	d260	♂	Papua New Guinea: Putuwé	-5.231, 142.532		MW202326
<i>Nungia xiaolonghaensis</i> (Cao & Li, 2016)	MRB078	♂	Malaysia: Tanah Rata	4.46, 101.40	MW187118	MW202327
<i>Nungia</i> sp. "NPNGK"	d259	♂	Papua New Guinea: Tualapa	-5.283, 142.498	MW187119	
<i>Nungia</i> sp. "NSGPQ"	d178	♂	Singapore	1.44, 103.70	MW187120	MW202328
<i>Nungia</i> sp. "NUBWH"	SWK12-3204	♀	Malaysia: Mulu NP	4.042, 114.814	MW187121	MW202329
<i>Nungia</i> sp. "NUMUL"	SWK12-1943	♂	Malaysia: Mulu NP	4.0405, 114.817	MW187122	MW202330
<i>Capeyorkia</i> cf. <i>vulpecula</i> (Thorell, 1881)	MRB087	♂	Papua New Guinea: Bundun	-6.8600, 146.6178	MW187123	
<i>Capeyorkia</i> sp. "NPNGE"	d261	♂	Papua New Guinea: Varirata NP	-6.07, 145.40		MW202331
<i>Capeyorkia</i> sp. "NPNGF"	d258	♂	Papua New Guinea: Goroka	-9.436, 147.364	MW187124	MW202332

UCE Data

DNA was isolated using the Qiagen DNeasy Blood and Tissue Kit, following the spin-column protocol. Quality of the isolation was estimated using a NanoDrop 2000c Spectrophotometer, and samples were repeated where possible if the 260:280 nm UV absorbance ratio fell outside the range of 1.4 to 2.2. For most taxa 1 to 4 legs were used for DNA extraction, but the entire prosoma was used for *Padillothorax badut* (specimen d548) and *Helpis minitabunda* (specimen NZ19-9152). For the target enrichment UCE sequencing, dual-indexed TruSeq-style libraries were prepared following methods previously used in arachnids (e.g., Starrett et al. 2017; Derkarabetian et al. 2018; Hedin et al. 2018; Kulkarni et al. 2019). Targeted enrichment was performed using either the myBaits Arachnida 1.1Kv1 (Arbor Biosciences; Faircloth 2017; Starrett et al. 2017) or the Spider 2Kv1 kit (Arbor Biosciences; Kulkarni et al. 2019) following the myBaits v4.01 protocol (<https://arborbiosci.com/wp-content/uploads/2018/04/my-Baits-Manual-v4.pdf>). Libraries were sequenced on partial lanes of Illumina NovaSeq 6000 S4 runs with 150 bp paired end reads. To the resulting set of reads we added those from two amycooid taxa, *Breda* and *Colonus*, obtained by Maddison et al. (2020), to assist as outgroups. Raw demultiplexed reads were processed with Phyluce version 1.6 (Faircloth 2016), quality control and adapter removal were conducted with the Illuminaprocessor wrapper (Faircloth 2013), and assemblies were created with SPAdes version 3.14.1 (Nurk et al. 2013), using the meta option, at default settings.

From among the contigs thus assembled, those matching particular UCE probes were pulled out using the Phyluce pipeline at default settings. Because some taxa were captured using the arachnid probeset (outgroups *Attulus*, *Breda*, *Colonus*, *Salticus*), and others using the spider probeset (remaining outgroups, and all baviines), a blended probeset file was needed to best pull out UCE contigs, because each of the arachnid and spider probesets includes loci not included by the other. Kulkarni et al.'s (2019) spider probeset includes (i) some of Starrett et al.'s (2017) arachnid probes directly, (ii) others for the same loci but modified to target spiders better, and (iii) others for new

loci. Because Kulkarni et al. do not identify probes of the second category as such, we sought to identify whether spider probes are orthologous to arachnid probes. We then deleted from the probeset file those arachnid probes matching spider probes, as including duplicate homologs reduces data recovery (contigs matching two probes are removed by Phyluce for being problematical). To determine homology, contigs from 18 diverse species in the Salticinae, 12 captured with arachnid probes, 6 with spider probes, were each matched against both arachnid and spider probesets. Any instance of a contig matching both a spider probe and arachnid probe, as assessed using a script examining .lastz files, was taken as indicating homology between the probes. Arachnid probes that showed no such hint of homology to spider probes were then added to Kulkarni et al.'s (2019) spider probeset to generate the blended probeset (see Suppl. material 1). The spider probeset includes 15015 probes and probe parts; the arachnid probeset, 14799; blended, 25689. The efficacy of the blended probeset can be seen in the numbers of loci recovered in the baviine dataset reported here: the arachnid probeset pulled out on average 134 loci from spider-enriched taxa and 411 from arachnid-enriched taxa; the spider probeset pulled out on average 1118 and 113 respectively; the blended probeset pulled out on average 1123 and 415. Nonetheless, many of the UCE loci recovered from the arachnid-enriched taxa were only among those taxa; this explains why many were subsequently deleted when a filter for occupancy among ingroups (see below) was applied.

Recovered UCE loci were aligned with MAFFT (Katoh and Standley 2013) and trimmed with Gblocks (Castresana 2000; Talavera and Castresana 2007), using -b1 0.5, -b2 0.5, -b3 10, -b4 4 settings in the Phyluce pipeline. Among the loci recovered, those with fewer than 6 taxa total or fewer than 3 ingroups were deleted. As in the analysis of Maddison et al. (2020), loci were also deleted over concerns about paralogy if their gene tree showed a very long branch, at least 5× longer than the second longest branch.

Data for 28S and mitochondrial genes

For the new Sanger-sequenced data, specimens were preserved, their DNA extracted, and sequences obtained for the nuclear gene 28S and the mitochondrial gene regions 16SNDI and COI following the protocols using the protocols of Zhang and Maddison (2013) and Maddison et al. (2014). Alignments were done by MAFFT with the L-INS-i option.

The same three gene regions were also present among the sequence capture genomic contigs as untargeted bycatch. We recovered them by constructing a local BLAST database of the contigs of each taxon, and querying it with 28S, 16SND1 and COI sequences from eight to nine different salticid species (*Bavia*, *Indopadilla*, *Bathippus*, *Harmochirus*, *Idastrandia*, *Langerra*, *Phintella*, *Platycryptus*, *Salticus*, *Attulus*, *Lyssomanes*), retaining any contigs matching with an e-value of less than 10^{-10} and length greater than 200. In a few cases, multiple contigs from a taxon were recovered as matching a single locus, but after alignment against others these could be interpreted as different parts of the target gene, and were thus stitched together to a single sequence.

Phylogenetic analysis

Maximum likelihood phylogenetic analyses were performed with IQ-TREE version 1.6.7.1 (Nguyen et al. 2015) using the Zephyr 3.1 package (Maddison and Maddison 2020) in Mesquite 3.61 (Maddison and Maddison 2019) on several datasets derived from the UCE, bycatch, and Sanger-sequenced data. The datasets were:

1. “UCEs” – The UCE dataset after filtering of loci, concatenated, unpartitioned.
2. “mtDNA+28S” – The concatenated data from 28S and mitochondrial sequences (10 full mtDNA, others Sanger and bycatch 16SND1 aligned against the full mtDNA). Analyzed with 2 partitions, 28S and mtDNA.
3. “restricted mtDNA+28S” – A restricted version of 28S and mtDNA with the long bycatch sequences trimmed to put the taxa with legacy Sanger data on almost equal footing (i.e., approximately as much data) with those with bycatch. 28S sites at start and end were trimmed until at least 3 of the shorter legacy Sanger sequences were represented. The same rule for trimming was used for the mtDNA before 16SND1, between 16SND1 and COI genes, and after COI. Analyzed with 2 partitions, 28S and mtDNA.
4. “UCEs+mtDNA+28S” – The UCE loci (dataset #1) concatenated to the restricted 28S and mtDNA data (dataset #3). Analyzed unpartitioned.

For the partitioned analyses, the options -m MFP -spp were used (extended model selection followed by tree inference, edge-linked partition model, with partition-specific rates); for the unpartitioned analyses, -m MFP (extended model selection followed by tree inference, edge-linked partition model, no partition-specific rates).

Several species of elongate brown Asian and Australasian salticids were initially identified in the field as baviines, but were excluded from the Baviini by preliminary molecular analyses and closer morphological study, which showed them to be near *Nungia epigynalis* Żabka, 1985. To document this and clarify the limits of the Baviini, we did a small analysis based on 28S and 16SND1, using previously published sequences of baviines, astioids, and other groups from Maddison and Hedin (2003), Bodner and Maddison (2012), and Maddison et al. (2014) combined with new sequences of the species in question (Table 3). Details are given in the Taxonomy section under Vicirini: *Nungia*.

Raw sequence reads from UCE capture are deposited in the Sequence Read Archive (BioProject PRJNA667925, <https://www.ncbi.nlm.nih.gov/sra/PRJNA667925>) with accession numbers shown in Table 2. Genbank accession numbers of Sanger sequenced genes are shown in Tables 2 and 3. Alignments and trees are deposited in the Dryad data repository (<https://doi.org/10.5061/dryad.4f4qrf9j>).

Taxonomic authority

The taxonomic authority for all nomenclatural acts (synonymies, new combinations, new species) is W. Maddison.

Molecular phylogenetic results

Molecular data obtained

UCE data obtained are outlined in Table 2. The Phyluce pipeline recovered aligned matrices of 1837 loci using the blended spider-arachnid probeset. In these initially recovered loci, the 16 taxa originally sequence-captured with the spider probeset had on average 1123 loci and 797,222 base pairs of sequence; the four originally sequence-captured with the arachnid set had on average 415 loci and 158,475 base pairs. From the original 1837 loci, 511 were deleted because they had fewer than six taxa total or fewer than three ingroups. Thirteen loci were deleted for having the longest branch more than $5 \times$ longer than the second longest. This resulted in resulting in a final set of 1313 loci, in which the 16 spider-probeset taxa had on average 1076 loci and 775,244 base pairs of sequence; the four arachnid-probeset taxa had on average 104 loci and 53,936 base pairs. The strong decline in arachnid-probeset taxa from 415 loci to 104 after occupancy filtering suggests that Kulkarni et al.'s (2019) incorporation of arachnid-unique probes into the spider probeset included only a portion. The 1313 loci were concatenated into a single alignment with 1,050,217 sites.

The bycatch 28S sequences were 435–6894 bp long (average 5675.9) and aligned well with the Sanger 28S sequences using MAFFT at default settings. Bycatch 28S were obtained for three specimens for which previous Sanger sequences were available and identical (*I. kahariana* SWK12-1163, 1021 base pairs; *M. reinholdae* SWK-01991, 1037 bp; *S. cf. opaciceps* MRB079, 1067 bp) except for a one base difference at the start of the *I. kahariana* sequence. An initial alignment of 28S including UCE bycatch and legacy Sanger data was 18646 bp long, but the first 1593 bp and the last 9793 bp of the alignment were poorly aligned and represented by only a few bycatch sequences, and so were trimmed. After addition of a few other taxa and realignment, the final 28S alignment was 7281 bp long.

Among the bycatch contigs for 10 taxa were long sequences containing both the 16SND1 and COI regions, and whose size (12568–15601 bp) suggests they may be the whole or nearly whole mitochondrial genome (marked in the column “mtDNA” in Table 2). For other taxa, the mitochondrial contigs recovered as matching 16SND1 and COI were separate and fairly short (16SND1: 362, 1136, 1835 bp; COI: 467, 596, 1083 bp). Bycatch 16SND1 were obtained for two species for which previous Sanger sequences were available and identical. For *S. cf. opaciceps* (MRB079) the 362 bp bycatch sequence was identical to the 908 bp Sanger sequence in the 303 bp of overlap; the sequence used was their concatenation. For *Helpis*, the 956 bp Sanger sequence published by Maddison and Hedin (2003) matches exactly the longer bycatch sequence here obtained from a different specimen, NZ19-9152, also from New Zealand. The COI obtained from those same two specimens (Sanger and bycatch likewise, respectively) is identical except for one nucleotide, but the 721 bp sequence reported by Maddison et al. (2014) for a different specimen of *Helpis* from Papua New Guinea differs at 35 sites, and is thus likely a different species. The bycatch sequences were used in their entirety, except for a terminal 183 bp of a bycatch 16SND1 from *M. reinhol-*

dae SWK12-1991, which was deleted because it showed no clear alignment with that portion of other taxa; we suspect that portion may have mistakenly assembled with 16SND1 because of a shared poly-AT repeat.

The whole mtDNA sequences aligned well against each other using MAFFT at default settings. The shorter bycatch sequences and Sanger 16SND1 and COI aligned well against the whole mtDNA. The whole mtDNA sequences initially differed in their (arbitrary) starting point on the circular mitochondrial genome, but after a preliminary alignment they were adjusted to all begin at a conserved region in 16S. After adjustments by hand to align ND1 and COI without gaps, the other regions (before ND1, between ND1 and COI, and between COI and the end) were re-aligned using MAFFT.

Trimming of the 28S and mtDNA alignments as explained for dataset #3 (“restricted mtDNA+28S”) yielded a 28S alignment of 1181 base pairs, and a mitochondrial alignment of 2211 bp.

Phylogenetic results

The primary phylogenetic results are shown in Figs 1–3. The different datasets (UCE, Sanger, and combined) gave substantially concordant results, with just a few points of disagreement. All confirm the monophyly of the baviines, and divide the group into three major clades (marked in Figs 1–3), one with a relatively long embolus that appears freely moveable (the *Piranthus* clade), one with a short erect embolus and flat body (the genus *Padillothorax*), and one with a relatively short embolus largely fixed to the tegulum and a higher body (the *Bavia* clade). The relationship among these three groups varies by dataset: *Padillothorax* is sister to the *Piranthus* clade by the mitochondrial and 28S data (Fig. 3), but by the much larger UCE and combined datasets it is placed reasonably securely as a deep-branching sister to the *Bavia* clade.

Relationships within each of the three major clades is reasonably stable across datasets. Within the *Piranthus* clade, the morphologically distinctive *Piranthus* is monophyletic, as is *Maripanthus*. The morphologically similar *Padillothorax badut* and *P. mulu* are sisters, as are *P. flavopunctus* and *P. cf. flavopunctus*. Within the *Bavia* clade, molecular results more or less match morphological groups: *Bavia* with relatively large bodies, *Indopadilla* with ridged chelicerae, thoracic bulges, and exposed clypeal arthrochial membrane, and the elongate yellow-orange *Stagetillus*. Accordingly, the concepts of genera here come from both morphological and molecular evidence.

Taxonomic results

Tribe Baviini Simon, 1901

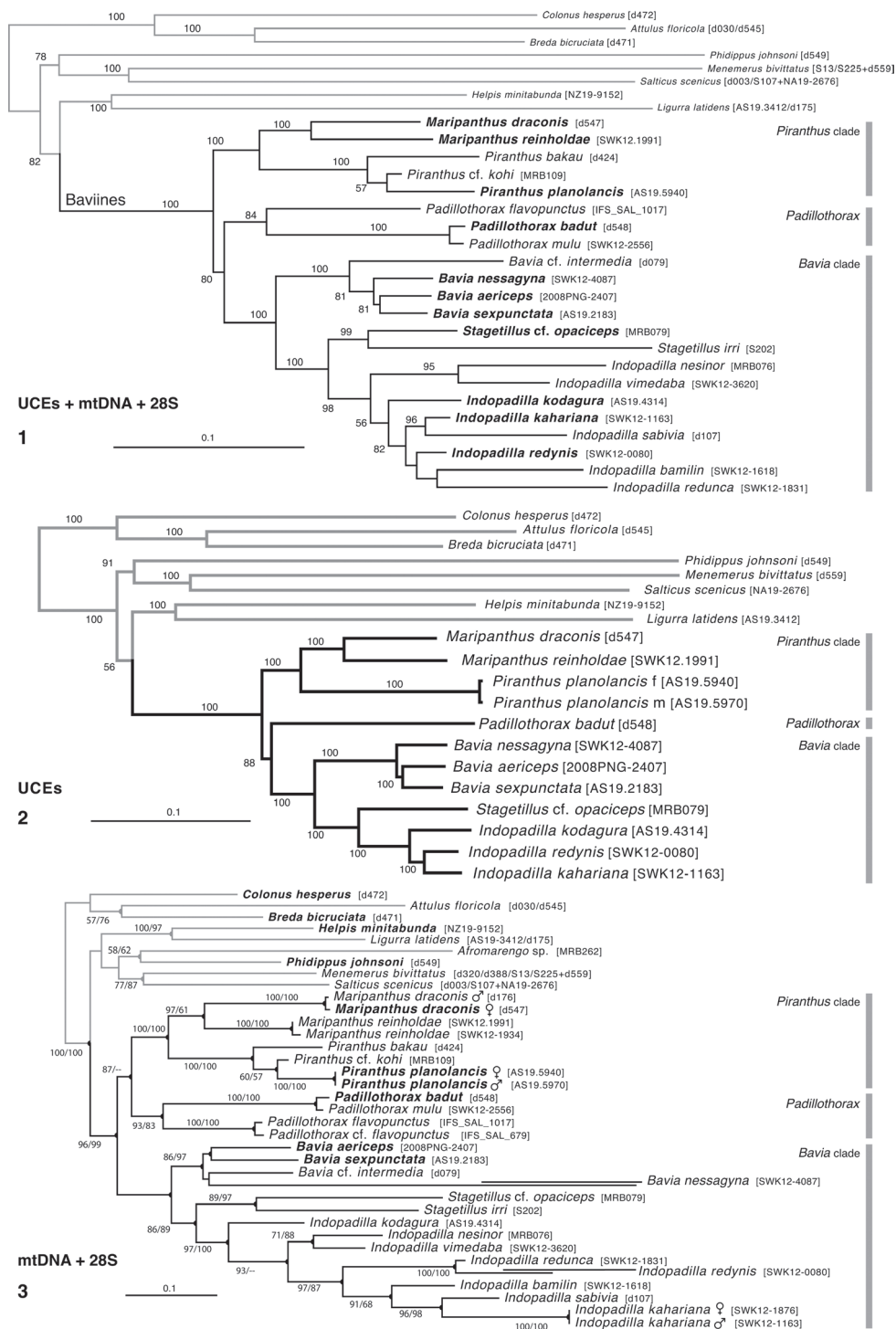
Genera included:

Bavia Simon, 1877

Indopadilla Caleb & Sankaran, 2019

Maripanthus Maddison, gen. nov.

Padillothorax Simon, 2001



Padillothorus Prószyński, 2018

Piranthus Thorell, 1895

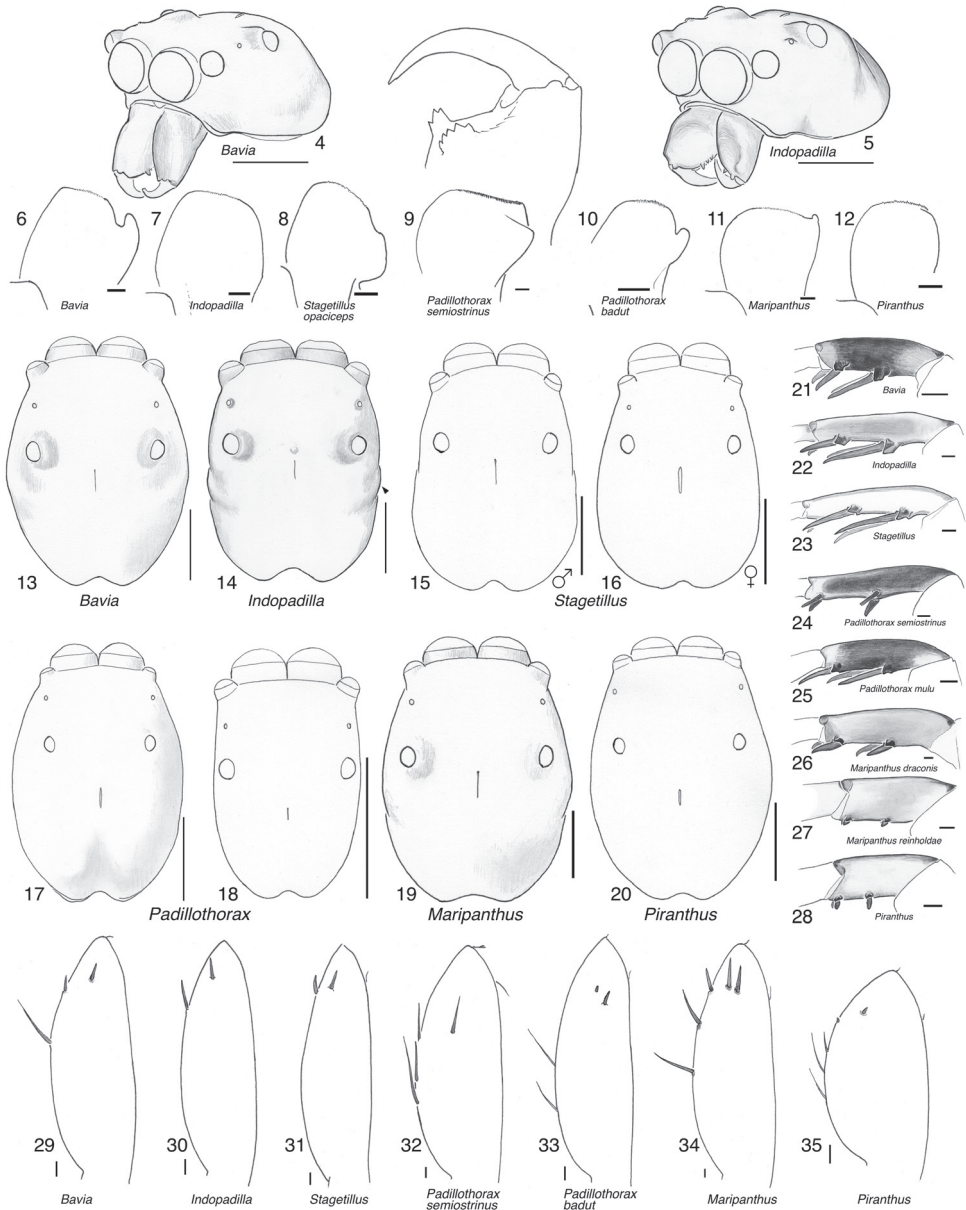
Stagetillus Simon, 1885

Narrow-bodied medium to large salticids in Asia and Australasia, pluridentate, with an embolus fixed to the tegulum or with some degree of mobility. The abdomen is usually long and the legs (except the first) relatively short. There is no known clearly understood morphological synapomorphy of the group. Nonetheless, molecular data groups together most tropical Asian salticids of this body form as baviines. Some long-bodied ballines (e.g., *Mantisatta* Warburton, 1900, *Copocrossa* Simon, 1901), marpissines (*Mendoza* Peckham & Peckham, 1894), astioids (*Holoplatys* Simon, 1885 and relatives, *Nungia* Żabka, 1985), chrysillines (*Epocilla* Thorell, 1887), and plexippines (*Telamonia* Thorell, 1887) might be confused for baviines, but most have distinctive features of their own. Most difficult to distinguish from baviines are perhaps the viciriine astioids *Nungia* and relatives (including *Pungalina* Richardson, 2013 and *Capeyorkia* Richardson, 2016). *Nungia* are generally smaller than baviines, with a more flat-topped carapace; they are quite distinct by molecular data (Maddison et al. 2014, and see below under Viciriini), but the palps are similar. *Nungia* is discussed further under Viciriini, below.

Padillothorus (see Prószyński 1984, 2018) is included tentatively among the baviines based primarily on the similarity of its body form with baviines, and its geographic distribution. *Padillothorus* has five retromarginal cheliceral teeth (Reimoser, 1927), which is typical for baviines. Although *Ligdus* Thorell, 1895 might appear as a candidate to belong in the Baviini, with narrow body and raptorial front legs, the juvenile type specimen (in NHM London, examined) is such a close match to *Copocrossa* Simon, 1901 as to be possibly a senior synonym thereof. *Ligdus* shares with *Copocrossa* and *Mantisatta* the peculiar feature of a first metatarsus bent ventrally almost 90 degrees near its base. Because of its apparent relationship with these ballines, *Ligdus* is therefore moved to the Ballini.

Figures 4–35 illustrate character variation in baviines, some of which is used to diagnose genera. Among baviines, the genera vary in these characters:

Figures 1–3. Phylogeny. **1** Maximum Likelihood tree (best of 20 replicates) from combined data set of 1313 UCE loci, plus mitochondrial 16SND1 and COI regions, plus 28S (dataset #4 in Methods). Baviines whose names are in bold, and all outgroups, have UCE data. Numbers are percentage of 500 bootstrap replicates showing the clade **2** Maximum Likelihood tree (best of 50 replicates) from concatenated data from 1313 UCE loci (dataset #1 in Methods). Numbers are percentage of 1000 bootstrap replicates showing the clade **3** Maximum Likelihood tree (best of 50 replicates) from concatenated data from mitochondrial data and 28S (dataset #2 in Methods). Taxa in bold have data from the entire mitochondrial genome, or nearly so. Numbers are percentage of 1000 bootstrap replicates showing the clade for the full dataset (#2), followed by the bootstrap percentage for the restricted mtDNA+28S dataset (#3 in Methods). Spots at nodes show those clades that also appear in the ML tree in the restricted dataset. The branches to *B. nessagyna* and *I. redynis* are long, compacted visually by cutting and sliding part of the length over itself; the actual length therefore should be seen as longer by the length of the overlap.



Figures 4–35. Variation in traits among baviines **4, 5** oblique views of female prosoma **4** *Bavia nessagyna* (specimen IDWM.20004; note convex front face of chelicerae, and typical thorax) **5** *Indopadilla redunca* (holotype IDWM.20011; note concave front face of chelicerae, and thoracic bulges) **6–12** left male endite (9 also with chelicera) **6** *Bavia nessagyna* (holotype IDWM.20005) **7** *Indopadilla redunca* (specimen SWK12-M0009) **8** *Stagetillus opaciceps* (specimen JK.08.08.19.0001) **9** *Padillothorax semiostrinus* (specimen JK.20.06.20.001) **10** *Padillothorax badut* (specimen SWK12-4688) **11** *Maripanthus jubatus* (specimen AS19.4373) **12** *Piranthus planolancis* (specimen AS19.5970) **13–20** carapace (all females except **15**) **13** *Bavia nessagyna* (specimen IDWM.20004) **14** *Indopadilla redunca* (holotype IDWM.20011) **15** *Stagetillus opaciceps* male (specimen JK.13.02.26.0017) **16** *Stagetillus* cf. *opaciceps* female (specimen MRB079).

Shape of the carapace – flatter (height < 36% of length) in most *Piranthus* and *Padillothorax*, higher in others. *Indopadilla* has distinctive bulges on the thorax sides (Figs 5, 14).

Lateral margin of male endites – *Indopadilla* and *Piranthus* males have the endite with a simple rounded margin, but the other genera have varying projections (Figs 6–12). *Maripanthus* bears a sharp distal-retrolateral corner. *Bavia* and *Padillothorax* have a lobe, in some thumb-like (Figs 6, 10), in others broad and triangular (Fig. 9). *Stagetillus opaciceps* has a large broad lobe projecting retrolaterally (Fig. 8), though *S. irri* lacks this lobe, and instead has only a mild corner at the retrolateral distal tip, not too different from *Indopadilla*.

Position of the fovea (Figs 13–20) – well back of the posterior eyes in *Piranthus*, *Padillothorax*, and *Padillothorus* (see p. 95 of Prószyński 1984); just behind the PME in others.

Sockets of leg I macrosetae – in the *Bavia* clade, the sockets of macrosetae extend downward as lateral flange (Figs 21–23), especially notable on the metatarsus, whose macrosetae are at least as long as the metatarsus is wide. In the *Piranthus* clade, sockets and macrosetae are much shorter (Figs 26–28), except in males of *Maripanthus draconis* and *M. jubatus*, which have fairly long macrosetae on the first metatarsus. *Padillothorax* is variable (Figs 24, 25).

Macrosetae of first femur (Figs 29–35) – *Padillothorax* is unusual among salticids in having one or two macrosetae more or less centrally placed on the prolateral face of the first leg femur. Most other salticids have femoral macrosetae, but with few exceptions (in *Epocilla* [Ali et al. 2018: fig. 2], *Padilla* Peckham & Peckham, 1894 [Andriamalala 2007], and some marpissines [Edwards 2006]) they are in a more dorsal or distal position; in *Padillothorax* they are at least one quarter of the femur's length from the distal tip, approx. midway between dorsal and ventral.

In several baviine genera, not each others' closest relatives, there is a characteristic series of markings consisting of small patches of pale scales on the thorax: one patch medially between the PLE, a short longitudinal stripe at the top of the thoracic slope, and one behind each PLE (e.g., *Bavia*, Fig. 53; *Indopadilla*, Fig. 84, *Maripanthus*, Fig. 222).

The taxonomic account below presents in sequence the *Bavia* clade, *Padillothorax*, and then the *Piranthus* clade.

Figures 4–35. Continued. **17** *Padillothorax semiostrinus* (specimen JK.20.06.20.001) **18** *Padillothorax mulu* (from Mulu Nat. Pk.) **19** *Maripanthus reinholdae* (specimen SWK12-1934) **20** *Piranthus planolancis* (specimen AS19.5940) **21–28** Metatarsus of first leg, retrolateral view. All female except **24** male. All are of left legs except **23, 25, 28** which are of right leg, digitally flipped **21** *Bavia nessagyna* (specimen IDWM.20004) **22** *Indopadilla kahariana* (specimen SWK12-1876) **23** *Stagetillus* cf. *opaciceps* (specimen MRB079) **24** *Padillothorax semiostrinus* (specimen SWK12-EP0105) **25** *Padillothorax mulu* (specimen SWK12-EP0105) **26** *Maripanthus reinholdae* (specimen SWK12-1934) **27** *Maripanthus draconis* (from Gunung Belemut, Johor) **28** *Piranthus planolancis* (specimen AS19.5940) **29–35** prolateral surface of male first leg femur. **29** *Bavia* cf. *capistrata* (specimen from Singapore) **30** *Indopadilla kahariana* (specimen from Lambir Hills Nat. Pk.) **31** *Stagetillus opaciceps* (specimen JK.08.08.19.0001) **32** *Padillothorax semiostrinus* (specimen JK.20.06.20.001) **33** *Padillothorax badut* (specimen SWK12-4688) **34** *Maripanthus draconis* (specimen from Johor, Gunung Lambak) **35** *Piranthus bakau* (holotype). Scale bars: 0.1 mm (**6–12, 21–35**), 1.0 mm (**4, 5, 13–20**).

The *Bavia* Clade (*Bavia*, *Indopadilla*, *Stagetillus*)

Bavia Simon, 1877

Bavia Simon 1877. Type species *Bavia aericeps* Simon, 1877

Acompse L. Koch 1879. Type species *Acompse suavis* L. Koch, 1879 = *B. aericeps*.

Species included.

Bavia aericeps Simon, 1877

Bavia capistrata (C. L. Koch, 1846), combination restored, removed from synonymy with *Evarcha flavocincta* (C. L. Koch, 1846)

Bavia fedor Berry, Beatty & Prószyński, 1997

Bavia nessagyna Maddison, sp. nov.

Bavia gabrieli Barrion, 2000

Bavia intermedia (Karsch, 1880)

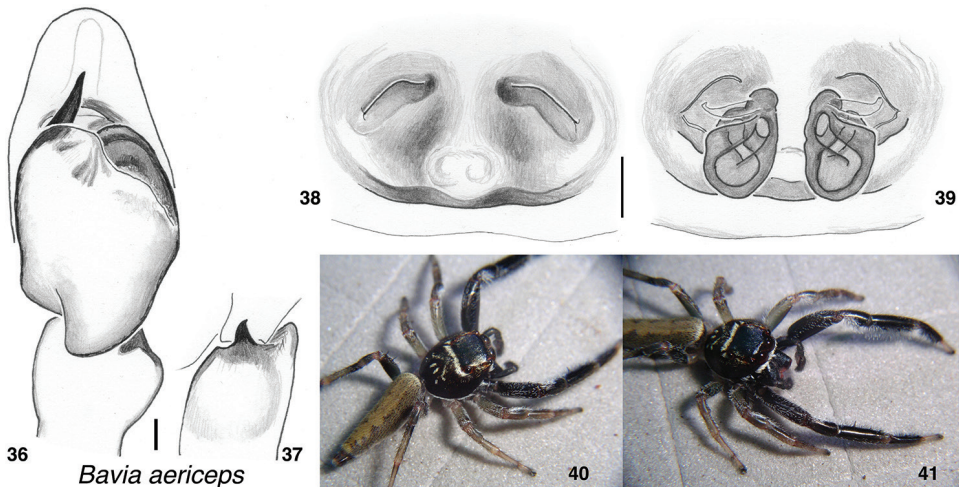
Bavia maurerae (Freudenschuss & Seiter, 2016), comb. nov., transferred from *Epidelaxia*

Bavia planiceps (Karsch, 1880)

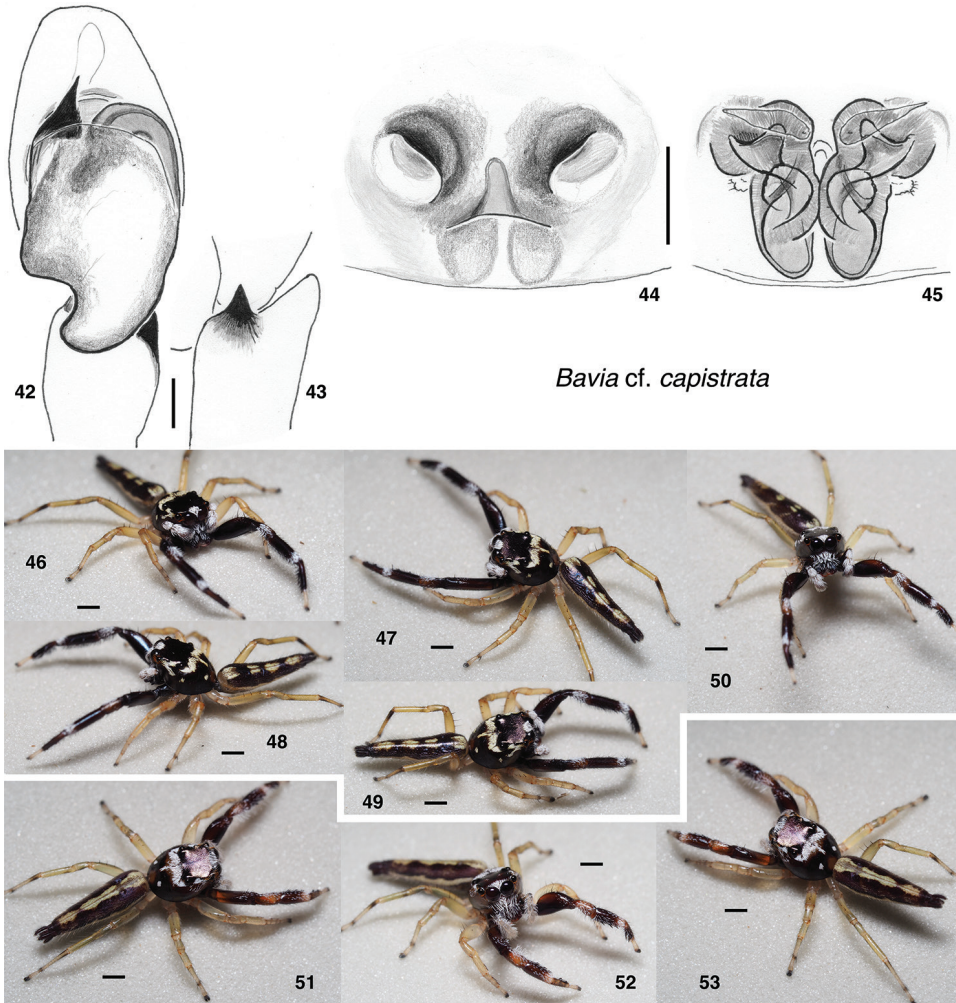
Bavia sexpunctata (Doleschall, 1859)

Bavia valida (Keyserling, 1882)

Diagnosis. Larger-bodied than most other baviines. Carapace relatively broad and having hexagonal shape, widest at or just behind the PLEs (Fig. 13). Chelicerae lack the sharp lateral ridge (Fig. 4) of *Indopadilla*. Embolus shorter than length of tegulum, arising in all known species on bulb's distal prolateral corner. ECP on a promi-



Figures 36–41. *Bavia aericeps* **36** male left palp, ventral view (specimen 2008PNG-2407, Papua New Guinea, 5.231°S, 142.532°E) **37** same, retrolateral view of tibia **38** female epigyne, ventral (specimen SMF 60114, Samoa) **39** same, vulva. **40, 41** male (specimen 2008PNG-1517, Papua New Guinea, 5.283°S, 142.498°E). Distance between substrate grooves 10 mm. Scale bars: on genitalia 0.1 mm.



Figures 42–53. *Bavia* cf. *capistrata*. **42** male left palp, ventral view (specimen AS19.1118, Singapore) **43** same, retrolateral view of tibia **44** epigyne, ventral (specimen AS19.1128, Singapore) **45** vulva, dorsal **46–49** Male AS19.1118 **50** Male AS19.2341 (Singapore) **51–53** female AS19.1128 (Singapore). Scale bars: on genitalia 0.1 mm; on bodies 1.0 mm.

nent medial bulge. Male endite with small thumb-like lobe laterally (Fig. 6), as in the *Padillothorax badut* group.

Illustrations are given here of some of the well-known species of *Bavia*, including *B. aericeps* (Figs 36–41) and *B. sexpunctata* (Figs 54–63). *B. capistrata* was synonymized without explanation by Prószyński (2017) with the extremely different *Evarcha flavocincta*, possibly because of superficial similarities in the palp. C. L. Koch's (1846) illustration of the male of *Maevia capistrata* is clearly a *Bavia* by body form and markings. The only doubt about the status of C. L. Koch's species is which species of *Bavia* is it precisely. Candidates include the one figured by Cao, Li, and Žabka (2016),

the one figured here as *B. cf. capistrata* (Figs 42–53), and *B. nessagyna* (Figs 64–75). The one figured here as *B. cf. capistrata* could be different from that figured by Cao, Li, and Žabka. The former shows a slightly wider embolus and more delicate ECP, and possibly more contrasting markings. Regardless, C. L. Koch's species is removed from synonymy with *Evarcha flavocincta* and returned to *Bavia*.

A video of the living female *B. cf. capistrata* (specimen AS19.1128) is available in Maddison (2020).

In addition to the species below, we have seen an undescribed species near *B. nessagyna* from Mulu National Park (single female) and a species near *B. intermedia* (single male, here represented as specimen d079 in the Sanger data).

***Bavia nessagyna* Maddison, sp. nov.**

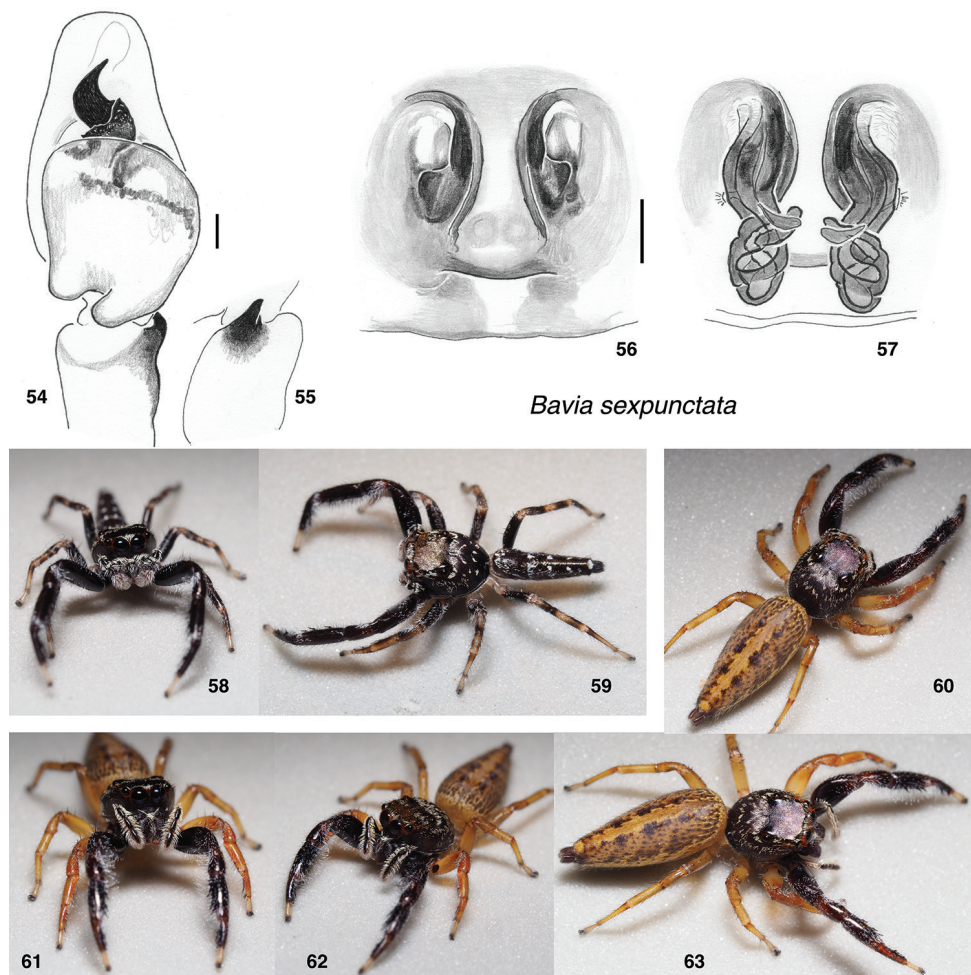
<http://zoobank.org/38524691-9D72-4BD7-9EED-76B3E580EA43>

Figs 5, 6, 13, 21, 64–75

Type material. All from MALAYSIA: Sarawak: Lambir Hills Nat. Pk., and in UBCZ. **Holotype:** male IDWM.20005 from Bukit Pantu Trail, 4.2032°N, 114.0305°E to 4.2035°N, 114.0304°E, 210 m el. 5 April 2012 Maddison/Piasek/Ang WPM#12-135. **Paratypes:** Male SWK12-4726 from Inoue Trail, 4.2002°N, 114.0346°N, to 4.2004°N, 114.0342°E, 200 m el. 4 April 2012 Maddison/Piasek/Ang WPM#12-130; female SWK12-4087 from Inoue Trail, 4.1990°N, 114.0375°E to 4.1988°N, 114.0370°E, 120 m el. 1 April 2012 Maddison/Piasek WPM#12-113; female IDWM.20004 from Lepoh-Ridan Trail, 4.2022°N, 114.0279°E to 4.2019°N, 114.0278°E 170 m el. 2 April 2012 Maddison/Piasek WPM#12-124; female IDWM.20006 from Bukit Pantu Trail, 4.2028°N, 114.0305°E to 4.2032°N, 114.0305°E, 210 m el. 5 April 2012 Maddison/Piasek/Ang WPM#12-134; female IDWM.20003 from Pantu Trail, 4.2030°N, 114.0399°E to 4.2032°N, 114.0396°E, 150–160 m el. 6 April 2012 Piasek/Ang WPM#12-145.

Etymology. From the Greek *nessa*, duck, and *gyne*, female, referring to the resemblance of the epigyne to a duck's bill. *Other names:* In WPM's lab notebooks the informal code for this species was "BVDUC-S".

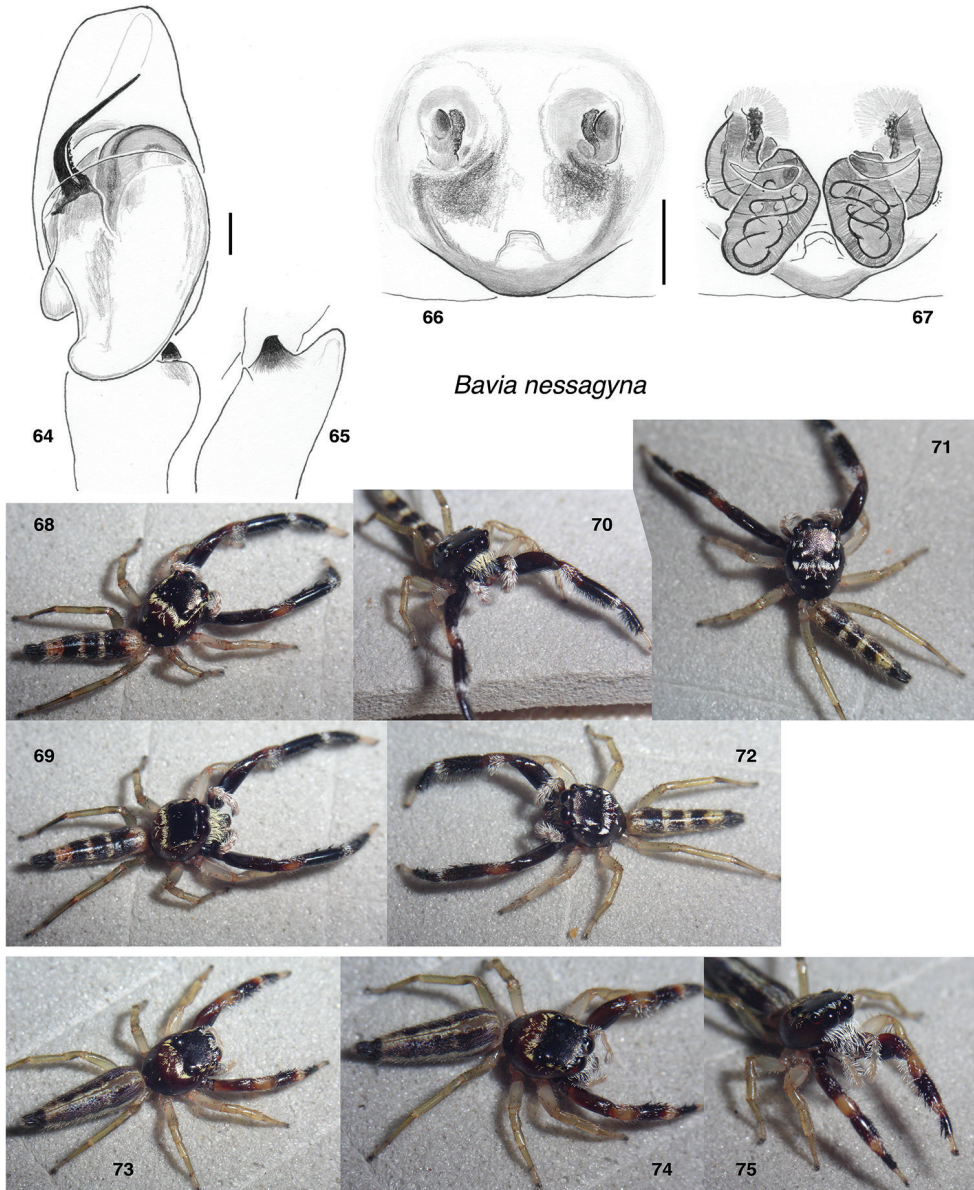
Diagnosis. One of the more delicate *Bavia*, along with *B. capistrata*, having legs II–IV very much paler than I, and thus resembling *Indopadilla*. Its distinction from *B. fedor* is slight: the embolus of both appears as a curved and narrowing blade with a series of retrolateral teeth. The teeth are short, triangular, and closely spaced in *B. nessagyna*, but larger in *B. fedor*, appearing as broad pillars whose bases are well separate (photographs of holotype kindly supplied by J. Boone, Bishop Museum). In *B. nessagyna* the teeth are not on the embolus proper but on a TmA that parallels the embolus (Fig. 64). In *B. fedor* it is unclear whether the teeth are on a TmA or on the embolus itself; Prószyński's illustration (Berry, Beatty and Prószyński 1997) shows no division into two processes, but it may be that they are closely adpressed. Even still, the overall shapes of the embolic division differ: broad at the base in *B. nessagyna* but abruptly narrowing; narrower at the base in *B. fedor* and narrowing more gradually. Epigyne with arcing ridges lateral to



Figures 54–63. *Bavia sexpunctata*. **54** male left palp, ventral view (Singapore, Upper Peirce Reservoir) **55** same, retrolateral view of tibia **56** epigyne, ventral (Singapore, Bukit Timah) **57** vulva, dorsal **58, 59** male (specimen AS19.2175, Singapore) **60–63** female (specimen AS19.0230, Singapore). Scale bars: on genitalia 0.1 mm.

the openings in *B. fedor*; without such a ridge in *B. nessagyna*. *B. nessagyna* differs from *B. cf. capistrata* in the distinct embolus, less contrasting markings, and the abdominal markings more transverse than longitudinal.

Description. Male (based on holotype, specimen IDWM.20005). Carapace length 3.6; abdomen length 4.8. **Carapace** (Fig. 71): Broad, seeming even broader because of small tuft of setae at widest point just posterior to PLEs. Integument of ocular area black, thorax dark brown, except in alcohol pale orange yellow area just behind the ocular area. Bands of cream coloured scales lie just posterior to and lateral to the ocular area; thorax with a few small spots of cream scales, the two posterior ones of which are prominent and well separated, as in *B. capistrata*. **Clypeus** dark and glabrous, but



Figures 64–75. *Bavia nessagyna* sp. nov. **64** male left palp, ventral view (holotype IDWM.20005) **65** same, retrolateral view of tibia **66** epigyne, ventral (specimen IDWM.20003) **67** vulva, dorsal **68, 69** male (specimen SWK12-4726) **70–72** male (specimen SWK12-0590) **73–75** female (specimen SWK12-4087). Distance between substrate grooves 10 mm. Scale bars: on genitalia 0.1 mm.

a disorderly fringe of long cream setae overhangs the chelicerae (Fig. 70). **Chelicerae** simple and mostly vertical, dark, with cream setae that, with those of the clypeus, give the appearance of an unkempt moustache. At least two teeth on retromargin (paratype

with 6). **Palp** as in Fig. 64; embolus thin and accompanied by toothed TmA. Femur dark basally, but terminally is pale, as are all more distal segments. Endites with thumb-like lobe laterally (Fig. 6). **Legs** II–IV notably paler than legs I, which bear annulae of white scales on patella and distally on tibia. Metatarsus I dark; tarsus pale. Ventral fringe of black setae beneath tibia and metatarsus I. **Abdomen** with dorsal markings primarily transverse, with four transverse pale bands separated by three dark bands.

Female (based on paratype IDWM.20003). Carapace length 3.3; abdomen length 5.9. **Carapace** as in male, but lacking tuft at widest point. **Clypeus** and **Chelicerae** as in male. Five retromarginal teeth. **Legs** similar to those of male, but with first leg not quite so dark, and without the ventral fringe so distinctly developed. **Abdomen** with only a hint of transverse bands, instead dominated by longitudinal stripes: a narrow central pale band flanked by wide dark bands. **Epigyne** with ECP beneath a posteriorly-projecting mound (Figs 66–67).

Natural history. All specimens from Lambir Hills were collected on big-leaved foliage (e.g., palms) except for IDWM.20004 whose collecting record says simply “foliage”.

Additional material examined. One female from MALAYSIA: Sarawak: Lambir Hills Nat. Pk., Inoue Trail, 4.2002°N, 114.0346°E to 4.2004°N, 114.0342°E, 200 m el. 4 April 2012 Maddison/Piasek/Ang WPM#12-130. One male from MALAYSIA: Sarawak: Bako Nat. Pk., Mangroves, beach forest, 1.722°N, 110.446°E, 0 m el. 8 March 2012 Maddison/Piasek/Ang/Lee WPM#12-003.

Indopadilla Caleb & Sankaran, 2019

Indopadilla Caleb & Sankaran, 2019. Type species *Indopadilla darjeeling* Caleb & Sankaran, 2019.

Species included.

Indopadilla annamita (Simon, 1903), comb. nov., transferred from *Bavia*

Indopadilla bamilin Maddison, sp. nov.

Indopadilla darjeeling Caleb & Sankaran, 2019

Indopadilla kahariana (Prószyński & Deeleman-Reinhold, 2013), comb. nov., transferred from *Bavia*

Indopadilla kodagura Maddison, sp. nov.

Indopadilla insularis (Mamel, Sankaran & Sebastian, 2015)

Indopadilla nesinor Maddison, sp. nov.

Indopadilla redunca Maddison, sp. nov.

Indopadilla redynis Maddison, sp. nov.

Indopadilla sabivia Maddison, sp. nov.

Indopadilla sorsorol (Berry, Beatty & Prószyński, 1997), comb. nov., transferred from *Bavia*

Indopadilla suhartoi (Prószyński & Deeleman-Reinhold, 2013), comb. nov., transferred from *Bavia*

Indopadilla thorelli (Simon, 1901)

Indopadilla vimedaba Maddison, sp. nov.

Diagnosis. Front face of chelicerae concave or flat in both males and females, bordered laterally by a sharp ridge (Fig. 5). The ridge projects laterally in some males (e.g., Fig. 98, triangle, or see the male of *I. vimedaba* figured by Prószyński 1987, p. 105, as “*Stagetilus semiostrinus*”). (Males of *Bavia* may have chelicerae with a flat front face, and males of *Padillothorax* may have the front face concave medially, but none have such a sharp or extended lateral ridge.) Clypeus very narrow at centre, exposing a broad expanse of arthrodial membrane that in most species is white (Figs 96, 115, 128; Żabka 1988; Prószyński and Deeleman-Reinhold 2013 fig. 12; Malamel et al. 2015 fig. 9; Caleb et al. 2019 figs. 4, 21; dark in *I. kahariana*, *I. darjeeling*, *I. bamilin*). Spermatheca anterior to copulatory openings (posterior in other baviines). Retromarginal teeth of male not clustered onto a raised hump; rather, the teeth occur on a long sharp ridge that extends medially from base of fang (e.g., Prószyński 1987, p. 105). Male endite rounded, lacking lobe or sharp corner (Fig. 7). Thorax with a bulge just behind the PLE that gives the carapace a “muscular” appearance (Figs 5, 14; see triangle on Fig. 14). (This area contains the muscle attachments for the palps, first legs, and possibly the second legs.) Abdominal markings varied but include a pale longitudinal stripe along each side that is broken approx. half way toward the back, followed by a more posterior pale spot that extends slightly dorsally (Figs 79, 99, 103). When the embolus is long (e.g., Fig. 93), it arises simply as an extension of the tegulum, not being clearly divided from the tegulum as in *Piranthus* and *Maripanthus*.

This distinctive group may have many dozens or even hundreds of species, judging from the rate of discovery of new species among the few specimens being collected. We show in Figs 129–142 some of the apparently-new species that we are not naming. Matching males and females with such sparse collecting can be difficult. We have co-collected both males and females of *I. kahariana*, and they fall together on the molecular phylogeny (Fig. 3). Among the new species, only two are represented by both sexes, *I. redunca* and *I. vimedaba*. We interpret the male *I. bamilin*, *I. kodagura*, and *I. sabivia* as not being matches for the female *I. nesinor* because they are distinct on the molecular phylogeny or have mismatching genitalia (length of embolus vs. copulatory ducts; elaboration of RTA vs. ECP).

Embolus length varies through *Indopadilla*, short in many species, in other species (e.g., *I. kodagura*, *I. suhartoi*) as long as in some *Piranthus* and *Marapathus*. While we might be tempted to split the group into two – *Indopadilla* with a long embolus in South Asia and southeast Asia, and a new genus with a short embolus in southeast Asia – the most complete molecular data nests the long-embolus *I. kodagura* among short embolus species (Fig. 1). Also, even if the long and short embolus species formed mutually monophyletic groups, dividing them would break one very distinctive and easily recognized clade (cheliceral ridge, thoracic bulges, wide arthrodial membrane on face, etc.) into two much more subtle groups. We therefore maintain the whole group as a single distinctive genus.

The peculiar carapace bulge and exposed arthrodial membrane on the clypeus hint to the possibility that *Indopadilla* may use unusual biomechanics. The third leg claw tufts appear noticeably larger than the others. *Indopadilla* are excellent jumpers, difficult

to collect even on a beating sheet, from which they can escape in a single decisive bound. They are usually collected from foliage. A video of living males of *I. kodagura* and the undescribed species “BVBTN” (Figs 134–136) is available in Maddison (2020).

***Indopadilla bamilin* Maddison, sp. nov.**

<http://zoobank.org/537ADFA4-923D-4295-8824-D22388ED5BCA>

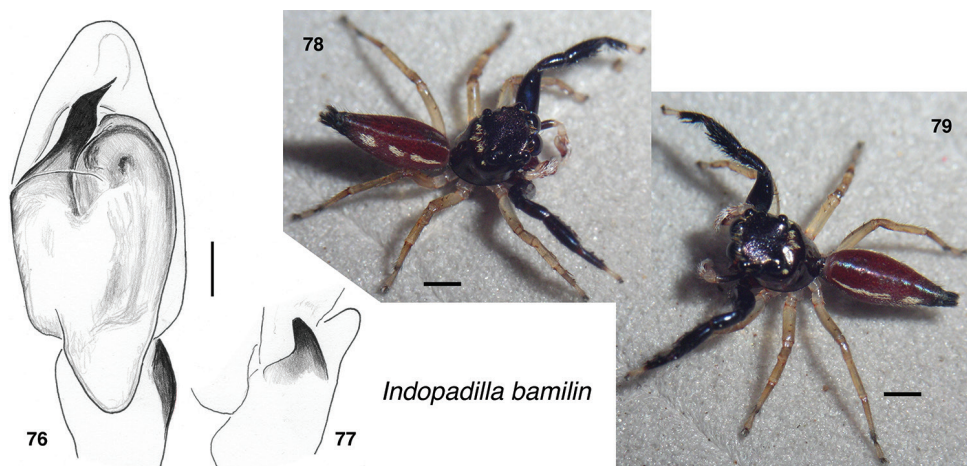
Figs 76–79

Type material. *Holotype* male (specimen SWK12-1618, in UBCZ) from MALAYSIA: Sarawak: Mulu Nat. Pk., Clearwater Cave Trail, 4.0597°N, 114.8292°E to 4.0592°N, 114.8291°E, 60 m el. 14 March 2012 Maddison/Piasecki/Ang WPM#12-027.

Etymology. An arbitrary combination of letters, ungendered. *Other names:* In Maddison (2015b) and WPM’s lab notebooks the informal code for this species was “BVVML”.

Diagnosis. Both embolus and RTA short and simple (Fig. 76). Other species with such a short embolus have a distinct TmA (*I. annamita*, *I. kahariana*, *I. redunca*, *I. sabivia*), which seems lacking in *I. bamilin*. First legs and body dark. None of the known females is an obvious match for this male in terms of markings or molecular phylogenetic placement, but also the unmatched females have longer copulatory ducts than would be expected for such a short embolus, or have a more dramatic ECP than expected for the simple RTA.

Description. **Male** (based on holotype, specimen SWK12-1618). Carapace length 2.3; abdomen length 3.0. **Carapace** dark brown, slightly paler around fovea, with a few patches of pale scales on thorax (Figs 78, 79). **Clypeus** dark, narrow; status of arthrochial membrane unclear, as chelicerae are somewhat sunken into the prosoma. **Chelicerae** vertical, brown, concave in front and with lateral ridge. Retromarginal teeth at least three, on long ridge. **Palp** femur dark; more distal segments pale. Embo-



Figures 76–79. *Indopadilla bamilin* sp. nov., male holotype SWK12-1618 **76** left palp, ventral view **77** same, retrolateral view of tibia **78, 79** holotype. Scale bars: on palp 0.1 mm; on bodies 1.0 mm.

lus short, undivided (i.e., no TmA; Fig. 76). Tibia with dorsal lobe distally (Fig. 77). Endite rounded laterally, without corner or lobe. **Legs** strongly contrasting between black leg I and pale legs II–IV. First patella entirely black. **Abdomen** dark red in life, with longitudinal band of pale scales on each side broken as typical for the genus.

***Indopadilla kahariana* (Prószyński & Deeleman-Reinhold, 2013), comb. nov.**
Figs 22, 30, 80–92

Bavia kahariana Prószyński & Deeleman-Reinhold, 2013: 115–117, figs 1–9.

Notes. We include illustrations of the described *Indopadilla kahariana*, to show living specimens and to show the genitalia in detail. Christa Deeleman-Reinhold kindly compared the type specimens to our illustrations and confirmed the match. A photograph of a living female is shown by Koh and Bay (2019, page 203, fig. A). In WPM's field and lab notebooks the informal code for this species was "BVSMB".

***Indopadilla kodagura* Maddison, sp. nov.**

<http://zoobank.org/013153B4-32EC-4F6A-A921-E7BB652AF67A>

Figs 93–99

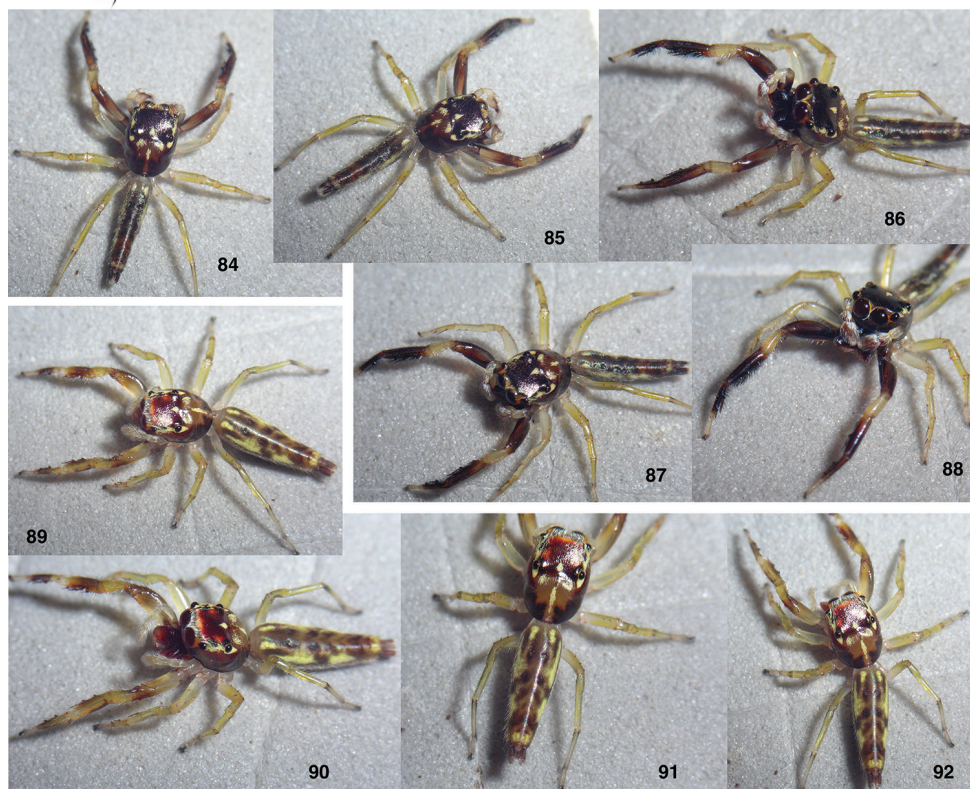
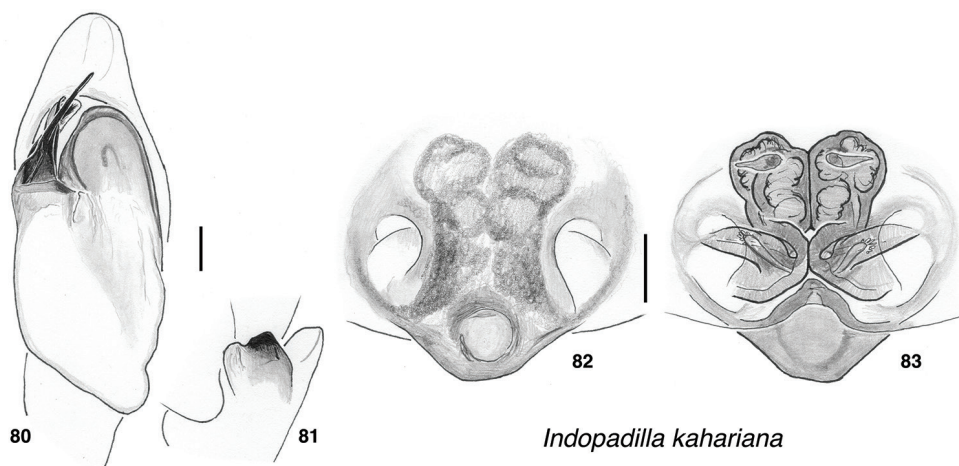
Type material. *Holotype* male (NCBS-BN351, also known as AS19.4314), in NCBS collection, from INDIA: KARNATAKA: Kodagu: Yavakapadi, Honey Valley area, forest & edge, 12.215°N, 75.659°E to 12.216°N, 75.661°E, 1300 m elev. 25 June 2019 W. Maddison & K. Marathe WPM#19-077.

Etymology. In the Kodava language, *kodagura* means from Kodagu. *Other names:* In WPM's field or lab notebooks the informal code for this species was "BVHVW".

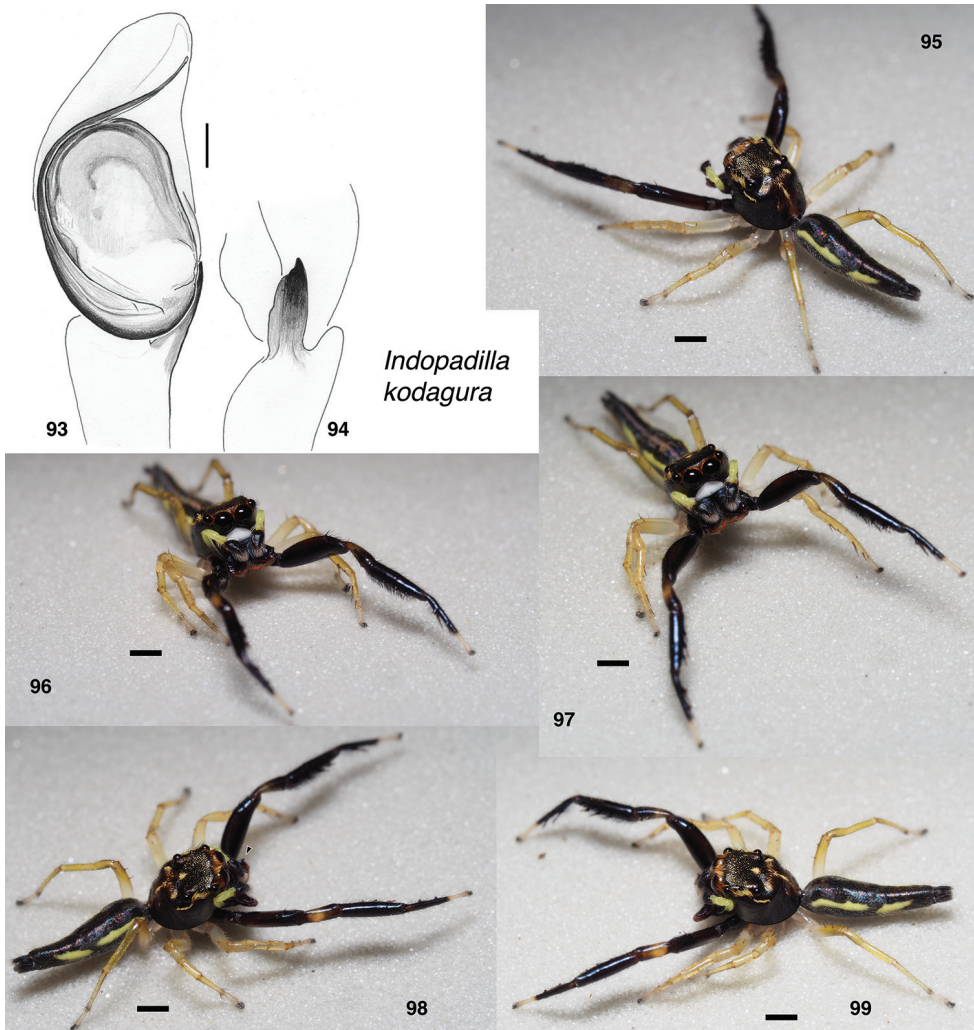
Diagnosis. Very similar to *I. insularis*, contrastingly marked in dark brown and yellow, with the face appearing white because the clypeus is withdrawn toward the eyes to expose a bright white arthrodial membrane. Like *I. insularis*, *I. darjeeling*, *I. sonsorol*, *I. suhartoi*, and *I. thorelli* in having a long thin embolus, but even longer than in those species, arising from the retrolateral basal corner of the bulb.

Description. **Male** (based on holotype, specimen NCBS-BN351). Carapace length 2.6; abdomen length 4.0. **Carapace** integument dark brown to black except to either side of fovea and narrow medial stripe on thorax, and with small patches of yellow scales in pattern typical for *Indopadilla*. **Clypeus** dark, extremely narrow, exposing white arthrodial membrane. **Chelicerae** dark, with lateral ridge bearing a tooth (Fig. 98, triangle). At least five retromarginal teeth, on long ridge. **Palp** yellow except for black cymbium. Embolus simple, long (Fig. 93); RTA a flat blade. **Legs** strongly contrasting between dark brown to black first legs, and yellowish posterior legs. Darkness of first legs relieved by pale tarsus, and honey coloured path on patella. **Abdomen** black except for two prominent yellow-white patches along each side.

Natural history. A video of the living holotype is available in Maddison (2020).



Figures 80–92. *Indopadilla kahariana*. **80** male left palp, ventral view (Mulu Nat. Pk., 4.045°N, 114.816°E) **81** Same, retrolateral view of tibia **82** epigyne, ventral (specimen SWK12-1876) **83** vulva, dorsal **83–88** male (SWK12-1163) **89–92** Female (SWK12-1876). Distance between substrate grooves 10 mm. Scale bars: on genitalia 0.1 mm.



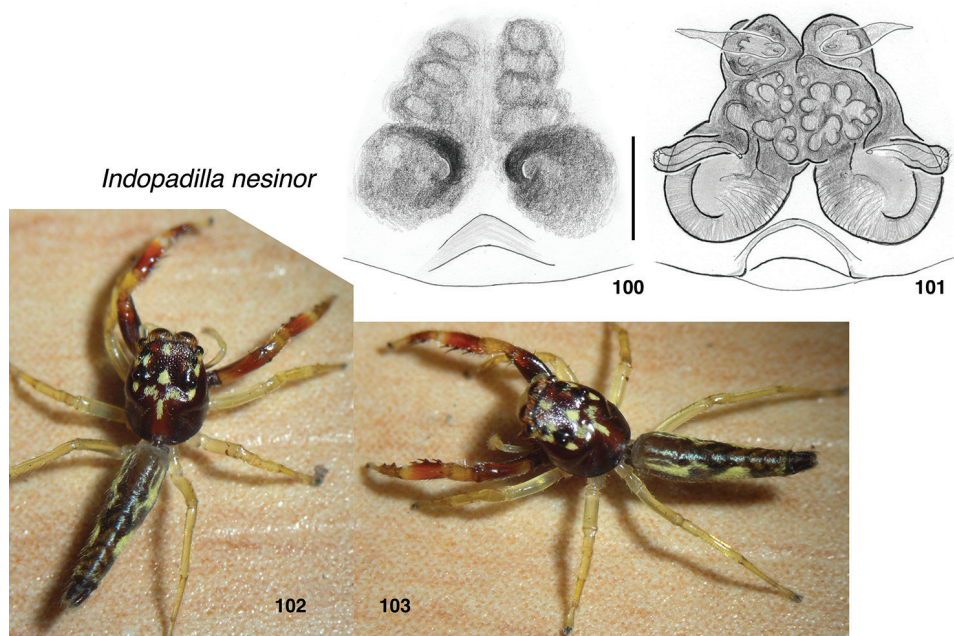
Figures 93–99. *Indopadilla kodagura* sp. nov., holotype. **93** male left palp, ventral view **94** same, retro-lateral view of tibia **95–99** male. Scale bars: on palp 0.1 mm; on bodies 1.0 mm.

***Indopadilla nesinor* Maddison, sp. nov.**

<http://zoobank.org/C34E99A9-07C6-4ECD-976A-3FEA32CB0E98>

Figs 100–103

Type material. *Holotype* female (specimen MRB076), in LKCNHM, from SINGAPORE: Nee Soon Swamp Forest, beating vegetation, 1.39°N, 103.81°E, 12 May 2005. W. Maddison, D. Li, I. Agnarsson, J. X. Zhang. WPM#05-015. *Paratype* female (specimen JK.14.05.19.0015) from SINGAPORE: Central Catchment Nature Reserve Upper Peirce Reservoir 1.3811°N, 103.8156°E, J. K. H. Koh 19 May 2014.



Figures 100–103. *Indopadilla nesinor* sp. nov., female holotype MRB076 **100** epigyne, ventral **101** vulva, dorsal **102, 103** Body. Scale bars: on epigyne 0.1 mm.

Etymology. An arbitrary combination of letters, ungendered. *Other names:* In WPM's lab notebooks the informal code for this species was "BVNES".

Diagnosis. As in *I. vimedaba*, the face appears white because of the exposed arthrochial membrane, whose boundary with the very narrow clypeus is indistinct. Differs from *I. vimedaba* in having chevroned abdominal markings visible in alcohol and epigynal openings small and copulatory ducts densely tangled and fused (Fig. 101).

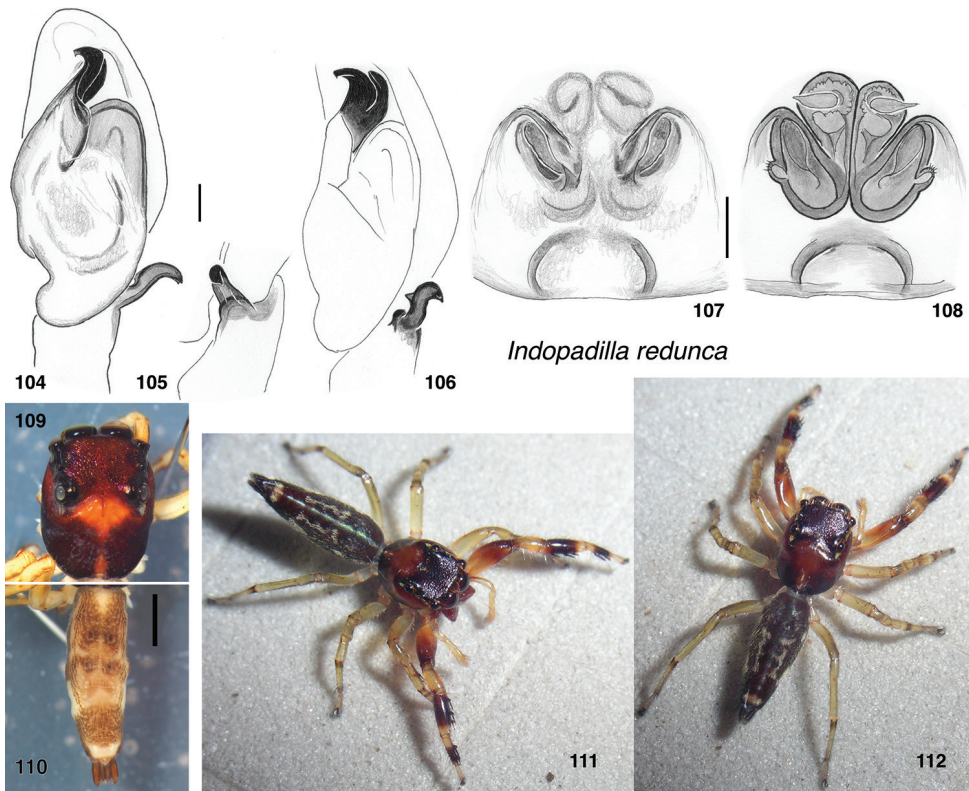
Description. Female (based on holotype, specimen MRB076). Carapace length 2.5; abdomen length 3.6. **Carapace** integument in alcohol dark brown, paler in ocular area and along midline of thorax, with patches of yellow scales (Fig. 102). **Clypeus** extremely narrow, but broad arthrochial membrane is exposed and bright white. **Chelicerae** brown, with concave front and lateral ridge. At least four retromarginal teeth. **Legs** pale except first, whose femur is brown darkening to black ventrally, and whose tibia and metatarsus are red-brown in the middle. **Abdomen** dark except for large patches of yellow scales along each side. **Epigyne** with shallow ECP and small openings (Fig. 100).

***Indopadilla redunca* Maddison, sp. nov.**

<http://zoobank.org/F3D55C28-3A7A-48CC-82FA-D91D0A363106>

Figs 5, 7, 14, 104–112

Type material. All from MALAYSIA: Sarawak: Mulu Nat. Pk. **Holotype.** Female (specimen IDWM.20011, in UBCZ), from Botanical Trail, 4.0380°N, 114.8137°E,



Figures 104–112. *Indopadilla redunca* sp. nov. **104** male left palp, ventral view (holotype SWK12-M0009) **105** same, retrolateral view of tibia **106** same, oblique ventral-retrolateral view **107** epigyne, ventral (specimen SWK12-1831) **108** Vulva, dorsal **109** male holotype, carapace **110** same, abdomen **111**, **112** Female (SWK12-1831). Distance between substrate grooves 10 mm. Scale bars: on genitalia 0.1 mm.

50 m el. 18 March 2012 W. Maddison WPM#12-059. **Paratype** female (specimen SWK12-1831, in UBCZ) from Botanical Trail, 4.0404°N, 114.8151°E to 4.0405°N, 114.8154°E, 50 m el. 16 March 2012 Maddison/Piascik/Ang WPM#12-039. **Paratype**. Male (specimen SWK12-M0009, in UBCZ) from Nightwalk Trail, 4.0446°N, 114.8154°E to 4.0450°N, 114.8156°E, 50 m el. 24 March 2012 Maddison/Piascik/Ang WPM#12-090. **Paratype** male (specimen JK.12.01.22.0024, in LKCNHM) from Sungai Paku Waterfall Trail, 04.0372°N, 114.8247°E, J. K. H. Koh 22 January 2012.

Etymology. Latin, meaning bent backward, referring to both the RTA and the ridge in front of the epigynal openings. **Other names:** In Maddison (2015b) and WPM’s field or lab notebooks the informal code for this species was “BVMTT”. In J. Koh’s notebooks it was referred to as “Bent RTA”.

Notes. The living paratype male 12.01.22.0024 is shown as figure E on p. 203 of Koh and Bay 2019.

Diagnosis. Male palp distinctive for bent RTA and thick curled embolus accompanied by TmA (Fig. 104). Epigyne similar to that of *I. redynis*, with cavernous ECP,

but with each opening framed by an anterior curved ridge. Posterior third of abdomen dark except for prominent pale transverse band just in front of anal tubercle. First femur pale basally, lacking dark spot of *I. redynis*.

Description. Male (based on paratype, specimen SWK12-M0009). Carapace length 2.9; abdomen length 3.6. **Carapace** in alcohol dark brown except medium brown near fovea, and a small medium brown stripe medially on thoracic slope. **Clypeus** dark, glabrous, very narrow in middle, exposing a white arthrochial membrane beneath. **Chelicerae** dark, concave and with lateral ridge. At least four retromarginal teeth, on long sharp ridge. **Palp** pale except dark gray retrolateral face of femur. Embolus thick and curved, accompanied by similarly curved TmA (Figs 104, 106). RTA projects out away from axis of palp, curved toward the proximal (Figs 105 106). **Legs** strongly contrasting between the first legs (dark, except for patella, tarsus, and much of femur). **Abdomen** as described under Male-female matching.

Female (based on holotype, specimen IDWM.20011). Carapace length 3.2; abdomen length 4.1. **Carapace** dark brown, paler around fovea and in a narrow medial band on thoracic slope. **Clypeus** narrow, dark, glabrous, exposing white arthrochial membrane. **Chelicerae** vertical, concave in front. Five retromarginal teeth. **Legs** pale except for first leg, whose tibia and metatarsus are dark brown in the middle, and the femur which grades to dark brown terminally. **Abdomen** marked as described under Male-female matching. **Epigyne** (Figs 107, 108) with large ECP medially. Openings behind arcing ridges.

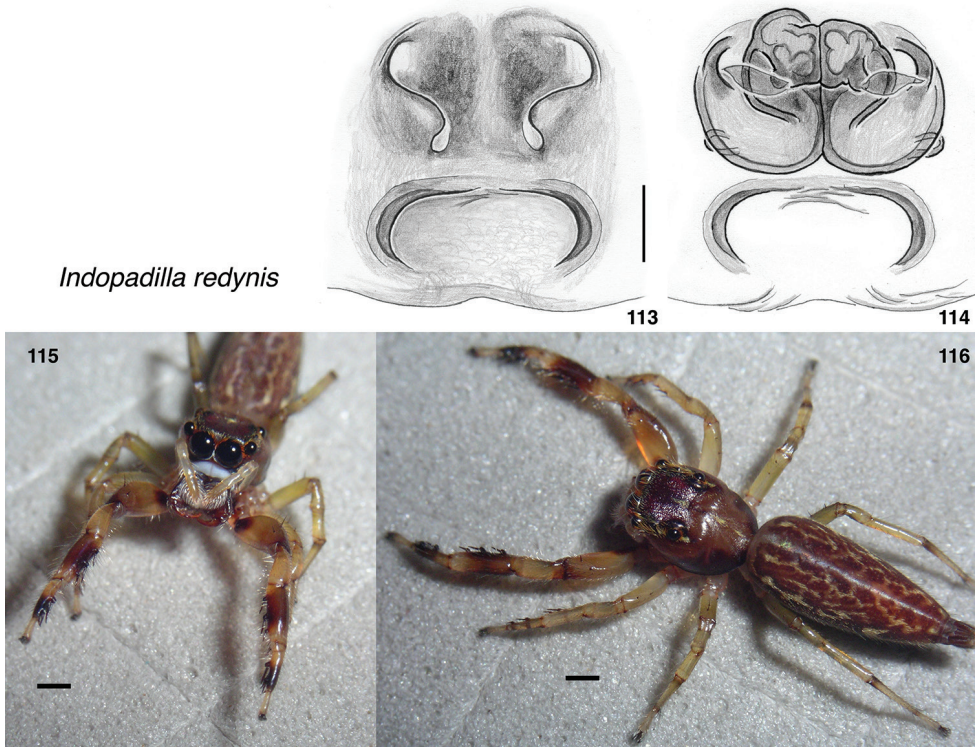
Male-female matching. The male and female, both collected at Mulu National Park, are matched primarily on the basis of markings and expected genitalic correlations. They share abdominal markings (Figs 110–112): just in front of the anal tubercle is a prominent pale transverse mark, more prominent than in other species, and in front of the pale mark is a dark more or less unmarked area that extends to cover the posterior third of the abdomen. Just in front of that, in the middle third, are two uneven narrow broken longitudinal bands, besides which are similar uneven pale bands on the side. While other *Indopadilla* species have uneven longitudinal bands, no others known have the bands so restricted by a dark posterior third, nor have the pale pre-anal band so prominent. In genitalia, the large ECP is expected to correspond to a dramatic RTA, which the matched male has. A female was chosen as holotype as it is in best condition, and the molecular data are from a matching female.

***Indopadilla redynis* Maddison, sp. nov.**

<http://zoobank.org/66E4CC75-6E34-479F-9A02-D304027C9EB5>

Figs 113–116

Type material. Holotype female (specimen IDWM.20012, in UBCZ) from MALAYSIA: Sarawak: Kubah Nat. Pk., roadside, 1.603–4°N, 110.185°E, 350 m el. 7 March 2012 Maddison/Piasek/Ang/Lee WPM#12-002. **Paratype** female (specimen SWK12-0080, in UBCZ) from MALAYSIA: Sarawak: Kubah Nat. Pk., Waterfall Trail, 1.605–6°N, 110.185–7°E, 300 m el. 7 March 2012 Maddison/Piasek/Ang/Lee WPM#12-001.



Figures 113–116. *Indopadilla redynis* sp. nov. **113** epigyne, ventral (holotype IDWM.20012) **114** vulva, dorsal **115, 116** Female (SWK12-0080). Scale bars on epigyne 0.1 mm; on bodies 1.0 mm.

Etymology. An arbitrary combination of letters, ungendered. *Other names:* In WPM’s lab notebooks the informal code for this species was “BVMT2”; it was also sometimes confused with *I. redunca* and labelled “BVMTT”.

Diagnosis. Similar in colour and epigyne to *I. redunca*. The epigyne differs in having the anterior part of the cavernous ECP with a more sharply defined boundary, the openings not behind a curved ridge, and the edge of the opening clearly sinuate (Fig. 113). The abdominal dorsum has fine reticulate markings throughout, not showing the unmarked posterior third. First leg markings match those of *I. redunca* except that anterior base of first femur with dark patch. Pale area on thoracic slope much broader than in *I. redunca*.

Description. Female (based on holotype, specimen IDWM.20012). Carapace length 3.6; abdomen length 5.7. **Carapace** integument medium to dark red-brown, except upper part of thorax between and beside eyes, continuing as a broad medial pale area to pedicel. **Clypeus** dark, extremely narrow, exposing broad white arthrodial membrane. **Chelicerae** light brown, concave in front. Five teeth on retromargin. **Legs** pale except dark brown on middle of first tibia and metatarsus, and darker patch at

front base of first femur. **Abdomen** red-brown, with delicate reticulate pale markings. **Epigyne** (Fig. 113) with large cavernous ECP; openings sinuate, resembling those of dendryphantines.

***Indopadilla sabivia* Maddison, sp. nov.**

<http://zoobank.org/28AEEB1A-86D2-4F38-B400-D4C1C4D089DC>

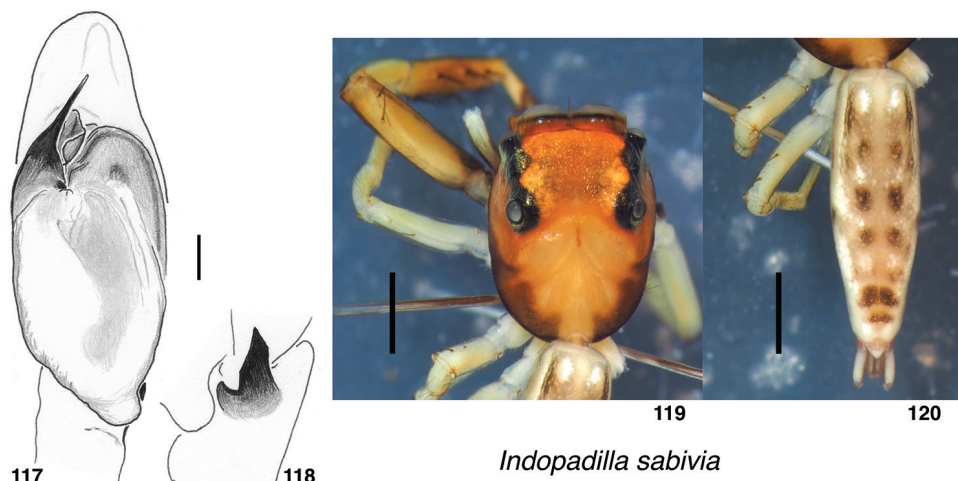
Figs 117–120

Type material. **Holotype** male (specimen d107, in UBCZ) from MALAYSIA: SABAH: Village of Kiabau. Central Sabah. 5.8315°N, 117.2245°E, 23 November 2000 K. Ober #00.437.

Etymology. An arbitrary combination of letters, ungendered. *Other names:* In WPM's lab notebooks the informal code for this species was "BVSAB".

Diagnosis. Palp similar to *I. kahariana* with a short sharp embolus with a TmA behind it, but the TmA is broader and more retrolaterally placed than in *I. kahariana*. RTA with sharp point, unlike the broad flat RTA of *I. kahariana*. These two species are sister groups on the molecular phylogeny (Fig. 1).

Description. **Male** (based on holotype, specimen d107). Carapace length 2.8; abdomen length 3.8. Overall appearance similar to that of *I. kahariana*, paler coloured than many male *Indopadilla*, honey to medium brown. **Carapace** medium brown to honey coloured, darker on sides, with ocular area and larger portion of dorsal thorax quite pale. **Chlypeus** narrow, exposing white arthrochial membrane. **Chelicerae** brown, with lateral ridge. Six retromarginal teeth, on long ridge. **Palp** pale except basal part



Figures 117–120. *Indopadilla sabivia* sp. nov., male holotype (specimen d107) **117** left palp, ventral view **118** same, retrolateral view of tibia **119, 120** Body. Scale bars: on palp 0.1 mm; on body 1.0 mm.

of femur. Embolus short and sharp, with broad TmA behind (Fig. 117). **Legs** mostly honey coloured, first somewhat darker and with ventral fringe on patella through metatarsus. **Abdomen** in alcohol similar to that of female *I. kahariana*, with series of darker paired spots dorsally and elongated pale spots along the side.

***Indopadilla vimedaba* Maddison, sp. nov.**

<http://zoobank.org/28AEEB1A-86D2-4F38-B400-D4C1C4D089DC>

Figs 121–128

Stagetilus semiostrinus: Prószyński, 1987: figs on pages 105–105 (misidentification).

Padillothorax semiostrinus: Prószyński 2018: 174–175, figs 28F–L (misidentification).

Type material. **Holotype** male (specimen JK 13.09.03.0011), in LKCNHM, from SINGAPORE: Nee Soon Swamp, 2 September 2013. J. K. H. Koh.

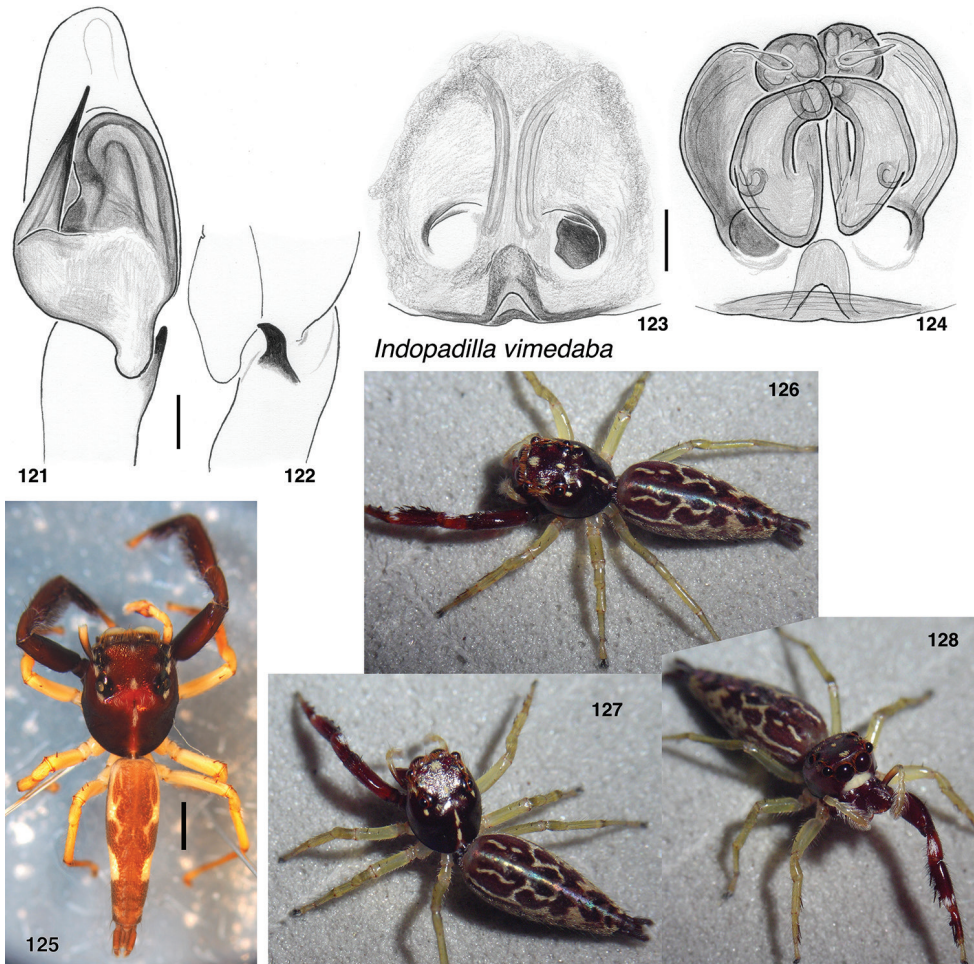
Etymology. An arbitrary combination of letters, ungendered. *Other names:* In Maddison (2015b) and WPM's field or lab notebooks the informal code for this species was "BVMDB".

Notes. As noted under *Padillothorax*, this species was mistaken for *Padillothorax semiostrinus*, and illustrated by Prószyński (1987) under that name. He illustrates a male and female in the same vial 15151 in the MNHN Paris from the "Malayana" peninsula.

Diagnosis. Palp with embolus longer than half the length of the bulb, straight and tapering (Fig. 121). Other *Indopadilla* have the embolus either longer and curved, or shorter. Epigyne with small but distinct ECP on back margin medially; openings simple and posterior (Fig. 123). Body dark brown except for highly contrasting but narrow pale cream markings, reticulate on abdomen.

Description. Male (based on holotype, specimen JK 13.09.03.0011). Carapace length 2.4; abdomen length 3.5. **Carapace** in alcohol dark brown to black, slightly paler around fovea and in narrow medial band along thoracic slope, which also has some white scales; other patches of white scales along borders of ocular area. **Clypeus** extremely narrow at centre, and beneath it is a broad expanse of white arthrodival membrane; precise boundary between the clypeus and arthrodival membrane indistinct. **Chelicerae** with strong lateral ridge that extends into a flange near the fang, as drawn by Prószyński (1987: 105). Three promarginal teeth and at least five retromarginal. **Palp** honey coloured except darker base of femur. Embolus a narrow long triangle (Fig. 121). **Legs** honey coloured except much larger first leg, which bears a ventral fringe. **Abdomen** dark above and below, with two pair of lateral pale spots, the anterior of which connects with a few thin pale lines.

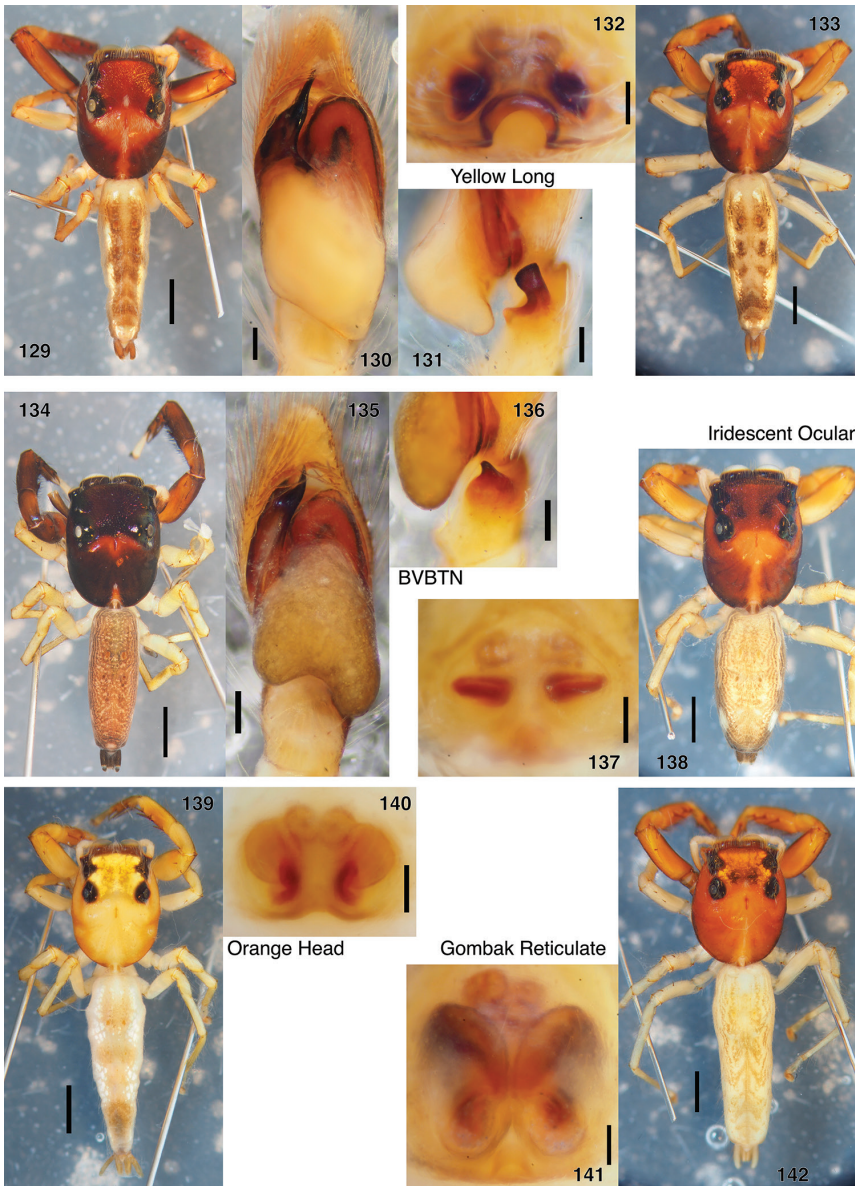
Female (based on specimen SWK12-3620). Carapace length 3.3; abdomen length 5.4. **Carapace** integument in alcohol medium red-brown except for narrow medial pale band along thoracic slope. **Clypeus** extremely narrow, exposing broad white arthrodival membrane (Fig. 128). **Chelicerae** concave in front with lateral ridge. At least four retromarginal teeth. **Legs** pale except first leg, dark except tarsus. **Abdomen** brown



Figures 121–128. *Indopadilla vimedaba* sp. nov. **121** male left palp, ventral view (holotype JK.13.09.03.0011) **122** same, retrolateral view of tibia **123** epigyne, ventral (specimen SWK12-3620) **124** vulva, dorsal **125** holotype male **126–128** female SWK12-3620. Scale bars: on genitalia 0.1 mm; on bodies 1.0 mm.

with distinct reticulation of pale scales. **Epigyne** (Fig. 123) with simple openings, from which broad copulatory ducts proceed anteriorly before narrowing considerably and proceeding to the posterior; then back anteriorly to the spermathecae.

Male-female matching. The male and female described above were not co-collected, but they match well the male and female (MNHN 15151, photographs examined) described by Prószyński, which were in the same vial, and thus likely co-collected. These males and females match in markings: the first leg is all dark except the tarsus; the abdominal dorsum is dark with some narrow pale lines, the venter dark; the pale medial band of the integument of the thoracic slope is narrow; there is a narrow band of pale scales on the midline low on the thoracic slope; the triangle of scales near the fovea is narrow. The male has fewer lines in its abdominal markings than the female,



Figures 129–142. Unidentified or undescribed *Indopadilla*, all in LKCNHM except **134–136**, in UBCZ. **129–131** male “Yellow Long” (specimen JK08.04.29.0029, Brunei, 4.6044°N, 114.6450°E), body, ventral palp, retrolateral palp tibia **132**, **133** female “Yellow Long” (specimen JK.12.03.14.0031, Brunei, 4.7036°N, 114.6264°E), epigyne, body **134–136** male “BVBTN” (specimen AS19.2286, Singapore, 1.3562°N, 103.7748°E to 1.3572°N, 103.7734°E), body, ventral palp, retrolateral palp tibia **137**, **138** female “Iridescent Ocular” (specimen JK.13.02.16.3005, Brunei 4.5764°N, 115.0731°E), epigyne, body **139**, **140** female “Orange Head” (specimen JK.12.03.21.0011, Brunei, 4.5833°N, 114.5047°E), body, epigyne (shown alive as fig. B on p. 203 of Koh and Bay 2019) **141**, **142** female “Gombak Reticulate” (specimen JK.98.03.05.0001, Singapore, 1.3619°N, 103.7592°E), epigyne, body. Scale bars: on genitalia 0.1 mm; on bodies 1.0 mm.

but those it has are precise matches to the female. Other *Indopadilla* differ; e.g., another candidate female, *I. nesinor*, has the first leg considerably more strongly banded, suggesting her male should have a first patella paler than seen in Fig. 125, more like that of *I. redunca* (Koh and Bay 2019: 203, fig. E), whose female's leg is banded similarly to *I. nesinor*. Also, *I. nesinor* differs in having a pale underside of the abdomen, and different thoracic markings. The relatively long but wide embolus of the male is a good fit to the openings and first broad part of the duct of the matched female, being ~ 0.07 mm wide at its base and ~ 0.3 mm long. In contrast, the openings of *I. nesinor* are only ~ 0.02 mm wide, enough to accommodate only a small portion of the embolus.

Additional material examined. One female (specimen SWK12-3620, in UBCZ) from MALAYSIA: Sarawak: Mulu Nat. Pk., headquarters area, on & in buildings, 4.042°N, 114.814°E, 50 m el. 26–27 March 2012 Maddison/Ang WPM#12-100.

Stagetillus Simon, 1885

Stagetillus Simon, 1885. Type species *S. opaciceps* Simon, 1885.

Hyctiota Strand, 1911, syn. nov. Type species *H. banda* Strand, 1911.

Species included.

Stagetillus banda (Strand, 1911), comb. nov.

Stagetillus opaciceps Simon, 1885

Stagetillus irri Maddison, sp. nov.

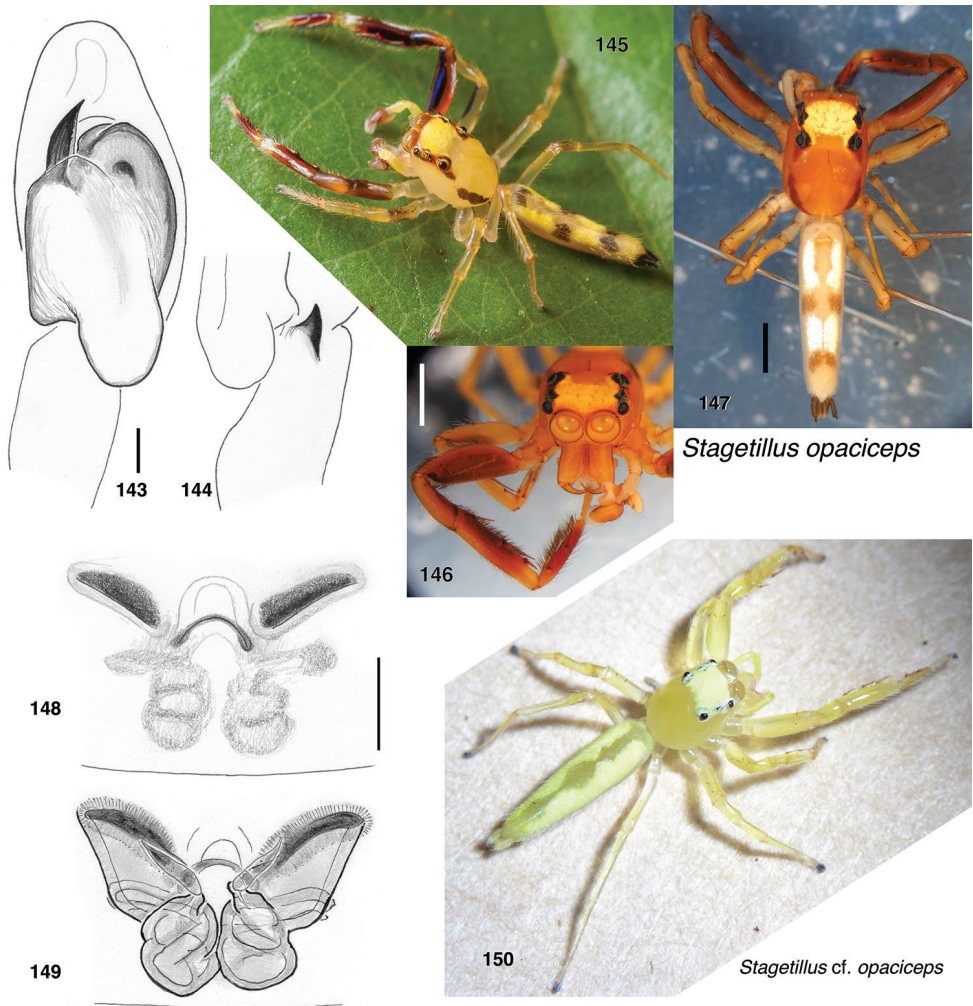
Notes. *Hyctiota banda* Strand, 1911 is based on a juvenile (SMF 2511 in SMF, examined) and not easily placed. Its being a baviine is suggested by its elongate body (most like that of *Indopadilla* or *Stagetillus*), plurident chelicerae, and Asian origin. Its macrosetae sockets resemble those of baviines (Figs 21–23). It lacks the thoracic bulge and ridged chelicerae of *Indopadilla*, and the flat carapace of *Padillothorax*. Like *Stagetillus*, the fovea is displaced slightly to the posterior. The two dark bands running through the PLE shown in Strand's (1911) original figure (no longer visible in specimen) resemble those of male *S. opaciceps*. The carapace is widest posteriorly, though not so clearly as in Figs 15 and 16. Although its synonymy with *Stagetillus* is not certain, by placing it with *Stagetillus*, a salticid genus otherwise incertae sedis is provisionally settled.

Diagnosis. Carapace distinctive in shape, widest point toward the posterior, approx. half way between the back eyes and the pedicel, and in colour, orange or yellow with the white digestive diverticulum showing beneath the transparent ocular quadrangle. Palp much like that of *Bavia*, with short blade-like embolus.

Stagetillus opaciceps Simon, 1885

Figs 8, 15, 16, 23, 31, 143–150

Stagetillus opaciceps Simon, 1885: 32.



Figures 143–150. *Stagettillus opaciceps* male, and a female tentatively identified as *S. opaciceps*. **143** Male left palp, ventral view (specimen JK.13.02.26.0017) **144** same, retrolateral view of tibia **145** living male from Belait, Brunei (photograph © Joseph Koh 2019) **146**, **147** male (specimen JK.08.08.19.0001) **148** female epigyne (specimen MRB079), ventral **149** vulva, dorsal **150** living female. Scale bars: on genitalia 0.1 mm; on bodies 1.0 mm.

Note. Prószyński's (1987) illustrations of Simon's type specimen characterize the male well. Two additional males illustrated here (Figs 143–147) are conspecific or at least very close (the male from Brunei, Figs 146, 147, has a slightly narrower embolus). Females of the species have not been reported, although we now tentatively identify, as the female of *S. opaciceps*, the specimen MRB079 from Ulu Gombak used by Maddison et al. (2014) for molecular phylogeny (Figs 148–150). That the female is a *Stagettillus* is suggested by its similarities to the male in size and body form, carapace shape, yellow coloration, and

visibility of the ocular digestive diverticulum. The modest ECP and epigynal openings are what might be expected from the small simple RTA and embolus of the known male of *S. opaciceps*. Given that Ulu Gombak is only 70 km from a known male of *S. opaciceps* (Figs 143, 144), the match of the Ulu Gombak female to *S. opaciceps* is credible. We therefore label the female, used here for molecular data, as *S. cf. opaciceps* (Figs 148–150). In WPM's lab notebooks the informal code for the female was "STULG".

Material examined. Male (specimen JK.13.02.26.0017, in LKCNHM) MALAYSIA: Negeri Sembilan, Hutan Lipur Ulu Bendul, 2.73°N, 102.0789°E, J. K. H. Koh 26 February 2013; Male (JK.08.08.19.0001, in LKCNHM) BRUNEI: Belait, Disturbed forest off Labi Road, 4.5858°N, 114.5067°E, J. K. H. Koh 19 August 2008. Female (specimen MRB079, in UBCZ) MALAYSIA: SELANGOR: Ulu Gombak Field Station. 3.325°N, 101.753°E, 250 m el. 16–19 May 2005. W. Maddison, D. Li, I. Agnarsson, J. X. Zhang, WPM#05-026.

***Stagetillus irri* Maddison, sp. nov.**

<http://zoobank.org/012F0D17-8A6A-4CE0-8EEB-8F0A3D2562AA>

Figs 151–157

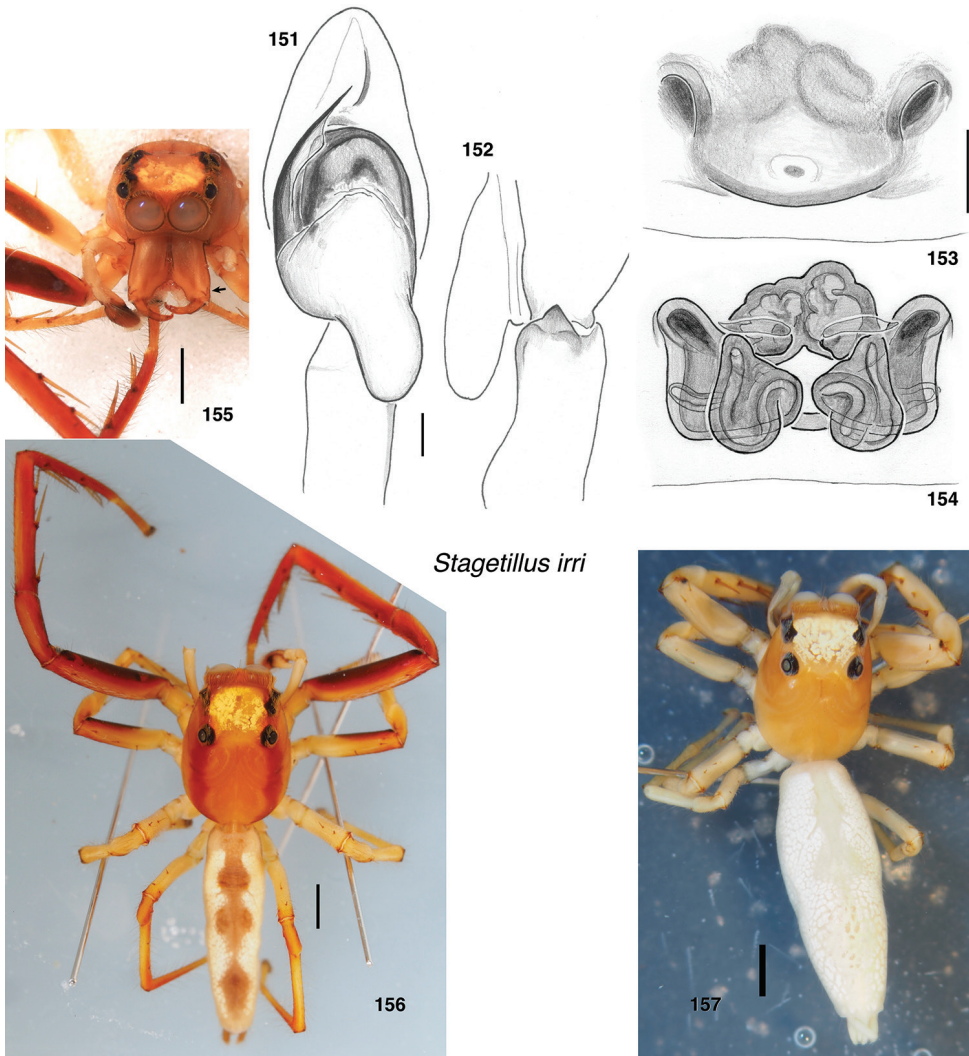
Type material. *Holotype* male (specimen IDWM.20023, in FSCA) and *paratype* female from PHILIPPINES: LUZON: Laguna Province, Los Baños, International Rice Research Institute, February 1993. R.R. Jackson (batch RRJ Ph 246/93). Other *paratypes* from same locality are 1 male (specimen IDWM.20022), December 1996, R.R. Jackson (batch RRJ Ph 292/96, in UBCZ); 3 females (specimens IDWM.20014, S202, and S203, in UBCZ), 1–16 December 1993, R.R. Jackson & G.B. Edwards; and 2 males 3 females, March 1993, R.R. Jackson (batch RRJ Ph 323/93, in FSCA).

Etymology. From the acronym for the type locality. *Other names:* This species was referred to by Maddison and Hedin 2003 as "unident. (Phil.)" In WPM's lab notebooks the informal code for this species was "STPHL".

Notes. The FSCA holds more material of this species, including from Mt. Makiling, near the type locality but at higher elevation (G. B. Edwards, pers. comm.).

Diagnosis. Similar in overall appearance to *S. opaciceps*, from which it differs in palp (narrower and longer embolus) and epigyne (shorter openings and having a central mound, presumably bearing the ECP). Male lacking the dense fringe beneath the first leg (Figs 155 vs. 146), but with a spur on the paturon (Fig. 155, arrow) that is lacking in *S. opaciceps* (Fig. 146). Male endite lacks the lateral bulge seen in *S. opaciceps*.

Description. Male (based on holotype, specimen IDWM.20023). Carapace length 3.3; abdomen length 4.6. *Carapace* yellow-orange with two darker stripes passing along PME, PLE, and to posterior margin, with transparent ocular areas showing bright white digestive diverticular beneath. Shape as in *S. opaciceps* (Fig 150). *Clypeus* narrow, more or less glabrous. *Chelicerae* orange, projecting slightly, with a spur on each paturon just above the fang base (arrow, Fig. 155). *Palp* pale except darker cymbium. Embolus arising at ~ 9:00 on the bulb, narrowing to a fine tip, with transparent



Figures 151–157. *Stagetillus irri* sp. nov. **151** male paratype IDWM.20022, left palp, ventral view **152** same, retrolateral view **153** female paratype S202, epigyne, ventral **154** same, vulva, dorsal. **155–156** male holotype IDWM.20023 **157** female paratype IDWM.20014. Scale bars: on epigyne 0.1 mm; on body 1.0 mm.

flange retrolaterally (Fig. 151). Long lobe of tegulum overhangs the tibia. RTA broad and obtuse. **Legs** pale yellow to dark orange, first pair darkest, with femora of first two pair darker below. First leg long, with only a weak fringe beneath. **Abdomen** with dark central band with three wider areas, flanked by bright white.

Female (based on paratype, specimen IDWM.20014). Carapace length 2.9; abdomen length 5.2. Entirely light in colour, from white to medium orange, except for the black of eyes, and small black patch at the front distal tip of the first leg femur. **Carapace** pale orange, with transparent ocular area showing bright white digestive

diverticular beneath. Shape as in *S. opaciceps* (Fig 157). **Chelicerae** orange, with five retromarginal teeth. **Legs** pale to dark honey-orange, except for black on prolateral tip of femur I. **Abdominal** integument transparent in alcohol, showing white digestive glands to either side of beige heart and mottled stercoral pocket. **Epigyne** (Fig. 153) similar to those of *Bavia*, with sclerotized openings on either side of a central mound.

Genus *Padillothorax*

Padillothorax Simon, 1901

Padillothorax Simon, 1901. Type species *Padillothorax semiostrinus* Simon, 1901.

Bavirecta Kanesharatnam & Benjamin, 2018, syn. nov. Type species *Bavirecta flavopuncta* Kanesharatnam & Benjamin, 2018.

Species included.

Padillothorax badut Maddison, sp. nov.

Padillothorax casteti (Simon, 1900), comb. nov., transferred from *Bavirecta*

Padillothorax exilis (Cao & Li, 2016), comb. nov., transferred from *Bavirecta*

Padillothorax flavopunctus (Kanesharatnam & Benjamin, 2018), comb. nov., transferred from *Bavirecta*

Padillothorax mulu Maddison, sp. nov.

Padillothorax semiostrinus Simon, 1901

Padillothorax taprobanicus Simon, 1902

Notes. The synonymy of *Bavirecta* with *Padillothorax* can be established now that the identity of the type species of the latter has been clarified (see below). The synapomorphies uniting them include the position of macrosetae on the first femur, flattened carapace, placement of fovea, pale thoracic “window” (Kanesharatnam and Benjamin 2018), and palp form. The deep genetic divide seen in Fig. 3 between *P. flavopunctus* and the *P. badut* species group (*P. badut* and *P. mulu*) might permit us to divide this into more than one genus, but this is unnecessary and not yet justified. The known *Padillothorax* species together make a recognizable genus, holding together well through their synapomorphies. In addition, there is no known data guiding us as to how to divide them and maintain monophyly, as we see no strong evidence resolving the trichotomy (*P. semiostrinus*, *P. flavopunctus*, *P. badut* + *P. mulu*).

Diagnosis. Distinctive for the macroseta(e) in the middle of the front surface of the first leg femur, the palp with narrow distally-pointing embolus, the pale trapezoidal “window” dorsally on the thorax (Kanesharatnam and Benjamin 2018), and the flat carapace with fovea well posterior to the eyes. The first femur’s prolateral macrosetae, either one or two, are present in both males and females (Figs 32, 33). While salticids usually have macrosetae dorsally or on the front surface distally (Figs 29–31, 34, 35), the more central location (more ventral and more basal, Figs 32, 33) of *Padillothorax* is unusual, known from only a few other genera (*Epocilla*, *Padilla*, some marpissines). The thoracic window is also different from the pale area on the top of the thorax seen in other baviines (e.g.,

Bavia nessagyna in alcohol), where it is neither as pale nor does it extend so far posteriorly as in *Padillothorax*. *Stagetillus* spp., and *Maripanthus draconis* have a pale thorax, but it is not framed by dark, as most of the thorax is pale. Palp is also distinctively simple: embolus narrow, pointing distally (i.e., appears erect in standard ventral view), fused to the tegulum, with no tegular fold covering its base as in *Bavia* and many *Indopadilla*. Epigynal openings anterior with simple copulatory ducts proceeding posteriorly. Abdomen with distinct transverse bands. First legs distinctly the longest. Male endite with lobe or sharp corner, unlike *Indopadilla* (whose endite is rounded, without lobes or corners).

***Padillothorax semiostrinus* Simon, 1901**

Figs 9, 17, 24, 32, 158–167

Padillothorax semiostrinus Simon, 1901: 71.

Notes. There has been confusion about the identity of *P. semiostrinus*. Prószyński (1987 p. 105) illustrated as *P. semiostrinus* a male and female from Simon's collection that clearly belong to the group here called *Indopadilla*, as Prószyński's illustrations show the group's typical diagnostic features. If his illustrations had shown *P. semiostrinus*, then *Indopadilla* would have been junior synonym of *Padillothorax*. However, Prószyński's illustrations are misidentified, representing a species quite distinct from *P. semiostrinus*, and which we describe above as *Indopadilla vimedaba*. Simon's (1901a, b) descriptions are sufficient to show the distinctions. He notes the thorax of *P. semiostrinus* almost twice as long as the ocular quadrangle (approx. equal in Prószyński's drawings and in *Indopadilla* generally), the carapace flatter than *Bavia* (as high or higher in *Indopadilla*), the fovea well back of the posterior eyes (immediately behind in *Indopadilla*), the retromarginal cheliceral teeth on a conical elevation (*Indopadilla* without elevation), and the male endite with a corner (well rounded in male *Indopadilla*). The last two distinctions are clear also in Simon's illustration (1901b, p. 461), which shows the teeth on a mound and the lateral margin of the chelicera simple, in contrast to Prószyński's illustration which shows the teeth not on a mound but spread along a ridge, and the lateral margin of the chelicera with an extended ridge (as in *Indopadilla*). Even Simon's name, *Padillothorax*, emphasizes the similarity to *Padilla*, whose distinctive carapace (flat, long, with short ocular quadrangle) is quite unlike the more standard carapace shown in Prószyński's drawings and *Indopadilla* in general. Thus, Prószyński's drawings are misidentified. He was likely misled by the vial's label, which appears much like those of Simon's other types.

As to what is *Padillothorax semiostrinus*, we have not been able to examine the type specimens, as they have not yet been located in the MNHN Paris. However, specimens found recently in Singapore and Taiwan match well Simon's (1901a) description, which we translate here to English (with the assistance of Charmaine Gorrie and Anna Bazzicalupo):

"♂. Length 7.5 mm. Cephalothorax low, long and oval, red-brown, darker towards the border; texture very wormy-coriaceous except for the middle of the thoracic part which is smoother. Cephalic area in front and at both sides, [and?] near the eyes, decorated with white-silver hairs. Two wide medial thoracic bands, nearly

contiguous; a thin marginal line decorated with white-silver hairs. Few white hairs around the eyes. Clypeus very narrow, bald. Abdomen narrow and very long, decorated above with dark violet, a medial band that is wide, entire, and yellow-brick red, bordered in front with lines and behind with a series of spots covered with silver-white hairs, marked on each side with a straight line in front and two white oblique [or crosswise?] lines behind. Venter reddish-yellow. Spinnerets dark. Chelicerae shiny black, short and diverging, convex outside, inside somewhat ribbed, inferior margin having a sunken furrow, then very raised and armed with a series of contiguous teeth, the middle larger. Mouth area black. Laminae truncate at the tip, convex, but with a compressed corner that is slightly extended. Sternum yellow. First pair of legs much longer and thicker than the others, femur clavate, tibia long and ovate, dark brown, coxa and femur black, tarsus yellow, tibia and metatarsus with fringe of reasonably long but not very dense black hairs. Remaining legs pale yellow, armed by a few small spines, as in *Bavia*. Palps reasonably small, pale yellow, thick with white hairs; tibia and patella rather short, equipped at the outside with a [long?] apophysis with a straight front and a black and acute tip."

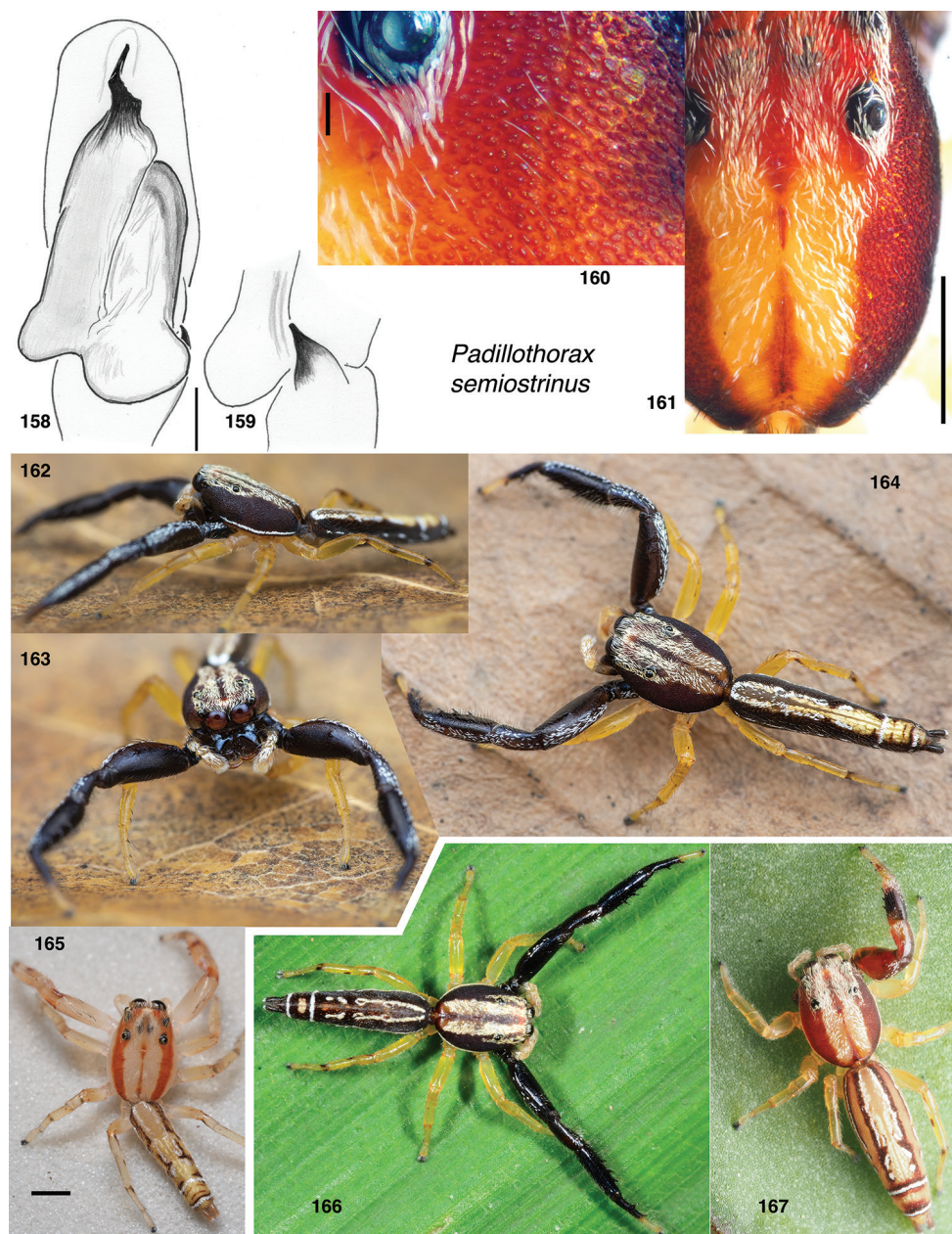
There are two apparent or possible conflicts between this description and the specimen seen in Figs 158–164. The most serious conflict is that the RTA in Fig. 158 is short, but Simon's description suggests the RTA is long. However, we were unable to understand the apparent use of genitive "*apophysi*" in "*tibia patella brevior, extus ad apicem apophysi sat longa, antice directa, apice nigra et acuta, instructa*". What exactly is long: the tip of the apophysis, the apophysis, or the outer edge of the tibia to the tip of the apophysis? Second, his description refers to marks at the back of the abdomen that are "*obliquus*", which would differ from Figs 164, 166 if it were translated as "oblique", but match if translated as "crosswise". Otherwise Simon's description and his mouth-parts illustration are an excellent match to the Singapore specimen, including the distinctive pair of nearly-touching wide thoracic bands, the pattern of the abdomen, the thorax rugosity except in the middle, the shape of the carapace and position of the fovea, the shininess and shape of the chelicerae, the mound bearing the retromarginal cheliceral teeth, the shape of the endite, the colours of the legs, and the yellow sternum.

We therefore provisionally identify the specimen of Figs 9, 17, 24, 32, 158–164 as *P. semiostrinus*. Although we might have added "cf." to its label to indicate our uncertainty ("*P. cf. semiostrinus*"), we avoid this so as to propose a stable concept of the species that could endure if Simon's types are never found.

A juvenile found in Singapore (Fig. 165) suggests the likely appearance of females. Males and females of this or a very similar species have been found in Taiwan, not yet examined, but with photographs posted in the website Facebook (Figs 166, 167).

Natural history. The male in Singapore was found in the open on a simpoh air leaf (*Dillenia suffruticosa*). A video of the living juvenile (specimen AS19.2448) is available in Maddison (2020).

Material examined. Adult male (specimen JK.20.06.20.001), in LKCNHM, from Singapore: Mandai Road, 1.4106°N, 103.7631°E. Y. Ng 20 June 2020. Juvenile (specimen AS19.2448), in UBCZ, from Singapore: Palau Ubin, 1.406°N, 103.971°E, 11 June 2019 Maddison/Morehouse et al. WPM#19-048.



Figures 158–167. *Padillothorax semiostrinus* **158–164** male JK.20.06.20.001 from Singapore **158** male left palp, ventral view **159** same, retrolateral view of tibia **160** oblique dorsal-lateral view just below posterior eye, showing sculpturing **161** carapace, dorsal view **162–164** living male (photographs © Yongi Ng 2020) **165** juvenile (specimen AS19.2448, Singapore) **166** male (from Taichung, Taiwan, photograph © Liu Shu Fen 2020) **167** female (from Taichung, Taiwan, photograph © Otto Lee 2020). Scale bars: 0.1 mm (**158–160**); 1.0 mm (**161, 165**).

***Padillothorax flavopunctus* (Kanesharatnam & Benjamin, 2018), comb. nov.**

Bavirecta flavopuncta Kanesharatnam & Benjamin, 2018: 4–8. figs 1–3.

Notes. This species shares the diagnostic features of the genus, including macrosetae on the middle of the front face of the first femur. *P. flavopunctus* has two such macrosetae on each femur, as in *P. badut* and *P. mulu*, but larger and placed even more proximally. We have concerns that the paratype female (IFS_SAL_679) is not conspecific with the male holotype, but if not conspecific, it is a closely related species, both by its strong morphological similarity (body form, markings) to the male and by its molecular proximity to a juvenile (IFS_SAL_1017) collected alongside the male at the type locality.

***Padillothorax badut* Maddison, sp. nov.**

<http://zoobank.org/1EA4DDD5-DE4A-456E-90AD-16C6E5B42FCF>

Figs 10, 33, 168–175

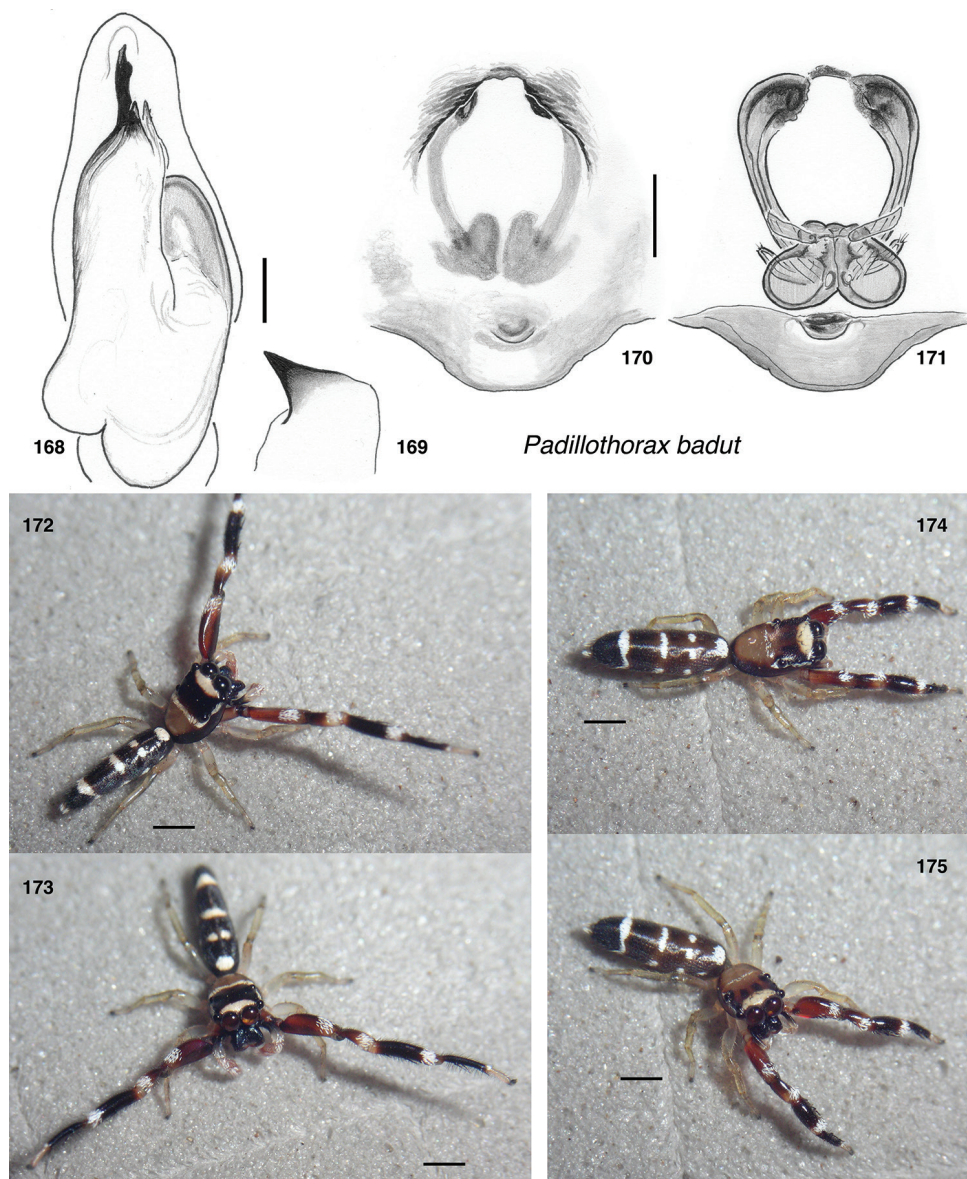
Type material. All from MALAYSIA: Sarawak: Lambir Hills Nat. Pk., and in UBCZ.

Holotype male (specimen IDWM.20007) from Bukit Pantu Trail, 4.2035°N, 114.0304°E to 4.2039°N, 114.0303°E, 210 m el. 5 April 2012 Maddison/Piasek/Ang WPM#12-136; **paratype** female (specimen SWK12-4350) from Lepoh-Ridan Trail, 4.2019°N, 114.0278°E to 4.2019°N, 114.0275°E, 190 m el. 2 April 2012 Maddison/Piasek WPM#12-125; **paratype** male (specimen SWK12-4688) from Inoue Trail, 4.2000°N, 114.0353°E to 4.2002°N, 114.0350°E, 190 m el. 4 April 2012 Maddison/Piasek/Ang WPM#12-128; **paratype** female (specimen IDWM.20008) from Bukit Pantu Trail, 4.2035°N, 114.0304°E to 4.2039°N, 114.0303°E, 210 m el. 5 April 2012 Maddison/Piasek/Ang WPM#12-136.

Etymology. From the Malay word *badut*, meaning clown. In the field we called these (and *P. mulu*) the “banded clowns”. *Other names:* In Maddison (2015b) and WPM’s field or lab notebooks this species was grouped with *P. mulu* under the informal name “BVBND”, until it was distinguished from that species as “BVBND-L”.

Diagnosis. Very similar to *P. mulu*, differing most notably in details of genitalia. The embolus of *P. badut* lacks the prolateral basal ridges and has a longer terminal part; the epigyne has the openings hidden beneath a fold.

Notes. This and the other new Malaysian species (*P. mulu*) are very similar in appearance, thin and banded; together we consider them as the *P. badut* species group. When the first legs are held forward in life (e.g., Fig. 174), the spider appears as a series of transverse white bands approximately evenly spaced from anterior to posterior: the first leg annuli, the two transverse bands on the carapace, and the four transverse bands on the abdomen. Their bodies are more delicate and parallel-sided than other *Padillothorax*, and they have more complex emboli.



Figures 168–175. *Padillothorax badut* sp. nov. **168** male left palp, ventral view (holotype IDWM.20007) **169** same, retrolateral view of tibia **170** epigyne, ventral (specimen IDWM.20008) **171** vulva, dorsal **172**, **173** Male (SWK12-4688) **174**, **175** female (SWK12-4350). Scale bars: on genitalia 0.1 mm; on bodies 1.0 mm.

Description. Male (holotype, specimen IDWM.20007). Carapace length 2.3; abdomen length 3.1. **Carapace** (Fig. 172): Black to dark brown except for band just back of the anterior eye row, and the pale trapezoidal window on thorax. Unusually flat (carapace height 0.72), with ocular area and most of the thorax on a plane, declining sudden-

ly only near back of thorax. Fovea well behind the PLEs (by more than their diameter). **Chlypeus** very narrow, dark. **Chelicerae** vertical, glabrous, dark. Teeth not examined in holotype, but another male from Lambir Hills has five retromarginal teeth, together in a mound as in *P. semiostrinus*. **Palp** pale except for base of femur. Base of embolus with two peaked projections on the retrolateral side (Fig. 168). Endite with lateral lobe (Fig. 10). **Legs**: First legs very distinctly longest and darkest, red-brown to black except for strong annulae with white scales. Legs II–IV pale yellow with just a smudge of dark laterally on a few segments of the fourth leg. **Abdomen**: narrow, with four white transverse bands.

Female (paratype, specimen IDWM.20008). Carapace length 2.1; abdomen length 3.1. Colour and structure matches that of male in nearly all aspects, with the most distinct difference being the slightly shorter first legs. **Cheliceral** teeth not examined in this specimen, but another female from Lambir Hills has four retromarginal teeth, together in a mound. **Epigyne** (Fig. 170) with two anterior openings, hidden under folds, and simple copulatory ducts visible without clearing. The copulatory duct has a diverticulum for the accessory gland extending laterally just before entering the simple spermatheca.

Natural history. On large-leaved understory plants such as palms. In life, they often hold the front legs out or to the front.

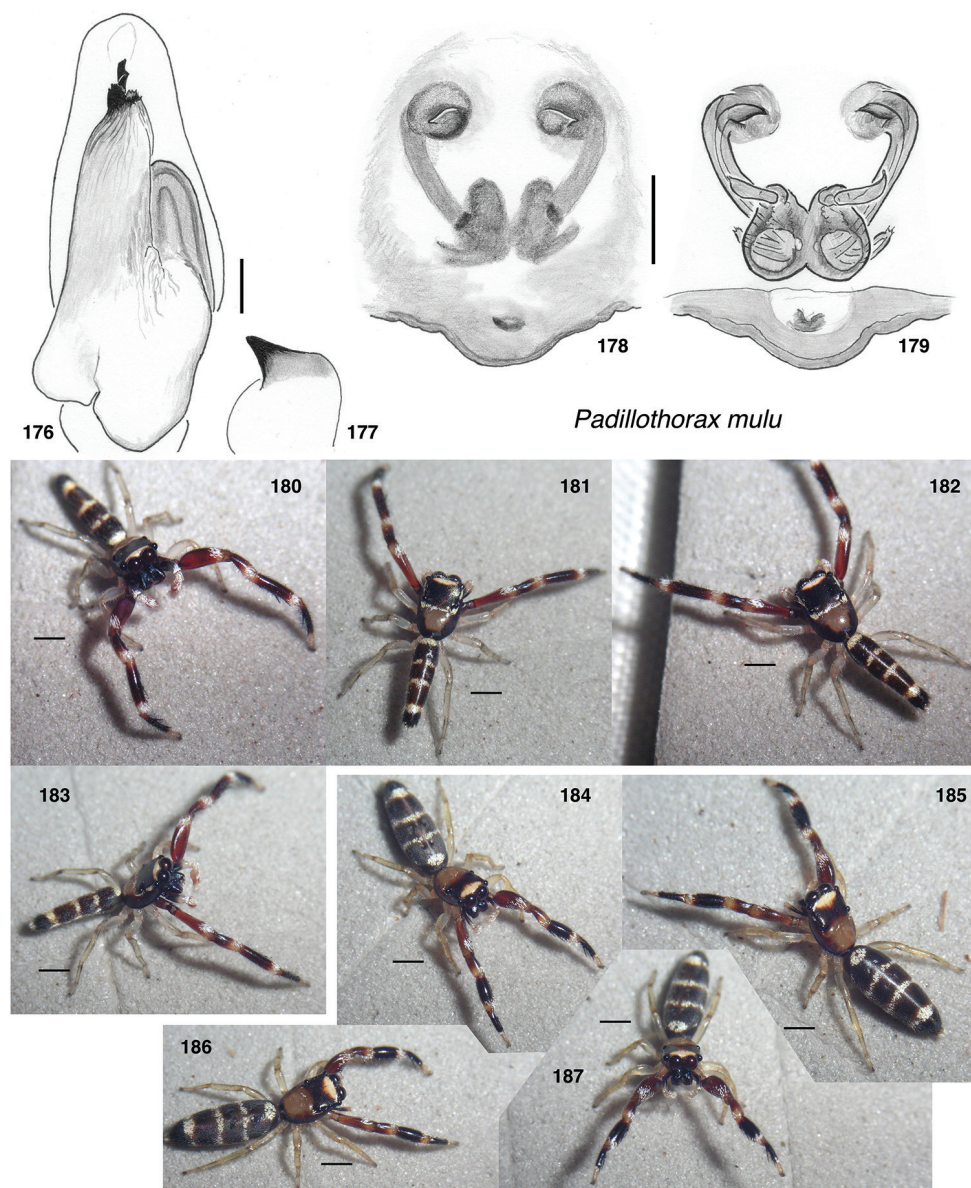
Additional material examined. All from MALAYSIA: Sarawak: Lambir Hills Nat. Pk., collected 4–6 April 2012 by Maddison/Piascik/Ang, in UBCZ. One female (specimen d548) from Inoue Trail, 4.2000°N, 114.0353°E to 4.2002°N, 114.0350°E, 190 m el. WPM#12-128. One male two females from Bukit Pantu Trail, 4.2028°N, 114.0305°E to 4.2032°N, 114.0305°E, 210 m el. WPM#12-134. One female from Bukit Pantu Trail, 4.2043°N, 114.0302°E to 4.2047°N, 114.0303°E, 210 m el. WPM#12-138. One female two juveniles from Bukit Pantu Trail, 4.2047°N, 114.0303°E to 4.2052°N, 114.0303°E, 200 m el. WPM#12-139. One female from Pantu Trail, 4.2027°N, 114.0401°E to 4.2030°N, 114.0399°E, 150 m el. WPM#12-144.

***Padillothorax mulu* Maddison, sp. nov.**

<http://zoobank.org/3B3E7E45-51BF-40F4-BD48-2E0CB877F732>

Figs 18, 25, 176–187

Type material. All from MALAYSIA: Sarawak: Mulu Nat. Pk., in UBCZ. **Holotype** male (specimen IDWM.20009) from Summit Trail near Camp 1, 4.0496°N, 114.8589°E to 4.0493°N, 114.8594°E, 220 m el. 21 March 2012 Maddison/Piascik/Ang WPM#12-067. **Paratype** female (specimen SWK12-EP0105) from Summit Trail near Camp 1, 4.0489°N, 114.8606°E to 4.0486°N, 114.8610°E, 280 m el. 21 March 2012 Maddison/Piascik/Ang WPM#12-071. **Paratype** male (specimen SWK12-2556) from Summit Trail near Camp 1, 4.0491°N, 114.8601°E to 4.0489°N, 114.8606°E, 270 m el. 21 March 2012 Maddison/Piascik/Ang WPM#12-070. **Paratype** female (specimen SWK12-EP0108) and male (specimen IDWM.20010) from Base Trail near Camp 1, 4.0543°N, 114.8534°E to 4.0544°N, 114.8531°E, 130 m el. 23 March 2012 Maddison/Piascik/Ang WPM#12-084.



Figures 176–187. *Padillothorax mulu* sp. nov. **176** male left palp, ventral view (holotype IDWM.20009) **177** same, retrolateral view of tibia **178** epigyne, ventral (specimen SWK12-EP0105) **179** vulva, dorsal **180–183** Male (SWK-2556) **184–187** female (SWK12-2574). Scale bars: on genitalia 0.1 mm; on bodies 1.0 mm.

Etymology. From the name of the type locality. *Other names:* In Maddison (2015b) and WPM’s field or lab notebooks this species was grouped with *P. badut* under the informal name “BVBND”, until it was distinguished from that species as “BVBND-M”.

Diagnosis. Very similar to *P. badut*, differing most notably in details of genitalia. The embolus of *P. mulu* is shorter, and has a toothed ridge on the prolateral base; the epigyne has the openings exposed on a more or less flat surface.

Description. Male (holotype, specimen IDWM.20009). Carapace length 2.5; abdomen length 3.5. Colour and structure matches that of *P. badut* as described above. Cheliceral teeth not examined. *Palp* pale except for base of femur. Base of embolus with various fine teeth; embolus shorter than in *P. badut* (Fig. 176).

Female (paratype, specimen SWK12-EP0105). Carapace length 2.1; abdomen length 3.3. Colour and structure matches that of *P. badut* as described above. Cheliceral teeth not examined in this specimen, but another female from Mulu has five retromarginal teeth. *Epigyne* (Fig. 178) similar to that of *P. badut*, except for the openings being exposed, not under a fold.

Natural history. As for *P. badut*, on large-leaved understory plants. They often hold the front legs out or to the front.

Additional material examined. All from MALAYSIA: Sarawak: Mulu Nat. Pk., in UBCZ. One female (specimen SWK12-EP0107) from Base Trail near Camp 1, 4.0543°N, 114.8534°E to 4.0544°N, 114.8531°E, 130 m el. 23 March 2012 Maddison/Piasek/Ang WPM#12-084. One female (specimen SWK12-2574) from Summit Trail near Camp 1, 4.0491°N, 114.8601°E to 4.0489°N, 114.8606°E, 270 m el. 21 March 2012 Maddison/Piasek/Ang WPM#12-070.

The Piranthus Clade (*Maripanthus*, *Piranthus*)

Maripanthus Maddison, gen. nov.

<http://zoobank.org/59175166-B0A7-4576-B294-856C7AE5FA5C>

Type species. *Maripanthus draconis* Maddison, sp. nov.

Species included.

Maripanthus draconis Maddison, sp. nov.

Maripanthus jubatus Maddison, sp. nov.

Maripanthus menghaiensis (Cao & Li, 2016), comb. nov. (transferred from *Nannenus*)

Maripanthus reinholdae Maddison, sp. nov.

Maripanthus smedleyi (Reimoser, 1929), comb. nov., transferred from *Bavia*

Etymology. An arbitrary combination of letters, reminiscent of *Marpissa* (as the females resemble) and *Piranthus* (to which it is closely related). To be treated grammatically as masculine.

Diagnosis. Epigynal atria long and gaping, anteriorly placed. Embolus long and beginning on the basal side of the tegulum, apparently freely articulated from the tegulum (as in the related *Piranthus*). Retromarginal cheliceral teeth close together, forming a single short ridge. Male endite with sharp corner (Fig. 11). Abdomen with central longitudinal pale band flanked by dark and stuttered into a chevron. Body unremark-

able for the Salticinae, in contrast to its sister genus *Piranthus* which are unusually flat and robust. The small *M. menghaiensis* and *M. reinholdae* in some respects resemble *Indopadilla* or small *Bavia*, but they lack the ridged chelicera l paturon of the former and the short embolus of the latter.

***Maripanthus draconis* Maddison, sp. nov.**

<http://zoobank.org/B511C74F-1343-48B8-ACDD-B01B20549324>

Figs 27, 34, 188–201

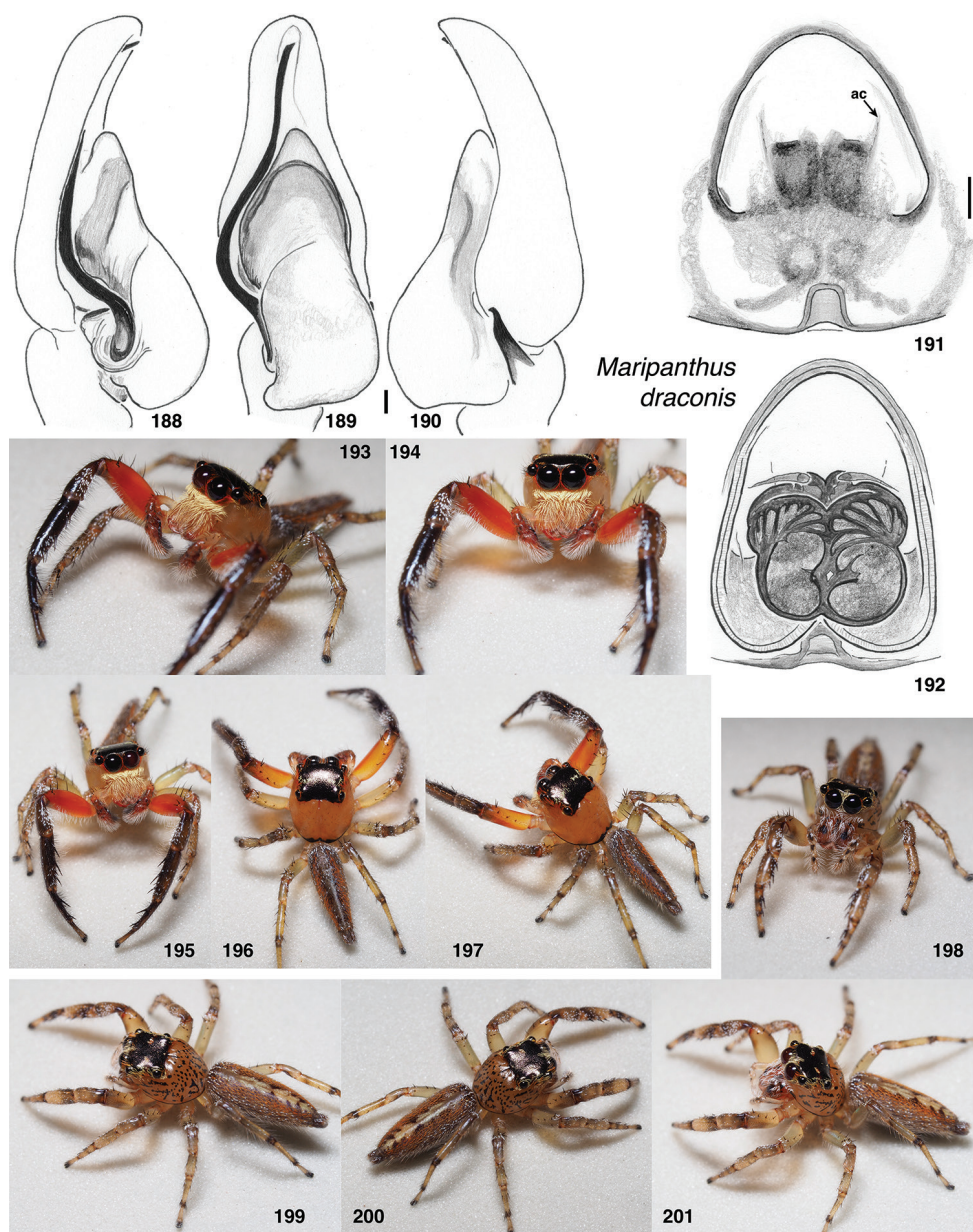
Type material. *Holotype* male (specimen AS19.2232), two *paratype* females (specimens AS19.2250 and d547), all in LKCNHM, from SINGAPORE: Bukit Timah Nature Reserve, stream at Jungle Falls Path. 1.3562°N, 103.7748°E to 1.3572°N, 103.7734°E 110–150 m elev. 12 June 2019 Maddison, Morehouse, & Marathe WPM#19-051. *Paratype* male (specimen WSG018) from SINGAPORE: Nee Soon Swamp Forest. Beating vegetation. 1.39°N, 103.81°E 12 May 2005. W. Maddison, D. Li, I. Agnarsson, J. X. Zhang. WPM#05-015.

Etymology. Greek, *δράκων*, referring to the fiery colours of the male. *Other names:* In Maddison (2015b) and WPM's field or lab notebooks the informal code for this species was "CFMAR". A specimen that is likely a closely related but distinct species is shown in Koh and Bay 2019 as "*Bavia*" sp. B Black-collared long-bellied jumping spider.

Diagnosis. Most similar to *M. smedleyi*, of which only the female is known; *M. draconis* differs in having longer epigynal atria (greater than half of epigynal length) and less distinct atrial cliff ("ac", Fig. 191). Similar to *M. jubatus* in being large bodied, but *M. draconis* differs in having a honey-coloured translucent thorax, which in the female is speckled with black, and which in the male contrasts strongly against the black ocular area. Male front is impressively red-orange, with red-orange first femora, palps, and rings around eyes, and a golden face. Embolus slightly shorter than the other three species for which males are known. Ventral bump on palp femur.

Description. Male (based on holotype, specimen AS19.2232). Carapace length 4.0; abdomen length 5.0. **Carapace** (Figs 196, 197) black in ocular area and in a thin line along ventral and posterior margin; thorax strongly contrasting honey coloured, glabrous except for a few vertical black setae. **Clypeus** covered with yellow-cream setae. **Chelicerae** vertical, a soft orange-red, covered with yellow-cream setae. Three promarginal and five retromarginal teeth. **Palp** femur pale, darkening to red-brown distally. Bulb elongate (Figs 188, 189); embolus arising on the prolateral basal corner and proceeding distally. Femur with small but distinct distal ventral bump. Endite with small corner projection. **Legs** with pale femora and darker markings more distally. First femur striking orange-red, patella to tarsus dark brown to black. First patella through metatarsus with sparse ventral fringe of setae that are black at base, white at tip. **Abdomen** with brown longitudinal medial band dorsally, flanked by scattered red scales, with some scattered white scales basally.

Female (paratype, specimen AS19.2250). Carapace length 4.2; abdomen length 6.1. **Carapace** (Fig. 199) integument black in ocular area, except for a pale spot on



Figures 188–201. *Maripanthus draconis* sp. nov. **188** male left palp, prolateral view (holotype AS19.2232) **189** same, ventral view **190** same, retrolateral view **191** epigyne, ventral (specimen AS19.2250) **192** vulva, dorsal **193–197** holotype **198–201** female AS19.2250. Scale bars: 0.1 mm.

each side just medial to the PME (in other females, these pale spots form a transverse band that intersects with a longitudinal medial pale band, forming a pale cross in the ocular area). Thorax honey-coloured with distinct black speckles. *Clypeus* with scattered white setae. *Chelicerae* brown with darker patches, with scattered white setae.

Three promarginal and five retromarginal teeth. **Legs** pale honey-coloured with various darker patches. **Abdomen** with central longitudinal pale chevroned band flanked by red scales. **Epigyne** with large atria leading to broad ducts (Figs 191, 192). Atria shallow laterally, declining rapidly at an “atrial cliff” (“ac”, Fig. 191) medial to which the surface is distinctly deeper. The ECP is apparently medial and small.

Natural history. In Singapore, beating vegetation in forest understory.

Additional material examined. In UBCZ. SINGAPORE: Bukit Timah Nature Reserve, stream at Jungle Falls Path. 1.3562°N, 103.7748°E to 1.3572°N, 103.7734°E, 110–150 m elev. 12 June 2019 Maddison, Morehouse, & Marathe WPM#19-051 (one female); Bukit Timah Nature Reserve. 1.355°N, 103.78°E, 29 May 2005. W. Maddison, D. Li, I. Agnarsson, J. X. Zhang. WPM#05-041 (1 female 1 juvenile). MALAYSIA: JOHOR: Gunung Belumut Recreational Forest. 2.066°N, 103.527°E, 60–100 m el. 24 May 2005. W. Maddison, D. Li, I. Agnarsson, J. X. Zhang. WPM#05-038 (1 male, 1 female, 6 juveniles); near Kluang, Gunung Lambak. 2.025°N, 103.344°E, 50–100 m el. 25 May 2005. W. Maddison, D. Li, I. Agnarsson, J. X. Zhang. WPM#05-039 (1 male). PAHANG: Tanah Rata. Jungle Trail 9 from Robinson Falls. 4.46°N, 101.40°E, 1200–1500 m el. 21–22 May 2005. W. Maddison, D. Li, I. Agnarsson, J. X. Zhang. WPM#05-035 (1 female). SELANGOR: Ulu Gombak Field Station, 3.325°N, 101.753°E, 250 m el. 16–19 May 2005. W. Maddison, D. Li, I. Agnarsson, J. X. Zhang. WPM#05-026 (1 female 1 juvenile); canyon near Ulu Gombak, 3.325°N, 101.765°E, 275 m el. 17 May 2005. W. Maddison, D. Li, I. Agnarsson, J. X. Zhang. WPM#05-027 (1 female 1 juvenile). SARAWAK: Fairy Caves, near Kuching, 1.381–2°N, 110.117–9°E, 20 m el. 10 March 2012 Maddison/Piascik/Ang/Lee WPM#12-011 (1 female). The female from Sarawak is listed with some hesitation. It may be conspecific with a male *Maripanthus* from Brunei, which appears to be a closely related but distinct species, with embolus initially directed distinctly more to the dorsal, and slight different carapace markings (specimen JK 08.08.23.0004, in LKCNHM, from Brunei: Ulu Temburong National Park, Ashton Trail 4.5428°N, 115.1528°E J K H Koh 23 August 2008).

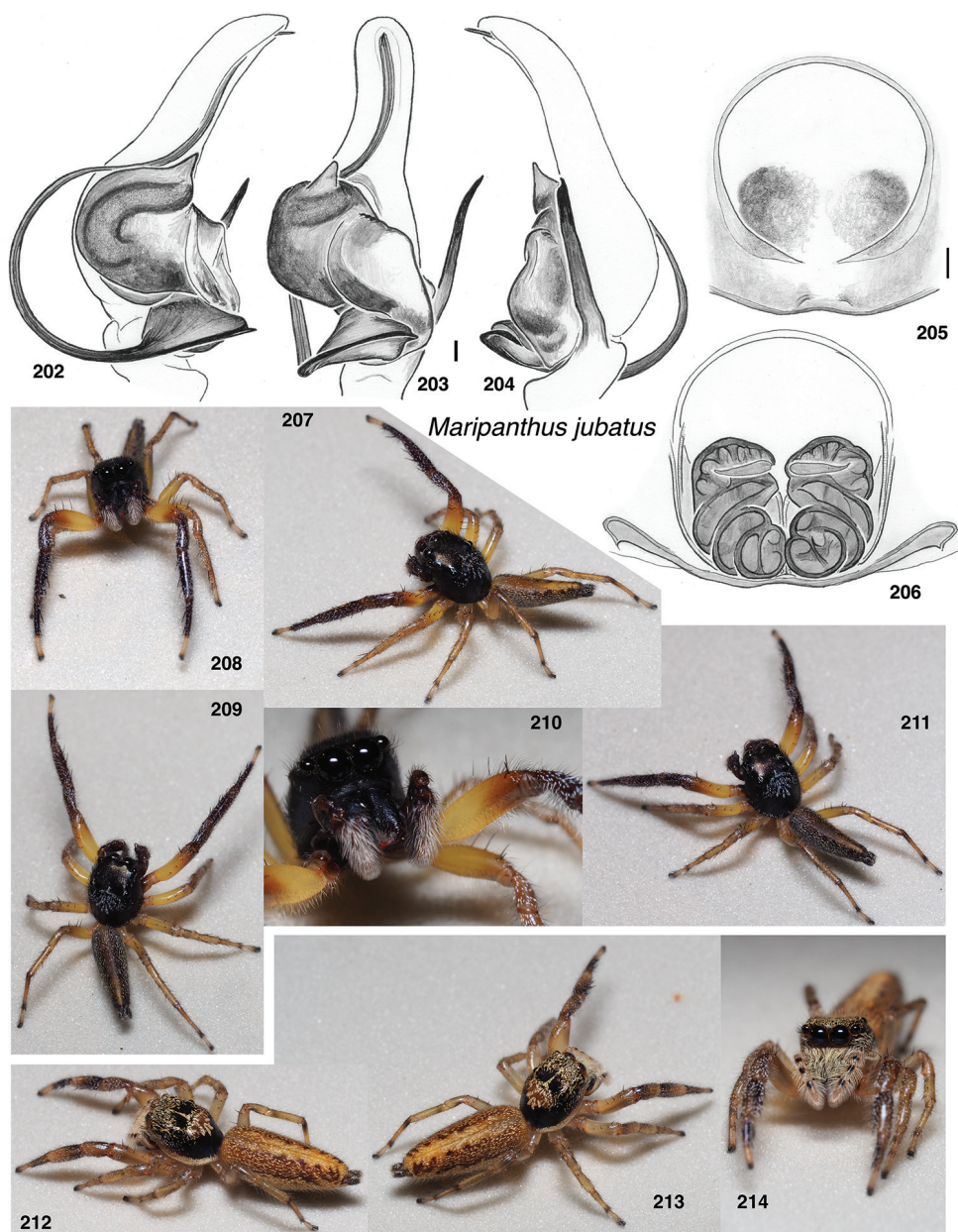
***Maripanthus jubatus* Maddison, sp. nov.**

<http://zoobank.org/BB40722F-B763-4501-B9E6-50F9C02EF23B>

Figs 11, 202–214

Type material. **Holotype** male (specimen NCBS-BN352, also known as AS19.4373) and **paratype** female (specimen NCBS-BN353, also known as AS19.4996), in NCBS collection, from INDIA: KARNATAKA: Kodagu: Yavakapadi, Honey Valley area, buildings and roadside, 12.22°N, 75.66°E, 1100 m elev. 23–28 June 2019 W. Maddison & K. Marathe WPM#19-069.

Etymology. Latin, meaning maned or crested, referring to the field of short black setae on the male ocular area. **Other names:** In WPM’s field or lab notebooks the informal code for this species was “CFMA2”.



Figures 202–214. *Maripanthus jubatus* sp. nov. **202** male left palp, prolateral view (holotype NCBS-BN352) **203** same, ventral view **204** same, retrolateral view **205** epigyne, ventral (specimen NCBS-BN353) **206** vulva, dorsal **207** holotype **208–211** male NCBS-BN354 **212–214** female NCBS-BN353. Scale bars: 0.1 mm.

Diagnosis. Similar size and body form to *M. draconis*, but differs most notably in solid dark integument of the carapace and face. Male palp with dramatically long embolus and RTA.

Description. Male (based on holotype, NCBS-BN352). Carapace length 3.9; abdomen length 4.8. **Carapace** (Figs 207–211) black, with scattered white scales on the top of the thorax. Front half of ocular area covered with vertical black setae, giving the appearance of a mane from in front (Fig. 210). **Clypeus** black, with long black setae. **Chelicerae** vertical, black. At least five retromarginal teeth. **Palp** black, but cymbium with white setae. Embolus long and swooping (Figs 202–204), beginning with a broad base over the tibia, proceeding prolaterally, then dorsally, then distally. RTA long and more or less straight. Femur lacks the ventral bump seen in *M. draconis*. Endite with small corner projection. **Legs** similar to those of *M. draconis*, with some segments of first legs dark, but differs in having the first femur pale honey darkening terminally to brown, and tarsus pale. **Abdomen** light brown mid-dorsally, darker laterally and with scattered cream coloured scales.

Female (based on paratype, NCBS-BN353). Carapace length 4.2; abdomen length 5.1. **Carapace** black except medium brown areas (yellow in alcohol) around fovea and along margin, covered with yellow cream scales in band along ventral margin, and dorsally on ocular area and anterior part of thorax (Figs 212–214). Clypeus covered with long cream-coloured setae. **Chelicerae** dark, covered with long cream setae. Three pro-marginal and five retromarginal teeth. **Legs** pale honey-coloured with various darker patches. **Abdomen** like that of male, but paler (Fig. 213). **Epigyne** (Fig. 205) similar to that of *M. draconis*, but with ECP split into a pocket on each side.

Natural history. Found in dry hanging banana leaves.

Additional material examined. All in NCBS collection. One male (specimen NCBS-BN354, also known as AS19.4403) from INDIA: KARNATAKA: Kodagu: Yavakapadi, on top of car, 12.2408°N, 75.6547°E, 23 June 2019 K. Marathe WPM#19-068. One male one female (specimens NCBS-BN355 and NCBS-BN355) from INDIA: KARNATAKA: Kodagu: near Madikeri, Rainforest Retreat, banana plantation, 12.480°N, 75.709°E, 30 June 2019 K. Marathe WPM#19-103.

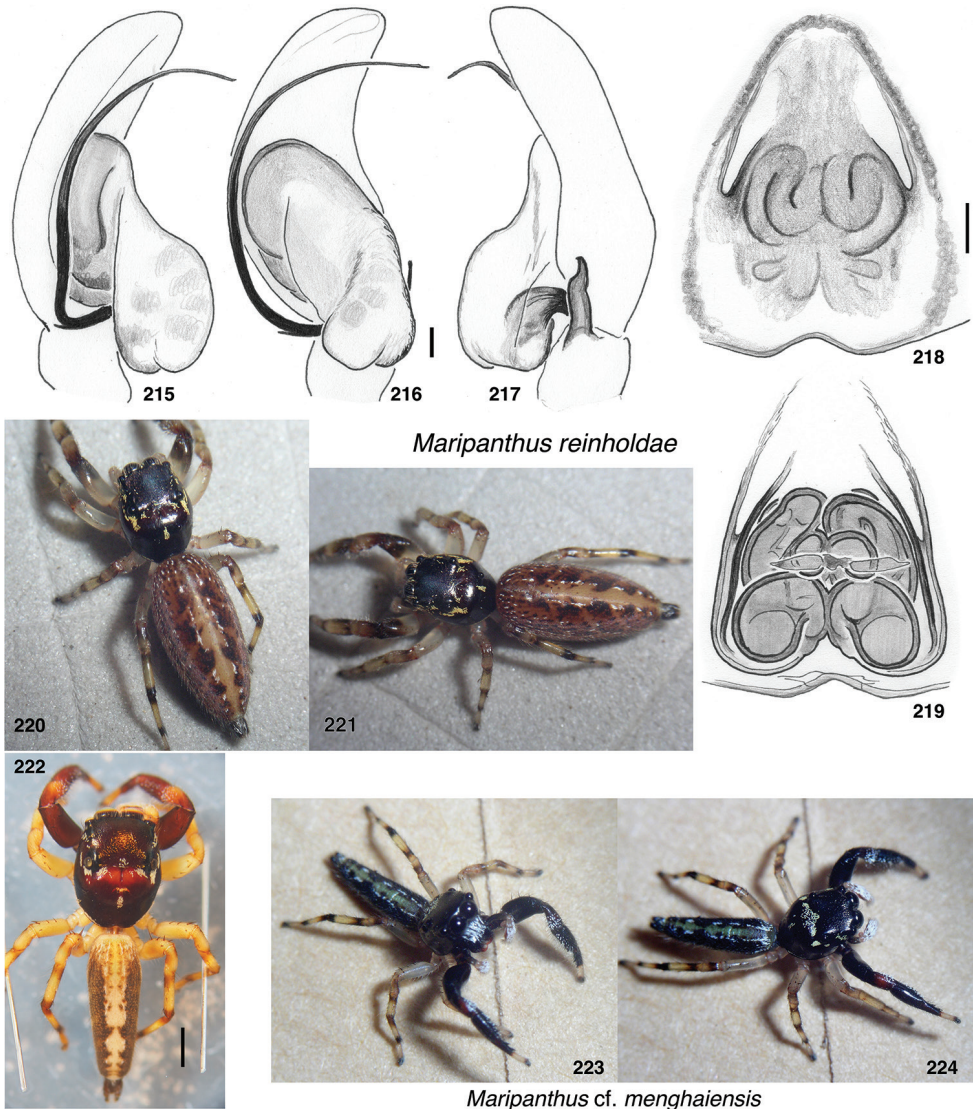
***Maripanthus menghaiensis* (Cao & Li, 2016), comb. nov.**

Figs 223, 224

Nannenus menghaiensis Cao & Li, 2016: 82–85, figs 28–29.

Note. *Nannenus menghaiensis* is here transferred to *Maripanthus* (and thus to the Baviini) based on its many close similarities with *M. reinholdae*, which itself is placed in *Maripanthus* by both morphological and molecular data. *M. menghaiensis* has an elongate body and pattern of thoracic and abdominal markings very much like those of other baviines (and unlike *Nannenus*, which is a compact-bodied ground dweller). See Diagnosis of *M. reinholdae* for distinctions therefrom.

A male (specimen IDWM.20013) that is either *M. menghaiensis* or a very closely related species is shown in Figs 223 and 224 (in UBCZ, from MALAYSIA: SELANGOR:



Figures 215–224. *Maripanthus reinholdae* sp. nov. and *M. cf. menghaiensis* **215–222** *Maripanthus reinholdae* **215** male left palp, prolateral view (holotype JK.11.12.24.0006) **216** same, ventral view **217** same, retrolateral view **218** epigyne, ventral (specimen SWK12-1934) **219** vulva, dorsal **220, 221** female SWK12-1934 **222** holotype male **223, 224** male *M. cf. menghaiensis* (specimen IDWM.20013). Scale bars on genitalia 0.1 mm; on body 1.0 mm.

Ulu Gombak Field Station, 3.325°N, 101.753°E, 250 m el. 16–19 May 2005. W. Maddison, D. Li, I. Agnarsson, J. X. Zhang. WPM#05-026). Its palp is very much like that figured by Cao, Li and Žabka (2016), but it differs slightly in the base of the embolus and a narrower embolus.

***Maripanthus reinholdae* Maddison, sp. nov.**

<http://zoobank.org/5B8BB349-2D63-42E2-AD0A-4426B4BAD0D9>

Figs 19, 26, 215–222

Type material. *Holotype* male (specimen JK 11.12.24.0006), in LKCNHM, from BRUNEI: Ulu Temburong National Park, Canopy Walk Trail, 4.5522°N, 115.1578°E, J. K. H. Koh 24 Dec. 2011. *Paratype* female (specimen SWK12-1934, in UBCZ), from MALAYSIA: Sarawak: Mulu Nat. Pk., Botanical Trail, 4.0406°N, 114.8170°E to 4.0404°N, 114.8176°E, 50 m el. 16 March 2012 Maddison/Piascik/Ang WPM#12-044. *Paratype* female (specimen SWK12-1991, in UBCZ), also from Mulu Nat. Pk., Kenyalang Trail, 4.0229°N, 114.8128°E to 4.0228°N, 114.8134°E, 55 m el. 17 March 2012 Maddison/Piascik/Ang WPM#12-047.

Etymology. Named in honour of Christa Deeelman-Reinhold, whose extensive work on southeast Asian spiders has greatly increased our knowledge of the area's fauna. She has discovered and described over 350 new species, including 54 new salticids. *Other names:* In Maddison (2015b) and WPM's field or lab notebooks the informal code for this species was "BVBGB". This species is shown in Koh and Bay 2019 as "*Bavia*" sp. C Two-lined long-bellied jumping spider; the upper photograph on p. 208 is of the holotype.

Diagnosis. Very similar to *M. menghaiensis*, and like it smaller and more *Indopadilla*-like in body form than *M. draconis* and *M. jubatus* (shorter first legs, more elongate abdomen). Differs from *M. menghaiensis* in the longer epigynal openings, and in details of the palp's bulb. In view from the retrolateral, the embolus is first directed to the distal then quickly turns dorsally (*M. menghaiensis*, embolus begins toward the dorsal). When the embolus comes out from behind the tegulum it is directed slightly proximally (slightly distally in *M. menghaiensis*). The embolus is thinner near the tip than in *M. menghaiensis*.

Description. Male (based on holotype, specimen JK.11.12.24.0006; living holotype shown on p. 208 of Koh and Bay 2019). Carapace length 2.9; abdomen length 4.0. **Carapace** (Fig. 222) black except for brown around fovea. Cream scales form a band crossing the thorax behind the PLEs, a small streak on the midline of the thoracic slope, and a narrow band along the lateral margins. **Clypeus** dark but centrally with a cluster of erect white scales that overhang the chelicerae. **Chelicerae** simple, vertical, dark. Plurident. **Palp** pale except for dark femur. Embolus long, arising retrolaterally before curling under the bulb prolaterally then proceeding distally (Figs 215–217). A short spur diverges from the embolus before it turns distally (Figs 215, 216). RTA vertical except for a bend and curl distally. Endite with small sharp corner, similar but smaller to that in the larger species of *Maripanthus*. **Legs** pale honey coloured except for first, which is black in all segments except the tarsus. Third and fourth legs darker near more distal joints. **Abdomen** thin, dark, with a pale mid-dorsal band, just lateral to which are indistinct longitudinal streaks of white scales.

Female (based on paratype, specimen SWK12-1934). Carapace length 3.7; abdomen length 5.0. **Carapace** as in male, but slightly paler in integument. **Chelicerae** with

three promarginal and five retromarginal teeth. **Legs** as in male but with first legs only slightly darker than the others. **Abdomen** brown with central pale chevroned band, and thin white streaks as in male. **Epigyne** (Fig. 218) similar in conformation to *M. draconis* and *M. jubatus*, but with atria smaller and copulatory ducts not so compacted.

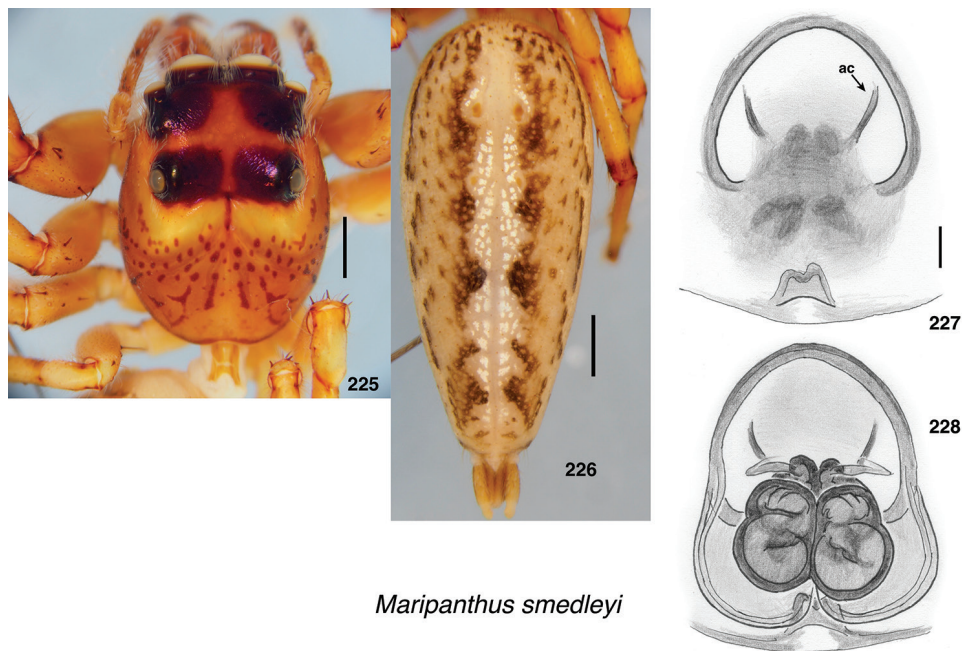
Additional material examined. One female (specimen JK.12.02.04.0010, in LKCNHM) from Brunei: Belait, Trail To Wasai Teraja Secondary Forest, 4.2911°N, 114.4231°E, J. K. H. Koh 4 February 2012.

***Maripanthus smedleyi* (Reimoser, 1929), comb. nov.**

Figs 225–228

Bavia smedleyi Reimoser, 1929: 130–132, fig. 4, holotype female SMF 1127 in SMF from Siberut, Sumatra, examined.

Notes. This species is close to *M. draconis*, with similar body form and markings (Figs 225, 226), but differing in details of the epigyne (Figs 227, 228). The atria are shorter, $\sim \frac{1}{2}$ length of the epigyne. Within the atria, the central depressed area is separated from the lateral raised areas by a more distinct and more heavily sclerotized “atrial cliff” (“ac”, Fig. 227). The spermathecae are smaller.



Maripanthus smedleyi

Figures 225–228. *Maripanthus smedleyi*, female holotype (SMF 1127) **225** carapace **226** abdomen **227** epigyne, ventral **228** vulva, dorsal. Scale bars: on genitalia 0.1 mm; on body 1.0 mm.

Piranthus Thorell, 1895

Piranthus Thorell, 1895. Type species *Piranthus decorus* Thorell, 1895.

Species included.

Piranthus api Maddison, sp. nov.

Piranthus bakau Maddison, sp. nov.

Piranthus decorus Thorell, 1895

Piranthus kohi Maddison, sp. nov.

Piranthus mandai Maddison, sp. nov.

Piranthus planolancis Malamel, Nafin, Sudhikumar & Sebastian, 2019

Diagnosis. Carapace surface rugose, with a coarse reticulate sculpturing throughout. Carapace flat (height well less than half the length), with ocular area and front part of thorax on a plane, and fovea well back of PLE, 1.3–1.5 × further from front of carapace than is the back of the PLE. Legs robust, especially the first pair. Embolus begins at pro-lateral basal corner of bulb; epigyne with central septum. Tip of abdomen black.

Two of the species (*P. bakau* and *P. kohi*) are distinctive for their black-and-white banding, three others (*P. decorus*, *P. mandai*, and *P. planolancis*) are more simply marked with brown and black, while the last (*P. api*) is a red-orange-black ember.

The four new species described here extend the range of *Piranthus* eastward as far as Borneo. The two previously described species, *P. decorus* (Thorell 1895; Caleb and Sanap 2017) and *P. planolancis* (Malamel et al. 2019; Nafin et al. 2020), are from Myanmar and India. A video of a living female of *P. planolancis* (specimen AS19.5940) is available in Maddison (2020).

Piranthus api Maddison, sp. nov.

<http://zoobank.org/4ABD7844-3008-4206-8EA2-20FE15058E44>

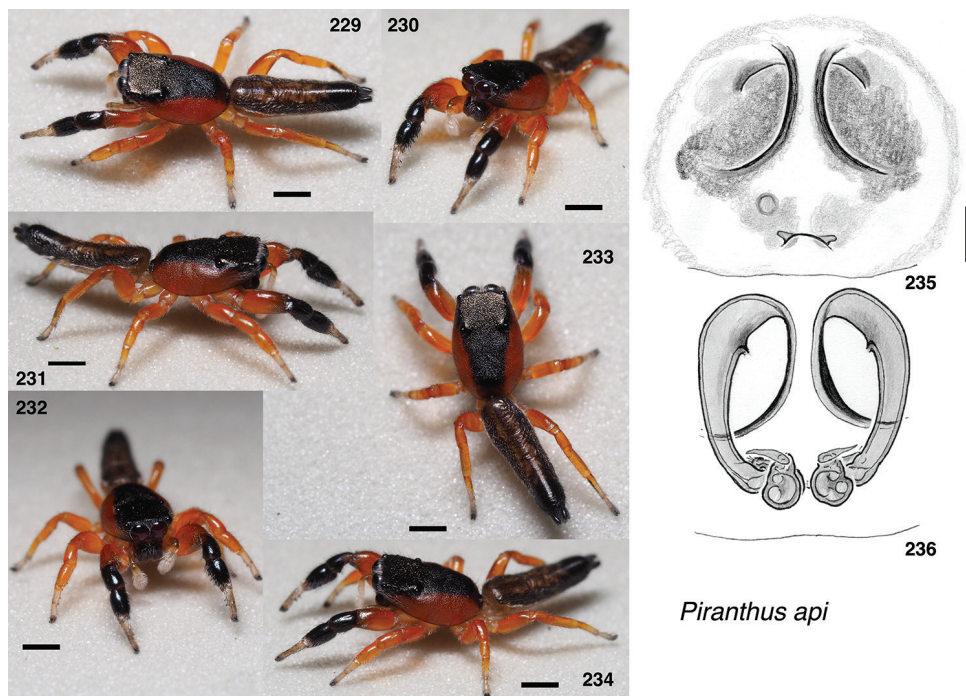
Figs 229–236

Type material. *Holotype* female (specimen AS19.3205), in LKCNHM, from SINGAPORE: Sungei Buloh Wetland Reserve, near Visitor Centre, 1.440°N, 103.734°E, 19 June 2019 Maddison/Marathe/Morehouse/et al. WPM#19-064.

Etymology. From the Malay word, “api”, meaning “fire”, referring to the colour. *Other names:* In WPM’s field or lab notebooks the informal code for this species was “PIORG”.

Diagnosis. A distinctively narrow species with bright red-orange legs.

Description. Female (holotype, specimen AS19.3205). Carapace length 3.0; abdomen length 3.5. **Carapace** narrow and low, orange-red-brown with central black area covering ocular area and medial part of thorax (Figs 229, 233). **Clypeus** black. **Chelicerae** short and vertical, dark. **Legs** red-orange except for black patella and tibia of first legs. **Abdomen** dark brown above, with median longitudinal paler band that in alcohol appears as to uneven parallel cream bands, extending backward until the black end of the abdomen. **Epigyne** (Fig. 235) with medial septum and a small medial ECP.



Figures 229–236. *Piranthus api* sp. nov., female holotype (specimen AS19.3205) **229–234** body **235** epigyne, ventral **236** vulva, dorsal. Scale bars: on epigyne 0.1 mm; on body 1.0 mm.

Natural history. The two specimens were both found deep within large grass tussocks overhanging a moist ditch. A video of the living holotype is available in Maddison (2020).

Additional material examined. A second female (specimen AS19.3217, in UBCZ), raised in captivity, same data as the holotype.

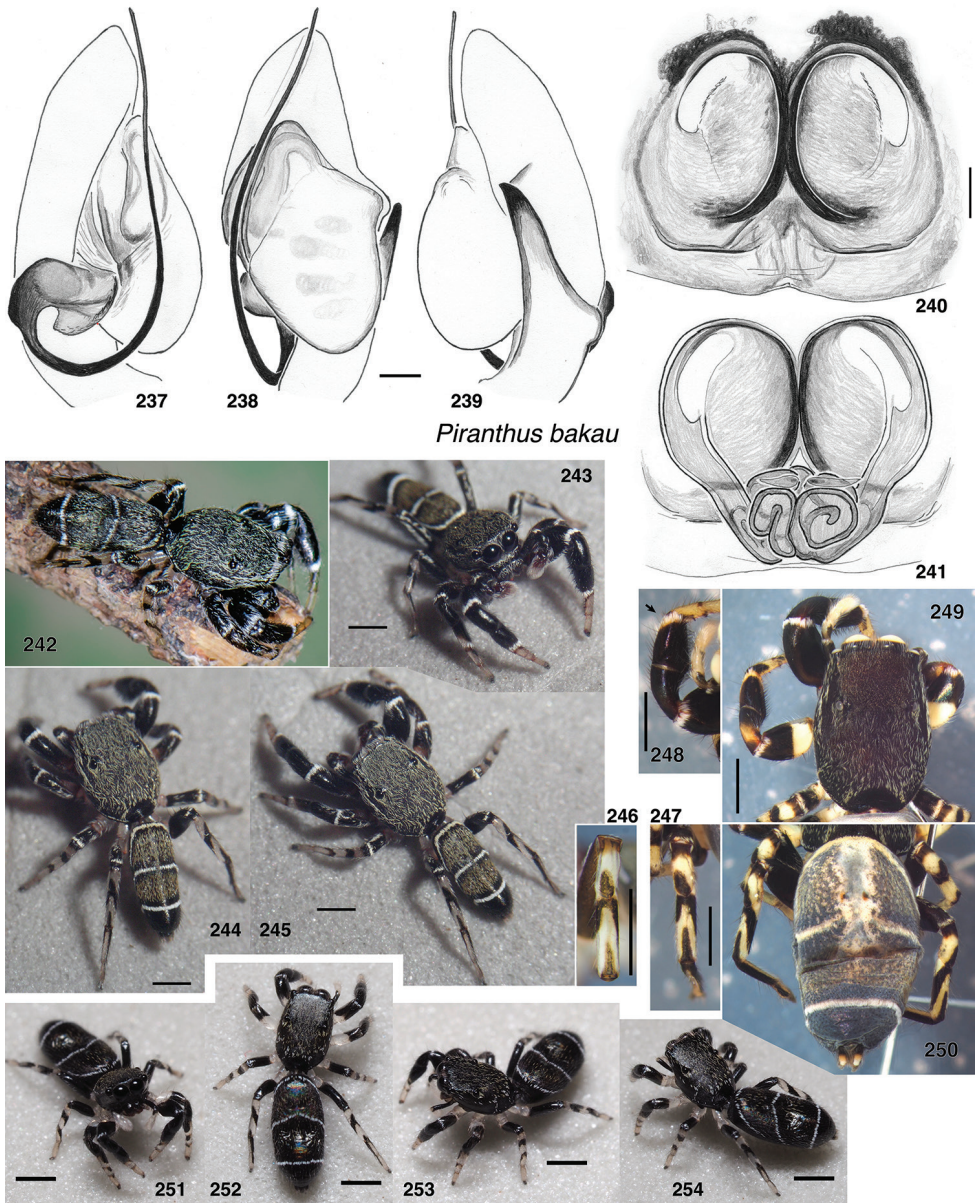
***Piranthus bakau* Maddison, sp. nov.**

<http://zoobank.org/1273542D-3BE3-404B-870E-246EEAA12967>

Figs 237–254

Type material. *Holotype* male (specimen SWK12-0561, also known as d424), in UBCZ, from MALAYSIA: Sarawak: Bako Nat. Pk., Mangroves, beach forest, 1.722°N, 110.446°E, 0 m el. 8 March 2012 Maddison/Piascik/Ang/Lee WPM#12-003.

Etymology. Referring to the type locality and to the holotype's habitat, mangroves (Malay, *bakau* = mangrove). *Other names:* In Maddison (2015b) and WPM's lab notebooks the informal code for this species was "BKOMG". This species is shown in Koh and Bay 2019 as the male of "*Bavia*" sp. D Strong-armed flat jumping spider.



Figures 237–254. *Piranthus bakau* sp. nov. **237** male left palp, prolateral view (holotype SWK12-0561) **238** same, ventral view **239** same, retrolateral view **240** epigyne, ventral (specimen AS19.2895) **241** vulva, dorsal **242** male JK.11.04.17.0040 (photograph © Joseph K. H. Koh) **243–245** male holotype (SWK12-0561) **246** male holotype left fourth patella and tibia, dorsal view (right leg digitally flipped to appear as left) **247–254** female specimen AS19.2895 **247** left fourth patella and tibia, dorsal view **248** left first leg, prolateral view **249** adult female prosoma **250** adult female abdomen **251–254** same specimen while immature. Scale bars on genitalia 0.1 mm; on bodies and legs 1.0 mm.

Diagnosis. This and the closely similar *P. kohi* differ from other known *Piranthus* in having white transverse banding on the body and legs, and the posterior legs striped with black and translucent white. *P. bakau* (Figs 237–254) differs from *P. kohi* (Figs 255–269) in having:

- Second white transverse band on the dorsum of the abdomen (i.e., the first behind the basal band) complete or broken by only a slight space;
- Sides of thorax lacking the three distinct narrow vertical lines seen in *P. kohi* (at most only a hint of two);
- Carapace lateral to the PLE with a bare patch, lacking golden scales, extending from PME back to behind PLE, and lateral to the bare patch is a stripe of denser golden scales (Figs 245, 249);
- First and second tibia bicoloured (black with white tip, arrow in Fig. 248);
- Second femur bicoloured (white basally, black terminally, Fig. 249);
- Black dorsal band on the fourth tibia incomplete, beginning mid-segment and reaching to the end (Figs 246, 247).
- Carapace slightly flatter than in *P. kohi*.
- Embolus (Fig. 237) notably longer than in *P. kohi* (Fig. 255), closely resembling that of *P. planolancis* (Nafin et al. 2020);
- Epigyne with cavernous atria framed by a curved medial ridge, and relatively long copulatory ducts leading to a posterior tangle of tubes and spermathecae.

Juveniles have markings consistent with those of adults, and thus can be distinguished by the non-genitalic features above.

Description. Male (based on holotype, SWK12-0561). Carapace length 2.7; abdomen length 3.0. **Carapace** with rugose surface, black on ocular area, dark brown otherwise, covered thinly with narrow golden to white scales except bare patch lateral to PLE, and on posterior slope. **Clypeus** narrow, dark, with a few white setae. **Chelicerae** small and vertical, dark, with a few pale setae. **Palp** (Figs 237–239) black except band of white scales terminally on femur, and cymbium, which is dark basally but then fades to white distally. Embolus long, arising on prolateral basal corner of bulb, looping first dorsally, then proximally, then distally. RTA a long blade. Endite margin rounded laterally. **Legs** relatively larger (compared to the body) than in many baviines, with first pair especially robust. First and second legs mostly dark and with terminal white annuli on the segments. First patella and tibia with ventral fringe of black setae. Third and fourth leg segments from patella to tarsus translucent white with black bands and stripes. Fourth tibia and patella with a pattern of short black and white bands. On the tibia, a black dorsal band begins not basally but half way to the end, and extends distally to the tip; basally, it is interrupted by white (Fig. 246; compare with Fig. 266). **Abdomen** with three narrow transverse white bands, a basal one, a second one behind that, and a third one behind that. Posterior to the third band the abdomen is a shiny black, but anterior it is dusted with golden setae.

Female (based on specimen AS19.2895). Carapace length 3.0; abdomen length 4.1. The specimen was collected and photographed as a small juvenile (Figs 251–254); as an adult its basic appearance is similar (Figs 249, 250). Structure and markings of carapace and legs as in male. **Abdomen** with second transverse band oblique. **Epigyne** (Fig. 240) with medial septum dividing deep broad atria. What serves as the ECP is not obvious; there may be two, folds posterior to the atrium on each side, midway between the epigastric furrow and the posteriormost part of the medial septum. If so, it may be intermediate between *P. decorus*, with a medial ECP (Caleb and Sanap 2017), and *P. planolancis* (Malamel et al. 2019; Nafin et al. 2020), with a pair of distantly separated lateral ECPs (Nafin et al. 2020: fig. 17).

Male-female matching. *P. bakau* and *P. kohi* are similar in general appearance, have overlapping geographical ranges, and have been collected to date with only adult males or adult females at a locality, not both. This leads to a question of which male matches which female. Unless there are additional closely similar species in the same areas, the inferred matching is well supported by the differences in markings, carapace shape, and lengths of embolus/copulatory ducts. The male of *P. bakau* and the female from Tengkorak inferred to match it share the diagnostic traits mentioned above. Doubt might arise because of one difference in their markings: the female has the second transverse abdominal band more oblique, with its two sides meeting at a central peak, while in the holotype the band is straight across. However, the second male, from Brunei, shows a peak (Fig. 242). A juvenile co-collected with the male holotype has the band peaked, and looks very much like the female when immature. The female is not designated as a paratype, however, because of the possibility it is a different but very closely related species, given the geographical distance between it and the holotype and their different habitats.

Natural history. Holotype male collected from mangroves; female from Tengkorak collected by shaking vines and understory trees near waterfall.

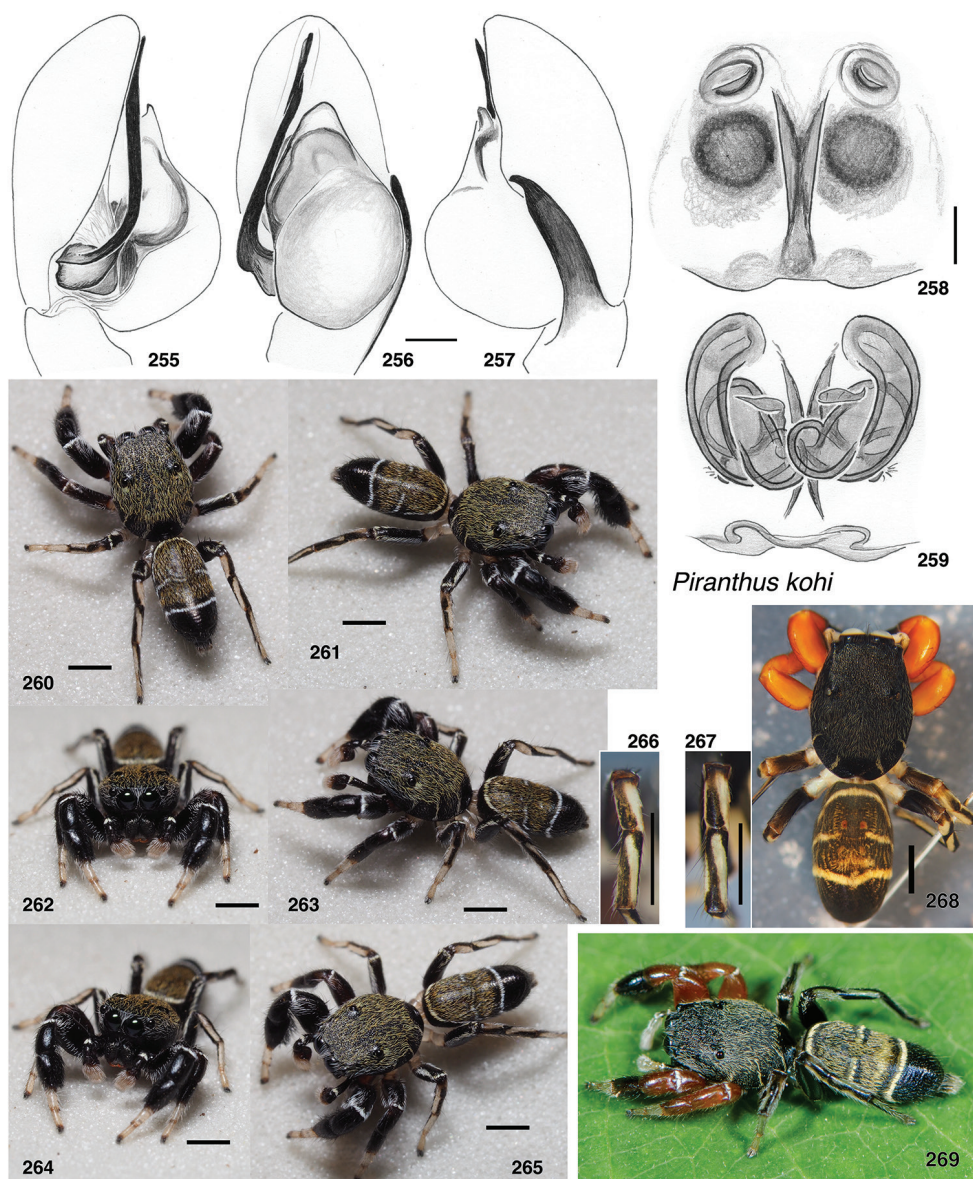
Additional material examined. Two juveniles with same data as holotype. Also, one male (specimen JK.11.04.17.0040), in LKCNHM, from BRUNEI: Tutong, Tasek Merimbun, Zone C2, Palau Luba, Sungai Melunchur, 4.5817°N, 114.6872°E, J. K. H. Koh 17 Apr. 2011. One female (specimen AS19.2895), in UBCZ, from MALAYSIA: JOHOR: Gunung Belemut Forest, Lata Tengkorak, 2.055°N, 103.543°E, 250 m elev. 16 June 2019 Maddison/Morehouse/et al. WPM#19-057.

***Piranthus kohi* Maddison, sp. nov.**

<http://zoobank.org/DBAC788B-2FDE-4D43-98C5-0C623368A800>

Figs 255–269

Type material. **Holotype** male (specimen AS19.1813), in LKCNHM, from SINGAPORE: Sungei Buloh Wetland Reserve, 1.440–1.447°N, 103.730–103.735°E, 10 June 2019 Maddison/Morehouse/et al. WPM#19-045. **Paratype** female (specimen JK 19.07.19.0001), in LKCNHM, from SINGAPORE: Pulau Ubin, Balai Quarry Trail, 1.4178°N, 103.9850°E, leg. P. Ng 19 July 2019.



Figures 255–269. *Piranthus kohi* sp. nov. **255** male left palp, prolateral view (holotype AS19.1813) **256** same, ventral view **257** same, retrolateral view **258** epigyne, ventral (specimen JK.12.04.11.0032) **259** Vulva, dorsal **260–265** holotype **266** male holotype left fourth patella and tibia, dorsal view **267** female left fourth patella and tibia, dorsal view (specimen JK.19.07.19.0001) **268** female JK.19.07.19.0001 **269** Female JK.12.04.11.0032 (photograph © Joseph K. H. Koh). Scale bars: on genitalia 0.1 mm; on bodies and legs 1.0 mm.

Etymology. This elegant species is named in honour of Joseph Koh Kok Hong, arachnologist, conservationist, and diplomat. Koh has worked tirelessly to build peace with nature. Through his collecting and excellent books (Koh 1989; Koh and Leong 2013;

Koh and Bay 2019), he has substantially promoted our knowledge of southeast Asian spiders and stimulated interest in their diversity and beauty. Koh collected the first known specimen of this species, in Brunei, and enabled our field work in Singapore during which the holotype and other specimens were collected. *Other names*: In WPM's lab notebooks the informal code for this species was "SUBSG". This species is shown in Koh and Bay 2019 as the female of "*Bavia*" sp. D Strong-armed flat jumping spider.

Diagnosis. *P. kohi* (Figs 254–269) shares with *P. bakau* (Figs 237–254) the pattern of transverse white bands, but differs from it in having:

- Three distinct vertical lines on each side of the thorax;
- Carapace lateral to the PLE more or less uniformly covered in white to gold setae;
- Second transverse dorsal band of the abdomen well broken at the middle;
- First and second tibiae and femora solid dark, not bicoloured;
- Black dorsal stripe extends the full length of tibia 4 (Figs 266, 267);
- Shorter embolus and copulatory ducts.

Juveniles can be distinguished by the non-genitalic features above.

Description. Male (based on holotype, AS19.1813). Carapace length 2.5; abdomen length 2.5. **Carapace** with rugose surface, black, dusted above with narrow golden scales. Sides and back of thorax bare except for three narrow and distinct vertical lines of pale setae. **Clypeus** black. **Chelicera** vertical and black. **Palp** black except for white cymbium. Embolus arising on prolateral basal corner, proceeding ventrally then curving distally (Figs 255, 256). RTA a long blade. **Legs** robust, especially the first pair. First two pairs black except for tarsus and metatarsus, and white annulae terminally on femur. First patella and tibia with ventral fringe of black setae. Fourth tibia and patella with a pattern of long black and white bands. On the tibia, a black band reaches from the base (on the prolateral side) all the way to the dorsal tip, forming an oblique dorsal band (Fig. 266; compare with Fig. 246). **Abdomen** similar to that of *P. bakau*, with three transverse white bands, anterior to the third of which the abdomen is dusted with golden setae, posterior to it a shiny black. Second transverse white band with a broad gap in both male and female.

Female (based on specimen, 12.04.11.0032). Carapace length 3.4; abdomen length 4.0. Structure and markings as in male, but generally more reddish, especially first and second legs, which are red-orange-brown in the femur and patella (and tibia of the second pair). **Epigyne** (Fig. 258) with central septum, but lacking the large cavernous atria of other *Piranthus* species.

Male-female matching. See comments under *P. bakau*. Male and female *P. kohi* share the diagnostic traits mentioned above. The matching is supported by both males and females occurring in Singapore and in similar mangrove habitats – eight specimens from Sungei Buloh including 4 males; 6 specimens from Palau Ubin including 2 females.

Natural history. Specimens in Singapore were found beating trees and vines in a mangrove area. It appeared that our greatest success in finding them was when shaking woody vines. Their motion when alive has a different sense than other baviines; rather

than the sharply-jumping *Indopadilla*, or the frequently waving *Padillothorax badut* group, or the more sedate *Piranthus planolancis* and *P. api*, *P. kohi* is constantly flicking up and down the first legs, palps, and abdomen, somewhat like ant mimicking salticids. A video of the living holotype is available in Maddison (2020).

Additional material examined. SINGAPORE: Sungei Buloh Wetland Reserve, 1.440–1.447°N, 103.730–103.735°E, 10 June 2019 Maddison/Morehouse/et al. WPM#19-045 (3 additional males raised in captivity, 2 juveniles, UBCZ); Sungei Buloh Wetland Reserve, Coastal Trail, 1.446°N, 103.730°E to 1.445°N, 103.735°E, 19 June 2019 Maddison, Marathe, Ng WPM#19-063 (2 juveniles, UBCZ); Pulau Ubin, Chek Jawa, 1.4122°N, 103.9908°E, 11 June 2019 Maddison, Sung, & Outomuro WPM#19-047 (1 female raised in captivity, 2 juveniles, UBCZ); Lim Chu Kang Mangroves, Tree trunks and limbs, 1.44°N, 103.70°E, 13 May 2005 W. Maddison, I. Agnarsson, J. X. Zhang. WPM#05-020 (2 juveniles, UBCZ). MALAYSIA: SELANGOR: Ulu Gombak Field Station, 3.325°N, 101.753°E, 250 m el., 16–19 May 2005 W. Maddison, D. Li, I. Agnarsson, J. X. Zhang. WPM#05-026 (1 juvenile, specimen MRB109, UBCZ). BRUNEI: Belait, Kuala Balai, Sungai Mendarum Damit Freshwater Swamp Forest, 4.4386°N, 114.3581°E, J. K. H. Koh 11 Apr. 2012 (1 female, specimen JK 12.04.11.0032, in LKCNHM). The specimen from Ulu Gombak, used in the molecular study, matches *P. kohi* well in markings, but it is a juvenile and thus labelled conservatively in the phylogenies as *P. cf. kohi*.

***Piranthus mandai* Maddison, sp. nov.**

<http://zoobank.org/8715C1FA-D05B-4876-9E12-BFA2EC4EB81C>

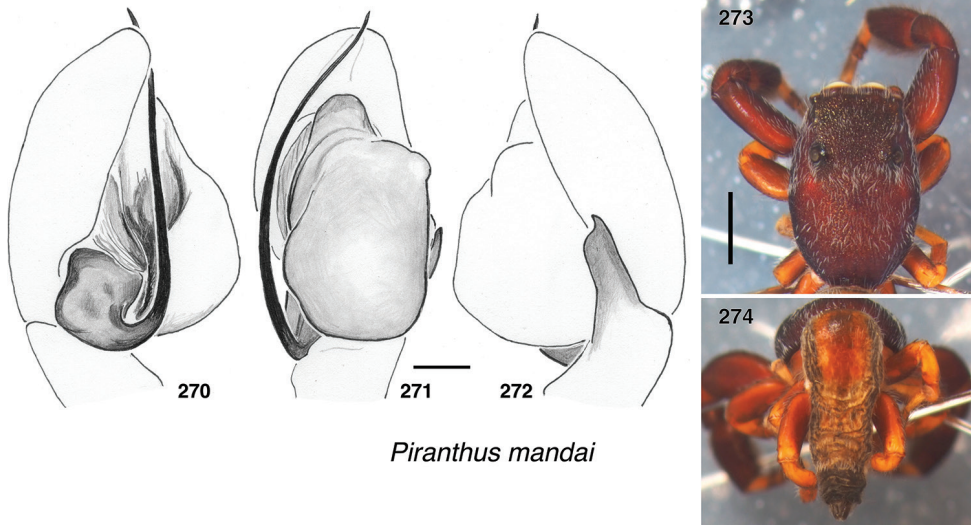
Figs 270–274

Type material. *Holotype* male (specimen JK.91.05.31.0001), in LKCNHM, from SINGAPORE: Mandai Track 15 Trail, 1.4106°N, 103.7783°E, J K H Koh 31 May 1991.

Etymology. Named for the type locality. *Other names:* In lab notebooks the informal code for this species was “SGOMG”.

Diagnosis. In colouration similar to *P. planolancis*, browns and blacks, but with body more compact and robust, as in *P. bakau* and *P. kohi*. Embolus with only a small loop before proceeding distally, and thus *P. mandai* is second in sequence from least to most rotated embolic bases: *P. kohi* (Fig. 255), *P. mandai* (Fig. 270), *P. planolancis* (Nafin et al. 2020), *P. bakau* (Fig. 237).

Description. **Male** (holotype, specimen JK.91.05.31.0001). Carapace length 2.7; abdomen length 2.5. **Carapace** with rugose surface, black and dark brown, with a sparse covering of narrow scales that is more or less uniform: there is no bare patch beside the PLE, and no distinct three vertical thoracic lines, but there is a slight condensation of scales into a single vertical thoracic line, similar to that in *P. bakau*. **Clypeus** narrow and dark. **Chelicerae** vertical, dark, with a few pale scales basally. **Palp** brown. Palp similar to that of *P. planolancis*, but RTA much shorter (Figs 270–272), the shortest known among *Piranthus*. **Legs** light to dark brown, with indistinct markings (Figs 273, 274)



Figures 270–274. *Piranthus mandai* sp. nov., male holotype (specimen JK.91.05.31.0001) **270** left palp, prolateral view **271** same, ventral view **272** same, retrolateral view **273** prosoma **274** abdomen. Scale bars: on palp 0.1 mm; on body 1.0 mm.

similar to those of *P. planolancis*; darkest in the femur, patella, and tibia of the first leg, and the femora of the other legs. **Abdomen** brown above, lacking the transverse bands of *P. bakau* and *P. kohi*, but with the dark end of the abdomen (Fig. 274).

Tribe Vicirini Simon, 1901

Nungia Żabka, 1985

Nungia Żabka, 1985. Type species *Nungia epigynalis* Żabka, 1985.

Note. At least 16 species of elongate dull brown salticids collected in field work in Asia and New Guinea were initially thought to be baviines (example photographs, Figs 275–282), but an analysis of two genes (Fig. 283) in nine of the species show that they form a clade with the similar *Nungia epigynalis*, nested within the Vicirini. Photographs of them were released by Maddison (2015b) under the name *Nungia*. Their distinction from baviines is also morphological. They have unident or fissident chelicerae and a carapace that is dark, matte (not shiny), distinctly flat-topped, and relatively square. The male first legs are fringed below; the embolus is usually short and fixed to the tegulum. The group is unreported but diverse in New Guinea (based partly on collecting by WPM, Maddison and Zhang 2011; *Nungia* there mistakenly reported under “*Bavia* and related genera”), as might be expected for a member of the Astioida. *Capeyorkia* falls within this group (Fig. 282, 283; NPNGE and NPNGF are listed as *Capeyorkia* because of similarity of palps), and likely *Pungalina* as well. Both *Pungalina*

and *Capeyorkia* may merit synonymy with *Nungia*. At least some species of *Muziris* Simon, 1901 belong here as well. Also within the group are two species misplaced in *Bavia*, one in *Diplocanthopoda*, and one in *Cosmophasis*. While we might have delayed their consideration until a future revision of *Nungia*, we address them here as part of organizing the baviines. We therefore make the following new combinations:

Nungia hatamensis (Thorell, 1881), comb. nov., transferred from *Diplocanthopoda* Abraham, 1925. See Fig. 280.

Nungia modesta (Keyserling, 1883), comb. nov., transferred from *Bavia*. Based on Keyserling's (1883) figures, body form and colouration typical of the New Guinea *Nungia*.

Nungia papakula (Strand, 1911), comb. nov., transferred from *Bavia*. Male and female syntypes in SMF examined; appears closely related to *N. hatamensis* and a likely senior synonym of *Muziris wiehlei* Berland, 1938. See Fig. 281.

Nungia xiaolonghaensis (Cao & Li, 2016), comb. nov., transferred from *Cosmophasis* Simon, 1901. See Fig. 279.

Some of these new combinations, and others made above in baviines, correct mistaken placements that may have resulted from convergence in the general form of the male palp. The palps of *Nungia hatamensis*, *Nungia xiaolonghaensis*, *Maripanthus menghaiensis*, *Bavia capistrata*, and *Bavia maurerae* do in fact resemble those of the genera in which they had been placed, respectively, *Diplocanthopoda* (a hasariine), *Cosmophasis* (a chrysilline), *Nannenus* (a nannenine), *Evarcha* (a plexippine), and *Epidelaxia* (a nannenine). Those genera are all in the Saltafresia, a group phylogenetically distinct from the astioids and baviines. The resemblance is largely restricted to the palps, as the remainder of the body is quite distinct in each case. Convergent evolution of the basic form of the palp is widespread in salticids, insofar as the palps are simple and variation in a single dimension (embolus length) can generate palps that look superficially quite similar. The general shape of the palp should be used with caution in determining relationships.

Species incertae sedis

The following species are too poorly known to assign to a known baviine genus, or for that matter to confirm their placement in the Baviini:

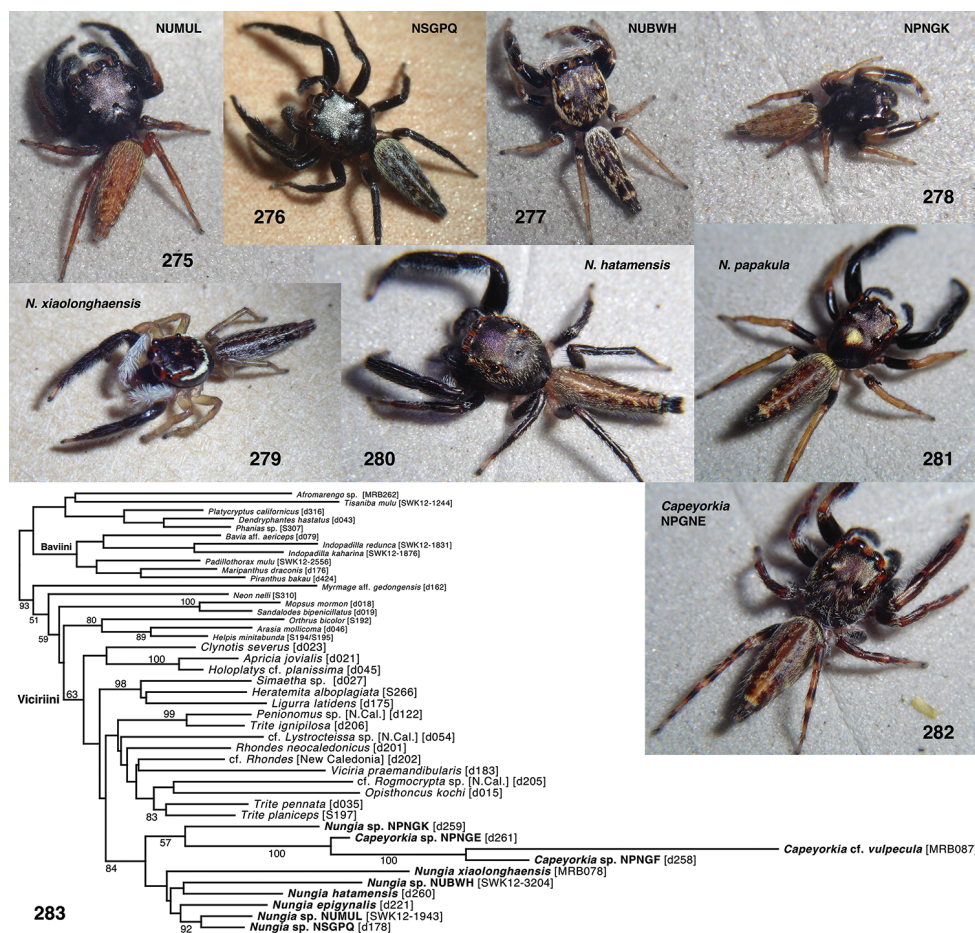
Bavia albolineata Peckham & Peckham, 1885

Bavia decorata (Thorell, 1890)

Bavia hians (Thorell, 1890)

Bavia sinoamerica Lei & Peng, 2011

Of these, *B. sinoamerica* is almost certainly not a baviine by body shape. Based on the form of the palp, and its being unident with a compact body, it may be a hasariine. *B. albolineata* has a palp that is credibly baviine, but its location in Madagascar and diverging chelicerae suggest it is not baviine.



Figures 275–283. *Nungia* and *Caeporykia* species and their phylogenetic placement, using informal species code names; all males except 277, female. **275** *Nungia* sp. “NUMUL”, Sarawak (specimen SWK12-1943) **276** *Nungia* sp. “NSGPQ”, Singapore (specimen d178) **277** *Nungia* sp. “NUBWH”, Sarawak (specimen SWK12-3204) **278** *Nungia* sp. “NPNGK”, Papua New Guinea (specimen d259) **279** *Nungia xiaolonghaensis*, Pahang (specimen MRB078) **280** *Nungia hatamensis*, Papua New Guinea (specimen d260) **281** *Nungia papakula*, Papua New Guinea, 9.436°S, 147.364°E (specimen 2008PNG-3538) **282** *Caeporykia* sp. “NPNGE”, Papua New Guinea (specimen d261) **283** molecular phylogeny placing *Nungia* species and related (in bold) within the vicirine astioids, based on IQ-TREE maximum likelihood analysis (50 replicates, partitioned) of 28S and 16SND1 sequences, with bootstrap percentages from 500 replicates (shown only within the Astioida).

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Supplementary material I

Blended spider and arachnid UCE probe set

Authors: Wayne P. Maddison, Imara Beattie, Kiran Marathe, Paul Y. C. Ng, Nilani Kanesharatnam, Suresh P. Benjamin, Krushnamegh Kunte

Data type: UCE probes

Explanation note: File blending the Starrett et al. (2017) arachnid probeset and the Kulkarni et al. (2019) probeset, used to recover UCEs from contigs. The Methods section of the paper and the README file explain.

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Link: <https://doi.org/10.3897/zookeys.1004.57526.suppl1>

A new species of *Campoletis* Förster (Hymenoptera, Ichneumonidae) with a key to species known from China, Japan and South Korea

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Abstract

A new species of the genus *Campoletis* Förster, 1869, *C. deserticola* Sheng & Zhou, **sp. nov.**, collected from Zhangwu, Liaoning Province and Songshan National Natural Reserve, Yanqing, Beijing, China, is described and illustrated. A taxonomic key to the species of *Campoletis* known in China is provided.

Keywords

Campopleginae, taxonomy, parasitoid wasp

Introduction

Campoletis Förster, 1869, a relatively large genus of the subfamily Campopleginae (Hymenoptera, Ichneumonidae), comprises 112 described species (Yu et al. 2016; Riedel 2017; Vas 2019a, b), of which 23 are from the Eastern Palearctic region (Kokujev 1915; Kusigemati 1972; Horstmann 1979; Yu et al. 2016; Vas 2019a) (14 of them are found across the whole Palearctic and three of them are found in both the Eastern Palearctic and the Oriental), seven are from the Oriental region (Gupta 1974;

Kusigemati 1987, 1990; Yu et al. 2016), 41 from the Western Palaearctic region (Yu et al. 2016; Riedel 2017; Vas 2019b), seven from the Neotropical region, 50 from the Nearctic region (Yu et al. 2016), and three species are from the Australasian region (Cameron 1903, 1911; Crosby 1994; Yu et al. 2016).

The Western Palaearctic species of *Campoletis* were revised by Riedel (2017); subsequently, three new species of *Campoletis* have been described by Vas (2019a, b) from Mongolia and South-Eastern Europe. Prior to this publication seven species of *Campoletis* had been known from China (Kokujev 1915; Uchida 1957; Kusigemati 1990; He et al. 1996; Sheng and Sun 2014).

The Project “Research Station of Liaohe-River Plain Forest Ecosystem, Chinese Forest Ecosystem Research Network”, set in the desert area in Liaoning Province, has being undertaken by Y-WW’s research group since 2014. One of the purposes of the investigation is recording biodiversity. Large numbers of ichneumonids were collected and in the present research, a new species of *Campoletis* is described which was collected in the desert. With paratypes collected from Yanqing, Beijing, it is described and illustrated herein, and compared with its congeners.

Materials and methods

Institutional abbreviations

- GSFGPM** General Station of Forest and Grassland Pest Management, National Forestry and Grassland Administration, China;
HUM Hokkaido University Museum, Sapporo, Japan;
RSLPFE Research Station of Liaohe-River Plain Forest Ecosystem, Chinese Forest Ecosystem Research Network, Changtu, Liaoning, China.

Specimen collection

Specimens were collected with interception traps (IT) as described by Li et al. (2012) in RSLPFE (Fig. 1) and in the Songshan National Natural Reserve, Yanqing, Beijing.

The forest in RSLPFE are mainly comprised of *Caragana korshinskii* Kom., *Ulmus pumila* L., *Salix matsudana* Koidz., *Crataegus pinnatifida* var. *major* N. E. Brown, *Populus* sp., *Lespedeza bicolor* Turcz. The forest floor is covered by *Allium macrostemon* Bunge, *Echinochloa crusgali* (L.) Beauv. and *Medicago sativa* L.

The forest in Songshan National Natural Reserve, Yanqing, Beijing, hold *Ulmus pumila* L., *Salix* spp., *Lespedeza bicolor* Turcz., *Vitex negundo* var. *heterophylla* (Franch.) Rehd., *Platycladus orientalis* (L.) Franco, *Pinus tabulaeformis* Carr.

The holotypes of *Campoletis chlorideae* Uchida, 1957 and *Tranosema rugosipropodeum* Uchida, 1942 deposited in the HUM were examined.

Morphological terminology is mostly based on Broad et al. (2018). Images were taken using a Leica M205A stereo microscope with LAS Montage MultiFocus. Type specimens are deposited in the Insect Museum, GSFGPM.



Figure 1. Habitat of *Campoletis deserticola* Sheng & Zhou, sp. nov., the holotype locality in Zhangwu County, Liaoning Province.

Taxonomy

Campoletis Förster, 1869

Campoletis Förster, 1869:157. Type-species: *Mesoleptus tibiator* Cresson.

Diagnosis (from Townes 1970; Gupta 1974; Riedel 2017). Inner margin of eye slightly indented opposite antennal socket. Apical margin of clypeus usually with a median tooth. Lower margin of mandible with narrow lamella, lower tooth of mandible slightly narrower than upper tooth, same length or slightly shorter. Malar space 0.5–1.0× as long as basal width of mandible. Areolet receiving 2m-cu usually basad of middle. Nervellus intercepted; discoidella almost unpigmented, reaching nervellus. Lateral suture between tergite 1 and sternite 1 distinctly below mid-height. Glymma present and deep. Ovipositor 1.6 to 3.5 as long as apical depth of metasoma.

Key to the *Campoletis* known in China, Japan and South Korea

- 1 Fore wing vein 2m-cu vertical or almost vertical, lower-posterior angle of second discal cell right-angled or almost right-angled **2**
- Fore wing vein 2m-cu distinctly inclivous, lower-posterior angle of second discal distinctly acute **3**
- 2 Antenna stout, second flagellomere approximately as long as wide. Propodeum indistinctly areolated, costula absent. Tegula black *C. longicalcar* (Kokujev)
- Antenna slender, second flagellomere longer than width. Propodeum distinctly areolated, costula present. Tegula yellowish white *C. tibetana* (Kokujev)

- 3 Areolet sessile, receiving vein 2m-cu basad of middle. Head, mesosoma, all tergites and all coxae entirely black. Tegula light yellow... *C. rugosipropodeum* (Uchida)
- Areolet with distinct petiole, receiving vein 2m-cu at or basad of middle. Head, mesosoma, tergites and coxae not entirely black. Tegula black, or yellow to brown 4
- 4 Costula absent. Tergite 2 as long as tergite 3. Area superomedia combined with area petiolaris. Tegula yellow *C. imperfecta* (Kokujev)
- Costula present. Tergite 2 longer than tergite 3. Area superomedia separated from area petiolaris by carina, at least junction between them discernible. Tegula black, or yellow to brown 5
- 5 Malar space 1.2× as long as basal width of mandible. Areolet receiving 2m-cu basad of middle. Area basalis reversed triangular..... *C. hongkongensis* Kusigemati
- Malar space as long as or shorter than basal width of mandible. Areolet receiving 2m-cu at or almost at middle, or area basalis trapezoidal (Fig. 11)..... 6
- 6 Tergite 2 at most as long as its posterior width 7
- Tergite 2 at least 1.25× as long as its posterior width 9
- 7 Occipital carina complete. Frons without median longitudinal carina; Notaulus almost entirely absent. Ovipositor sheath 1.1–1.2× as long as second tergite. All coxae black. Tegula brown..... *C. deserticola* Sheng & Zhou, sp. nov.
- Lower portion of occipital carina incomplete. Frons with median longitudinal carina; Notaulus present. Ovipositor sheath 0.8× as long as second tergite. Fore and mid coxae yellow brown, at least not entirely black. Tegula whitish yellow . 8
- 8 Lower tooth of mandible shorter than upper tooth. Areolet receiving 2m-cu basad of middle. Area superomedia combined with area petiolaris, without carina between them. subbasal and apical portions of hind tibia blackish, median portion whitish..... *C. takizawai* Kusigemati
- Lower tooth of mandible as long as upper tooth. Areolet receiving 2m-cu at middle. Area superomedia separated from area petiolaris by distinct carina. Hind tibia entirely yellowish brown..... *C. gastrolinae* Kusigemati
- 9 Ovipositor sheath 0.64× as long as hind tibia. Hind femur red. Posterior portion of tergite 3 and subsequent tergites reddish brown *C. chlorideae* Uchida
- Ovipositor sheath at most 0.5× as long as hind tibia. Basal and apical portions of hind femur black. Tergites black, at most sides of tergites 3–7 more or less reddish..... *C. annulata* (Gravenhorst)

***Campoletis deserticola* Sheng & Zhou, sp. nov.**

<http://zoobank.org/018A514B-3CBB-447B-9A91-E130F1E817AE>

Figures 2–15

Material examined. Holotype: CHINA • ♀; Liaoning, Zhangwu, Aershan; 273 m; 18.VI.2020; Ya-Wei Wei leg. **Paratypes:** CHINA • 2♀♀23♂♂; Beijing, Yanqing, Songshan National Natural Reserve; 672 m; 17–26.IX.2011; IT by Shi-Xiang Zong leg. • 1♀1♂; Liaoning, Zhangwu, Aershan; 273 m; 18.VI.2020; Ya-Wei Wei leg.

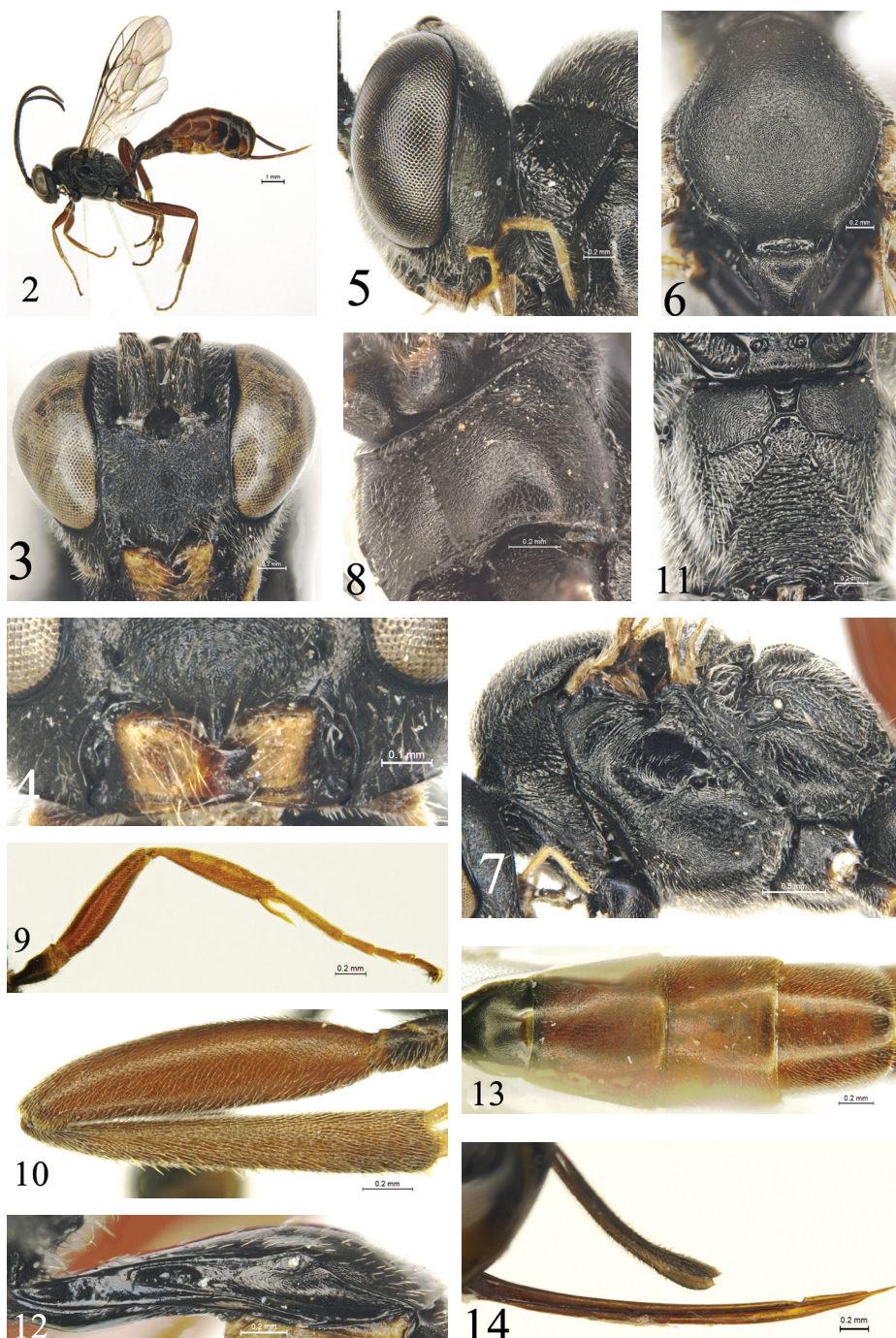
Diagnosis. *Campoletis deserticola* Sheng & Zhou, sp. nov. can be distinguished from all other species of *Campoletis* by combination of the following:

Body granulate to finely granulate, without evident punctures. Face (Fig. 3) and main portion of clypeus rough, with indistinct, irregular fine punctures. Malar space $0.8\text{--}0.9\times$ as long as basal width of mandible. Mesoscutum and scutellum (Fig. 6) with even leathery culpture. Anterolateral portion of postscutellum with deep circular depressions (Fig. 11). Propodeum (Fig. 11) with dense gray setae; area externa roughly shagreened; area petiolaris with dense transverse wrinkles. Head except mandible, mesosoma and all coxae entirely black. All femora brownish red. Tergites 2–4 almost entirely reddish brown.

Description. Female. Body length 6.4–7.2 mm. Fore wing length 4.7–5.0 mm. Ovipositor sheath length 0.9–1.1 mm.

Head. Inner margins of eyes slightly convergent ventrally. Face (Fig. 3) $1.4\times$ as wide as long from dorsal margin to clypeal fovea, evenly slightly convex, rough, with indistinct irregular fine punctures; dorsal margin with a V-shaped concavity medially. Clypeal suture entirely absent. Basal portion of clypeus (Figs 3, 4) with texture as that of face; apical margin smooth, shiny, with strong median tooth. Mandible (Fig. 4) distinctly narrowed to ends of teeth, with sparse brownish yellow setae; upper tooth as long as lower tooth. Malar area, gena (Fig. 5) and vertex shagreened. Malar space $0.8\text{--}0.9\times$ as long as basal width of mandible. Gena distinctly convergent posteriorly, in dorsal view $0.5\times$ as long as width of eye. Postocellar line $1.2\times$ as long as ocular-ocellar line. Frons with texture as that of face. Antenna with 28–30 flagellomeres. Ratios of lengths from first to fifth flagellomeres 1.5:1.2:1.1:1.1:1.0. Occipital carina complete, reaching hypostomal carina above base of mandible.

Mesosoma. Lateral concavity of pronotum (Figs 5, 7) wide, shallow, lower half with distinct oblique wrinkles; dorsoposterior portion shagreened. Epomia present. Mesoscutum (Fig. 6) with leathery culpture, evenly convex; notaulus absent. Scutoscuteellar groove almost smooth, shiny. Scutellum slightly convex, with fine leathery culpture. Postscutellum shagreened, anterolateral portion with deep circular depressions (Fig. 11). Mesopleuron (Fig. 7) with leathery culpture; in front of speculum slightly concave with longitudinal wrinkles; upper anterior portion with oblique longitudinal wrinkles. Upper end of epicnemial carina reaching anterior margin of mesopleuron, at 0.5 height of posterior margin of pronotum; ventral part (Fig. 8) complete, strongly elevated. Metapleuron slightly convex, with texture as lower portion of mesopleuron; lower-posterior portion with short oblique wrinkles. Ratio of length of hind tarsomeres from first to fifth approximately 5.6:2.4:1.6:1.0:1.3. Claw with two or three teeth. Wings slightly brownish, hyaline. Fore wing with vein 1cu-a distal to M&RS by approximately $0.2\times$ length of 1cu-a; 1cu-a distinctly inclivous. Areolet quadrilateral, with distinct petiole, receiving vein 2m-cu at approximately 0.4 distance from vein 2rs-m to 3rs-m; 2rs-m almost as long as 3rs-m. Postnervulus strongly inclivous, intercepted at lower 0.3. Hind wing vein 1-cu $1.5\times$ as long as cu-a. Propodeum (Fig. 11) with dense gray setae; area basalis reversed trapezoid, shiny, almost smooth; area externa roughly shagreened; area superomedia rough with indistinct fine punctures; area denipara with indistinct oblique wrinkles; area petiolaris with dense, distinct transverse



Figures 2–14. *Campoletis deserticola* Sheng & Zhou, sp. nov. Holotype, female **2** habitus, lateral view **3** head, anterior view **4** clypeus and mandibles **5** head and pronotum, lateral view **6** mesoscutum and scutellum **7** mesosoma, lateral view **8** mesosoma, ventrolateral view **9** fore leg, lateral view **10** hind femur and tibia, lateral view **11** propodeum **12** first tergite, lateral view **13** postpetiole and tergites 2–4, dorsal view **14** ovipositor and ovipositor sheath, lateral view.

wrinkles. Area superomedia and area petiolaris confluent, junction between them discernible. Propodeal spiracle small, almost circular, connecting pleural carina by ridge.

Metasoma. Metasomal tergites weakly shagreened. First tergite (Fig. 12) $2.2\text{--}2.3\times$ as long as its apical width, anterior portion and posterior margin smooth, shiny; spiracle small, circular, located at apical 0.33 . Second tergite (Fig. 13) trapezoidal, $1.4\times$ as long as its anterior width, $0.9\times$ as long as its posterior width; longer than third tergite. Third tergite approximately $0.7\times$ as long as posterior width, sides parallel. Ovipositor sheath $0.55\text{--}0.65\times$ as long as hind tibia, $0.85\text{--}0.95\times$ as long as first tergite, $1.1\text{--}1.2\times$ as long as second tergite. Ovipositor (Fig. 14) slightly curved upwards.

Coloration (Fig. 2). Black, except for following: mandible except teeth yellow brown. Apical three segments of maxillary palpi, tegulae and lateral margins of tergite 7 brown. Femora, sides of fore tibia (Fig. 9), hind tibia (Fig. 10) except base, main portion of tergite 2, tergites 3 and 4 and anterior portion of tergite 5 brownish red. Inner side of fore tibia and fore tarsus yellowish brown. Mid tarsus brown. Base of hind tibia and tarsus brownish black. Pterostigma and veins brown.

Male (Fig. 15). Body length $6.0\text{--}7.2$ mm. Fore wing length $4.3\text{--}5.0$ mm. Antenna with $31\text{--}34$ flagellomeres. Similar to female, except following: fifth tergite almost entirely brownish red; posterior median portion of sixth tergite brown.

Distribution. CHINA: Beijing, Liaoning.

Etymology. The specific name is derived from the habitat of the holotype locality.

Remarks. The new species is similar to *Campoletis gastrolinae* Kusigemati, 1972 and *C. cognata* (Tschek, 1871) in having the head and mesosoma black; tergites 2–3 red to reddish brown; hind femur completely or predominantly red; apical margin of



Figure 15. *Campoletis deserticola* Sheng & Zhou, sp. nov. Paratype, male. Habitus, lateral view.

clypeus with strong median tooth; second tergite approximately as long as (*C. cognata* at most 1.2×) posterior width. It can be distinguished from *C. gastrolinae* by the following combination of characters: frons without median longitudinal carina; notaulus absent; areolet receiving vein 2m-cu distinctly basal of its middle; Area superomedia and area petiolaris confluent; ovipositor sheath 1.1–1.2× as long as second tergite; coxae entirely black; tergites 6–8 mainly black. *C. gastrolinae* has the frons with median longitudinal carina; notaulus extending to the middle of the mesoscutum; the areolet receiving vein 2m-cu is placed at its middle; Area superomedia and area petiolaris separated by distinct carina; the ovipositor sheath is 0.8× as long as the second tergite; fore and mid coxae yellow; tergites 6–8 partly yellowish brown.

The new species can be distinguished from *C. cognata* by the following couplet inserted into Riedel's (2017) Identification key:

- 34 Prepectal carina angled in the area of the sternaulus and divided into a transverse and pleural part, both similar; genal carina obliterated ventrally; ovipositor sheath c. 0.9–1.2× longer than the first tergite; fore tibia leaner, more than 6× longer than wide (as fig. 46)..... *C. pleuralis* ♀♂
- Prepectal carina continuous without transverse branch or angle in the pleural part; genal carina complete ventrally and arched outwards, meeting the hypostomal carina just before the mandible base; ovipositor sheath c. 0.8–0.95× as long as the first tergite; fore tibia rather swollen, less than 6× longer than wide (fig. 48)..... **34'**
- 34' Malar space 0.8–0.9× as long as basal width of mandible. Hind tibial spur distinctly shorter than half length of hind first tarsomere. Second tergite 0.9× as long as its apical width. Basal flagellomeres black. Hind tibial spun yellow. All coxae of male black..... *C. deserticola* Sheng & Zhou, sp. nov. ♀♂
- Malar space 0.6–0.7× as long as basal width of mandible. Hind tibial spur at least 0.5× as long as hind first tarsomere. Second tergite 1.1–1.2× as long as its apical width. Basal flagellomeres yellowish. Hind tibial spun reddish. fore and middle coxae of male yellow..... *C. cognata* (Tschek) ♀♂

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The genus *Nipponodrasterius* Kishii (Coleoptera, Elateridae, Agrypninae), a junior synonym of the genus *Gamepenthès* Fleutiaux (Coleoptera, Elateridae, Elaterinae), with review of the Japanese *Gamepenthès* species

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Abstract

The genus *Nipponodrasterius* Kishii, 1966 was established as a member of the subfamily Conoderinae Fleutiaux, 1919 (now tribe Oophorini Gistel, 1848; subfamily Agrypninae Candèze, 1857) based on *N. alpicola*. The genus was suggested to be unlikely to belong to Agrypninae because it lacks diagnostic features of the Agrypninae. However, there are no taxonomic treatments for the genus or species. Here, we review the status of the genus and species by examining the holotype of *N. alpicola*. Consequently, the genus was found to be a junior synonym of the genus *Gamepenthès* Fleutiaux, 1928 and *N. alpicola* was found to be a junior synonym of *G. pictipennis* (Lewis, 1894). We review all species of *Gamepenthès* in Japan and provide a key to species.

Keywords

Japan, Megapenthini, new synonym, Oophorini, Palearctic region, taxonomic review

Introduction

The monotypic elaterid genus *Nipponodrasterius* Kishii, 1966 was established as a member of the subfamily Conoderinae Fleutiaux, 1919 (currently tribe Oophorini Gistel, 1848; subfamily Agrypninae Candèze, 1857) based on *Nipponodrasterius alpicola* Kishii, 1966. This species is known only from the holotype collected on a mountain (altitude 2800 meters) in central Honshu, Japan. Its sex was not determined in the original description. The original description separates the genus from known members of tribe Oophorini using the following characteristics: rather flat body, antennomeres II and III small, antennomeres IV–X clearly serrate, elytral surface clearly granulated, and tarsomere IV shortly bilobed. Kishii (1987) redescribed this genus, modifying the original description slightly. He changed the description “tarsomere IV shortly bilobed” in Kishii (1966) to “tarsomere IV slightly enlarged apically”. Moreover, he added an important character state to the generic description, claws without basal setae. Ôhira (1994) focused on the status of the claws and suggested that this genus is unlikely to belong to Agrypninae, because the presence of basal setae on the claws is a diagnostic feature of members of Agrypninae, absent only in genus *Danosoma* Thomson, 1859 (Hayek 1973). Ôhira (1994) did not examine specimens of the genus directly and did not revise the status of the genus.

We observed that *N. alpicola* is similar to species of the genus *Gamepenthès* Fleutiaux, 1928 in the tribe Megapenthini Gurjeva, 1973, subfamily Elaterinae Leach, 1815 based on these diagnostic features and a drawing of the dorsal habitus in the original description. In considering the systematic position of *N. alpicola*, the direction of the mouth-parts and the structure of the head capsule, procoxal cavity, prosternal process, mesocoxal cavity and mesosternum are also important characters (Ôhira 1970a; Stibick 1979; Schimmel 2003), however, these features were not described in Kishii (1966, 1987). The holotype of the type species required re-examination.

Five *Gamepenthès* species are distributed in Japan: *G. ornatus* (Lewis, 1894); *G. pictipennis* (Lewis, 1894); *G. similis* (Lewis, 1894); *G. versipellis* (Lewis, 1894); *G. yoshidai* Ôhira, 1995. Ôhira (1995a) reviewed the four Japanese species, except for *G. yoshidai*, and showed that they are clearly separated from each other by their aedeagi. Ôhira (1995a) provided a key to distinguish them, based mainly on body color, although members of the genus often show color variation. Subsequently, Ôhira (1995b) described a new species as *G. yoshidai* without showing its aedeagus. Hence, we examine the holotype of *N. alpicola* and review the Japanese *Gamepenthès* species including *G. yoshidai* in order to resolve the problem of *Nipponodrasterius*. Additionally, we provide a new key to these species based on external morphology.

Material and methods

We examined the holotype of *N. alpicola* and non-type specimens of the five Japanese *Gamepenthès* species, as well as the only paratype of *G. yoshidai*. The type specimens are in the collection of the Osaka Museum of Natural History (OMNH; Osaka, Japan).

The non-type specimens are in the personal collection of the authors (Osaka, Japan) and will be donated to the OMNH in the future. Unique identifier numbers of the non-type specimens are: GO001–GO014; GP001–GP012; GS001–GS010; GV001–GV017; GY001, GY002. We found a slide of the male genitalia of the holotype of *N. alpicola* in OMNH (Fig. 5L), although its sex and genitalia were not mentioned in the original description. On the slide, the aedeagus of the holotype, missing the phallobase, had been mounted in balsam and distorted due to pressure exerted by the cover slip (Fig. 5J).

The methods used for observing and dissecting specimens, taking photographs, creating line drawings, and depositing the dissected parts follow Arimoto and Suzuki (2020).

The classification of the family Elateridae follows Kundera et al. (2019), Bouchard et al. (2011), and Cate (2007). The morphological nomenclature system follows Costa et al. (2010) and Douglas (2011). The diagnosis of *Gamepenth**es* was based on information from Ôhira (1970a, 1995a), Schimmel (2003), and evidence found during this study. The non-type specimens were identified using descriptions and figures in Lewis (1894) and Ôhira (1995a, b).

Measurements and indices

Measurements and indices were made following Arimoto and Suzuki (2020). Measurements are shown in millimeters. The following abbreviations are used:

BL	Body length from head to elytral apices
BW	Maximum body width
MAE	Maximum distance across the eyes
MBE	Minimum distance between the eyes
OI	Ocular index: $MAE/MBE \times 100$
PL	Maximum pronotum length including hind angles
PML	Length of the midline of pronotum
PAW	Minimum pronotum width between anterior angles
PW	Maximum pronotum width including hind angles
PI	Pronotum index: $PL/PW \times 100$
PWI	Pronotum width index: $PAW/PW \times 100$
EL	Maximum elytra length
EW	Maximum elytra width
EI	Elytra index: $EL/EW \times 100$
BI	Body index: $EL/PL \times 100$

Taxonomy

Genus *Gamepenth**es* Fleutiaux, 1928

*Gamepenth**es* Fleutiaux, 1928: 158 (original description; type species: *Megapenth**es octomaculatus* Schwarz, 1898; by original designation).

Nipponodrasterius Kishii, 1966: 9 (original description; type species: *Nipponodrasterius alpicola* Kishii, 1966; by original designation); Kishii 1987: 62 (redescription).
syn. nov.

Diagnosis. Head capsule oval in lateral view. Supra-antennal carina complete, rounded, depressed medially. Frontoclypeal region narrowed medially. Mouth-parts inferior. Antennae serrate from antennomere IV, without median longitudinal carina; antennomere IV longer than II–III combined in many, shorter than II–III combined in a few. Pronotum with median basal furrow, without sublateral incision near hind angles; hind angles unicarinate. Pronotosternal sutures not grooved or very shallowly grooved in front. Posterior edge of hypomer on straight mesally and then broadly rounded. Procoxal cavity partly closed behind by mesal projection of hypomer on. Prosternal process concave between procoxae, with subapical tooth in lateral view. Side of scutellum parallel on anterior half. Mesocoxal cavity open to mesepimer on and mesepisternum. Mesosternum separated by suture from metasternum. Outer edge of metacoxal plates wide in most, but narrowed in a few. Elytral surface with rasp-like punctures; elytral apical edge serrate and with small spines, serration very slight in some and then almost rounded. Tarsi simple; claws simple, without basal setae.

Ôhira (1970a, 1995a) stated that the apical elytral edge is more or less truncate; however, this is based on a misunderstanding.

Distribution. Oriental region (Bhutan, China, India, Indonesia, Laos, Malaysia, Myanmar, Nepal, Philippines, Taiwan, Thailand, Vietnam): 30 species (Schimmel 2003, 2004, 2006; Schimmel and Tarnawski 2009). Palearctic region (Japan, Russia): five species (Kishii 1999; Prosvirov 2013).

Ecology. Adults of the genus are often observed visiting flowers during the daytime. In Japan, *Gamepenth*es has been recorded visiting the flowers of *Sambucus* sp. and *Viburnum* sp. (family Adoxaceae), *Angelica* sp. (Apiaceae), *Aralia cordata* Thunb. (Araliaceae), *Clethra barbinervis* Siebold et Zucc. (Clethraceae), *Neoshirakia japonica* (Siebold et Zucc.) Esser (Euphorbiaceae), *Castanea crenata* Siebold et Zucc. (Fagaceae), *Hydrangea paniculata* Siebold and *H. serrata* (Thunb.) Ser. var. *acuminata* (Siebold et Zucc.) Nakai (Hydrangeaceae), and *Cimicifuga* sp. (Ranunculaceae) (Ôhira, 1995a). This study adds flowers of *Tilia japonica* (Miq.) Simonk. (Malvaceae) to the records.

While most adult *Gamepenth*es individuals are not attracted to lights at night, *G. similis* has been collected by light traps (Ootsuka et al., 1981). We examined a few specimens of *G. ornatus* and *G. pictipennis* collected using simple light traps made with weak fluorescent lights.

Included species from Japan. Five species: *G. ornatus* (Lewis, 1894); *G. pictipennis* (Lewis, 1894); *G. similis* (Lewis, 1894); *G. versipellis* (Lewis, 1894); *G. yoshidai* Ôhira, 1995.

Key to species of the genus *Gamepenth*es from Japan

- 1 Body size large (BL: over 5.1 mm) (Fig. 1A, B, D, E); antennomere II shorter than wide in male (Fig. 3A, C), almost as long as wide or slightly longer than

- wide in female (Fig. 3B, D); antennomere IV longer than II–III combined (Fig. 3A–D) **2**
- Body size small (BL: under 5.0 mm) (Fig. 1C); antennomere II longer than wide (Fig. 3E, F); antennomere IV shorter than II–III combined (Fig. 3E, F) ***G. similis* (Lewis, 1894)**
- 2** Antennomere IV robust (1.36–1.72 times longer than wide in male, 1.66–1.79 times longer than wide in female) (Fig. 3A, B); lateral half of metacoxal plates not narrowed laterad, with sides wide (Fig. 3G); apical edge of elytra serrate (Fig. 3I) **3**
- Antennomere IV elongate (1.74–2.06 times longer than wide in male, 1.96–2.17 times longer than wide in female) (Fig. 3C, D); lateral half of metacoxal plates narrowed laterad, with sides narrow (Fig. 3H); apical edge of elytra rounded, without spines (Fig. 3J) **4**
- 3** Body size smaller (BL: under 6.5 mm in male, under 7.1 mm in female) (Fig. 1A); pronotum moderately widened posterad (PWI: 150–156 in male, 161–174 in female) (Fig. 4A, B) ***G. ornatus* (Lewis, 1894)**
- Body size larger (BL: over 6.5 mm in male, over 7.0 mm in female) (Fig. 1D); pronotum strongly widened posterad (PWI: 172–184 in male, 176–191 in female) (Fig. 4C, D) ***G. versipellis* (Lewis, 1894)**
- 4** Body robust (EI: 222–244, BI: 209–247) (Fig. 1B); prosternal process weakly inclined dorsad (20–25°) (Fig. 4E) ***G. pictipennis* (Lewis, 1894)**
- Body slender (EI: 259–265, BI: 254–282) (Fig. 1E); prosternal process strongly inclined dorsad (43–50°) (Fig. 4F) ***G. yoshidai* Ôhira, 1995**

***Gamepenthesis ornatus* (Lewis, 1894)**

Figures 1A, 3A, B, 4A, B, 7A

Megapenthesis ornatus Lewis, 1894: 47 (original description; type locality: Yuyama, Kumamoto Prefecture, Kyushu, Japan).

Gamepenthesis ornatus (Lewis, 1894); Kishii 1959: 58 (changed generic status).

Megapenthesis ornatus aberrant form *basalis* Nakane, 1958: 87 (original description; type locality: Mt. Osore-zan, Aomori Prefecture, Honshu, Japan).

Material examined. 2 females, Japan, Honshu, Nara Prefecture, Yoshino District, Kamikitayama Village, Amagase, 11 VII 2004, Hisayuki Arimoto leg. [females: GO001, GO002]; 1 male, Japan, Honshu, Nara Prefecture, Yoshino District, Totsukawa Village, Asahi, Mt. Syakaga-take, 1450 m, 4 VIII 2019, Hisayuki Arimoto leg., from flowers of *Tilia japonica* [male: GO003]; 3 males, 1 female, Japan, Honshu, Wakayama Prefecture, Tanabe City, Mt. Gomadan-zan, 18 VII 2019, Hisayuki Arimoto leg. [males: GO004–GO006; female: GO007]; 2 females, Japan, Honshu, Nara Prefecture, Tenkawa Village, near Gyôjagaeshi Tunnel, 900 m, 16 VII 2017, Hisayuki Arimoto leg. [GO008, GO009]; 1 male, Japan, Honshu, Wakayama Prefecture, Tanabe City, Mt. Jyôgamori-yama, 18 VII 2019, Hisayuki Arimoto leg. [GO010]; 1 female,

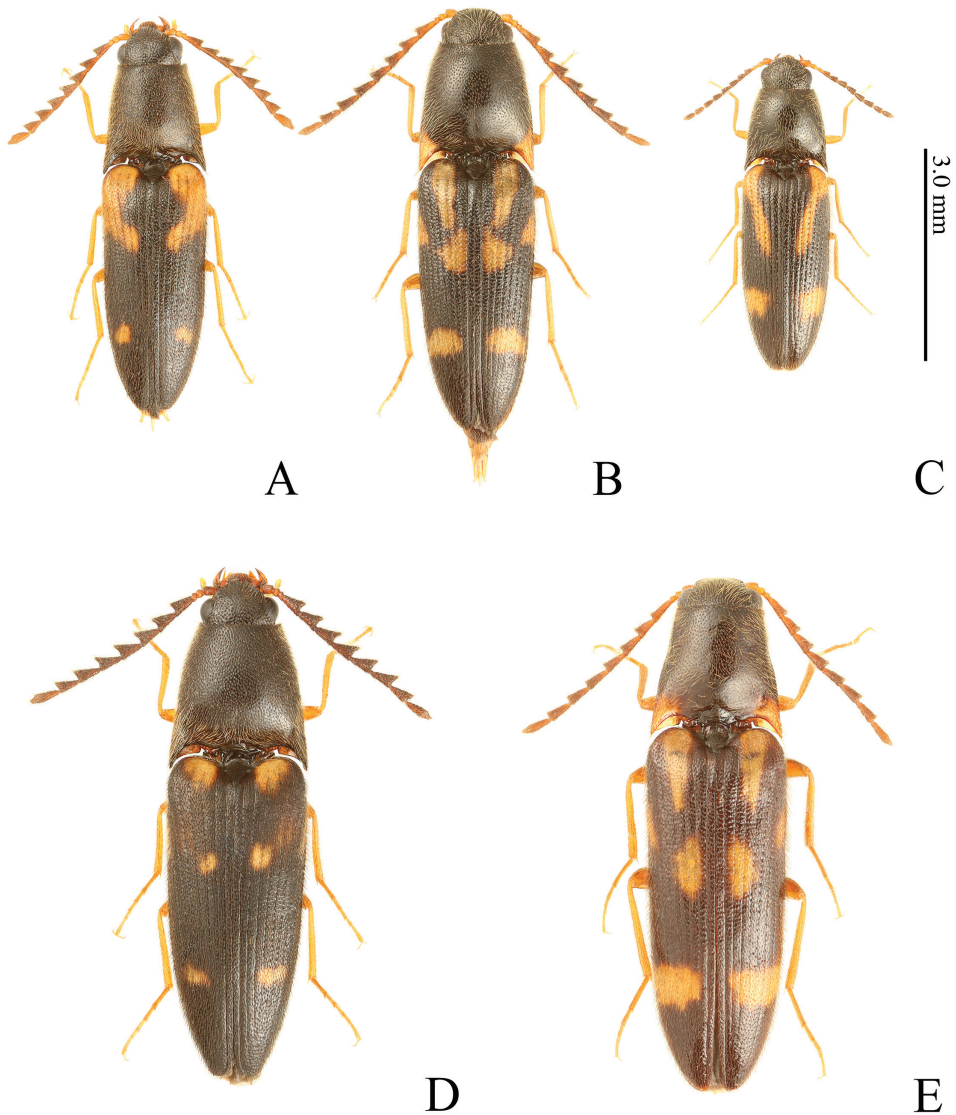


Figure 1. *Gamepenthos* spp., male, habitus, dorsal view **A** *G. ornatus* [GO003] **B** *G. pictipennis* [GP010] **C** *G. similis* [GS003] **D** *G. versipellis* [GV006] **E** *G. yoshidai* [GY001].

Japan, Honshu, Okayama Prefecture, Tomada District, Kagamino Town, Neji, 8–15 VII 2016, Akihiko Watanabe leg., by light FIT [GO011]; 1 male, Japan, Kyushu, Kumamoto Prefecture, Uki City, Mt. Shiraiwa-yama, 16–17 VII 2016, Ryô Noda leg. [GO012]; 2 females, Japan, Kyushu, Miyazaki Prefecture, Nishiusuki District, Gokase Town, Mt. Shiraiwa-yama, 1347 m, 32°34'13.7"N, 131°06'51.6"E, 30 VII 2011, Kôichi Arimoto leg. [GO013, GO014].

Diagnosis. Body robust (EI: 238–254, BI: 220–236). Prothorax black in male, brown in female. Each elytron with pale orange U-shaped marking basally. Antenna-

mere II shorter than wide in male, almost as long as wide in female; III shorter than wide in male, longer than wide in female; IV robust (1.36–1.53 times longer than wide in male, 1.69–1.79 times longer than wide in female), longer than II–III combined (1.53–1.99 times as long as II–III combined in male, 1.02–1.10 times as long as in female). Prosternal process weakly inclined dorsad (24–38°). Metacoxal plates not narrowed outwards on lateral half; outer edge wide. Apical edge of elytra serrate. Apex of parameres beyond pre-apical expansions equilateral triangular (apex length 0.8–0.9 times width of parameres at expansion).

Measurements. Male (6 spec.). BL: 5.29–6.18; BW: 1.41–1.72; MAE: 0.893–1.07; MBE: 0.599–0.719; OI: 148–154; PL: 1.47–1.82; PML: 1.24–1.51; PAW: 0.925–1.08; PW: 1.41–1.70; PI: 105–107; PWI: 150–156; EL: 3.47–4.12; EW: 1.41–1.72; EI: 238–246; BI: 226–236. Female (8 spec.). BL: 5.86–7.03; BW: 1.57–1.93; MAE: 0.929–1.12; MBE: 0.620–0.764; OI: 141–150; PL: 1.71–2.12; PML: 1.42–1.81; PAW: 0.956–1.14; PW: 1.57–1.93; PI: 106–111; PWI: 161–174; EL: 3.90–4.67; EW: 1.57–1.93; EI: 242–254; BI: 220–230.

Distribution. Japan: Honshu, Shikoku, Kyushu.

Comparative notes. *Gamepenth ornatus* and *G. versipellis* (Lewis, 1894) are often found sympatrically and are remarkably similar. They are distinguished by apical expansion of parameres beyond apical-lateral hooks (*G. ornatus*, apex length 0.8–0.9 times width of parameres at expansion; *G. versipellis*, 0.5–0.6 times width of parameres at expansion) (Fig. 7A, D).

Ôhira (1995a) distinguished *G. ornatus* from *G. versipellis* in the key by the antennomere II (*G. ornatus*, longer than wide; *G. versipellis*, shorter than wide) and color of the basal outer edge of the elytra (*G. ornatus*, pale orange, Fig. 1A; *G. versipellis*, black, Fig. 1D). However, in both species, the males' antennomere II is shorter than wide (Fig. 3A), and in females, it is almost as long as or slightly longer than wide (Fig. 3B). Moreover, their elytral base is variable in color, and we found specimens [GO001, GO016] of *G. versipellis* with a pale orange basal outer edge of the elytra. The two species are difficult to distinguish using antennomere II and elytral color. In females, pronotum coloration is a good diagnostic character (*G. ornatus*, brown, Fig. 4B; *G. versipellis*, red, Fig. 4D) because no pronotum color variation has been found in either species. Considering the possibility that females with non-red pronota have been found, pronotum shape is the best diagnostic character for both sexes of the two species except for aedeagus (*G. ornatus*, PWI 150–156 in male and 161–174 in female; *G. versipellis*, PWI 172–184 in male and 176–191 in female) (Fig. 4A–D).

***Gamepenth pictipennis* (Lewis, 1894)**

Figures 1B, 2A–D, 3C, D, 4E, 5, 6, 7B

Melanoxanthus pictipennis Lewis, 1894: 48 (original description; type locality: Fukushima [Kisofukushima in Nagano Prefecture] and Natakugawa [Nakatsugawa in Gifu Prefecture], Honshu, Japan).

Gamepenth pictipennis (Lewis, 1894); Kishii 1959: 58 (changed generic status).

Gamepenthès pictipennis aberrant form *mizunoi* Kishii, 1968: 14 (original description; type locality: Tokugô-tôge Pass, Nagano Prefecture, Honshu, Japan).

Nipponodrasterius alpicola Kishii, 1966: 9 (original description; type locality: Sampuku-tôge Pass, Kashio, Ôshika Village, Shimoina District, Nagano Prefecture, Honshu, Japan). **syn. nov.**

Material examined. *Holotype* of *Nipponodrasterius alpicola*. Male, Japan, Honshu, Nagano Prefecture, Shimoina District, Ôshika Village, Kashio, Sampuku-tôge Pass, 17–20, VII, 1956, H. Nitta leg. Verbatim label data (Fig. 5J): “*Nipponodrasterius* / *alpicola* / Kishii. 1966 / DET. T. KISHII. ‘66”; “HOLOTYPE”; “Sampuku pass / South Alps, Japan / July 17–20, 1956 / Coll. Nitta”; “2489”.

Non-type material. 1 male, Japan, Hokkaido, Uryû District, Horokanai Town, Syumarinaï, 31 VII 1982, Koji Hosokawa leg. [GP001]; 1 female, Japan, Honshu, Gunma Prefecture, Ôsawa, 19 VII 1975, M. Yagi leg. [GP002]; 1 male, Japan, Honshu, Yamanashi Prefecture, Sudama Town, Masutomi spa, 9 VIII 1989, Yutaka Ishikawa leg. [GP003]; 1 female, same place as the former, 1300 m, 26 VII 1999, Yutaka Ishikawa leg. [GP004]; 1 female, same place as the former, ca 1300 m, base of the western end of the Okuchichibu Mountains, 18 VII 1990, Yutaka Ishikawa leg. [GP005]; 1 male, Japan, Honshu, Yamanashi Prefecture, Kôshû City, Enzan, Hikawa Forest Road, 20 VIII 1989, K. Shindô leg. [GP006]; 1 male, Japan, Honshu, Gifu Prefecture, Takayama City, Shôkawa Town, Oganigô, Ôkuro Valley, 30 VI 2007, Hisayuki Arimoto leg. [GP007]; 1 female, Japan, Honshu, Gifu Prefecture, Ôno District, Shôkawa Village, Ogamigô, 12 VIII 1995, N. Yuzawa leg. [GP008]; 1 male, Japan, Honshu, Nara Prefecture, Tenkawa Village, Tsubonouchi Forest Road, 1200m, 21 VII 2008, Hisayuki Arimoto leg. [GP009]; 1 male, 1 female, Japan, Honshu, Okayama Prefecture, Tomada District, Kagamino Town, Neji, 8–15 VII 2016, Akihiko Watanabe leg., by light FIT [male: GP0010; female: GP011]; 1 male, Japan, Kyushu, Ôita Prefecture, Toyogoôno City, Ogata Town, Mt. Furusobo-san, 30 VII 2017, Yûji Tsutsumiuchi leg. [GP012].

Diagnosis. Body robust (EI: 222–244, BI: 209–247). Prothorax black; hind angles of pronotum yellow to orange in many, black in some. Each elytron with three separate yellow markings basally; basal markings connected in many, variably reduced in some. Antennomere II shorter than wide; antennomere III shorter than wide in male, slightly longer than wide in female; IV elongate (1.74–2.00 times longer than wide in male, 1.96–2.05 times longer than wide in female), longer than II–III combined (1.47–1.79 times as long as II–III combined in male, 1.21–1.40 times as long as II–III combined in female). Prosternal process weakly inclined dorsad (20–25°). Metacoxal plates narrowed outwards, with outer edge narrow. Apical edge of elytra rounded, without spines. Apex of parameres beyond pre-apical expansions widely triangular (apex length 0.1–0.2 times width of parameres at expansion).

Measurements. Male (8 spec.). BL: 5.13–6.51; BW: 1.42–1.88; MAE: 0.903–1.10; MBE: 0.623–0.793; OI: 132–145; PL: 1.34–1.85; PML: 1.27–1.62; PAW: 0.937–1.13; PW: 1.37–1.76; PI: 101–111; PWI: 146–161; EL: 3.32–4.29; EW:

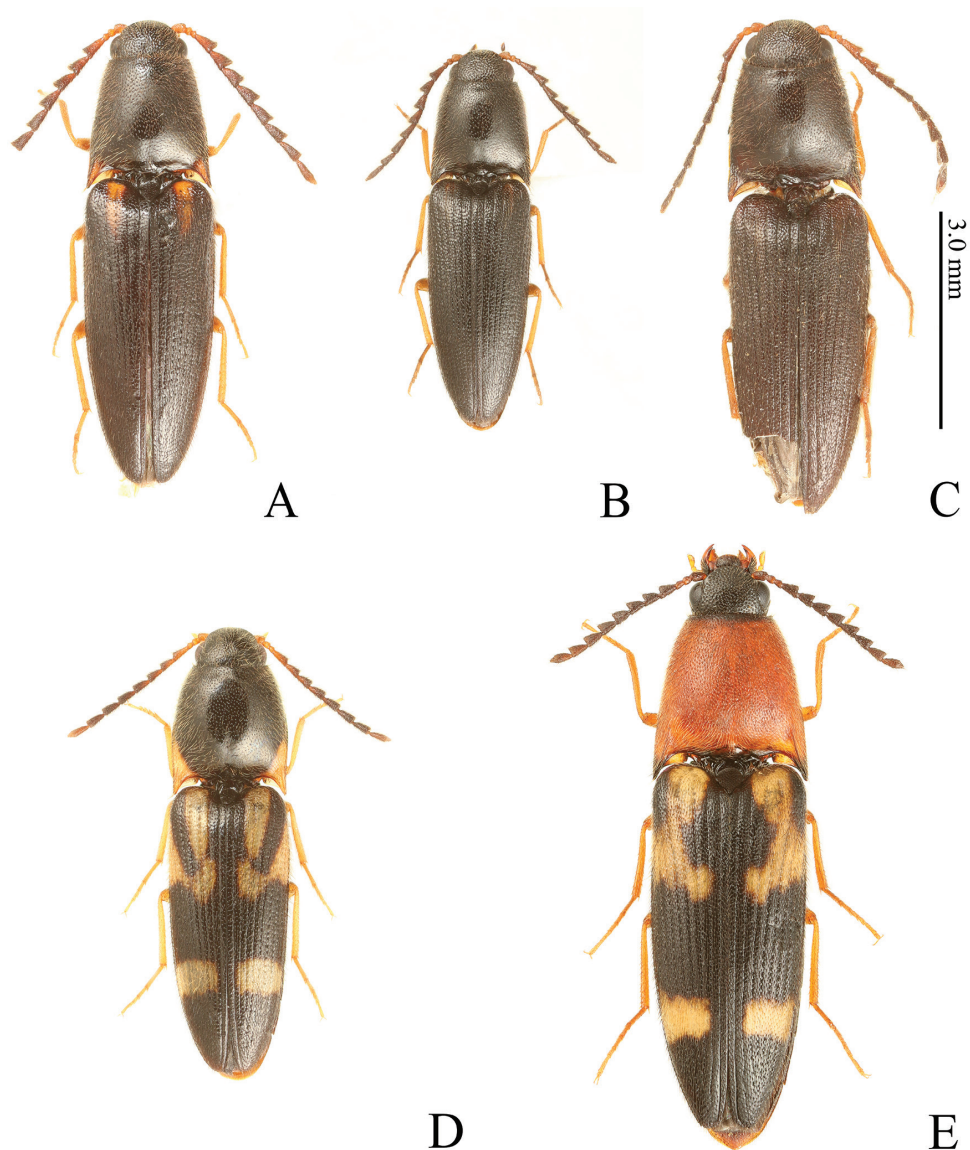


Figure 2. *Gamepenthès* spp., color variation **A** *G. pictipennis*, male [GP003] **B** *G. pictipennis*, male [GP012] **C** *G. pictipennis*, male, holotype of *Nipponodrasterius alpicola* **D** *G. pictipennis*, female [GP010] **E** *G. versipellis*, female [GV007].

1.42–1.88; EI: 222–238; BI: 212–247. Female (5 spec.). BL: 5.65–7.25; BW: 1.55–1.96; MAE: 0.915–1.14; MBE: 0.653–0.856; OI: 133–140; PL: 1.61–2.11; PAW: 0.943–1.17; PML: 1.40–1.87; PW: 1.47–1.91; PI: 108–112; PWI: 155–163; EL: 3.57–4.72; EW: 1.55–1.96; EI: 228–244; BI: 209–237.

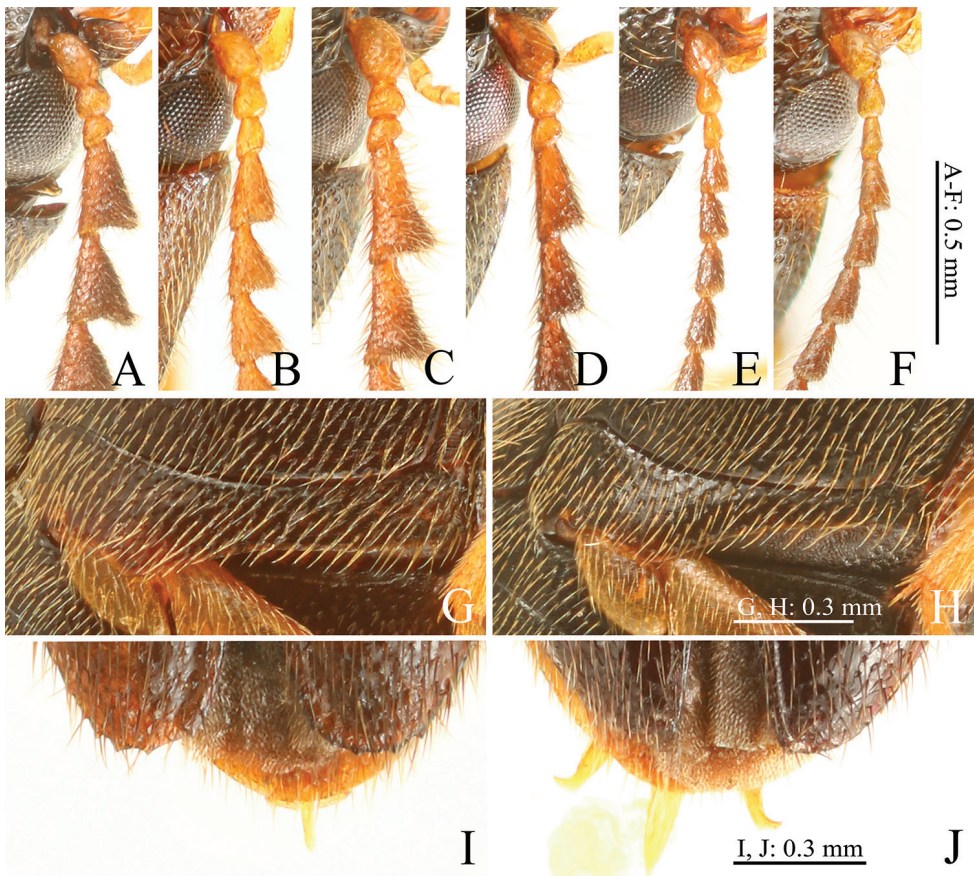


Figure 3. *Gamepenthess* spp. **A–F** right basal antennomeres **G, H** left metacoxal plate **I, J** apices of elytra **A** *G. ornatus*, male [GO003] **B** *G. ornatus*, female [GO009] **C** *G. pictipennis*, male [GP010] **D** *G. pictipennis*, female [GP011] **E** *G. similis*, male [GS003] **F** *G. similis*, female [GS006] **G, I** *G. versipellis* [GV011] **H** *G. pictipennis* [GP010] **J** *G. pictipennis* [GP003].

Distribution. Japan: Hokkaido, Honshu, Shikoku, Kyushu. Russia: Kunashir Island. The specimen examined from Hokkaido [GP001] is from the northern limit of the distribution of the genus.

Gamepenthess similis (Lewis, 1894)

Figures 1C, 3E, F, 7C

Melanoxanthus similis Lewis, 1894: 182 (original description; type locality: Fukushima [Kisofukushima in Nagano Prefecture], Nikko in Tochigi Prefecture and Osaka in Osaka Prefecture, Honshu, Japan).

Gamepenthess similis (Lewis, 1894); Kishii 1959: 59 (changed generic status).

Note. Ôhira (1970a) transferred *Melanoxanthus similis* to the genus *Gamepenthes*, although Kishii (1959) had already suggested that the species belongs to *Gamepenthes*.

Material examined. 1 male, Japan, Honshu, Fukushima Prefecture, 31 VII 1989, K. Shindô leg. [GS001]; 1 male, 2 females, Japan, Honshu, Kyoto Prefecture, Kyoto City, Sakyô Ward, Hirogawara-obana Town, Sasari-tôge Pass, 698 m, 35.27546°N, 135.72935°E, 1 VIII 2020, Kôichi Arimoto leg., by beating shrubs [male: GS008; females: GS009, GS010]; 1 male, Japan, Honshu, Nara Prefecture, Tenkawa Village, Tsubonouchi Forest Road, 21 VII 2008, Hisayuki Arimoto leg. [GS002]; 2 males, Japan, Honshu, Wakayama Prefecture, Tanabe City, Mt. Gomadan-zan, 18 VII 2019, Hisayuki Arimoto leg. [GS003, 004]; 1 male, 1 female, Japan, Honshu, Tottori Prefecture, Saihaku District, Daisen Town, Mt. Dai-sen, 30 VII 2016, Akihiko Watanabe leg. [male: GS005; female: GS006]; 1 female, Japan, Honshu, Hiroshima Prefecture, Hikimi-tôge Pass, 7 VIII 1983, T. Itô leg. [GS007].

Diagnosis. Body robust (EI: 223–247, BI: 231–266). Prothorax black. Each elytron with yellow diagonal long marking basally. Antennomere II distinctly longer than wide; III longer than wide; IV robust (1.58–1.64 times longer than wide), shorter than II–III combined (0.67–0.76 times as long as II–III combined). Pronotum gradually widened posterad. Prosternal process weakly inclined dorsad (23–37°). Metacoxal plates not narrowed outwards, with outer edge wide. Apical edge of elytra rounded, without spines. Apex of parameres beyond apical-lateral hooks widely triangular (apex length 0.4 times width of parameres at expansion).

Measurements. Male (6 spec.) BL: 4.22–4.65; BW: 1.21–1.31; MAE: 0.706–0.786; MBE: 0.487–0.576; OI: 136–145; PL: 1.11–1.25; PML: 0.924–1.07; PAW: 0.702–0.805; PW: 1.13–1.24; PI: 97.6–101; PWI: 154–165; EL: 2.84–3.21; EW: 1.21–1.31; EI: 234–247; BI: 246–266. Female (4 spec.). BL: 4.39–4.95; BW: 1.31–1.42; MAE: 0.728–0.819; MBE: 0.523–0.600; OI: 136–140; PL: 1.25–1.41; PML: 1.03–1.20; PAW: 0.736–0.832; PW: 1.20–1.37; PI: 103–105; PWI: 153–165; EL: 2.92–3.34; EW: 1.31–1.42; EI: 223–237; BI: 231–244.

Distribution. Japan: Honshu, Shikoku, Kyushu.

Gamepenthes versipellis (Lewis, 1894)

Figures 1D, 2E, 3G, 3I, 4C, D, 7D

Megapenthes versipellis Lewis, 1894: 47 (original description; type locality: Chiûzenji in Tochigi Prefecture and Kashiwagi in Nara Prefecture, Honshu, and Junsai, Sapporo and Otaru in Hokkaido, Japan).

Gamepenthes versipellis (Lewis, 1894); Kishii 1958: 29 (changed generic status).

Megapenthes versipellis aberrant form *nigerrimus* Nakane, 1958: 86 (original description; type locality: Mt. Osore-zan, Aomori Prefecture, Honshu, Japan).

Megapenthes versipellis aberrant form *sexpunctatus* Nakane, 1958: 86 (original description; type locality: Mt. Osore-zan, Aomori Prefecture, Honshu, Japan).

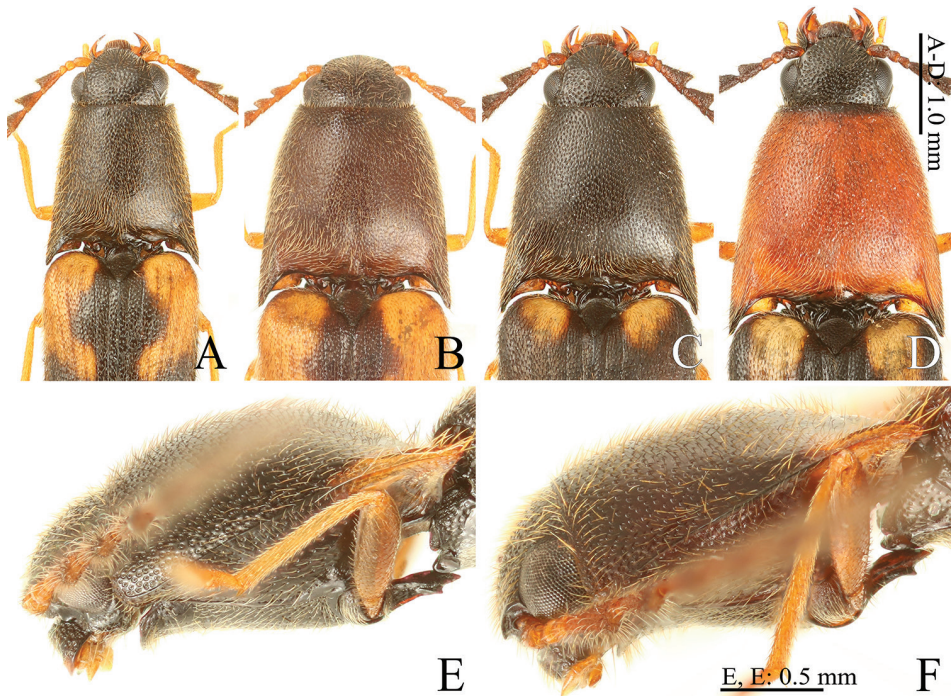


Figure 4. *Gamepenthès* spp., head and prothorax **A** *G. ornatus*, male [GO003] **B** *G. ornatus*, female [GO002] **C** *G. versipellis*, male [GV006] **D** *G. versipellis*, female [GV007] **E** *G. pictipennis*, male [GP010] **F** *G. yoshidai*, male [GY001] **A–D** dorsal view **E, F** lateral view.

Megapenthès versipellis aberrant form *octopustularus* Nakane, 1958: 87 (original description; type locality: Mt. Osore-zan, Aomori Prefecture, Honshu, Japan).

Megapenthès versipellis aberrant form *interruptus* Nakane, 1958: 87 (original description; type locality: Mt. Osore-zan, Aomori Prefecture, Honshu, Japan).

Megapenthès versipellis var. *shirozui* Kishii, 1958: 31 (original description; type locality: Mt. Kuju-san, Ôita Prefecture, Kyushu, Japan).

Note. The species exhibits elytral color variation. Based on this, Nakane (1958) and Kishii (1958) described four forms and one variant.

Material examined. 1 female, Japan, Hokkaido, Samani District, Samani Town, Mt. Apoi-dake, 9 VIII, 1974, H. Miyauchi leg. [GV001]; 1 male, Japan, Honshu, Nagano Prefecture, Mt. Kisokomaga-take, 31 VII 1976, Ryôji Toyoshima leg. [GV002]; 1 male, Japan, Honshu, Nagano Prefecture, Mt. Yatsuga-take, 26 VII 1979, Katsuhiko Kitagawa leg. [GV003]; 1 male, Japan, Honshu, Gifu Prefecture, Ôno District, Shôkawa Village, Ogamigô, 12 VIII 1995, N. Yuzawa leg. [GV004]; 1 male, Japan, Honshu, Nara Prefecture, Yoshino District, Kamikitayama Village, Mt. Ôdaigahara, 14 VII 1985, Hisayuki Arimoto leg. [GV005]; 1 male, 3 females, Japan, Honshu, Nara Prefecture, Yoshino District, Totsukawa Village, Asahi, Mt. Syakaga-take, 1450 m,

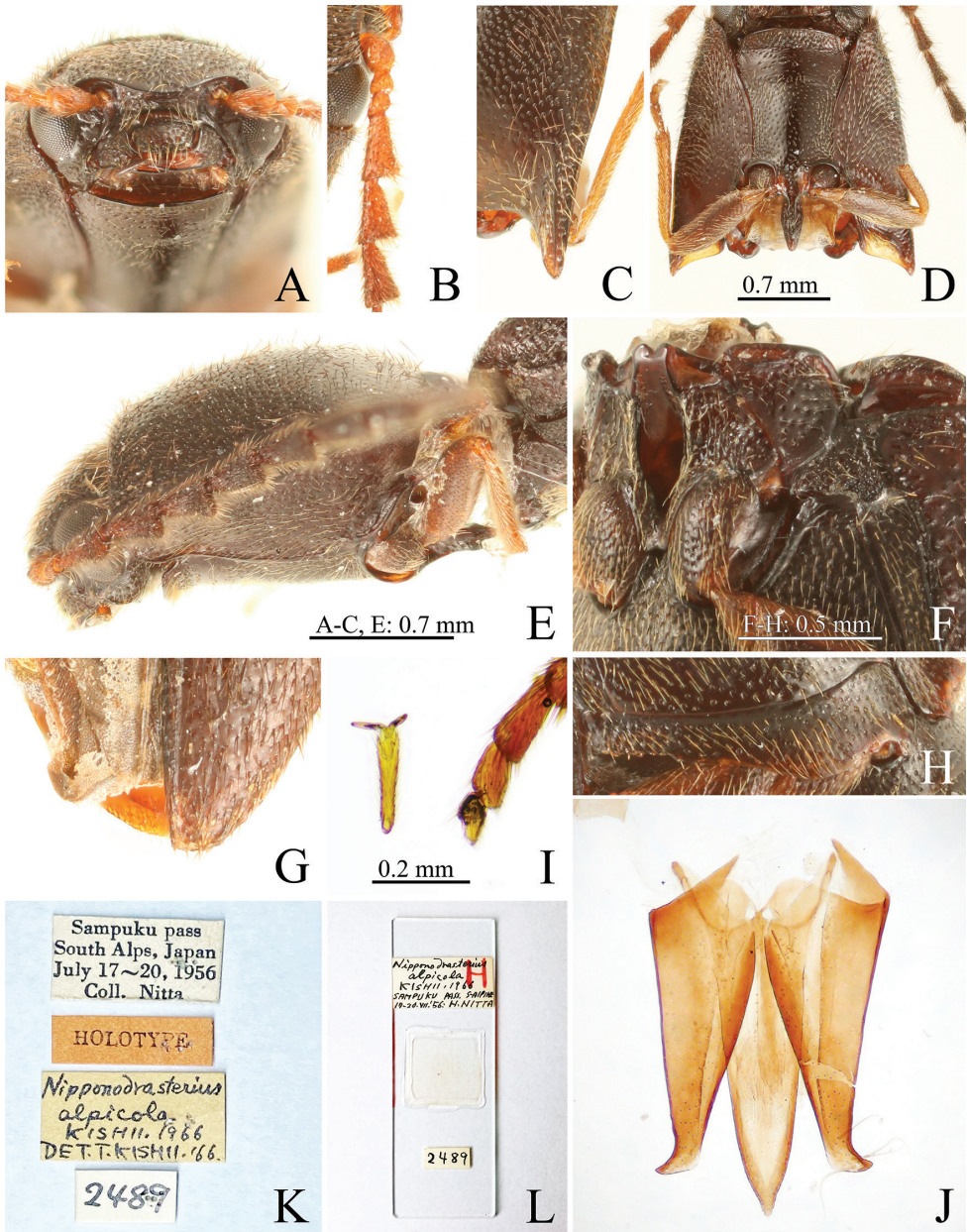


Figure 5. Holotype of *Nipponodrasterius alpicola* **A** head, anterior view **B** right basal antennomeres **C** hind angles of pronotum **D** prothorax, ventral view **E** prothorax, lateral view **F** mesosternum **G** apices of elytra **H** right metacoxal plate **I** left mid tarsus and claw **J** aedeagus **K** labels **L** aedeagus slide.

4 VIII 2019, Hisayuki Arimoto leg., from flowers of *Tilia japonica* [male: GV006; females: GV007–GV009]; 2 males, Japan, Honshu, Nara Prefecture, Kamikitayama Village, Amagase, 11 VII 2004, Hisayuki Arimoto leg. [GV010, GV011]; 1 male,

Japan, Honshu, Nara Prefecture, Tenkawa Village, 23 VII 1989, H. Nomura leg. [GV012]; 1 female, Japan, Honshu, Hyôgo Prefecture, Shisô City, Haga Town, Tokura, Mt. Hyôno-sen, 1 VII 2015, S. Sugimoto leg. [GV013]; 1 female, Japan, Shikoku, Ehime Prefecture, Mt. Ishizuchi-san, 26 VII 1979, Kiyoshi Matsuda leg. [GV014]; 1 male, 2 females, Japan, Kyushu, Miyazaki Prefecture, Nishiusuki District, Gokase Town, Mt. Shiraiwa-yama, 1347 m, 32°34'13.7"N, 131°06'51.6"E, 30 VII 2011, Kôichi Arimoto leg. [male: GV015; females: GV016, GV017].

Diagnosis. Body robust (EI: 226–243, BI: 206–222). Prothorax black in male; female with pronotum and hypomeron red, prosternum black. Each elytron with pale orange U-shaped marking basally; basal marking partly reduced in some. Antennomere II shorter than wide in male, slightly longer than wide in female; III shorter than wide in male, longer than wide in female; IV robust (1.48–1.72 times longer than wide in male, 1.66–1.75 times longer than wide in female), longer than II–III combined (1.72–1.99 times as long as II–III combined in male, 1.08–1.14 times as long as II–III combined in female). Prosternal process weakly inclined dorsad (17–26°). Metacoxal plates not narrowed outwards, with outer edge wide. Apical edge of elytra serrate. Apex of parameres beyond pre-apical expansions widely triangular (apex length 0.5–0.6 times width of parameres at expansion).

Measurements. Male (8 spec.). BL: 6.60–7.53; BW: 1.92–2.19; MAE: 1.07–1.19; MBE: 0.709–0.831; OI: 141–154; PL: 1.98–2.33; PML: 1.73–1.96; PAW: 1.10–1.22; PW: 1.92–2.19; PI: 103–110; PWI: 172–184; EL: 4.30–5.03; EW: 1.88–2.11; EI: 229–243; BI: 206–222. Female (9 spec.). BL: 7.08–9.24; BW: 2.03–2.60; MAE: 1.12–1.30; MBE: 0.753–0.907; OI: 142–149; PL: 2.20–2.77; PML: 1.89–2.38; PAW: 1.15–1.39; PW: 2.03–2.60; PI: 106–112; PWI: 176–191; EL: 4.64–6.04; EW: 2.02–2.58; EI: 226–241; BI: 207–219.

Distribution. Japan: Hokkaido, Honshu, Shikoku, Kyushu. Russia: Kunashir Island. This species was also recorded from China and Oriental region (Cate 2007). Schimmel (2003, 2004, 2006) and Schimmel and Tarnawski (2009) recognized 18 species from China and Indochina: however, *G. versipellis* had not been confirmed from the area. Therefore, the records of *G. versipellis* from China and the Oriental region were probably based on misidentifications of allied species, such as *G. hubeiensis* Schimmel, 2003, *G. holzschuhi* Schimmel, 2003, *G. kresli* Schimmel & Tarnawski, 2009, *G. sausai* Schimmel, 2003 and *G. sichuanensis* Schimmel, 2003.

Gamepenthes yoshidai Ôhira, 1995

Figures 1E, 4F, 7E

Gamepenthes yoshidai Ôhira, 1995b: 27 (original description; type locality: Mt. Tsurugi-san, Tokushima Prefecture, Shikoku, Japan).

Material examined. Paratype. 1 female, Japan, Shikoku, Tokushima Prefecture, Miyoshi City, Mt. Tsurugi-san, Minokoshi, 31 VII 1982, Yûji Kurota leg.

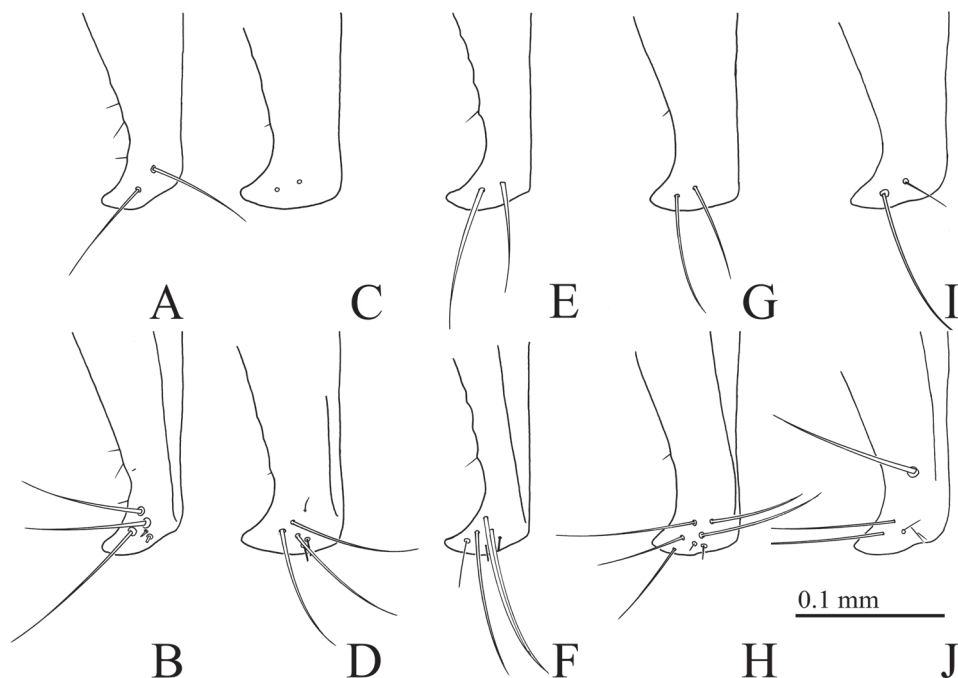


Figure 6. *Gamepenth pictipennis*, male, apex of left paramere of aedeagus **A, B** [GP006] **C, D** [GP007] **E, F** [GP009] **G, H** [GP012] **I, J** holotype of *Nipponodrasterius alpicola* **A, C, E, G, I** dorsal side **B, D, F, H, J** ventral side.

Non-type material. 2 males, Japan, Shikoku, Tokushima Prefecture, Naka District, Naka Town (formerly Kisawa Village), Mt. Takashiro-yama, 31 VII 1993, Mit-suo Kakô leg. [GY001, GY002].

Diagnosis. Body slender (EI: 259–265, BI: 254–282). Prothorax black; hind angles of pronotum yellow. Each elytron with three separate yellow markings basally. Antennomere II shorter than wide in male, almost as long as wide in female; III shorter than wide in male, longer than wide in female; IV elongate (1.92–2.06 times longer than wide in male, 2.17 times longer than wide in female), longer than II–III combined (1.27–1.77 times as long as II–III combined). Prosternal process strongly inclined dorsad (43–50°). Metacoxal plates narrowed outwards on lateral half, with outer edge narrow. Apical edge of elytra rounded, without spines. Apex of parameres beyond pre-apical expansions widely triangular (apex length 0.3–0.4 times width of parameres at expansion).

Measurements. Male (2 spec.). BL: 6.96–7.29; BW: 1.87–1.98; MAE: 1.17–1.21; MBE: 0.711–0.752; OI: 161–164; PL: 1.72–1.87; PML: 1.51–1.65; PAW: 1.17–1.23; PW: 1.74–1.87; PI: 98.8–100; PWI: 148–152; EL: 4.85–5.13; EW: 1.87–1.98; EI: 259; BI: 275–282. Female (1 spec.). BL: 7.20; BW: 1.89; MAE: 1.15; MBE: 0.743; OI: 154; PL: 1.98; PML: 1.71; PAW: 1.16; PW: 1.82; PI: 109; PWI: 157; EL: 5.02; EW: 1.89; EI: 265; BI: 254.

Distribution. Japan: Shikoku. This species may be endemic to Shikoku, Japan.

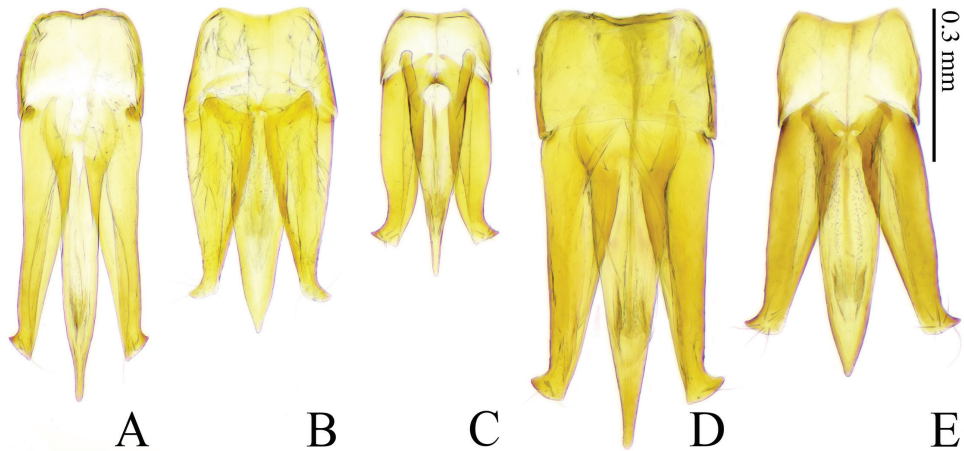


Figure 7. *Gamepenthos* spp., male, aedeagus, ventral side **A** *G. ornatus* [GO006] **B** *G. pictipennis* [GP006] **C** *G. similis* [GS008] **D** *G. versipellis* [GV003] **E** *G. yoshidai* [GY002].

Discussion

The holotype of *N. alpicola* has an oval head capsule in lateral view (Fig. 5E), inferior mouth-parts (Fig. 5E), mesocoxal cavity open to the mesepimeron and mesepisternum (Fig. 5F), mesosternum separated by suture from metasternum (Fig. 5F), and claws simple and without basal setae (Fig. 5I). These features are diagnostic for members of the subfamily Elaterinae (Stibick 1979). Moreover, the holotype has the following key features for the genus *Gamepenthos* of the tribe Megapenthini (Ôhira 1970a; Schimmel 2003): supra-antennal carina complete and depressed medially (Fig. 5A), vertical distance between supra-antennal carina and labrum narrowed medially in anterior view (Fig. 5A), antennomeres II and III short (Fig. 5B), antennomeres IV–X serrate (Fig. 5B), hind angles of pronotum unicarinate (Fig. 5C), procoxal cavity partly closed by a projection of the hypomeron, prosternal process concave between procoxae (Fig. 5D) and with subapical tooth (Fig. 5E), and elytral surface with small tubercle-like prominences on anterior edge of punctures (Fig. 2C) (the elytral surface clearly granulated in Kishii 1966). Kishii (1987) stated that tarsomere IV of *N. alpicola* was slightly enlarged apically, but the tarsomere IV of the holotype is simple, which matches the diagnosis of *Gamepenthos* and Megapenthini (Fig. 5I). Therefore, we concluded that *Nipponodrasterius* should be a junior synonym of *Gamepenthos*.

We found a slide of the male genitalia labeled as belonging to the holotype of *N. alpicola* (matching specimen number and label information) in OMNH (Fig. 5K, L), although the sex and genitalia of the holotype were not mentioned in the original description. We found that *N. alpicola* should be a junior synonym of *G. pictipennis* by comparing the aedeagi of the Japanese *Gamepenthos* species (Figs 5J, 6, 7) and their aedeagus shown in Ôhira (1970b, 1995a). *Gamepenthos pictipennis* is also distinguished from its congeners by a combination of body size, antennae, prosternal pro-

cess, metacoxal plates, and apical edge of the elytra (see above key and diagnoses). The holotype of *N. alpicola* shares these features (Fig. 5). We also found that *G. pictipennis* has variable pronotum and elytral coloration, ranging from a black base with clear yellow markings (Figs 1B, 2D) to having fewer yellow markings (Fig. 2A) to entirely black (Fig. 2B). Even the black specimens show slight yellow markings, and the hind angles of the pronotum and anterior parts of that elytra are slightly yellow tinged (Fig. 2B), as in the holotype (Figs 2C, 5C). We conclude the holotype of *N. alpicola* is a melanic specimen of *G. pictipennis*.

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Checklist of rodents and insectivores of the Mordovia, Russia

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Abstract

A list of 40 species is presented of the rodents and insectivores collected during a 15-year period from the Republic of Mordovia. The dataset contains more than 24,000 records of rodent and insectivore species from 23 districts, including Saransk. A major part of the data set was obtained during expedition research and at the biological station. The work is based on the materials of our surveys of rodents and insectivorous mammals conducted in Mordovia using both trap lines and pitfall arrays using traditional methods.

Keywords

Insectivores, Mordovia, rodents, spatial distribution

Introduction

There is a need to review the species composition of rodents and insectivores in all regions of Russia, and the work by Tovpinets et al. (2020) on the Crimean Peninsula serves as an example of such research. Studies of rodent and insectivore diversity and distribution have a long history, but there are no lists for many regions of Russia of

rodent and insectivorous species. Lists of species have been updated for a few regions, with some species excluded and others added. The Republic of Mordovia is one of these regions, where eminent theriologists (S.I. Ognev, S.S. Turov, L.G. Morozova-Turova, I.I. Barabash-Nikiforov, L.P. Borodin, M.N. Borodina, P.L. Borodin) once worked. The inventory of the mammalian fauna of Mordovia resumed at the beginning of the 21st century as part of dissertation research and continues to this day. Over this period, not only has the species composition of the region changed but also the status of many species.

The Mordovian fauna is heterogeneous and consists of four different ecological and faunal complexes of species—taiga, coniferous and broad-leaved forests, and steppe—which are widely distributed in several natural areas (Andreychev 2020).

Here, we publish a checklist of rodent and insectivore records across the Republic of Mordovia. This checklist was based on comprehensive surveys of small mammals carried out from 2006 to 2020.

Insectivores are represented in Mordovia by 12 species belonging to three families.

Family Erinaceidae Fischer, 1814

1. Northern white-breasted hedgehog, *Erinaceus roumanicus* Barrett-Hamilton, 1900
2. West European hedgehog, *Erinaceus europaeus* Linnaeus, 1758

Family Talpidae Fischer, 1814

1. European mole, *Talpa europaea* Linnaeus, 1758
2. Russian desman, *Desmana moschata* (Linnaeus, 1758)

Family Soricidae Fischer, 1814

1. Eurasian common shrew, *Sorex araneus* Linnaeus, 1758
2. Laxmann's shrew, *Sorex caecutiens* Laxmann, 1788
3. Least shrew, *Sorex minutissimus* Zimmermann, 1780
4. Taiga shrew, *Sorex isodon* Turov, 1924
5. Eurasian pygmy shrew, *Sorex minutus* Linnaeus, 1766
6. Eurasian water shrew, *Neomys fodiens* (Pennant, 1771)
7. Southern water shrew, *Neomys anomalus* Cabrera, 1907
8. Lesser white-toothed shrew, *Crocidura suaveolens* (Pallas, 1811)

Rodents are represented by 29 species belonging to eight families.

Family Sciuridae Fischer, 1817

1. Red squirrel, *Sciurus vulgaris* Linnaeus, 1758
2. Spotted suslik, *Spermophilus suslicus* Gldenstaedt, 1770
3. Bobak marmot, *Marmota bobak* (Mller, 1776)

Family Castoridae Hemprich, 1820

1. Eurasian beaver, *Castor fiber* Linnaeus, 1758

Family Gliridae Thomas, 1897

1. Forest dormouse, *Dryomys nitedula* (Pallas, 1779)
2. Garden dormouse, *Eliomys quercinus* (Linnaeus, 1766)
3. Fat dormouse, *Glis glis* (Linnaeus, 1766)
4. Hazel dormouse, *Muscardinus avellanarius* (Linnaeus, 1758)

Family Sminthidae Brandt, 1855

1. Northern birch mouse, *Sicista betulina* (Pallas, 1779)

Family Allactagidae Vinogradov, 1925

1. Great jerboa, *Allactaga major* (Kerr, 1792)

Family Spalacidae Gray, 1821

1. Greater mole rat, *Spalax microphthalmus* Gldenstaedt, 1770
2. Family Cricetidae Fischer, 1817
3. Bank vole, *Myodes glareolus* (Schreber, 1780)
4. Northern red-backed vole, *Myodes rutilus* (Pallas, 1779)
5. European water vole, *Arvicola amphibius* (Linnaeus, 1758)
6. Root vole, *Microtus oeconomus* (Pallas, 1776)
7. Gray dwarf hamster, *Cricetulus migratorius* (Pallas, 1773)
8. Common hamster, *Cricetus cricetus* (Linnaeus, 1758)
9. Muskrat, *Ondatra zibethicus* (Linnaeus, 1766)
10. Steppe lemming, *Lagurus lagurus* Pallas, 1773
11. Common vole, *Microtus arvalis* (Pallas, 1779)
12. East European vole, *Microtus rossiaemeridionalis* Ognev, 1924
13. Field vole, *Microtus agrestis* (Linnaeus, 1761)
14. European pine vole, *Microtus subterraneus* (de Selys-Longchamps, 1836)

Family Muridae Illiger, 1811

1. Striped field mouse, *Apodemus agrarius* (Pallas, 1771)
2. Pygmy wood mouse, *Apodemus uralensis* (Pallas, 1811)
3. Yellow-necked wood mouse, *Apodemus flavicollis* (Melchior, 1834)
4. Harvest mouse, *Micromys minutus* (Pallas, 1771)
5. House mouse, *Mus musculus* Linnaeus, 1758
6. Norway rat, *Rattus norvegicus* (Berkenhout, 1769)

Genetic studies of two similar species, *Microtus arvalis* and *M. rossiaemeridionalis*, have not been conducted in the region. Approaches and criteria for differentiation of two similar species, *Erinaceus roumanicus* and *E. europaeus*, have been applied for a number of specific morphological and craniometric characteristics (Zaitsev 1984; Frost et al. 1991). First, *E. roumanicus* has a patch of white hair on its belly. And *E. europaeus* has no white hair on its belly. Differences in the skull are also apparent; in *E. roumanicus*, the premaxillary-maxillary suture has one or two inflections (in *E. europaeus* it is smooth), the length of the premaxillary-nasal suture does not exceed 9.0 mm (in *E. europaeus* >9.0 mm), and the maximum length of the nasal bones in their back part is greater than or equal to 3.0 mm (*E. europaeus* <3.0 mm) (Zaitsev 1984; Frost et al. 1991; Zaitsev et al. 2014). The color of the needles of these two species can serve as a criteria for their differences. Six species (*Eliomys quercinus*, *Cricetulus migratorius*, *Lagurus lagurus*, *Myodes rutilus*, *Microtus subterraneus*, and *Neomys anomalus*) reported from the Republic of Mordovia were not detected during our surveys. However, these species were captured by our colleagues, either long ago or even in the last year, and most of them (*E. quercinus*, *C. migratorius*, *L. lagurus*, and *M. rutilus*) were recorded in the Mordovian state nature reserve, Temnikovsky district (Borodina et al. 1970). *Microtus subterraneus* has recently been found in Mordovia (Kirillova et al. 2019). This record represents the easternmost occurrence of of this species. Previously, this underground vole was recorded in neighboring regions of Mordovia, namely near the village of Zhelannoe in Ryazan region and from Zametchinsky district in Penza region. This species is rare and included in Red Data Books of several Russian regions, including the Leningrad, Tver, Penza, Moscow, Pskov reion, and Novgorod regions. The appearance of a new species for Mordovia can be explained by its expansion into new territories. This is confirmed by the new record of this species from the Smolensk region (Belyaev 2020). In addition, a species atypical of the Mordovian fauna, *Neomys anomalus*, is now known (Borodin 2013).

From an ecological perspective, mesophilous species comprise the largest group, which includes 26 species. Some xerophilous species (*M. bobak*, *Sp. suslicus*, *Al. major*, *Sp. microphthalmus*, *Cr. migratorius*, *Cr. cricetus*, *L. lagurus*, and *M. minutus*) occur only in steppe habitats. Only in the steppe areas of Mordovia are there concentrated populations of *S. microphthalmus* (Andreychev 2018, 2019) and *M. bobak* (Andreychev et al. 2015). Populations of *S. microphthalmus* in Mordavia are vulnerable, as in other parts of its range (Zagorodniuk et al. 2018). Grazing is important here for *M. bobak*, as has been shown for Ukraine (Rashevskaya and Semeniuk 2015; Tokarsky 2015; Savchenko and Ronkin 2018).

Dendrophile rodents are represented by only seven species: *D. nitedula*, *G. glis*, *M. avellanarius*, *E. quercinus*, *S. vulgaris*, *A. flavicollis*, and *A. uralensis*. Of these species, the most studied in the region are *D. nitedula* (Andreychev and Boyarova 2020; Andreychev and Kiyaykina 2020), *A. flavicollis*, and *A. uralensis* (Andreychev and Kuznetsov 2012).

Thirteen species are associated with human settlements, *C. suaveolens*, *E. roumanicus*, *S. minutus*, *S. araneus*, *S. isodon*, *C. cricetus*, *M. glareolus*, *M. arvalis*, *A. agrarius*, *A. uralensis*, *A. flavicollis*, *M. musculus*, and *R. norvegicus*, and these have been repeatedly recorded in residential areas. However, only three species, *M. musculus*, *R. norvegicus*, and *C. suaveolens*, are truly commensal.

The rodent and insectivore fauna of Mordovia is in general large, as it includes both steppe and taiga species. The largest rodent of Mordovia is *C. fiber*, which is widely distributed in the region's water bodies (Andreychev 2017). The rodent and insectivore fauna of Mordovia is larger than in adjacent regions. However, the fauna lacks some species that exist in adjacent regions: Ulyanovsk region - *Allocricetulus evermanni* Brandt, 1859 (Red Book 2008); Penza region - *Spermophilus major* Pallas, 1778, *Sicista strandi* (Formozov, 1931) (Il'in et al. 2006); Nizhny Novgorod region – *Rattus rattus* (Linnaeus, 1758), *Tamias sibiricus* (Laxmann, 1769), *Pteromys volans* (Linnaeus, 1758), *Myodes rufocanus* (Sundevall, 1846) (Krivonogov et al. 2008); Chuvash region – *Tamias sibiricus* (Laxmann, 1769), *Pteromys volans* (Linnaeus, 1758) (Red Book 2010); and Ryazan region - *Rattus rattus* (Linnaeus, 1758), *Pteromys volans* (Linnaeus, 1758) (Red Book 2011). Thus, seven species of rodents and insectivores present in adjacent regions are absent from the fauna of Mordovia.

Taxonomic coverage

The dataset contains more than 24,000 registrations of rodent and insectivore species from the districts of the Republic of Mordovia, including Saransk (Table 1, Appendix 1).

Taxonomic ranks

Kingdom: Animalia

Phylum: Chordata

Class: Mammalia

Order: Eulipotyphla, Rodentia

Family: Erinaceidae, Talpidae, Soricidae, Sciuridae, Castoridae, Gliridae, Sminthidae, Allactagidae, Spalacidae, Cricetidae, Muridae

Genus: *Talpa*, *Desmana*, *Sorex*, *Neomys*, *Crocidura*, *Sciurus*, *Spermophilus*, *Marmota*, *Castor*, *Dryomys*, *Eliomys*, *Glis*, *Muscardinus*, *Sicista*, *Allactaga*, *Spalax*, *Myodes*, *Arvicola*, *Microtus*, *Cricetulus*, *Cricetus*, *Ondatra*, *Lagurus*, *Microtus*, *Apodemus*, *Micromys*, *Mus*, *Rattus*

Species: *Erinaceus roumanicus*, *Erinaceus europaeus*, *Talpa europaea*, *Desmana moschata*, *Sorex araneus*, *Sorex caecutiens*, *Sorex minutissimus*, *Sorex isodon*, *Sorex minutus*, *Neomys fodiens*, *Neomys anomalus*, *Crocidura suaveolens*, *Sciurus vulgaris*, *Spermophilus suslicus*, *Marmota bobak*, *Castor fiber*, *Dryomys nitedula*, *Eliomys quercinus*, *Glis glis*, *Muscardinus avellanarius*, *Sicista betulina*, *Allactaga major*, *Spalax microphthalmus*, *Myodes glareolus*, *Myodes rutilus*, *Arvicola amphibius*, *Microtus oeconomus*, *Cricetulus migratorius*, *Cricetus cricetus*, *Ondatra zibethicus*, *Lagurus lagurus*, *Microtus arvalis*, *Microtus rossiaemeridionalis*, *Microtus agrestis*, *Microtus subterraneus*, *Apodemus agrarius*, *Apodemus uralensis*, *Apodemus flavicollis*, *Micromys minutus*, *Mus musculus*, *Rattus norvegicus*

Table 1. Registration points of rodents and insectivores collected in the Mordovia.

Species no.	Species	Points no. (from Appendix 1)
1	<i>Erinaceus roumanicus</i>	17, 25, 31, 32, 46, 63, 75, 99, 102
2	<i>Erinaceus europaeus</i>	34, 103
3	<i>Talpa europaea</i>	1, 8, 11, 17, 24, 33, 36, 40, 44, 53, 56, 63, 64, 67, 73, 76, 81, 85, 97, 98, 102, 103, 105
4	<i>Desmana moschata</i>	68, 73, 76, 81, 95, 97, 101
5	<i>Sorex araneus</i>	6, 8, 11, 22, 24, 28, 33, 35, 40, 45, 51, 53, 56, 63, 64, 67, 73, 77, 83, 89, 98, 102, 103
6	<i>Sorex caecutiens</i>	37, 71, 67, 76, 93, 97, 102, 103
7	<i>Sorex minutissimus</i>	76
8	<i>Sorex isodon</i>	14, 37, 52, 59, 62, 66, 74, 94, 96, 102, 103
9	<i>Sorex minutus</i>	10, 11, 22, 24, 26, 33, 35, 40, 45, 51, 53, 56, 58, 63, 65, 67, 73, 77, 82, 91, 98, 102, 103
10	<i>Neomys fodiens</i>	12, 17, 33, 40, 47, 49, 53, 55, 63, 69, 73, 76, 80, 84, 86, 97, 101, 102, 103, 105
11	<i>Neomys anomalus</i>	76
12	<i>Crocidura suaveolens</i>	20, 36, 76, 102
13	<i>Sciurus vulgaris</i>	17, 31, 34, 38, 44, 56, 63, 67, 73, 76, 88, 97, 100, 102
14	<i>Spermophilus suslicus</i>	7, 31, 23, 33
15	<i>Marmota bobak</i>	1, 21, 31, 32, 39, 62
16	<i>Castor fiber</i>	1, 8, 11, 17, 24, 33, 36, 40, 44, 53, 56, 63, 64, 67, 73, 76, 81, 85, 97, 98, 102, 103, 105
17	<i>Dryomys nitedula</i>	36, 76, 102, 103
18	<i>Eliomys quercinus</i>	17, 76
19	<i>Glis glis</i>	4, 38, 42, 76, 102
20	<i>Muscardinus avellanarius</i>	17, 56, 102, 103
21	<i>Sicista betulina</i>	76, 100, 102, 103
22	<i>Allactaga major</i>	31, 33, 69, 85
23	<i>Spalax microphthalmus</i>	11, 19
24	<i>Myodes glareolus</i>	1, 8, 11, 17, 24, 33, 36, 40, 44, 53, 56, 63, 64, 67, 73, 76, 81, 85, 97, 98, 102, 103, 105
25	<i>Myodes rutilus</i>	76
26	<i>Arvicola amphibius</i>	1, 8, 11, 17, 24, 33, 36, 40, 44, 53, 56, 63, 64, 67, 73, 76, 81, 85, 97, 98, 102, 103, 105
27	<i>Microtus oeconomus</i>	24, 61, 70, 76, 92, 102, 103
28	<i>Cricetulus migratorius</i>	76
29	<i>Cricetus cricetus</i>	3, 5, 9, 16, 18, 24, 33, 37, 50, 62, 98, 104
30	<i>Ondatra zibethicus</i>	1, 8, 11, 17, 24, 33, 36, 40, 44, 53, 56, 63, 64, 67, 73, 76, 81, 85, 97, 98, 102, 103, 105
31	<i>Lagurus lagurus</i>	31, 76
32	<i>Microtus arvalis</i> s.l.	1, 8, 11, 17, 24, 33, 36, 40, 44, 53, 56, 63, 64, 67, 73, 76, 81, 85, 97, 98, 102, 103, 105
33	<i>Microtus agrestis</i>	72, 76, 87, 102, 103
34	<i>Microtus subterraneus</i>	102
35	<i>Apodemus agrarius</i>	10, 11, 22, 24, 27, 33, 35, 40, 45, 51, 53, 56, 58, 63, 65, 67, 73, 77, 82, 91, 98, 102, 103
36	<i>Apodemus uralensis</i>	1, 8, 11, 17, 24, 33, 36, 40, 44, 53, 56, 63, 64, 67, 73, 76, 81, 85, 97, 98, 102, 103, 105
37	<i>Apodemus flavicollis</i>	2, 29, 30, 33, 41, 54, 56, 57, 60, 63, 73, 78, 79, 90, 97, 103
38	<i>Micromys minutus</i>	13, 17, 31, 43, 48, 71, 76, 102
39	<i>Mus musculus</i>	10, 11, 22, 24, 27, 33, 35, 40, 45, 51, 53, 56, 58, 63, 65, 67, 73, 77, 82, 91, 98, 102, 103
40	<i>Rattus norvegicus</i>	1, 8, 11, 17, 24, 33, 36, 40, 44, 53, 56, 63, 64, 67, 73, 76, 81, 85, 97, 98, 102, 103, 105

Spatial coverage

The dataset covers the entire Republic of Mordovia within 53°38'N to 55°11'N and 42°11'E to 46°45'E.

Temporal coverage

The data were collected from 2006 to 2020.

Method

Most of the dataset was obtained in the Republic of Mordovia during expedition research and at the biological station. The work is based on the materials of our surveys of rodents and insectivorous mammals conducted in the Republic of Mordovia, using trap lines and pitfall arrays using traditional methods. Small rodents were captured using small spring snap-traps (120 × 55 mm) left over night in lines of from 50 to 100 traps with a distance of 5 m between them and baited with bread and sunflower oil. We also used live traps baited with salami and apple to catch dormice. Voucher specimens are stored in the personal collection A. Andreychev, Saransk (teriomordovia@bk.ru). Data on *Erinaceus roumanicus*, *Erinaceus europaeus*, *Talpa europaea*, *Desmana moschata*, *Sciurus vulgaris*, *Spermophilus suslicus*, *Marmota bobak*, *Castor fiber*, *Allactaga major*, *Spalax microphthalmus*, *Cricetus cricetus*, and *Ondatra zibethicus* were obtained via direct observations, recording and/or detection of the traces of their activities (tracks, burrows, etc.). Latin names of species are given according to the classical nomenclature (Wilson and Reeder 2005).

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Appendix I

Points of the Republic of Mordovia in which mammals are recorded.

Points no.	District	Location	Geographic coordinates
1	Lyambirskiy	Atemar	54.0980°N, 45.2138°E
2	Kochkurovskiy	Vorob'evka	54.0251°N, 45.1754°E
3		Vnukovka	54.0118°N, 45.1609°E
4		Novotyaglovka	53.5506°N, 45.1778°E
5	Ichalkovskiy	Lobaski	54.3662°N, 45.1007°E
6	Lyambirskiy	Cheremishevo	54.1579°N, 45.0604°E
7	Romodanovskiy	Malaya Chfarovka	54.2435°N, 45.1750°E
8		Romodanovo	54.2494°N, 45.2043°E
9		Kavtorovka	54.2187°N, 45.1491°E
10		Kurilovo	54.2854°N, 45.2805°E
11	Ruzaevskiy	Levzhenskij	54.0618°N, 45.0517°E
12		Popovka	54.0690°N, 45.0310°E
13		Klyucharevo	54.0846°N, 45.0121°E
14		Ruzaevka	54.0246°N, 44.5609°E
15		Bogolyubovka	54.0596°N, 44.5238°E
16		Tatarskij Shebdas	53.5851°N, 44.5444°E
17	Saransk	Saransk	54.1328°N, 45.1102°E
18		Zykovo	54.0495°N, 45.0589°E
19		Dobrovol'nyj	54.0807°N, 45.0506°E
20		Pushkino	54.0815°N, 45.1151°E
21		Makarovka	54.1037°N, 45.1717°E
22		Kulikovka	54.0689°N, 45.1217°E
23	Ardatovskiy	Zharenki	54.4420°N, 46.1421°E
24	Atyashevskiy	Tarasovo	54.3578°N, 46.1334°E
25	Chamzinskij	Rep'evka	54.2468°N, 45.4177°E
26		Gorbunovka	54.3030°N, 45.5188°E
27		Azar'evka	54.3367°N, 45.3987°E
28		Komsomol'skij	54.2672°N, 45.5183°E
29		Lyulya	54.2755°N, 45.5589°E
30	Ichalkovskiy	Vchkusy	54.4196°N, 45.3641°E
31	Bol'shebereznikovskiy	Simkino	54.1527°N, 46.1168°E
32	Dubenskij	Engalychevo	54.1846°N, 46.2649°E
33		Nikolaevka	54.2105°N, 46.3065°E
34		Purkaevo	54.2316°N, 46.3625°E
35	Kochkurovskiy	Novaya Pyрма	54.0017°N, 45.2922°E
36	Chamzinskij	Chamzinka	54.2318°N, 45.4739°E
37		Medaev	54.2593°N, 46.0009°E
38		Pyangelej	54.1778°N, 45.4172°E
39		Picheury	54.1847°N, 45.4883°E
40	Insarskiy	Luhmenskij Majdan	53.4460°N, 44.1146°E
41		Potulovka	53.4215°N, 44.2515°E

Points no.	District	Location	Geographic coordinates
42	Kadoshkinskiy	Adashevo	53.5712°N, 44.1884°E
43	Kovylkinskiy	Mordovskoe Kolomasovo	53.5837°N, 44.0684°E
44	Atyur'evskiy	Shustruj	54.1441°N, 43.2251°E
45		Kurtashki	54.1916°N, 43.2639°E
46	Zubovo-Polyanskiy	Achadovo	53.5385°N, 43.0009°E
47	Kovylkinskiy	Gumny	54.0067°N, 43.4337°E
48	Krasnoslobodskiy	Zheltonogovo	54.2875°N, 43.4456°E
49		Slobodskie Dubrovki	54.2483°N, 43.3468°E
50	Temnikovskiy	Bulaevo	54.3331°N, 43.3354°E
51	Torbeevskiy	Salazgor'	54.0718°N, 43.0735°E
52		Drakino	54.0269°N, 43.1445°E
53	Kadoshkinskiy	Pushkino	54.0528°N, 44.2329°E
54	Ruzaevskiy	Boldovo	53.5981°N, 44.3908°E
55	Staroshajgovskiy	Mal'keevka	54.2428°N, 44.4723°E
56		Staraya Terizmorga	54.1569°N, 44.3043°E
57	Lyambirskiy	Dal'nij	54.2883°N, 44.5892°E
58		Yazykovo	54.2680°N, 44.5864°E
59		Lopatino	54.1738°N, 45.0136°E
60	Ardatovskiy	Kurakino	54.5645°N, 46.0831°E
61		Staroe Ardatovo	54.5843°N, 46.1336°E
62	Bol'sheignatovskiy	Petrovka	54.5854°N, 45.2930°E
63		Kirzhemany	54.5850°N, 45.4432°E
64	Kovylkinskiy	Rybkindo	54.1531°N, 43.4799°E
65		Kovyl'yaj	54.1016°N, 43.5071°E
66	Krasnoslobodskiy	Krasnaya Podgora	54.2887°N, 43.4870°E
67		Lesnoj	54.2613°N, 43.5214°E
68		Zarechnoe	54.2469°N, 43.5124°E
69		Staraya Ryabka	54.2050°N, 43.5046°E
70		Samozlejka	54.1829°N, 43.4931°E
71	El'nikovskiy	Churino	54.3995°N, 43.4471°E
72		Russkie Poshaty	54.4078°N, 43.4436°E
73		Starye Pichingushi	54.3391°N, 43.5029°E
74	Temnikovskiy	Staryj Gorod	54.4175°N, 43.0609°E
75		Temnikov	54.3748°N, 43.1139°E
76		MGZ im. P.G. Smidovicha	54.4286°N, 43.1423°E
77		Kozlovka	54.3816°N, 43.2114°E
78		Sosnovka	54.4281°N, 43.1683°E
79	Ten'gushevskiy	Standrovo	54.3953°N, 42.3943°E
80		Shelubej	54.4074°N, 42.4291°E
81		Telimerki	54.4364°N, 42.4580°E
82		Feklisov	54.4289°N, 42.5073°E
83		Vedenyapino	54.4416°N, 42.5857°E
84	Atyur'evskiy	Arga	54.2034°N, 43.0912°E
85	Zubovo-Polyanskiy	Podlyasovo	54.1941°N, 42.4184°E
86		Svezhen'kaya	54.0035°N, 42.2674°E
87		Izvest'	53.5609°N, 42.2746°E
88		Vysya	53.5033°N, 42.2320°E
89		Gorodishche	53.4553°N, 42.2921°E
90		Zhukovka	53.5293°N, 42.4358°E
91		Shiringushi	53.5123°N, 42.4571°E
92		Ozernyj	54.2510°N, 42.4141°E
93		Lesnoj	54.2774°N, 42.4323°E
94		Romanovka	54.1481°N, 42.4416°E

Points no.	District	Location	Geographic coordinates
95	Zubovo-Polyanskiy	Leplej	54.1883°N, 42.4890°E
96	Ten'gushevskiy	Yuzga	54.3277°N, 42.5919°E
97	Torbeevskiy	Vindrej	54.1554°N, 42.5523°E
98	Ardatovskiy	Turgenevo	54.5150°N, 46.1648°E
99		Redkodub'e	54.4743°N, 46.0990°E
100		Lun'ga	54.4864°N, 45.5652°E
101		Lun'ginskij Majdan	54.5046°N, 45.4821°E
102	Ichalkovskiy	Smol'nyj	54.4592°N, 45.3690°E
103	Bol'shebereznikovskiy	Biologicheskaya stanciya MGU	54.1014°N, 46.0988°E
104		Special'nyj	54.0262°N, 45.5324°E
105	Kochkurovskiy	Mordovskoe Davydovo	53.5856°N, 45.4535°E

A new leafhopper species of the genus *Anagonalia* from India (Hemiptera, Cicadellidae, Cicadellinae)

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Abstract

A new leafhopper species, *Anagonalia lapnanensis* **sp. nov.**, is described from Arunachal Pradesh, India. A morphological variant is also described which, is interpreted as belonging to the same species due to negligible divergence in the COI mtDNA gene. Detailed illustration of males and female are provided.

Keywords

Auchenorrhyncha, intra-specific variation

Introduction

Members of the Asian leafhopper genus *Anagonalia* Young (Cicadellidae: Cicadellinae) are medium to large in size and either pale yellow to green with or without dark wings and usually with orange markings on the head and thorax (Fig. 1). Young (1986) established the genus *Anagonalia* with *Tettigoniella melichari* Distant from Sri Lanka (new name for *T. rubromaculata* Melichar, preoccupied) as the type species. Young (1986) also included two new species from south India, *A. koda* and *A. trava*, and synonymised *Tettigoniella affinis* Distant from north-east India with *A. melichari*. In addition to colour, the genus *Anagonalia* can be distinguished by its angulate anterolateral

margin of the crown near the eye, relatively flattened clypeus, and depressed clypellus (Figs 3, 21). According to Young (1986) the last two features separate *Anagonalia* from the closely related *Erragonalia* Young but the depression of the clypellus (best seen in lateral view) is very slight in some species of *Anagonalia*. Young also mentioned that the genus differs in lacking basiventral microsetae on the pygofer but these are present in *A. melichari* sensu Yang et al. (2017: fig. 6a). In the present study we describe a new species from north-eastern region of India, together with a variant, and provide illustrations of external features and male and female genitalia.

Materials and methods

Type specimens of the new species are deposited in National Pusa Collection, Division of Entomology, ICAR-Indian Agricultural Research Institute, New Delhi, India. Specimens were collected through Mercury vapour lamp light trap from Lapnan (India: Arunachal Pradesh), were processed by sorting, cleaning and mounting. Male genitalia dissection was carried out as described by Knight (1965). The abdomen was removed by inserting a sharp pin between the abdomen and thorax with gentle piercing. The abdomen was treated in 10% KOH for 2–4 h to remove unsclerotised material by gently prodding the abdomen with the head of a pin. Afterwards, the abdomen was rinsed thoroughly in water. The internal structures were then removed by a hooked pin, before being stored in glycerol vials for study. Photographs were taken with a Leica DFC 425C digital camera on the Leica M205FA stereozoom automontage microscope.

Molecular analysis using DNA extraction and PCR amplification

For mitochondrial cytochrome oxidase subunit I (mtCOI) analysis, the DNA was extracted from legs of specimens according to the manufacturer protocol, QIAGEN QIAamp DNA Investigator Kit. The isolated DNA was stored at -20 °C until required. The barcode region of mtCOI was amplified using the primers LCO1490: 5'-GGT-CAACAAATCATAAAGATATTGG-3'; HCO2198: 5'-TAAACTTCAGGGTGAC-CAAAAAATCA-3'. The PCR was performed with total reaction volume of 25 µl using DNA polymerase (Fermentas GmbH, St. Leon- Rot, Germany) under the following cycling protocol: 4 min. hot start at 94°, 35 cycles of denaturation for 30 s at 94°, annealing for 60 s at 47 °C, elongation for 50 s at 72 °C and a final extension 72 °C for 8 min in a C1000 Thermal cycler. The reaction mixture included (as described by KOD FX puregene™ manufacturer protocol) 4 µl of DNA template, 12.5 µl 2× PCR buffer, 10 µl 2mM dNTP, 1 unit TAQ (KODFX) enzyme, and forward and reverse primers were 0.3 µM each at final concentration. The products were checked on a 2% agarose gel and visualised under UV using Alphaview® software version 1.2.0.1. The amplified products were sequenced at SciGenome Pvt Ltd (Cochin, India). The sequences were assembled and aligned with BioEdit version 7.0.0 and deposited in NCBI GenBank (Table 1).

Table 1. Taxa included in phylogenetic analysis with GenBank accession numbers, with locality data.

Species	Geographic locality	GenBank sequence ID
<i>Anagonalia lapnanensis</i> sp. nov.	India: Arunachal Pradesh	MK073117*
<i>Anagonalia lapnanensis</i> variant	India: Arunachal Pradesh	MK073118*
<i>Atkinsoniella sulphurata</i>	China	HQ456375.1
<i>Atkinsoniella opponens</i>	China	HQ456374.1
<i>Atkinsoniella thalia</i>	China	HQ456372.1
<i>Atkinsoniella grabami</i>	China	HQ456377.1
<i>Hishimonus phycitis</i>	Not Available	KY654344.1

*Obtained from molecular work analysed for this paper

Phylogenetic analysis

To determine the sequence divergence between the two variants of *A. lapnanensis* sp. n., we performed a phylogenetic analysis including other taxa within Cicadellini and Opsini as outgroups (Table 1). The Basic Local Alignment Search Tool (BLAST) was used to query the National Center for Biotechnology Information (NCBI) non-redundant nucleotide database and protein database for other leafhopper COI sequence data in blastn searches. The sequences were aligned with the help of CLUSTAL W and a neighbour-joining tree was prepared with MEGA version 6 using Kimura-2-Parameter distance model (Tamura et al. 2013, Saitou and Nei 1987, Kimura 1980).

Anagonalia lapnanensis sp. nov.

<http://zoobank.org/02BF2478-0383-4C98-8C57-1C6EDEEE553A>

Figs 1–18

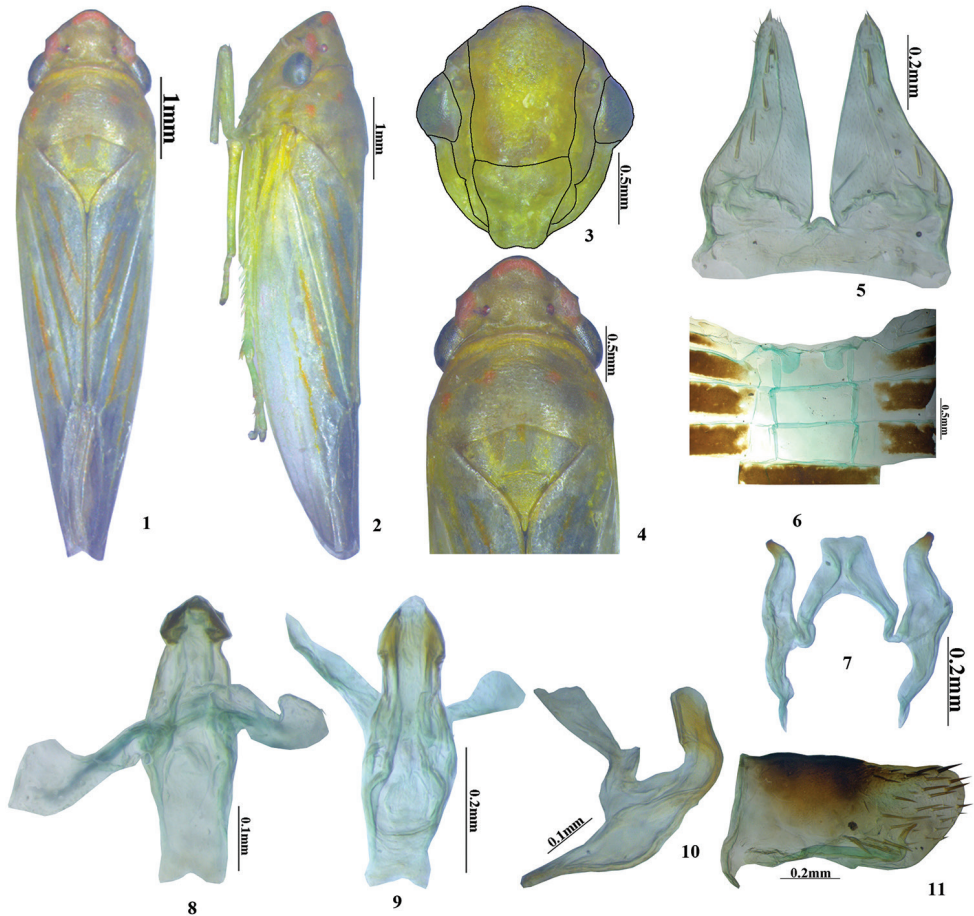
Material examined. *Holotype* ♂, INDIA: Arunachal Pradesh: Lapnan, (26°59'27.03"N, 95°28'58.29"E, 448m), 27.xi.2017, sweep net coll. Stuti (National Pusa Collection).

Paratypes 5♀, same data as holotype.

Diagnosis. The new species can be distinguished from other species of the genus in having pygofer process apically sinuate, short styles with indistinct lateral lobe, connective with short stem and strongly divergent arms, strongly bent aedeagal shaft with rectilinear apical part, and dorsal connective elongate and tapered distally.

Description. Colour (Figs 1–4) generally pale green with yellow tinge. Head with three orange spots on crown, anterior spot saddle shaped, lateral pair elliptical, and one median translucent black spot on anterior margin in ventral view. Pronotum with four orange spots approximately equidistant from anterior and posterior margin and to each other. Scutellum medially with an orange spot and yellow mottling at anterior margin. Forewing with prominent orange markings on veins.

Head with anterior margin of crown rounded, anterolateral margin of crown angulate before eyes; crown longer medially than next to eyes, length medially approximately half width across eyes; ocelli on crown, almost equidistant from anterior and

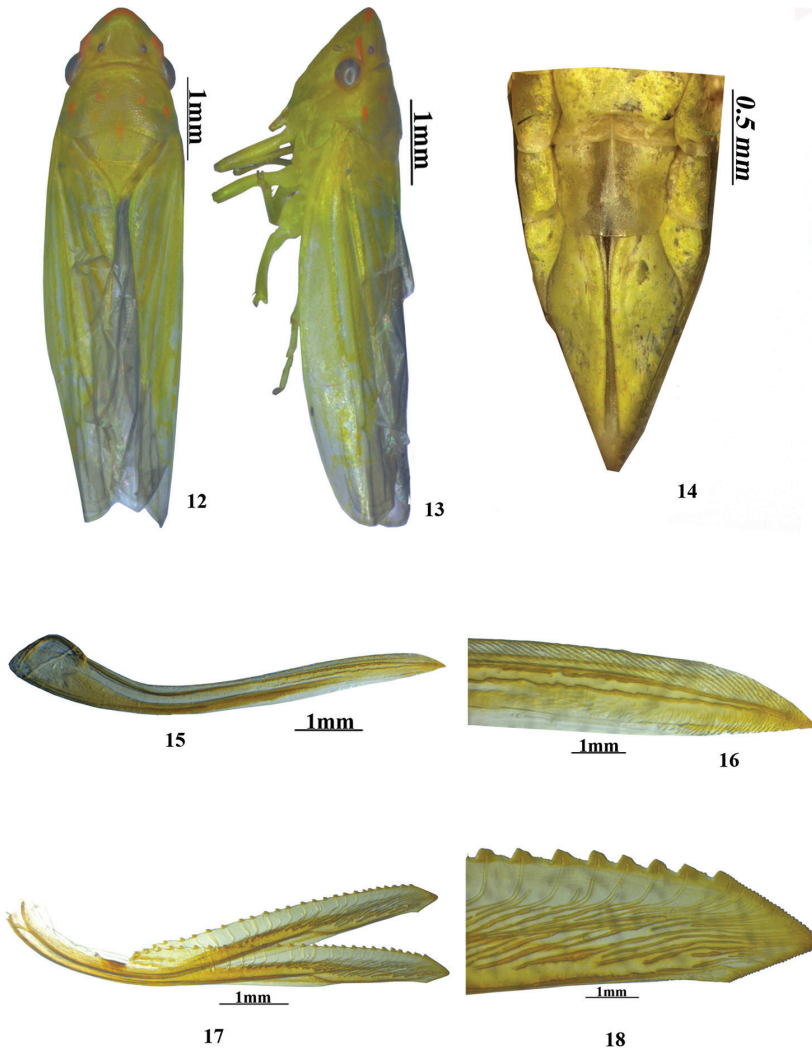


Figures 1–11. *Anagonalia lapnanensis* sp. nov. (male): **1** dorsal habitus **2** lateral habitus **3** face **4** head and thorax, dorsal view **5** subgenital plates and valve **6** sternal abdominal apodemes **7** styles and connective **8–10** aedeagus and dorsal connective, dorsal, ventral and lateral views **11** pygofer lateral view.

posterior margin, nearer to the lateral orange spots than to each other; ridge arising from eye up to ocelli, crown convex between ocelli. Face with frontoclypeus broad and relatively flat, laterofrontal suture extending onto crown; clypellus depressed distally (Fig. 3). Pronotum (Fig. 4) convex, posterior margin highly concave in middle, $1.3\times$ wider than long and $1.22\times$ longer than vertex.

Male second sternal abdominal apodemes (Fig. 9) short, not extending to next sternite.

Male genitalia. Pygofer (Fig. 11) in lateral view, $1.6\times$ longer than wide, with dispersed macrosetae on apical half; caudoventral margin with row of stout macrosetae; in ventral view, a long apically sinuate hook like process arising on posteroventral margin. Valve short, fused to pygofer. Subgenital plates (Fig. 5) $1.4\times$ as long as style, elongate, triangular, narrowed gradually towards apex, apex rounded, with a row of macrosetae along sub-lateral margin. Styles (Fig. 7) longer than wide, exceeding apex of connective.



Figures 12–18. *Anagonalia lapnanensis* (female): **12** dorsal habitus **13** lateral habitus **14** sternite VII **15**, **16** first valvula **17**, **18** second valvula.

tive, preapical lobe poorly developed. Connective (Fig. 7) Y-shaped with stem 1.5× longer than arms. Dorsal connective with arms tapered to apex. Aedeagus in dorsal view (Fig. 8), wider in the middle and slightly narrow at base and apex, in lateral view (Fig. 10) shaft strongly dorsally curved at midlength, of similar width throughout length, gonopore apical.

Female genitalia. Seventh sternite (Fig. 14) with posterior margin slightly convex; first valvulae (Figs 15, 16) slightly bent dorsally and tapered distally to acute apex; in lateral view dorsal irregular sculpturing extending from midlength to apex, subapically with ventral hyaline area extending to midlength. Second valvulae (Fig. 17) with dorsal sclerotised and hyaline area at $\frac{1}{4}$ th distance from base to apex, thereafter dorsal margin

sharply expanded and slightly tapered to near apex with approximately 26 teeth, there-
after apex triangular with fine teeth on dorsal and ventral margins (Fig. 18).

Measurements (mm). Male 6.8 long, 1.5 wide across eyes, 1.4 wide across hind
margin of pronotum. Female 6.3 long, 1.3 wide across eyes, 1.2 wide across hind mar-
gin of pronotum.

Etymology. This species is named after the place of collection, Lapnan, in
Arunachal Pradesh.

Remarks. The new species is similar externally to the types of *Tettigoniella affinis*
Distant from India, a species synonymised with *A. melichari* Distant from Sri Lanka by
Young (1986) but, as the types of *T. affinis* are female, their identity is uncertain (MD
Webb, pers. comm.). Based on figures seen of the types of *A. melichari* (Melanovsky &
Webb, in prep.), the specimens described here differ in shape of the male genitalia by the
pygofer process being strongly sinuate distally in lateral view, the aedeagal shaft apex be-
ing rectilinear in lateral view and the style lacking a preapical lobe. The specimen recorded
by Young (1986) of *A. melichari* is figured in insufficient detail to be certain of its identity.

Variant of the new species

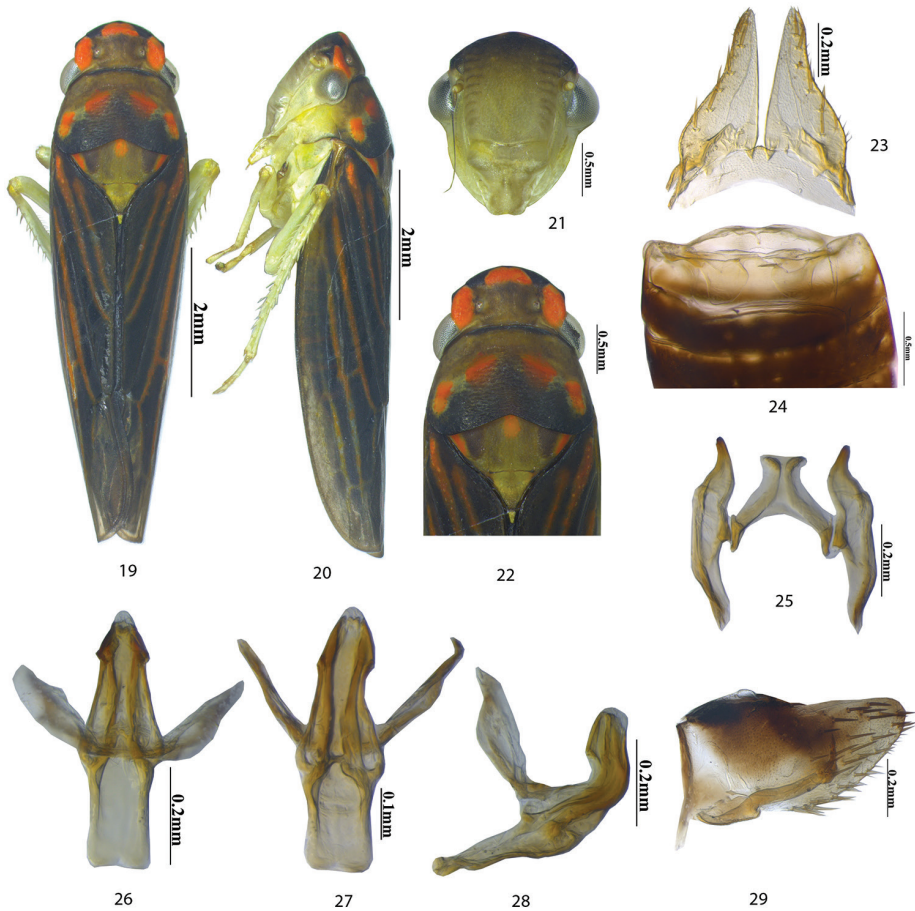
Material examined. Non-types 2♂, same data as holotype and paratypes, except
10.vii.2018.

Remarks. This variant differs from the holotype and paratypes of the new species
as follows: black with orange markings on head and thorax more prominent; scutellum
with three spots, one medial and two lateral; crown less produced anteriorly; aedeagus in
dorsal view narrower at apex and in lateral view apex wider subapically (see Figs 19–29).

To establish if the variant was a new species a molecular analysis was performed
(see Materials and methods). The neighbour-joining (NJ) tree (Fig. 30) from the phy-
logenetic analysis shows 100 % similarity and the Pairwise Distance matrix (Table 2)
had shown genetic distance 0.2 %, which is negligible according to the 3.5 % diver-
gence rule (De Barro et al. 2011). Thus it is inferred that the differences found in to-
potypical specimens are deemed to be variations of the new species rather than being
of a different species. This variation may be attributed to seasonal climatic differences,
i.e., the rainy season in July, and winter in November. Further confirmation of these
findings will require breeding experiments and or acoustic recordings.

Table 2. Percent pairwise corrected (K2P) genetic distance among different species of Cicadellini includ-
ing the new species and the variant for MrCOI.

Species	1	2	3	4	5	6	7
<i>Anagonalia lapnanensis</i> sp. nov.		0.002	0.074	0.078	0.081	0.076	0.141
<i>Anagonalia lapnanensis</i> variant	0.002		0.073	0.077	0.081	0.075	0.140
<i>Atkinsoniella sulphurata</i>	0.831	0.824		0.017	0.023	0.017	0.113
<i>Atkinsoniella opponens</i>	0.864	0.857	0.131		0.022	0.018	0.118
<i>Atkinsoniella thalia</i>	0.886	0.879	0.195	0.175		0.024	0.159
<i>Atkinsoniella grahami</i>	0.858	0.851	0.119	0.134	0.202		0.129
<i>Hishimonus phycitis</i>	1.329	1.328	1.141	1.151	1.319	1.248	



Figures 19–29. *Anagonalia lapnanensis* variant: **19** dorsal habitus **20** lateral habitus **21** face **22** head and thorax, dorsal view **23** subgenital plates and valve **24** sternal abdominal apodemes **25** styles and connective **26–28** aedeagus and dorsal connective, dorsal, ventral, and lateral views **29** pygofer, lateral view.

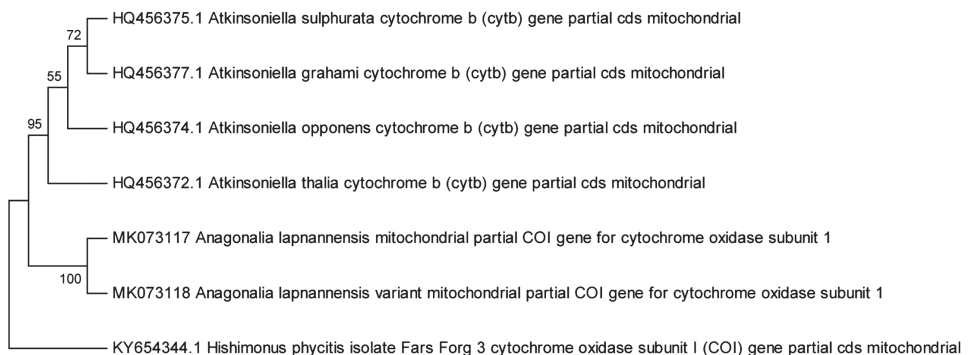


Figure 30. Phylogram showing relationships of *Anagonalia lapnanensis* sp. nov. and *A. lapnanensis* variant, with related species of tribe Cicadellini inferred using by neighbour-joining (NJ) tree method of mitochondrial COI sequences.

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